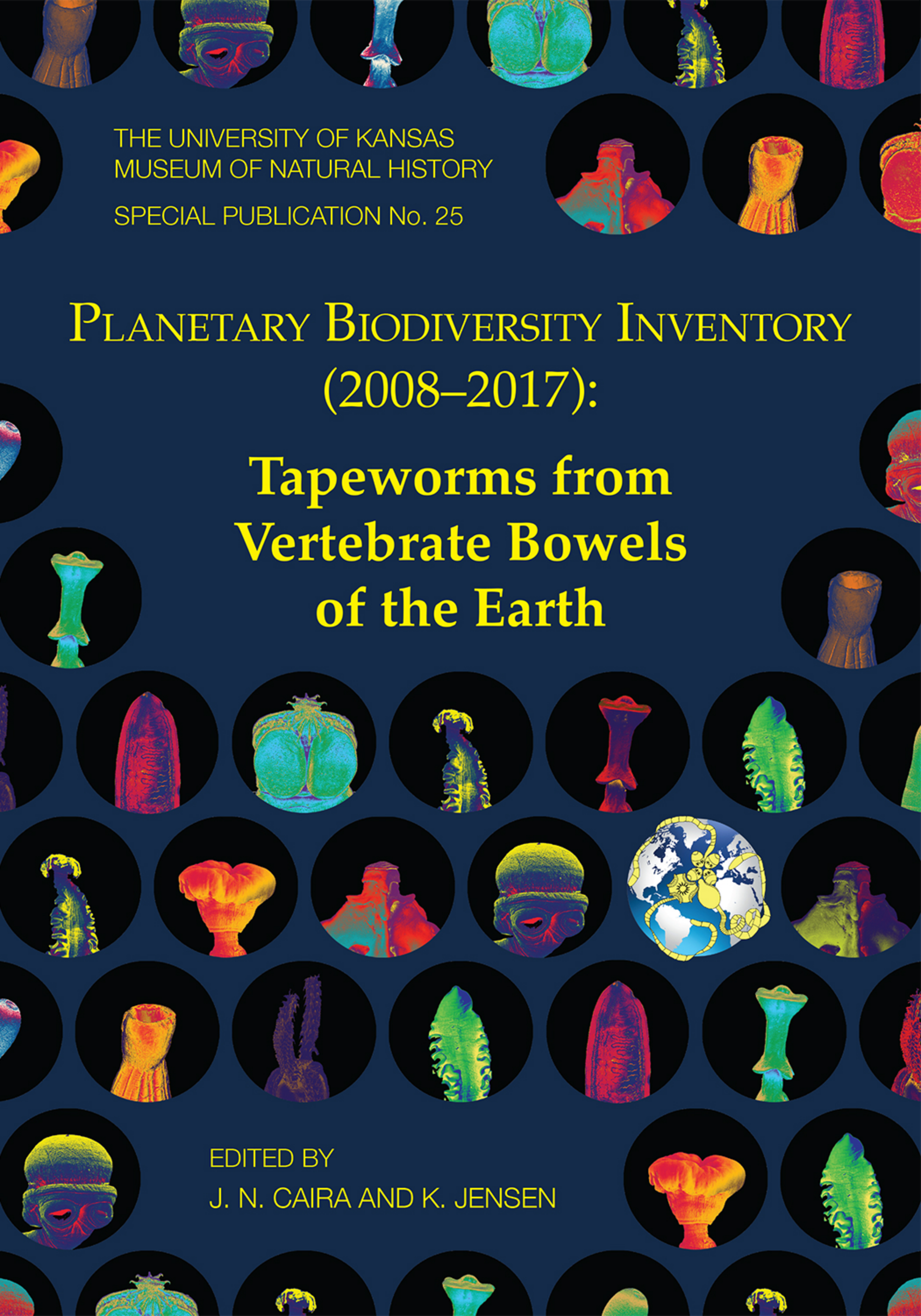

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Tapeworms from Vertebrate Bowels of the Earth

EDITED BY
J. N. CAIRA AND K. JENSEN

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20 JULY 2017

Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth

Edited by

JANINE N. CAIRA

Department of Ecology and Evolutionary Biology,
University of Connecticut,
Storrs, Connecticut, 06269-3043, USA

AND

KIRSTEN JENSEN

Department of Ecology and Evolutionary Biology,
Biodiversity Institute,
University of Kansas,
Lawrence, Kansas, 66045, USA

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CONTRIBUTORS

BEVERIDGE, IAN
Department of Veterinary Science, University of Melbourne, 250 Princes Highway, Werribee, Victoria 3030, Australia. E-mail: ibeve@unimelb.edu.au

BRABEC, JAN
Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, Branišovská 31, 370 05 České Budějovice, Czech Republic. E-mail: brabcak@paru.cas.cz

BUENO, VERONICA M.
Department of Ecology and Evolutionary Biology, University of Connecticut, 75 N. Eagleville Rd., Storrs, CT 06269-3043, USA. E-mail: veronica.m.bueno@uconn.edu

CAIRA, JANINE N.
Department of Ecology and Evolutionary Biology, University of Connecticut, 75 N. Eagleville Rd., Storrs, CT 06269-3043, USA. E-mail: janine.caira@uconn.edu

DE CHAMBRIER, ALAIN
Muséum d'Histoire Naturelle de Genève, P.O. Box 6434, CH-1211 Geneva 6, Switzerland. E-mail: nomimoscolex2@yahoo.fr

CIELOCHA, JOANNA J.
Biology Department, Science Center 220J, Rockhurst University, 1100 Rockhurst Road, Kansas City, MO 64110, USA. E-mail: joanna.cielocha@rockhurst.edu

DIMITROVA, YANA D.
Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, 2 Gagarin Street, 1113 Sofia, Bulgaria. E-mail: janadarck3@abv.bg

GALLAGHER, KAITLIN
Department of Ecology and Evolutionary Biology, University of Connecticut, 75 N. Eagleville Rd., Storrs, CT 06269-3043, USA. E-mail: kaitlin.gallagher@uconn.edu

GEORGIEV, BOYKO B.
Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, 2 Gagarin Street, 1113 Sofia, Bulgaria. E-mail: boyko_georgiev@yahoo.com

GREIMAN, STEPHEN E.
Department of Biology, Georgia Southern University, P.O. Box 8042-1, Statesboro, GA 30460, USA. E-mail: sgreiman@georgiasouthern.edu

HANSEN, HAAKON
Norwegian Veterinary Institute, Section for Parasitology, Ullevålsveien 68, 0454 Oslo, Norway. E-mail: haakon.hansen@vetinst.no

HASELI, MOHAMMAD
Department of Biology, Faculty of Sciences, University of Guilan, Rasht, Iran. E-mail: haseli@guilan.ac.ir

HAUKISALMI, VOITTO
Piettasenkatu 38 A 23, 33580 Tampere, Finland. E-mail: haukisal@gmail.com

HERZOG, KAYLEE S.
Department of Ecology and Evolutionary Biology and the Biodiversity Institute, University of Kansas, 1200 Sunnyside Ave., Lawrence, KS 66045, USA. E-mail: ksherzog@ku.edu

Hoberg, Eric P.
Animal Parasitic Diseases Laboratory, Agricultural Research Service, US Department of Agriculture, Beltsville, MD, 20705-2350, USA and Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., 20560-0163, USA.
E-mail: Eric.Hoberg@ars.usda.gov

Ivanov, Verónica A.
Instituto de Biodiversidad y Biología Experimental y Aplicada - IBBEA (CONICET-UBA), and Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, Pabellón II, piso 4, Lab. 52, C1428EHA, Buenos Aires, Argentina. E-mail: ivanov@bg.fcen.uba.ar

Jensen, Kirsten
Department of Ecology and Evolutionary Biology and the Biodiversity Institute, University of Kansas, 1200 Sunnyside Ave., Lawrence, KS 66045, USA. E-mail: jensen@ku.edu

Kuchta, Roman
Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, Branišovská 31, 370 05 České Budějovice, Czech Republic. E-mail: krtek@paru.cas.cz

Littlewood, D. Timothy J.
Department of Life Sciences, Natural History Museum, Cromwell Road, London, SW7 5BD, UK.
E-mail: t.littlewood@nhm.ac.uk

Makarikov, Arseny A.
Institute of Systematics and Ecology of Animals, Siberian Branch of Russian Academy of Sciences, 11 Frunze Str., 630091, Novosibirsk, Russia. E-mail: makarikov@mail.ru

Mariaux, Jean
Muséum d'Histoire Naturelle de Genève, P.O. Box 6434, CH-1211 Geneva 6, Switzerland and Department of Genetics and Evolution, University of Geneva, CH-1205 Geneva, Switzerland.
E-mail: jean.mariaux@ville-ge.ch

Marques, Fernando P. L.
Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, tv. 14, no. 101, 05508-090 Cidade Universitária, São Paulo, Brasil. E-mail: fernando@ib.usp.br

Menoret, Adriana
Instituto de Biodiversidad y Biología Experimental y Aplicada - IBBEA (CONICET-UBA), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, Pabellón II, piso 4, Lab. 52, C1428EHA, Buenos Aires, Argentina. E-mail: menoret.a@bg.fcen.uba.ar

Oros, Mikuláš
Institute of Parasitology of the Slovak Academy of Sciences, Hlinkova 3, 040 01 Košice, Slovakia.
E-mail: oros@saske.sk

Phillips, Anna J.
Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., 20560-0163, USA. E-mail: phillipsaj@si.edu

Pickering, Maria
Department of Biological Sciences, Meredith College, 3800 Hillsborough Street, Raleigh, NC 27607-5298, USA. E-mail: mpickering@meredith.edu

Razafiarisolo, Tantely
Département de Biologie Animale, Université d'Antananarivo, B.P. 906 – 101 Antananarivo, Madagascar. E-mail: razafiarisolotantely@yahoo.com

Reyda, Florian B.
Biology Department, State University of New York, College at Oneonta, 120 Science I, Oneonta, NY 13820-4015, USA. E-mail: florian.reyda@oneonta.edu

Ruhnke, Timothy R.
Department of Biology, West Virginia State University, H101, Institute, WV 25112-1000, USA. E-mail: ruhnketr@wvstateu.edu

Scholz, Tomáš
Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, Branišovská 31, 370 05 České Budějovice, Czech Republic. E-mail: tscholz@paru.cas.cz

Schaeffner, Bjoern C.
Helmintologia Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, tv. 14, no. 101, 05508-090 Cidade Universitária, São Paulo, Brasil. E-mail: b.schaeffner@unimelb.edu.au

Tkach, Vasyl V.
Department of Biology, University of North Dakota, 10 Cornell Street Stop 9019, Grand Forks, ND 58202-9019, USA. E-mail: vasyl.tkach@und.edu

Vasileva, Gergana P.
Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, 2 Gagarin Street, 1113 Sofia, Bulgaria. E-mail: gpetrunova@gmail.com

Waeschenbach, Andrea
Department of Life Sciences, Natural History Museum, Cromwell Road, London, SW7 5BD, UK. E-mail: a.waeschenbach@nhm.ac.uk

Widmer, Vincent
Muséum d'Histoire Naturelle de Genève, P.O. Box 6434, CH-1211 Geneva 6, Switzerland. E-mail: vincent.widmer@unige.ch

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PREFACE

This document is organized into 22 peer-reviewed chapters. Each of the chapters focuses on an individual cestode group, begins with the status of knowledge of the group prior to the inception of the PBI project, and ends with an assessment of the current understanding of the group. In each case, diversity, classification, morphology, phylogenetic relationships, host associations, and geographic distribution are addressed. In all but one case, each chapter includes a list of valid taxa. Synonyms have not generally been listed; this was determined to be beyond the scope of the project given the immensity of such lists for some groups. With over 3,000 valid species, the generation of a list of species for the Cyclophyllidea was also determined to be beyond the scope of this project. However, a list of valid higher taxa is provided. Each of the 19 cestode orders is addressed alphabetically in separate chapters with two exceptions. The Mesocestoididae are treated as a family in the Cyclophyllidea. Although evidence supporting recognition of the former as an independent order is mounting, the case remains to be formally made based on more detailed investigations of this enigmatic group of mammal parasites. The Onchoproteocephalidea are the second exception. So as to emphasize the dual nature of the host associations and scolex morphology of its members, the freshwater fish-parasitizing taxa (formerly assigned to the order Proteocephalidea) are treated in a chapter as the Onchoproteocephalidea I separately from the taxa that parasitize elasmobranchs, which are treated as the Onchoproteocephalidea II. Use of quotation marks around taxon names (e.g., the order "Tetraphyllidea") is to remind readers of the definitively non-monophyletic nature of these groups.

The first and last chapters are more synthetic in nature. The first chapter provides an overview of the results of the project both in terms of its Intellectual Merit and Broader Impact elements (to use NSF terminology). The final chapter provides a molecular framework for the phylogenetic relationships among the cestodes as they are understood at the end of the PBI project. The final chapter also describes the molecular methods and taxon sampling employed to achieve that framework. This Special Issue concludes with an Appendix listing the more than 220 publications directly resulting from project efforts, all of which cite the PBI award (NSF DEB Nos. 0818696 and 0818823).

1 An overview of tapeworms from vertebrate bowels of the earth

By
Janine N. Caira[1], Kirsten Jensen[2], Boyko B. Georgiev, Roman Kuchta,
D. Timothy J. Littlewood, Jean Mariaux, Tomáš Scholz, Vasyl V. Tkach,
and Andrea Waeschenbach*

INTRODUCTION

In these times, it is rare that those who study Natural History are presented with an opportunity to take a global look at the diversity of any taxonomic group. This is extremely regrettable given this approach has been employed to such great advantage in centuries past by numerous distinguished naturalists, including, for example, Charles Darwin and Alfred Russel Wallace, whose discoveries ultimately served as the foundation of disciplines such as Evolution, Ecology, Biogeography, and Biodiversity, to name just a few. The demands and time restrictions of contemporary academia are among the factors contributing to the decline in such global work today, but the situation is exacerbated by limitations in funding. Based on the enthusiasm we experienced over the course of this project from all corners of the world, the decline is most decidedly *not*, the result of a lack of interest!

In an attempt to remedy the situation, in 2003, the National Science Foundation (NSF), in partnership with the ALL Species Foundation, and the Alfred P. Sloan Foundation, established the Planetary Biodiversity Inventories (PBI) program. This program was aimed at funding species-level inventories of major groups of organisms *across the planet*. For the relatively brief period of its existence, the PBI program did much to restore enthusiasm for exploring biodiversity on a global scale. In 2008, in the last year of the program, our project: ***A survey of tapeworms from vertebrate bowels of the earth*** was funded. For the next eight years, our international team scoured the earth discovering and describing tapeworms (i.e., cestodes) from birds, mammals, frogs, lizards, snakes, bony fishes, and elasmobranchs (i.e., sharks and stingrays). As mandated by NSF, the project also included substantial training and outreach activities. It is not an overstatement to say that this funding from the PBI program changed tapeworm systematics forever—transforming it into the synthetic discipline it is today. Lest the impact of this remarkable investment in this poorly known, and in fact often maligned, group of parasites be lost among the many other valuable endeavors funded by NSF, our project team collaborated to generate this Special Issue. It is our hope that in assembling the results of our activities and discoveries into a single document, the full magnitude and value of this creative program will not go unrecognized. It is also our hope that this document will serve to catalyze future work on this intriguing group of parasitic platyhelminths.

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[1] Corresponding author (janine.caira@uconn.edu)

[2] Corresponding author (jensen@ku.edu)

* Non-corresponding authors in alphabetical order.

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PROJECT GOALS

The overall objective of the project was to provide a global synthetic treatment of the diversity, classification, morphology, host associations, geographic distribution, and interrelationships of cestodes. To this end, the project had six primary goals. (1) To discover and describe as much cestode novelty as possible by examining a wide array of species of vertebrates from as many different countries as possible across the globe that had not previously been examined for cestodes. (2) To recollect from historically problematic regions and/or host taxa to resolve major outstanding taxonomic issues. (3) To collect specimens of as many different cestode species across as great a diversity of cestode taxa as possible and preserve them for novel morphological and molecular work. (4) To assess interrelationships at multiple levels based on phylogenetic analyses of molecular sequence data from multiple genes informed by morphological data. (5) To attempt to reconcile cestode classification at all levels with a revised understanding of their phylogenetic relationships. (6) To use historical data and new collections to begin to generate estimates of total global diversity for at least a subset of cestode orders.

THE TEAM

As Principal Investigators (PIs) of the project, Janine Caira (University of Connecticut) and Kirsten Jensen (University of Kansas) were responsible for overall project management. Co-Principal Investigator (Co-PI) Tim Littlewood and postdoctoral fellow Andrea Waeschenbach (The Natural History Museum, London) coordinated the molecular work. Co-PI Jean Mariaux (Muséum d'Histoire Naturelle de Genève) coordinated the ultra-speciose cyclophyllidean elements of the project. In total, over 250 individuals worked on the project in various roles; these are detailed below.

Given that tapeworm systematists self-organize by their cestode orders of interest, and thus also by the vertebrate classes parasitized by their cestode orders of interest, project personnel were assembled into four "host" teams. Each team was led by one to three taxonomists with expertise in the groups of cestodes that parasitize her/his/their particular host group. The *bird-hosted* cestode team was led by Jean Mariaux (Muséum d'Histoire Naturelle de Genève) and Boyko Georgiev (Bulgarian Academy of Sciences), the *mammal-hosted* cestode team by Vasyl Tkach (University of North Dakota), the *bony fish-hosted* cestode team by Tomáš Scholz and Roman Kuchta (both Czech Academy of Sciences), and Alain de Chambrier (Muséum d'Histoire Naturelle de Genève)—this team was also responsible for the holocephalan (ratfish) cestodes; the *elasmobranch-hosted* cestode team was led by Janine Caira and Kirsten Jensen. The dearth of cestodes reported from frogs, snakes, lizards, and their kin did not justify a separate team to cover the cestodes of these host groups, instead given that the cestode groups hosted by these vertebrates are the same as those hosted by bony fishes, Alain de Chambrier of the fish-cestode hosted team led the work on cestodes from herptiles.

Team leaders formulated and implemented the strategy for treating their respective cestode order(s). Each chose to enlist the assistance of additional taxonomic experts from across the globe. By host group, these experts included for *mammals*: Ian Beveridge (University of Melbourne), Voitto Haukisalmi (Forest Research Institute, Finland), and Vadim Kornyushin (National Academy of Sciences, Ukraine); *birds*: Eric Hoberg (Smithsonian Institution), Vadim Kornyushin (National Academy of Sciences, Ukraine), Pavel Nikolov (Bulgarian Academy of Sciences), Gergana Vasileva (Bulgarian Academy of Sciences); *bony fishes*: Alicia A. Gil de Pertierra (University of Buenos Aires), and Vladimíra Hanzelová and Mikulas Oros (Slovak

Academy of Sciences); *elasmobranchs*: Ian Beveridge (University of Melbourne), the late Louis Euzet (France), Claire Healy (Royal Ontario Museum), Verónica Ivanov (Universidad de Buenos Aires), Masoumeh Malek (University of Tehran), Fernando P. L. Marques (Universidade de São Paulo), Lassad Neifar (Faculté des Sciences de Sfax, Tunisia), Harry Palm (Universität Rostock), Florian Reyda (State University of New York at Oneonta), and Timothy Ruhnke (West Virginia State University). Each "host" team also generally included at least one to two postdoctoral fellows, as well as multiple graduate and undergraduate students. Additional detail on these individuals is provided in the Training section below.

A program assistant, Elizabeth Barbeau, supported in part with matching funds to this award from the University of Connecticut (UConn), was responsible for all clerical aspects of the project and was also heavily involved in the development and population of the project databases. The project website and databases were developed in collaboration with Yi Zhang, Josh Roy, and Jason Card from UConn's University Information Technology Services (UITS). The children's book *Meet the Suckers* was also a collaborative effort involving Virge Kask of UConn (backgrounds), Joachim Mohrenberg of Braunschweig, Germany (cartoons of children; http://www.mohrenberg.de/), and Elizabeth Barbeau (content design). The original cover art for this Special Issue was done by Kendel Craig, the winner of a competition we held with the design students of the American School in London, for this honor.

Collaboration across "host" teams was greatly facilitated by annual project meetings held in Geneva in 2009 and 2012, Melbourne in 2010 (following the International Congress of Parasitology), Kansas in 2011, London in 2013, and Brazil in 2014. The meetings in 2011 and 2014 coincided with the 7th and 8th International Workshops on Cestode Systematics, respectively. The former Workshop was largely funded by the PBI project and was organized by PI Jensen at the University of Kansas. The latter Workshop was organized by F. P. L. Marques at the University of São Paulo. The global community of Cestodologists also completed a paper (Chervy, 2009) detailing the long-awaited unified terminology for the surface features unique to cestodes known as microtriches under the pseudonym "Lenta Chervy"—a combination of the words "Tape" and "Worms" in Russian—which our global community of Cestodologists typically employs for their collaborative works.

FIELDWORK

The four "host" teams worked independently to identify the geographic regions and specific host groups to target for conducting fieldwork that would supplement material already in hand. In all cases, highest priority was given to major regions in which a particular vertebrate class had not previously been examined for cestodes. Regions known to be home to vertebrate orders, families, or genera containing species that had been reported to host a particular cestode group, but that included many species that had not yet been examined, were also targeted. With a few exceptions, our original plans to conduct combined field trips involving the collection of cestodes from more than one major vertebrate group were generally foiled by difficulties in obtaining collecting permits spanning several major vertebrate groups or, more often, by the logistical inefficiencies presented by the fact that different methods of capture, often in different types of habitats (e.g., forests vs. ocean, etc.), were required to obtain hosts of different vertebrate classes.

The primary localities surveyed by the four "host" teams over the course of the project are summarized in Figure 1. Cestodes were collected from the following 54 countries: Argentina, Australia, Bangladesh, Belize, Brazil, Bulgaria, Cambodia, Canada, Central African Republic, Chile, China, Costa Rica, Czech Republic, Democratic Republic of Congo, Ecuador, Egypt, Ethiopia, Falkland Islands, France, Gabon, Guatemala, Guyana, India, Indonesia, Iran, Italy, Ivory Coast, Kenya, Madagascar, Malawi, Malaysia, Mexico, Mozambique, New Caledonia, Norway, Peru, Philippines, Portugal, Republic of Kazakhstan, Russia, Senegal, Slovakia, Solomon Islands, South Africa, South Korea, Sudan, Taiwan, Thailand, Tunisia, Uganda, United Kingdom, Ukraine, United States (AK, CT, KS, MS, ND, NE, NY, RI, SC, TN, and TX), and Vietnam.

Collecting trips ranged in duration from a few days to several weeks. Field teams varied in size from one to five individuals. All foreign fieldwork was conducted in collaboration with local experts who provided logistical support as well as knowledge of local faunas. Primary local collaborators, by country are as follows: Mostafa Hossain (Bangladesh); Norlan Lamb and Roy Polonio (Belize); Natalia Da Mata Luchetti, Fernando P. L. Marques, Luis Eduardo Tavares, Marcos Tavares, José Luque, and Ricardo Takemoto (Brazil); Pavel Nikolov (Bulgaria); Touch Bunthang (Cambodia); Manigandan Lejeune Virapin (Canada); Francisco Concha, Günther Försterra, Daniel González-Acuña, and Vreni Häussermann (Chile); Dian Gao, Cai Kuizheng, Pin Nie, Gui Tang Wang, Shan Gong Wu, and Bing Wen Xi (China); Tayler Clarke, Ingo Wehrtmann, and Mario Espinoza (Costa Rica); Oscar Carreno and Gabriela Flores (Ecuador); Mohamed Bosseri and Amal Khalil (Egypt); Eshete Dejen Dresilign, Abebe Getuhun Gubale, and Seyoum Mengistou (Ethiopia); Joost Pompert (Falkland Islands); Bernard Marchand (France); Mathieu Bourgarel and Jean-Paul Gonzales (Gabon); Anirban Ash and Pradip K. Kar (India); Asri Yuinar (Indonesia); Razieh Ghayoumi and Masoumeh Malek (Iran); Andrea Gustinelli (Italy); Inza Kone (Ivory Coast); Steven Goodman, Marie Jeanne Raherilalao, Jeanne Rasamy, and Achille Raselimanana (Madagascar); R. Hashim, Susan Lim (late), and R. Ramli (Malaysia); Samuel Bila (Mozambique); Jean-Lou Justine (New Caledonia); Martin Mortenthaler, Aurora Ramírez Aricara, and Lidia Sánchez (Peru); Rafe Brown (Philippines); Graca Costa and Gui Menezes (Portugal); Vladimir Besprovaznnykh, Vladimir Chistyakov, and Alexey Ermolenko (Russia); Rokhaya Sall (Senegal); David Blair, Tingo Leve, and Richard Mounsey (Solomon Islands); Tracey Fairweather and Robert Leslie (South Africa); Ki Hong Kim (South Korea); Zuheir Mahmoud (Sudan); Hsuan-Ching Ho and Hsuan-Wien Chen (Taiwan); Lawan Chanhome (Thailand); Jim Ellis and Andrew Shinn (UK); Olga Lisitsyna and Yuriy Kvach (Ukraine); Michael Barger, Megan Bean, Sara Brant, Isaure de Buron, Anindo Choudhury, Joseph Cook, Stephen Curran, Bryan Frazier, Andrew Hope, David G. Huffman, John M. Kinsella, Robin Overstreet, Eric Pulis, and Jason Weckstein (USA); Tran T. Binh and Vu Quang Manh (Vietnam).

Across these localities, habitats sampled included coniferous forests (North America, South America, and Asia), temperate forests (North America, South America, and Europe), tropical forests (South America, Africa, Southeast Asia, and Australia), grasslands (prairies, pampas, veld, and steppes), polar regions (Svalbard), freshwater wetlands (lakes, ponds, rivers, and streams), inland seas, sea shores, oceanic islands and coral reefs, and the open ocean (epipelagic, mesopelagic, bathypelagic zones, as well as demersal and benthic zones).

At each locality, vertebrate hosts were captured using the method most appropriate for the habitat(s) represented. Terrestrial hosts were generally captured using mist net, snake stick, Sherman trap, pit fall trap, the occasional firearm, or rarely by hand. Aquatic hosts were collected by trawl, hand-line, long-line, gill net, or hand-spear. Institutional Animal Care and Use Committee (IACUC) protocols were generally issued to the leaders of the four "host" teams by their home institutions. In all cases, permission to collect was obtained from relevant authorities and all local laws and regulations were followed.

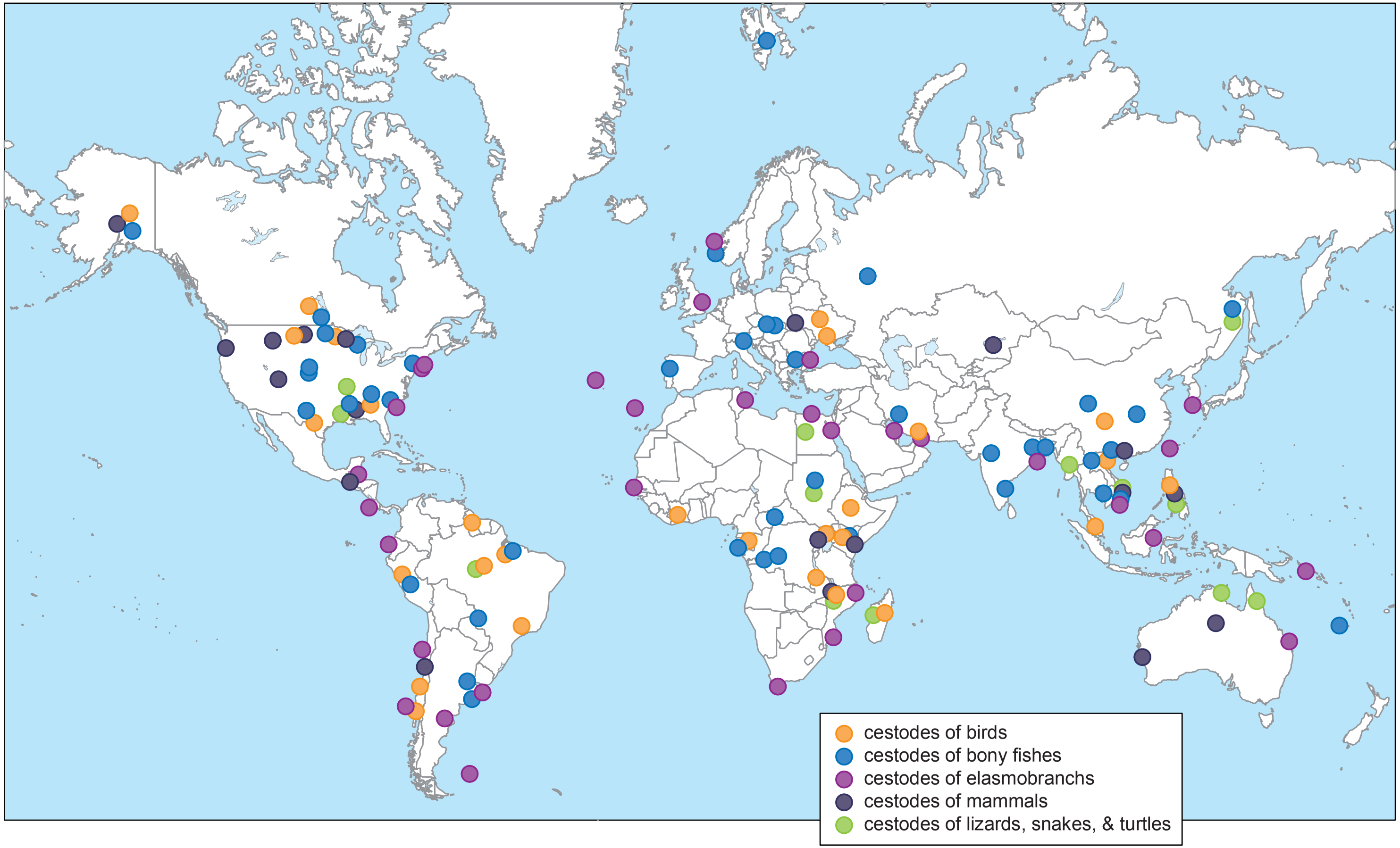

Figure 1. Locations of collecting events and expeditions (by major host group) conducted as part of this PBI project (2008–2017).

In total, 14,884 specimens of 1,906 vertebrate species were examined for cestodes. By major host group, these are as follows: 1,160 specimens representing 143 species of mammals; 3,473 specimens representing 989 species of birds; 219 specimens representing 59 species of snakes, lizards, and frogs; 8,226 specimens of over 500 species of bony fishes; and 1,806 specimens representing 215 species of elasmobranchs. Mammals examined represented approximately 20% of the 139 mammal families, with an emphasis on the Soricomorpha (shrews). Birds examined represented approximately 50% of the 238 bird families, with an emphasis on the Passeriformes. Bony fishes represented approximately 18% of the 497 bony fish families, with an emphasis on Siluriformes and Cypriniformes. Elasmobranch collections represented approximately 40% of the 61 families, with an emphasis on deeper water taxa (e.g., Squaliformes [dogsharks] and Rajiformes [skates]), as well as on groups of Carcharhiniformes [ground sharks], Myliobatiformes [stingrays], and Lamniformes [mackerel sharks] not previously examined for cestodes.

As the title of the project suggests, our focus was on the tapeworms that live in the digestive system of vertebrates. To this end, our collections targeted adult tapeworms in the final (i.e., definitive) host. Tapeworms have wonderfully complex life-cycles, involving at least two, and sometimes three hosts, some of which are also vertebrates, but many of which are invertebrates. It was simply beyond the scope of the project to collect the larval and juvenile stages of tapeworms from these other hosts, although our molecular data tagged to adult vouchers may facilitate identification of many of these in the future.

NOVELTY AND DIVERSITY

Substantial novelty was discovered across a wide array of cestode orders. In total 215 new species were formally described. These included ten or more species in each of the orders Cyclophyllidea (36 new species), Diphyllidea (18 new species), Lecanicephalidea (29 new species), Onchoproteocephalidea I (20 new species), Onchoproteocephalidea II (25 new species), Rhinebothriidea (25 new species), "Tetraphyllidea" relics (10 new species), and Trypanorhyncha (31 new species). In addition, we estimate that material of hundreds of additional new species across orders was collected but remains to be processed. In total, 64 new genera were erected—the majority of these were members of the orders Cyclophyllidea (20 new genera), Lecanicephalidea (9 new genera), Onchoproteocephalidea I (9 new genera), Rhinebothriidea (5 new genera), and Trypanorhyncha (8 new genera).

A substantial body of revisionary work was also completed. In total, 135 new combinations were made across the 19 cestode orders. Major efforts included substantial (almost complete) revisions of the Caryophyllidea and the Bothriocephalidea. Given that most of the questionable species in both orders were originally collected from bony fishes in India and/or Bangladesh, these revisions were made possible through the collection of new material from type hosts in both of these countries. In the end, almost 200 species were synonymized in the Bothriocephalidea (at least 100 species of *Senga*) and Caryophyllidea (86 species).

In combination, the lists of valid taxa for each cestode order provide an informed assessment of the current diversity of cestodes overall. The total number of valid species across the planet today is at least 4,810 (but species are being described monthly so this number is already out of date!), and the total number of valid genera is 833. A breakdown of these totals by cestode order, and by family for the Cyclophyllidea, is provided in Table 1. These numbers do not include the species and genera, listed at the end of each chapter, that are considered *incertae sedis* nor does it include named, but undescribed species and genera that have appeared in molecular phylogenies. Thus, the global fauna of known cestodes is now approaching 5,000 species. The Cyclophyllidea remain by far the most speciose of the 19 cestode orders, with well over 50% of all known cestode diversity, in 437 genera. When numbers are combined for all species, the Onchoproteocephalidea are the second most speciose order, with 562 species, in 79 genera. This order is rivaled only by the Trypanorhyncha in terms of number of genera (i.e., 81), although not in terms of number of species (i.e., 315). Six orders (i.e., the Amphilinidea, Cathetocephalidea, Haplobothriidea, Litobothriidea, Nippotaeniidea, and Spathebothriidea) are on the low end of cestode diversity with less than ten species each. The limited nature of the host associations of each of these groups makes it likely their diversity will not greatly exceed these numbers even with additional collections.

The collection of fresh, properly fixed material led to a much deeper understanding of the morphological complexities of tapeworms. For example, many groups were examined with scanning electron microscopy (SEM) for the first time. Insights into the diversity of scolex configurations seen across tapeworms are provided in the plates of scanning electron micrographs for the following groups: Bothriocephalidea (see fig. 1 in Chapter 3 this volume, Kuchta and Scholz, 2017a), Caryophyllidea (see fig. 3 in Chapter 4 this volume, Scholz and Oros, 2017), Cathetocephalidea (see fig. 1 in Chapter 5 this volume, Caira et al., 2017a), Diphyllidea (see fig. 2 Chapter 7 this volume, Caira et al., 2017b), Diphyllobothriidea (see figs. 1–13 in Chapter 8 this volume, Kuchta and Scholz, 2017b), Haplobothriidea (see fig. 1 in Chapter 10 this volume, Kuchta and Scholz, 2017c), Lecanicephalidea (see fig. 1 in Chapter 11 this volume, Jensen et al., 2017), Litobothriidea (see figs. 2 and 3 in Chapter 12 this volume, Caira et al., 2017c), Nippotaeniidea (see fig. 1 in Chapter 13 this volume, Scholz et al., 2017), Onchoproteocephalidea I (see figs. 8–16 in Chapter 14 this volume, de Chambrier et al., 2017), Onchoproteocephalidea II (see fig. 2 in Chapter 15 this volume, Caira et al., 2017d), Phyllobothriidea (see fig. 1 in Chapter 16 this volume, Ruhnke et al., 2017a), Rhinebothriidea (see fig. 1 in Chapter 17 this volume, Ruhnke et al., 2017b), Spathebothriidea (see fig. 1 in Chapter 18 this volume, Kuchta and Scholz, 2017d), Tetrabothriidea (see fig. 2 in Chapter 19 this volume, Mariaux et al., 2017b), "Tetraphyllidea" relics (see figs. 2–7 in Chapter 20 this volume, Caira et al., 2017e), and Trypanorhyncha (see fig. 1 in Chapter 21 this volume, Beveridge et al., 2017). However, light microscopic work also highly benefited from the collection of newly fixed material as is evident in the beautiful light micrographs provided for the Cyclophyllidea (see figs. 6–21 in Chapter 6 this volume, Mariaux et al., 2017a).

HOST ASSOCIATIONS

Our emphasis on vertebrates in this project is because they, or more specifically their "bowels," *are* the habitat of adult cestodes. Once all vertebrate species on the planet have been examined, the assessment of the global cestode fauna will be complete. However, the daunting nature of that task is illustrated by the magnitude of current estimates of vertebrate diversity: 32,855 species of bony fishes (Eschmeyer and Fong, 2017), 10,404 species of birds (Clements et al., 2016), 10,104 species of snakes and lizards (Uetz, 2017), 7,621 species of amphibians, 5,416 species of mammals (Wilson and Reeder, 2005), 1,269 species of elasmobranchs (Eschmeyer and Fong, 2017), 346 species of turtles (Uetz, 2017), and 52 species of holocephalans (Eschmeyer and Fong, 2017). Nonetheless, our estimates of the number of valid cestode species known from each of these major vertebrate host groups, based on type host species, are interesting to consider. In order of decreasing magnitude these are: 1,540 cestode species are described from mammals, 1,639 species from birds, 1,034 species from elasmobranchs, 465 species from bony fishes, 97 species from snakes and lizards (i.e., squamates), 24 species from amphibians, 11 species from holocephalans, and four species from turtles.

TABLE 1. Number of valid genera and species, and major vertebrate groups parasitized by each cestode order (incl. families for cyclophyllideans only); citation for each chapter treating the respective cestode order is also given. * Major host groups listed in order of decreasing cestode diversity; minor host groups enclosed in parentheses. † Number of species of *Mesocestoides* according to Chertkova and Kosupko (1978).

Cestode group	**Major vertebrate host group***	**No. of valid genera**	**No. of valid species**	**Source**
Amphilinidea	bony fishes, turtles	6	8	Scholz and Kuchta (2017) (Chapter 2 this volume)
Bothriocephalidea	bony fishes	48	132	Kuchta and Scholz (2017a) (Chapter 3 this volume)
Caryophyllidea	bony fishes	42	122	Scholz and Oros (2017) (Chapter 4 this volume)
Cathetocephalidea	elasmobranchs	3	6	Caira et al. (2017a) (Chapter 5 this volume)
Cyclophyllidea	birds, mammals, lizards & snakes, (amphibians)	437	3,034	Mariaux et al. (2017a) (Chapter 6 this volume)
Acoleidae Fuhrmann, 1899	birds	2	5	
Amabiliidae Braun, 1900	birds	10	32	
Anoplocephalidae Blanchard, 1891	mammals, lizards & snakes, birds	81	480	
Catenotaeniidae Spasskii, 1950	mammals	6	36	
Davaineidae Braun, 1900	birds, mammals	37	450	
Dilepididae Fuhrmann, 1907	birds, mammals	90	750	
Dioicocestidae Southwell, 1930	birds	5	21	
Dipylidiidae Railliet, 1896	mammals	3	15	
Gryporhynchidae Spasskii & Spasskaya, 1973	birds	16	76	
Hymenolepididae Perrier, 1897	birds, mammals	130	923	
Mesocestoididae Perrier, 1897	mammals, birds	2	13†	
Metadilepididae Spasskii, 1959	birds	10	15	
Nematotaeniidae Lühe, 1910	amphibians	5	19	
Paruterinidae Fuhrmann, 1907	birds, (mammals)	24	125	
Progynotaeniidae Fuhrmann, 1936	birds	6	24	
Taeniidae Ludwig, 1886	mammals	4	50	
Diphyllidea	elasmobranchs	6	59	Caira et al. (2017b) (Chapter 7 this volume)
Diphyllobothriidea	mammals	18	70	Kuchta and Scholz (2017b) (Chapter 8 this volume)
Gyrocotylidea	holocephalans	1	10	Kuchta et al. (2017) (Chapter 9 this volume)
Haplobothriidea	bony fishes	1	2	Kuchta and Scholz (2017c) (Chapter 10 this volume)
Lecanicephalidea	elasmobranchs	29	90	Jensen et al. (2017) (Chapter 11 this volume)
Litobothriidea	elasmobranchs	1	9	Caira et al. (2017c) (Chapter 12 this volume)
Nippotaeniidea	bony fishes	1	6	Scholz et al. (2017) (Chapter 13 this volume)
Onchoproteocephalidea				
Onchoproteocephalidea I	bony fishes, lizards & snakes, amphibians, (turtles), (mammal)	68	316	de Chambrier et al. (2017) (Chapter 14 this volume)
Onchoproteocephalidea II	elasmobranchs	11	246	Caira et al. (2017d) (Chapter 15 this volume)
Phyllobothriidea	elasmobranchs, (holocephalans)	24	69	Ruhnke et al. (2017a) (Chapter 16 this volume)
Rhinebothriidea	elasmobranchs	22	136	Ruhnke et al. (2017b) (Chapter 17 this volume)
Spathebothriidea	bony fishes	5	6	Kuchta and Scholz (2017d) (Chapter 18 this volume)
Tetrabothriidea	birds, mammals	6	70	Mariaux et al. (2017b) (Chapter 19 this volume)
"Tetraphyllidea" relics	elasmobranchs	25	104	Caira et al. (2017e) (Chapter 20 this volume)
Trypanorhyncha	elasmobranchs	81	315	Beveridge et al. (2017) (Chapter 21 this volume)
	TOTAL	**833**	**4,810**	

With 1,034 cestode species described from a host group that includes only 1,269 species, clearly, elasmobranchs were found to play a surprisingly more prominent role as hosts of cestode diversity than anticipated, given their low diversity relative to that of other major vertebrate groups. The disproportionate richness of elasmobranch cestodes is also evident from the number of new species described over the PBI project. Of the 215 new species, 148 (69%) came from elasmobranchs. This is despite the fact that of the 14,884 specimens of 1,906 species of vertebrates examined over the course of the project, only 1,806 specimens (i.e., 12%) of 215 species (i.e., 11%) were elasmobranchs. In essence, the discovery of cestode novelty in elasmobranch hosts required substantially less collecting effort than the discovery of novelty in any of the other major host groups. Several factors could account for their disproportionately high diversity. For example, the cestode faunas of elasmobranchs comprise nine of the 19 cestode orders (i.e., the Cathetocephalidea, Diphyllidea, Lecanicephalidea, Litobothriidea, Onchoproteocephalidea II, Phyllobothriidea, Rhinebothriidea, "Tetraphyllidea" relics, and Trypanorhyncha). The only other vertebrates that rival elasmobranchs in this respect are the bony fishes, which collectively host members of seven cestode orders (i.e., the Amphilinidea, Bothriocephalidea, Caryophyllidea, Haplobothriidea, Nippotaeniidea, Onchoproteocephalidea I, and Spathebothriidea). However, in total, the nine orders in elasmobranchs include 1,034 species, whereas the seven orders in bony fishes include a total of only 465 species. Furthermore, whereas only three of the seven orders parasitizing bony fishes house more than 50 species, seven of the nine orders parasitizing elasmobranchs exceed this number and thus it is commonplace to find representatives of multiple, and in the cases of some stingrays, up to five, orders parasitizing the same species. Alternatively, given their relatively low diversity (i.e., 1,269 species), it is possible that elasmobranchs have simply been more thoroughly sampled than the other vertebrate groups. Indeed, we estimate that over 40% of elasmobranch species have been examined for cestodes. Unfortunately, comparative assessments are not currently available for mammals, birds, or bony fishes owing to their extremely high numbers of species.

We have taken advantage of the tractable nature of elasmobranchs to provide estimates of total global diversity for eight of the nine chapters treating elasmobranch cestodes based on data from both described and undescribed species. We believe these estimates are reasonable not only because of our relatively representative sampling across elasmobranch genera, but also because most species of elasmobranch cestodes exhibit oioxenous specificity for their hosts (*sensu* Euzet and Combes [1980]) in that each generally parasitizes only a single species of host. As a consequence, extrapolation from examined host species to unexamined host species is viable. The estimated total across these eight orders of cestodes parasitizing elasmobranchs is 3,857 species in the 1,269 species of elasmobranchs known. The somewhat more relaxed degree of host specificity seen in the trypanorhynchs (Palm and Caira, 2008) made estimation in that order more difficult. However, if we conservatively assume that on average a single species of trypanorhynch will be found parasitizing each elasmobranch species—which seems reasonable given that it is commonplace for more than a single species of trypanorhynch to parasitize the same host species—the global estimate for trypanorhynchs would be 1,269 species. This would bring the total for all nine orders of cestodes parasitizing elasmobranchs to 5,126.

Extending the above calculations to include all vertebrates so as to generate an estimate of the global cestode fauna overall is complicated by factors beyond the challenges of assessing the proportion of species examined to date for the highly speciose groups of vertebrates. Key among them is the fact that cestodes differ substantially in terms of their degree of host specificity.

While some cestodes exhibit strict specificity for their hosts, host specificity in others is much more relaxed, ranging from mesostenoxenous, to metastenoenous, or even to euryxenous (*sensu* Caira et al. [2003]). This renders a precise global diversity calculation impossible in the absence of detailed host specificity data. Nonetheless, we would offer the following estimate. The subset of the planet's 68,067 vertebrate species that have been examined, are known to host 4,810 species of cestodes. Based on their examination of a total of 3,473 specimens of 989 species of birds, Mariaux et al. (2017a, Chapter 6 this volume) estimated a global total of 8,000 species of cestodes in birds. We estimate the world's elasmobranchs collectively host 5,126 cestode species. Thus, a global cestode fauna of 20,000 species does not seem unrealistic.

As predicted at the inception of the project, a good proportion of cestode novelty was discovered in species that belong to host orders, families, or genera with species known to host other cestodes, but that had not yet been examined for cestodes. However, some unexpected novel host associations were documented. For example, bothriocephalidean cestodes were discovered for the first time from the order Lepisosteiformes (i.e., gars) (Brabec et al., 2015) and also from several families of teleosts not previously known to host this order of cestodes. Onchoproteocephalidea I were reported for the first time from the families Gekkonidae (i.e., geckos) (Coquille and de Chambrier, 2008) and Dactyloidae (i.e., anoles) (Coquille and de Chambrier, 2008). The cestode faunas of deepwater sharks were found to be especially depauperate in terms of diversity, prevalence, and intensity of infections (Caira and Pickering, 2013). Discoveries of novel host associations were generally independent of country, although some surprises, such as a remarkably high amount of cyclophyllidean cestode diversity in the birds of Chile, were encountered. Beyond host type, more important considerations, included for example, habitat type.

Rigorous parasite survey work requires the accurate identification of each and every vertebrate specimen examined, and given prevalence of infection is rarely 100%, and varies considerably across group, examination of multiple specimens of a species is typically required if cestode infections are to be detected. As a consequence, this work can help inform the taxonomy of host groups—especially of groups that are poorly known. This synergy was exemplified by our survey work on the cestodes of elasmobranchs, which had a considerable impact on the taxonomy and systematics of the elasmobranchs themselves. Beyond contributing to a monograph providing NADH2 data for over 4,200 specimens of nearly half of the elasmobranch species known on the planet (Naylor et al., 2012), the project yielded hundreds of tissue samples and images of live or newly sacrificed sharks and rays that were used to inform recent work by elasmobranch taxonomists describing tens of new species and many genera of elasmobranchs (e.g., Last et al., 2016a–c; Manjaji-Matsumoto and Last, 2016). This work in turn has helped to inform fisheries management and conservation efforts focused on these elasmobranch taxa. The elasmobranch team is not unique in this respect. The leaders of all four vertebrate teams are recognized as experts in the taxonomy of their respective vertebrate groups in their own right.

PHYLOGENETICS AND CLASSIFICATION

The highly collaborative nature of the PBI project led to unprecedented advances in our understanding of the phylogenetic relationships and classification of cestodes (see Chapter 22 this volume, Waeschenbach and Littlewood, 2017). Beyond collaborating with one another, taxonomic experts worked closely with molecular phylogeneticists, primarily at the Natural History Museum in London, to generate ordinal-level phylogenetic frameworks. The molecular phylogeneticists were responsible for developing a high-throughput pipeline for the generation of reliable sequence data for multiple genes for nearly 1,000 specimens; these data were complemented by sequence data from large fragments of the mitochondrial genome for representative taxa in 16 of the 19 orders. Taxonomic experts maximized the breadth of taxon sampling in all groups through the collection of new material preserved for molecular work. These individuals ensured the accuracy of the identities of specimens sequenced and, in most cases, prepared hologenophores (*sensu* Pleijel et al., 2008) of specimens sequenced that serve to anchor the identities of these specimens into the future, that were deposited in museums around the world. The large volume of reliable sequence data from accurately identified, vouchered specimens now available in GenBank serves as a valuable resource for those interested in exploring new uses for such data (see Chapter 22 this volume, Waeschenbach and Littlewood, 2017).

The results of these collaborations included phylogenetic frameworks for 14 of the 19 cestode orders. The markers targeted were the two nuclear genes 28S rDNA and 18S rDNA, the two mitochondrial genes COI and 16S rDNA. In total, sequence data for one or more of these genes were generated for over 950 species. The breakdown by gene is as follows: 18S rDNA for 903 specimens, 28S rDNA for 935 specimens, 16S rDNA for 726 specimens, and COI for 829 specimens. Total taxon coverage in these molecular phylogenetic works ranged from 20% (Lecanicephalidea) to 80% (Caryophyllidea) of described species in each order.

Some of the highlights of the insights gained from these comprehensive phylogenetic analyses are as follows. Across the cestodes overall, the non-monophyly of the elasmobranch-hosted order "Tetraphyllidea" was partially resolved by revision of existing ordinal-level classification of the cestodes. To help resolve the situation, the Rhinebothriidea, Phyllobothriidea, and Onchoproteocephalidea were erected as new orders (see Healy et al., 2009; Caira et al., 2014). To preserve the monophyly of all cestode orders, the latter was circumscribed to include both a subset of genera previously assigned to the elasmobranch-hosted tetraphyllidean family Onchobothriidae as well as all species formerly assigned to the order Proteocephalidea, the majority of which parasitize teleosts and herptiles. As a consequence, 19 orders of cestodes are now recognized. Absolutely no support for the monophyly of the group traditionally referred to as the Cestodaria, comprising the orders Amphilinidea + Gyrocotylidea, was seen in analyses in which data for these taxa were included from GenBank and thus we have avoided use of the term Cestodaria here. In contrast the monophyly of the remaining 17 orders (collectively referred to as the Eucestoda) to the exclusion of the Amphilinidea and Gyrocotylidea was highly supported.

Novel phylogenetic frameworks were generated for the Bothriocephalidea, Caryophyllidea, Cyclophyllidea, Diphyllidea, Diphyllobothriidea, Lecanicephalidea, Litobothriidea, Onchoproteocephalidea, Phyllobothriidea, Rhinebothriidea, "Tetraphyllidea" relics, and Trypanorhyncha. In several cases these analyses led to major revisions in classification. The order Trypanorhyncha was subdivided into the two new suborders Trypanobatoidea and Trypanoselachoidea—the former primarily parasitizing batoids as definitive hosts and the latter primarily parasitizing sharks (Olson et al., 2010). Complete family-level classifications were established for the Rhinebothriidea (see Ruhnke et al., 2015) and Lecanicephalidea (see Jensen et al., 2016) for the first time. In the former case two new families (the Anthocephaliidae Ruhnke, Caira & Cox, 2015 and Escherbothriidae Ruhnke, Caira & Cox, 2015) were erected; in the latter case four new families (the Aberrapecidae Jensen, Caira, Cielocha, Littlewood & Waeschenbach, 2016, Eniochobothriidae Jensen, Caira, Cielocha, Littlewood & Waeschenbach, 2016, Paraberrapecidae Jensen, Caira, Cielocha, Littlewood & Waeschenbach, 2016, and Zanobatocestidae Jensen, Caira, Cielocha, Littlewood

& Waeschenbach, 2016) were erected. The new family Rhoptrobothriidae Caira, Jensen & Ruhnke, 2017 is established within the "Tetraphyllidea" relics, in the present volume (Chapter 20 this volume, Caira et al., 2017e) for a bizarre group of cestodes that parasitizes eaglerays. The new subfamily Testudotaeniinae de Chambrier, Coqille, Mariaux & Tkach, 2009 was established for a group of onchoproteocephalideans from turtles (de Chambrier et al., 2009).

The remarkably beneficial nature of these partnerships is clear from the breadth and depth of the resulting analyses. These works serve to illustrate the remarkable synergism that can arise from interactions between individuals with the combinations of expertise. Many of these collaborations are likely to continue well into the future.

DISSEMINATION

The Global Cestode Database (GCD) (www.tapewormdb.uconn.edu), originally developed as part of a Partnership for Enhancing Expertise in Taxonomy (PEET) project in a FileMaker Pro platform, was transferred to an on-line MySQL platform over the course of the project so as to make the data it houses easily, freely available to the public. Substantial effort was invested in populating this database, which now houses taxonomic information and, in most cases also images, of 12,225 nominal cestode taxa (i.e., including synonyms, etc.). The GCD now serves as the main repository for housing comprehensive information on tapeworm taxonomy and systematics. It has been embraced by the global community of Cestodologists as the key resource for taxonomic and systematic work on tapeworms. Our biggest challenge, now that the PBI project has come to completion, is to develop a sustainable strategy for continuing the population of the GCD into the future so as to keep it current.

On-line MySQL specimen databases were developed *de novo* for each of the major groups of vertebrate hosts. The Elasmobranch Host Specimen Database (www.elasmobranchs.tapewormdb.uconn.edu) is particularly active and now houses data, and in most cases also images, of over 9,200 specimens of sharks and stingrays.

The project website (www.tapeworms.uconn.edu) has served, and given an agreement with the University of Connecticut to maintain the website into perpetuity, will continue to serve as the primary site for the electronic dissemination of the main results of the project. This site also serves as a portal to the GCD and the host specimen databases. The site also provides (i) a list of participants, (ii) information and images of field trips and project meetings and cestode workshops, (iii) a list of new taxa and synonymies resulting from the project, (iv) a list of the publications resulting from the project, (v) quick references and illustrations to larval, microthrix, and egg terminology, etc., and (vi) an illustrated glossary of tapeworm features (with original, standardized images of each feature) that a number of colleagues from across the globe now use as a resource for teaching.

In total, 220 publications focused on the taxonomy, systematics, phylogenetic relationships, and/or morphological features of cestodes resulted from the project. These were complemented by four additional papers focused on parasites belonging to other groups collected incidentally along with cestodes from hosts examined over the courses of the project. A full list of these publications is provided in the Appendix.

TRAINING

One of the major strengths of the project, and a factor that contributed significantly to its success, was the group of extremely capable, talented postdoctoral fellows, and graduate and undergraduate students that we were able to attract to participate in this research. These individuals were fully engaged in all aspects of the laboratory and field elements of the project.

Beyond the intricacies of the taxonomy and systematics of their respective target cestode groups, these individuals received training in the full complement of modern laboratory methods required to identify and describe tapeworms. Many also acquired skills in molecular and phylogenetic methods. A large number of these trainees were engaged in the preparation of publications describing the results; a number also served as authors of chapters in this Special Issue. These individuals are indicated with symbols in the list of project publications in the Appendix. The Training section below provides additional details.

The project employed a flexible strategy for supporting postdoctoral fellows that would match the needs of the four "host" teams with the interests of each fellow. In the cases of some of the foreign individuals, project funding was supplemented with funds from their own institutions. In total, 14 postdoctoral fellows were members of the project team. As a result of the highly collaborative nature of project personnel, most individuals received a blend of training from both foreign and US taxonomic experts. Most of the postdoctoral fellows were successful at obtaining permanent academic or research positions. Each fellow, his or her primary institution of training, and if different, his or her current place of employment, are as follows: Jitka Aldhoun (Natural History Museum in London), Jan Brabec (Czech Academy of Sciences), Joanna Cielocha (University of Kansas; Rockhurst University), Caroline Fyler (University of Connecticut; Martha's Vineyard High School), Voitto Haukisalmi (Finnish Museum of Natural History), Miloslav Jirků (Czech Academy of Sciences), Roman Kuchta (Czech Academy of Sciences), Arseny Makarikov (Russian Academy of Sciences [Siberian Branch]), Maria Pickering (University of Connecticut; Meredith College), Mikulas Oros (Czech Academy of Sciences; Slovak Academy of Sciences), Martina Orosové (Slovak Academy of Sciences), Anna Phillips (University of Connecticut; Smithsonian Institution), and Aneta Yoneva (Bulgarian Academy of Sciences). The efforts of postdoctoral fellow Andrea Waeschenbach (Natural History Museum in London) were instrumental to the success of the molecular phylogenetic elements of the project. Not only did she work closely with each project team to coordinate work on their respective cestode orders, but she also conducted much of the molecular work for the project. Data for sizeable subsets of additional taxa were generated by postdoctoral fellow Jan Brabec, as well as Co-PI Vasyl Tkach and collaborator Fernando Marques.

In total, 34 graduate students, 18 of whom were from the USA, worked on the project. The home countries of foreign graduate students included Argentina, Australia, Brazil, Bulgaria, Canada, Chile, Czech Republic, Iran, and Switzerland. Following their work on the project, among the US graduate students, four doctoral students accepted postdoctoral fellowships (some continuing on this project) and three are currently completing doctoral degrees; two master's students went on to pursue doctoral degrees, one is a research specialist, and one is a freelance scientific illustrator. Of the foreign students, five currently hold assistant professorships or research positions, and three are postdoctoral fellows; two of the master's students went on to pursue doctoral degrees.

Undergraduate students played an especially key role in the project; 59 students were involved, 45 of whom were from the USA. The 14 foreign students were based in Canada, Costa Rica, the Czech Republic, Germany, Ivory Coast, Madagascar, Senegal, Switzerland, and Tunisia. Beyond providing these students with valuable exposure to research, these students received training that helped prepare them to pursue advanced degrees: ten went on to graduate school, four to law school, four to medical school, one to veterinary school, and one is currently enrolled in a combined MD/Ph.D. program. One of the original undergraduates on the project, Stephen Greiman, completed his graduate training and is now an Assistant Professor at Georgia Southern University.

OUTREACH

Their marvelous beauty, obscure biology, and association with vertebrates make tapeworms ideal organisms for enlightening both children and the general public about some of the less well known organisms of the world. Beyond the project website, we engaged in two endeavors that specifically targeted these audiences. A prototype of a children's book focused on tapeworms was completed (Figs. 2, 3). This book, entitled *Meet the Suckers*, takes children inside the animals that live in a typical public Aquarium, introducing them to the wonders of the tapeworms that live inside the animals of an Aquarium. The story begins when Briar and Jakob, the two children featured in the book, receive a package that contains not only "worm-wear" goggles that allow them to see inside of animals, but also a gut-tube containing a "spokesworm" named Cyri. The children (and their cat Rusty) travel with Cyri to an Aquarium, where they learn all about the biology of the many different kinds of tapeworms that live inside of the various animals in each exhibit which they can "see" with their worm-wear goggles (in the book, these tapeworms are hidden under flaps that children reading the book must lift). In all cases, the tapeworms illustrated are the actual species that parasitize each host animal illustrated. Complete with a glossary and several resource pages (as well as a number of puns to keep adult readers entertained), the book highlights the wondrous nature, rather than the potentially distasteful aspects, of tapeworms. The book is authored by "Lenta Chervy" in recognition of the collaborative nature of its creation.

Aimed at a broader component of the general public, an exhibit entitled "The 'Faces' of Parasites," highlighting some of the results of the project, was developed and installed at the University of Kansas Natural History Museum. This exhibit features four LED panels with 4-foot high, colorized scanning electron micrographs, each of which dramatically portrays the scolex of a different novel tapeworm species discovered over the course of the project. The exhibit is augmented by host and collection visuals displayed on a tablet and actual specimens under a loupe for scale.

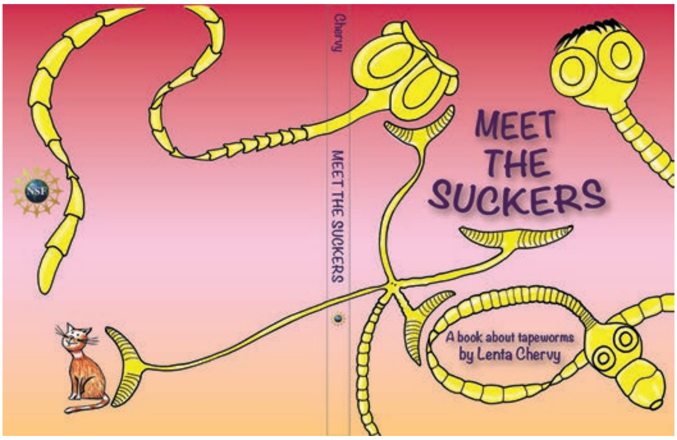

FIGURE 2. Cover design of the prototype of the children's book *Meet the Suckers*.

FINAL CONSIDERATIONS

This project focused on tapeworms—a gutless group of remarkable parasitic worms found in the digestive system of all major groups of vertebrate animals, including humans. The primary goals of the project were to collect tapeworms from as many different species of mammals, birds, bony fishes, snakes, lizards, turtles, sharks, and stingrays from around the world as possible, to discover and describe as much tapeworm novelty as possible from these hosts, and to establish robust frameworks of the evolutionary relationships of these parasites based on molecular and morphological information. Thanks to the energetic and highly

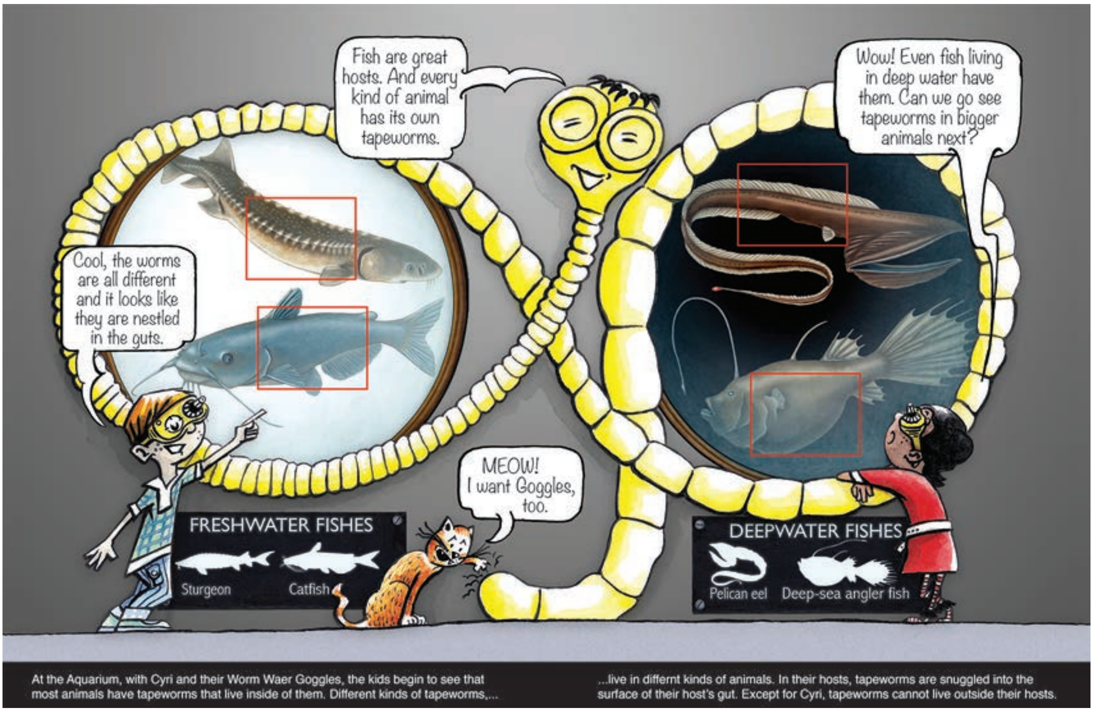

Figure 3. Example spread of the prototype of the children's book *Meet the Suckers* showing the children Briar and Jakob (and Rusty, the cat), accompanied by their "spokesworm" Cyri, at the Aquarium discovering the tapeworms that live inside bony fishes.

collaborative nature the global community of Cestodologists we believe we have exceeded our original goals! The over 210 new species described and over 60 new genera erected bring the global totals to at least 4,810 species and 833 genera. But, this is just the tip of the iceberg!

Our relatively informed estimate of the full magnitude of cestode diversity parasitizing the approximately 68,000 species of vertebrates inhabiting the planet is now a remarkable 20,000 species. As is clear from this estimate, we anticipate that only a subset of vertebrate species will be found to host tapeworms—the results of our survey work provide compelling evidence that vertebrate groups differ substantially in their suitability as hosts for tapeworms. For example, we have learned or, in some cases confirmed, that the following vertebrate groups host few or even no tapeworms. In *mammals* examples of such groups are the Artiodactyla (deer, etc.), Perissodactyla (horses, etc.), and Primata (monkeys, etc.); in *birds* these are the Procellariformes (petrels, etc.) and Sphenisciformes (penguins); in *bony fishes* these are, for example, the Scombridae (mackerels, tunas, etc.); in *elasmobranchs* these are the Squaliformes (dogfish, etc.) and "Scyliorhinidae" (cat sharks). In general the Squamata (snakes and lizards), Chelonii (turtles), and Amphibia (frogs and salamanders) also host few tapeworms. In contrast, the following vertebrate groups appear to be especially good hosts for tapeworms. The *mammal* groups are the Soricomorpha (shrews, etc.), Chiroptera (bats), Lagomorpha (rabbits, etc.), Carnivora (bears, etc.), and Marsupialia (kangaroos, etc.); the *bird* groups are the Passeriformes (sparrows, etc.), Charadriiformes (plovers, sandpipers, seagulls, etc.), Podicipediformes (grebes), and Anseriformes (ducks, geese, swans, etc.); the *bony fish* groups are the Siluriformes (catfish, etc.) and Cypriniformes (carp, etc.); the *elasmobranch* groups are the Myliobatiformes (stingrays, etc.) and Rhinopristiformes (guitarfish, etc.). As tapeworms are transmitted trophically (i.e., through the food web), the intermediate hosts of tapeworms are of particular interest because they can inform biases towards definitive host use.

Because so many of our new tapeworm species were discovered in host species not previously examined for tapeworms, regardless of country, in seeking to discover the remaining approximately two-thirds of the world's global tapeworm fauna, future survey work aimed at discovering additional novelty should focus on unexplored species in these more productive host groups and their close relatives. But, the way forward is not without significant challenges. As highly visible vertebrates, essentially all of these potential host taxa are charismatic creatures. Permits are becoming more difficult to obtain even for the collection of very small numbers of individuals of these taxa. This is unfortunate because, as noted above, tapeworm work has been instrumental in helping to inform the taxonomy and systematics of the vertebrate groups, and as a consequence has also informed policy and conservation efforts aimed at those vertebrate groups. Furthermore, although it is terrific that we now have a relatively robust estimate of the scope of the work required to complete the global picture of tapeworm diversity, the magnitude of that diversity raises important concerns in terms of the future of taxonomic expertise in tapeworms, and of cyclophyllideans in particular. Given the latter order already numbers over 3,000 species, and literally thousands of birds and mammals remain to be surveyed for tapeworms, we anticipate that a large proportion of the estimated 15,000 tapeworm species remaining to be described will likely be cyclophyllideans. In reality, a substantial boost in the number of active tapeworm taxonomists, and especially those working on taxa that parasitize birds and mammals, is required if we are to move forward with achieving the goal of completing the global inventory in a timely fashion. We have contemplated taking a Citizen Science approach to expand the workforce engaged in tapeworm taxonomy, but the challenges of collecting from vertebrates and the expertise required to preserve and prepare tapeworms properly for taxonomic work make this somewhat unrealistic. Reinvigoration of NSF's Partnership for Enhancing Expertise in Taxonomy (PEET) program, which was responsible for training a large proportion of those involved in the elasmobranch tapeworm taxonomy aspects of this project, including one of the PIs, would likely be an effective way to proceed.

The nature of tapeworm taxonomy requires an unusually high degree of methodological rigor when generating molecular sequence data if accurate identities are to be given to the specimens sequenced. Even the largest tapeworm specimens cannot be definitively identified with the naked eye because the majority of the diagnostic features of tapeworms are associated with their internal anatomy. To optimally view these features specimens need to be stained, cleared, and mounted on glass slides. To overcome this problem, project personnel made it a routine practice to sequence only a portion of a tapeworm specimen (usually taken from somewhere on the middle of the strobila) and to prepare the remainder of the specimen (usually scolex and terminal proglottid[s]) for morphological work to serve as a hologenophore to ground the identity of the specimen sequenced. In many instances this practice allowed us to detect issues with identifications when morphological and molecular results conflicted. It is our hope that this practice will be continued into the future for the value of having confirmed identities clearly justifies the extra time and effort required to prepare the hologenophores.

Basic phylogenetic frameworks are now available for most cestode orders. Nowadays, it is unusual to erect new orders of animals, but three new orders were erected between 2009 and 2014 largely as a result of PBI project efforts. As a consequence, ordinal-level classifications have largely been reconfigured to bring them into line with these frameworks, but that work is not yet complete. Much remains to be done with the “Tetraphyllidea” relics before their phylogenetic relationships with respect to one another and other orders are sufficiently well understood to allow a strategy for optimally subdividing them into monophyletic groups can be developed. Further investigation of the phylogenetic relationships of the Phyllobothriidea is likely to necessitate some reconfiguration of this group as well. Serious consideration should be given to establishing the Mesocestoididae as an independent order, given we have shown it to be the sister taxon of a clade that includes both the Cyclophyllidea and the Tetrabothriidea. The family-group level classifications of the Trypanorhyncha and Onchoproteocephalidea are in dire need of attention, as is the genus-level classification of the non-elasmobranch hosted onchoproteocephalideans. Finally, in the cases of most of the 19 orders exhaustive species-level phylogenies are not yet available.

Nonetheless, as a result of PBI project efforts, tapeworms and their vertebrate hosts have emerged as one of the most well-documented host-parasite systems in existence. All sorts of intriguing patterns are beginning to emerge, raising numerous intriguing questions. For example: Why are some groups of tapeworms more host-specific than others? Why do some vertebrate groups make better hosts for tapeworms than others? What circumstances led to the association of tapeworms with humans on more than one occasion over evolutionary time? Are tetrabothriideans essentially just cyclophylideans that parasitize marine mammals? Given that phylogenetic relationships of vertebrate host groups are also more well undestood, rigorous cophylogenetic studies can now be undertaken. Preliminary analyses have already raised a plethora of interesting fundamental questions about the evolution of cestodes and their hosts. For example: What evolutionary processes might account for the fact that, at least in some of the cestodes groups that parasitize elasmobranchs, highly host-specific taxa do not appear to have coevolved with their vertebrate?

Beyond what this system can tell us about the historical associations between tapeworms and their hosts, we hope it serves as a valuable resource for future work investigating the evolution and cophylogenetic relationships of parasites in general, and the processes that govern these associations. We are delighted to have been part of this exciting project and to be able to share our results with others. To this end, a PDF of the entire Special Publication is available at: http://hdl.handle.net/1808/24421 and http://tapeworms.uconn.edu/finalpub.html.

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2

Amphilinidea Poche, 1922

By
Tomáš Scholz[1] and Roman Kuchta

AMPHILINIDEA AS THEY WERE KNOWN PRIOR TO THE PBI PROJECT

Diversity and Classification. This is a small order of monozoic cestodes with eight valid species that differ in their body plan from "typical" tapeworms (i.e, taxa more or less corresponding to the subclass Eucestoda). The first amphilinidean was described as *Monostoma foliaceum* Rudolphi, 1819 (now *Amphilina foliacea* [Rudolphi, 1819] Wagener, 1858) by Rudolphi (1819), whereas the most recently described species is *Nesolecithus africanus* Dönges & Harder, 1966 (see Table 1). The order was erected by Poche (1922) who provided a comprehensive survey of this group that included the families Amphilinidae Claus, 1879 and newly proposed Schizochoeridae Poche, 1922; four new genera were also proposed at that time (Poche, 1922, 1926). Johnston (1931) erected the family Australamphilinidae Johnston, 1931.

Whereas there is little disagreement regarding the number of valid species (taxa described from the Indian subcontinent after Woodland [1923] are not recognized as valid by subsequent authors), little consensus exists as to the higher classification, including the number of genera (from 3 recognized by Bandoni and Brooks [1987] to as many as 8 accepted by Schmidt [1986], who retained *Hunteroides* Johri, 1959 [= syn. of *Gephyrolina* Poche, 1926 according to most authors] and *Gyrometra* Yamaguti, 1954 [= syn. of *Gigantolina* Poche, 1922]). In the most comprehensive monograph on the Amphilinidea, Dubinina (1982) recognized six genera in four families, whereas Bandoni and Brooks (1987), who used a cladistic approach to assess the interrelationships, host associations, and geographic distribution of amphilinideans based on a study of type and voucher specimens, accepted only three genera in one family split into two subfamilies.

In the most recent review of the order with keys to the genera, Gibson (1994) largely followed the classification of Dubinina (1982) accepting eight species in six genera, but did not follow her classification at a higher level. Instead, he accepted two families, the Amphilinidae and the Schizochoeridae, the latter with two subfamilies, the Schizochoerinae Poche, 1922 and the Austramphilininae. Rohde (1998) questioned the validity of both families and the two subfamilies of Schizochoeridae, retaining only a single family, the Amphilinidae, with the six genera recognized by Gibson (1994). Generic classification of this order is used herein, because the characteristics he used to differentiate individual genera seem to us to be well justified. These include: the course of the uterus and its form (tubular or sacciform), the shape of the body, the relative position and appearance of the terminal genitalia (male and female gonopores, i.e., ejaculatory duct and vagina which may form a common genital duct), the bifurcation and spination of the vagina, ovary shape, the shape and size of the seminal receptacle, and the presence of caudal lobes and a *ductus yamagutii* (see Gibson, 1994).

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[1] Corresponding author (tscholz@paru.cas.cz)

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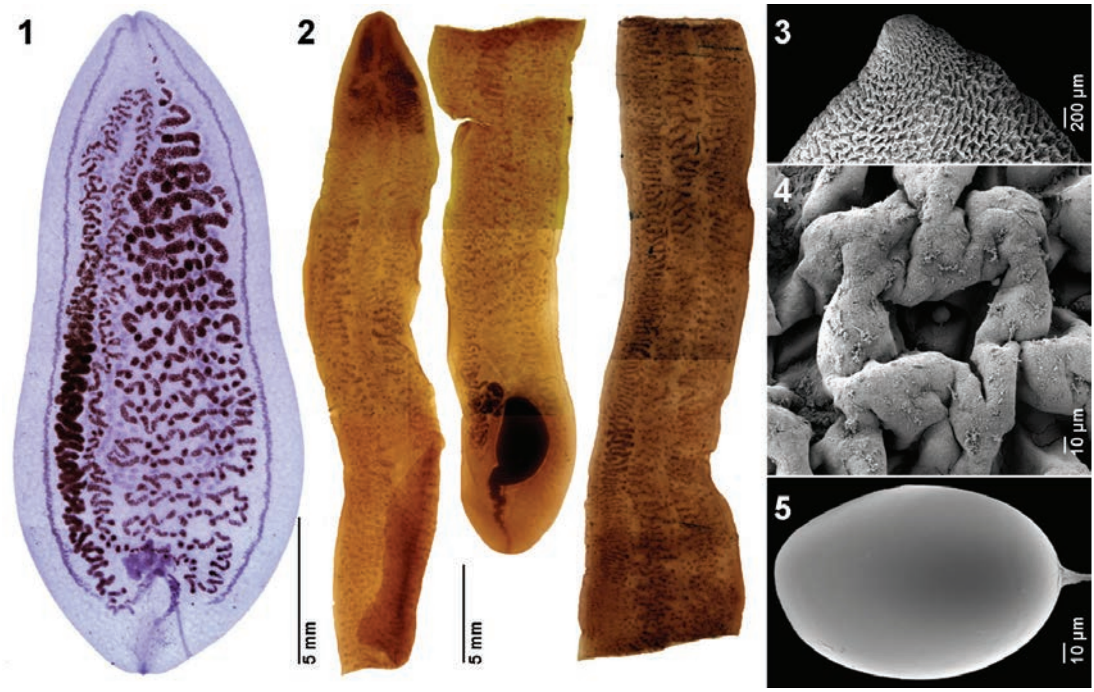
Dubinina (1982) proposed raising the order to the level of a class as the Amphilinida, but this classification has not been accepted by any subsequent authors except for Bazitov (1984) and Galkin (1999). Instead, most authors, including Joyeux and Baer (1936), Wardle and McLeod (1952), Yamaguti (1959—the Caryophyllidea were also included), and Schmidt (1986), considered the amphilinideans along with the Gyrocotylidea to compose the subclass Cestodaria.

MORPHOLOGY. The amphilinideans are large worms (several cm long) with a flattened leaf-like body not divided into proglottids (Figs. 1, 2). Their monozoic body is elongate to foliiform, without any distinct organs of attachment (i.e., scolex) (Figs. 3, 4), even though a small sucker-like organ may be present at the anterior end (Gibson, 1994). The protonephridial system comprises two lateral ducts opening posteriorly via a common pore. The testes are follicular, forming narrow, lateral bands. A cirrus-sac is absent; the vas deferens forms an ejaculatory bulb and ejaculatory duct distally. The genital pores open at or near the posterior extremity, usually separately, but are exceptionally joined to form a single pore. The ovary is located in the posterior region of the body and is variable in shape (bilobed symmetrical, bilobed asymmetrical, reniform, elongate, lobate, or compact). The vagina usually opens ventrally on the body, but is occasionally bifid, opening via ventral and dorsal pores. A seminal receptacle is present, varying in shape and size from small to very long; it may be connected to an accessory seminal receptacle. The vitellarium is follicular, with numerous follicles present in lateral bands between the testicular fields and lateral margins of the body. A long, tubular, N-shaped or looped, uterus extends between the ootype and the anterior extremity opening via a uterine pore at the anterior end of the body. The uterus runs anteriorly from the posterior ootype, then posteriorly on the same side of the body, changes to the other side of the body and again runs anteriorly to terminate close to the anterior end. This N-shaped arrangement of the uterus in three limbs, as in *Amphilina* Wagener, 1858, has not been documented in any other neodermatan group. The eggs are anoperculate (Fig. 5) and contain a lycophora or decacanth larva with ten hooks of two types at the posterior end; these hooks may be retained in the adult (Dubinina, 1982; Bandoni and Brooks, 1987; Gibson, 1994; Rohde, 1998).

The ultrastructure of amphilinideans has been studied extensively because of the group's peculiar morphology and biology which are important for the understanding of the evolutionary history of cestodes and parasitic flatworms (i.e., Neodermata) in general (Ehlers, 1985). Xylander (1987, 1988), Biserova et al. (2000), and Davydov and Kuperman (1993) have studied different organs and organ systems of *Amphilina foliacea*, a parasite of sturgeons (Acipenseriformes: Acipenseridae Bonaparte). In Australia, Rohde and co-authors, especially Garlick and Watson (for extensive list of references, see Rohde [1994, 1998]), studied *Austramphilina elongata* Johnson, 1931 from freshwater turtles.

HOST ASSOCIATIONS. All eight valid species occur as adults in the body cavity of their hosts: chondrosteans (sturgeons; Acipenseridae), evolutionarily ancient freshwater teleosts (Osteoglossiformes: Arapaimidae Bonaparte and Gymnarchidae Bleeker), more recently evolved marine teleosts (Perciformes: Haemulidae Gill and Mugilidae Jarocki), and one species in freshwater turtles (Testudines: Chelidae Gray).

The life-cycles of four species, *Amphilina foliacea*, *A. japonica* Goto & Ishii, 1936, *Austramphilina elongata*, and *Nesolecithus africanus* have been studied (Janicki, 1928; Rašín, 1931; Cole, 1968; Dubinina, 1974; Rohde and Georgi, 1983; Gibson et al., 1987; Rohde and Watson, 1989). Freshwater crustaceans, including amphipods, the freshwater prawn *Desmocaris trispinosa* (Aurivillius), the crayfish *Cherax destructor* Clark, and the freshwater shrimp *Paratya australiensis* Kemp and *Atya* sp. have been documented to serve as intermediate hosts of



FIGURES 1–5. Micrographs of selected amphilinideans. **(1)** Photomicrograph of whole mount of *Amphilina foliacea* ex *Acipenser ruthenus* L., Slovakia. **(2)** Photomicrograph of whole mount of *Australamphilina elongata* ex *Chelodina oblonga* imported from Indonesia. **(3–5)** Scanning electron micrographs of *Amphilina foliacea* ex *Acipenser ruthenus,* Slovakia. **(3)** Anterior region. **(4)** Surface of anterior region. **(5)** Egg.

amphilinideans (Janicki, 1928; Rašín, 1931; Dubinina, 1982; Gibson et al., 1987; Rohde, 1994).

Based on some degree of resemblance between amphilinidean life-cycles and those of bothriocephalideans and diphyllobothriideans (i.e., the use of crustaceans as intermediate hosts), and based on the body cavity as an atypical site of infection for egg-bearing adults in the definitive hosts, Janicki (1930) suggested that amphilinideans are essentially sexually mature plerocercoids derived from a strobilate adult form that had at one time been parasitic in the intestine of now extinct Tertiary "reptiles." However, this would seem unlikely, especially as Gibson et al. (1987) indicated that the two congeneric species, *Nesolecithus africanus* and *N. janickii*, present in osteoglossiform fishes in adjacent regions of West Africa and South America, have been separated, and have changed little, for more than 100 million years, well before the Tertiary period.

Bandoni and Brooks (1987) found a 70% fit between host and parasite phylogenies, suggesting a high degree of coevolution between amphilinideans and their teleost hosts. However, these authors based their phylogeny on morphological characteristics alone and a more robust phylogenetic hypothesis inferred from molecular sequence data is required to test their results.

GEOGRAPHIC DISTRIBUTION. The geographic distribution of species of this order is "patchy" and does not exhibit any apparent pattern. Bandoni and Brooks (1987) divided the amphilinideans into two groups, with members of the Amphilininae (i.e., 2 species of *Amphilina*) occurring in northern temperate regions and the Schizochoerinae (i.e., all 6 of the remaining species in their classification) occurring in the tropics and Southern Hemisphere. More specifically, both species of *Amphilina* occur in the Holarctic biogeographic realm. *Austramphilina elongata* is endemic to freshwaters of Australia. *Gephyrolina paragonopora* (Woodland, 1923) Poche, 1926 is known only from freshwaters of the Indian subcontinent, whereas *Gigantolina magna* (Southwell, 1915) Poche, 1922 has a much broader distribution, with records from marine perciform fishes off the Peninsular Malaysia, Pakistan, Sri Lanka, Sulawesi, and Tanzania. *Nesolecithus africanus* is known from freshwaters in Nigeria, whereas *N. janickii* Poche, 1922 and *Schizochoerus liguloideus* (Diesing, 1850) Poche, 1922 occur in Amazonia (South America) (Dubinina, 1982; Gibson et al., 1987). Bandoni and Brooks (1987) compared the geographic distribution of the amphilinideans with four current hypotheses of area relationships for the southern land masses and obtained high consistency index values (88 to 100%), which they interpreted as evidence that vicariance may be sufficient to explain the biogeographic distribution of amphilinideans.

Phylogenetic Relationships. The systematic position of the amphilinideans among neodermatans, and cestodes specifically, has been controversial. However, most authors have considered them to be an evolutionarily ancient order of cestodes that have not evolved proglottization or a modification of an anterior attachment organ as a scolex, as is the case in most eucestodes (Wardle and McLeod, 1952; Yamaguti, 1959; Schmidt, 1986; Khalil et al., 1994; Xylander, 2001). Bandoni and Brooks (1987) presented a hypothesis for the interrelationships of the amphilinideans based on morphological characters. They recognized three lineages that correspond to the three genera they considered valid, namely the basal *Amphilina* with two species, and a sister clade consisting of two species of *Gigantolina* and four species of *Schizochoerus*.

In fact, early molecular phylogenetic analyses have not shed much light on the phylogenetic relationships of amphilinideans because only a few species were sequenced and included in these analyses. In addition, the genes sequenced exhibited extremely high levels of divergence relative to other cestodes, making alignment difficult without losing a considerable amount of information (Olson et al., 2001). Mariaux (1998) generated sequence data for the 18S rDNA gene for *Schizochoerus liguloideus* from *Arapaima gigas* (Schinz) in Brazil and used this taxon as the outgroup for analyses of the Eucestoda. Olson and Caira (1999) showed extreme divergence of 18S rDNA sequence data in *S. liguloideus* in comparison to that of other cestode taxa. Subsequently, Olson et al. (2001) generated sequence data for both the 18S rDNA and 28S rDNA genes for two additional amphilinidean species, *Austramphilina elongata* from the eastern long-necked turtle (*Chelodina longicollis* [Shaw]) in Australia (18S rDNA, AJ287480; 28S rDNA, AF286907) and *Gigantolina magna* from the painted sweetlips (*Diagramma labiosum* Macleay) in the Coral Sea, Queensland, Australia (18S rDNA, AJ243681; 28S rDNA, AF286908). However, these authors also observed a high degree of divergence in 18S rDNA and also in 28S rDNA sequence data in these two species, making confident alignment of both genes difficult (Olson et al., 2001). Therefore, both amphilinidean species were excluded from their analyses although the sequence data were made publicly available.

The only assessment of interrelationships among any amphilinidean taxa was provided by Olson et al. (2008) who compared partial 28S rDNA (i.e., D1–D3 region) sequence data for three species (*Amph. foliacea*, *Aust. elongata*, and *G. magna*) and complete 18S rDNA sequence data for four species (*Amph. foliacea*, *Aust. elongata*, *G. magna*, and *S. liguloideus*). Based on 28S rDNA sequence data, *Amph. foliacea* was recovered as sister taxon to the lineage comprising *Aust. elongata* and *G. magna*. Their analysis of 18S rDNA sequence data alone yielded a tree with a different topology in which *Amph. foliacea* was sister to a group consisting of *Aust.*

elongata and *S. linguloideus*. However, support was generally weak. None of the analyses yielded tree topologies consistent with the classifications of Bandoni and Brooks (1987) or Gibson (1994).

CURRENT STATUS OF THE AMPHILINIDEA

DIVERSITY AND CLASSIFICATION. No major changes in the taxonomy of the order have been proposed as a result of PBI project efforts, because the typical hosts of amphilinideans were not targeted owing to difficulties in their collecting.

Individual genera are readily distinguishable using the above-mentioned morphological characteristics, and also by conspicuous differences in host use, geographic distribution, and (partly) habitat (1 monotypic genus occurs in marine teleosts whereas the remaining taxa are freshwater). At this point, the most questionable decision may be the distinction between *Schizochoerus* and *Nesolecithus*; both genera share a unique feature among amphilinideans (i.e., a distally bifid vagina), in addition to other key morphological characteristics such as an N-shaped uterus, a subglobular ovary, and the absence of a terminal depression. The genera differ in the shape of the body (elongate versus fusiform) and length of the seminal receptacle (very long in the former genus versus short in the latter genus). The independent status of these genera should be explored using molecular sequence data; at present, sequence data for only one of the three recognized species are available (see above).

Regarding the higher-level classification of the order, we follow Rohde (1998), who questioned Gibson's (1994) subfamilial and familial classification, especially because a polar egg stalk is present only in species of *Amphilina* (family Amphilinidae) and *Gephyrolina* (subfamily Schizochoerinae, family Schizochoeridae), but in no other genera. Molecular sequence data are incomplete and controversial (see above) but do not appear to fully support any of the classifications previously proposed (i.e., Dubinina, 1982; Bandoni and Brooks, 1987; Gibson, 1994). Therefore, we retain here only the Amphilinidae.

MORPHOLOGY. In fact, very few new data on the morphology of amphilinideans were generated over the course of the PBI project. Unlike previous decades, during which the ultrastructure of amphilinideans, especially that of *Austramphilina elongata* and *Amphilina foliacea*, was studied in detail (see above and Rohde, 1994), only four ultrastructural studies have been published since 2008; they dealt with *Amph. foliacea (*see Bruňanská et al., 2012, 2013; Poddubnaya, 2013) and *A. japonica* (see Poddubnaya and Xylander, 2010).

HOST ASSOCIATIONS. Except for a specimen of *Austramphilina elongata* collected from the northern long-necked turtle *Chelodina oblonga* Gray (as *Macrochelodina rugosa* [Ogilby]) (new host record) imported from Indonesia to the Czech Republic and examined by J. Bulantová (Faculty of Science, Charles University, Prague), no new information on host associations was generated over the course of the PBI project. As discussed in detail by previous authors, the spectrum of definitive hosts covers a selection of phylogenetically unrelated groups from freshwater chelonians to marine perciform teleosts. Doubtful records include those of *Amphilina coreana* Chu & Chu, 1991 (in fact a synonym of *A. japonica*) from Alaska pollock, *Theragra chalcogramm* (Pallas), and *A. foliacea* from channel catfish, *Ictalurus punctatus* (Rafinesque), by Naimova and Roitman (1989). Furthermore, *Amphilina tengaria* Jafri, 1993 reported from the Tengara catfish, *Mystus tengara* (Hamilton), in India is in fact a synonym of *Gephyrolina paragonopora*.

GEOGRAPHIC DISTRIBUTION. Except for the specimen of *Aust. elongata* imported from Indonesia (new geographic record, first one outside of Australia) mentioned above, no new geographic records of the amphilinideans were reported during the PBI project.

Phylogenetic Relationships. No hypotheses of amphilinidean interrelationships were generated as a result of the PBI project. Waeschenbach et al. (2012) generated data for a contiguous fragment of the mitochondrial genome (mtDNA) spanning 4,034–4,447 bp for 18 cestode species, including the amphilinidean *Gigantolina magna* from a marine perciform fish in Australia (new sequence JQ268545).

The data available at this time do not allow for the generation of robust phylogenetic inferences for either amphilinidean interrelationships, or for definitive resolution of the relationships between amphilinideans and the other cestode orders—and the Gyrocotylidea in particular. Sequence data for a limited selection of genes for only four species representing only 50% of the total diversity in the order are available. In addition, the nuclear ribosomal genes for which sequence data are available are highly divergent, limiting their use for assessing amphilidean phylogenetic relationships. Extreme divergence in their nuclear ribosomal genes also indicates that this group has had a long evolutionary history but key questions regarding host colonization or vicariance remain to be addressed by future research (Olson and Caira, 1999; Olson et al., 2001, 2008). In contrast, mitochondrial genome sequence data show promise for resolving amphilinidean relationships among cestodes (Waeschenbach et al., 2012).

CONCLUSIONS

The Amphilinidea is a small order, with only eight species recognized, albeit in six genera, of monozoic, large cestodes with a flattened leaf-like body. They occur as adults in the body cavity of chondrosteans, freshwater and marine teleosts, and one species in freshwater turtles. The life-cycle includes crustaceans serving as intermediate hosts. Amphilinideans are undoubtedly one of the two earliest diverging groups of cestodes. However, insufficient data exist to assess the interrelationships of this small order, or for unraveling patterns in their host associations and geographic distribution.

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TABLE 1. List of valid amphilinidean taxa with type hosts.

VALID TAXA

FAMILY AMPHILINIDAE CLAUS, 1879
- *Amphilina* Wagener, 1858 (syn. *Aridmostomum* Grimm, 1871)
  - *Amphilina foliacea* (Rudolphi, 1819) Wagener, 1858 (type) ex *Acipenser sturio*
  - *Amphilina japonica* Goto & Ishii, 1936 ex *Acipenser mikadoi*
- *Australamphilina* Johnston, 1931 (syn. *Kosterina* Ihle & Ihle-Landenberg, 1932)
  - *Australamphilina elongata* Johnston, 1931 (type) ex *Chelodina longicollis*
- *Gephyrolina* Poche, 1926 (syns. *Hunteroides* Johri, 1959; *Pseudogephyrolina* Gupta & Singh, 1992)
  - *Gephyrolina paragonopora* (Woodland, 1923) Poche, 1926 (type) ex *Macrones seenghala* (= *Sperata seenghala*)
- *Gigantolina* Poche, 1922 (syn. *Gyrometra* Yamaguti, 1954)
  - *Gigantolina magna* (Southwell, 1915) Poche, 1922 (type) ex *Diagramma crassispinum* (= *Plectorhinchus gibbosus*)
- *Nesolecithus* Poche, 1922
  - *Nesolecithus janickii* Poche, 1922 (type) ex *Arapaima gigas*
  - *Nesolecithus africanus* Dönges & Harder, 1966 ex *Gymnarchus niloticus*
- *Schizochoerus* Poche, 1922
  - *Schizochoerus liguloideus* (Diesing, 1850) Poche, 1922 (type) ex *Arapaima gigas*

3

Bothriocephalidea Kuchta, Scholz, Brabec & Bray, 2008

By
Roman Kuchta[1] and Tomáš Scholz

BOTHRIOCEPHALIDEA AS THEY WERE KNOWN PRIOR TO THE PBI PROJECT

Diversity and Classification. The Bothriocephalidea was erected as an independent order by Kuchta et al. (2008a) just before the inception of the PBI project. Prior to that, its taxa and those assigned to the second new order established by Kuchta et al. (2008a), the Diphyllobothriidea (see Chapter 8 this volume, Kuchta and Scholz, 2017), had collectively been considered to compose the single order Pseudophyllidea Carus, 1863. The taxa assigned to the Bothriocephlidea had traditionally been divided into four families: Bothriocephalidae Blanchard, 1849, Echinophallidae Schumacher, 1914, Philobythiidae Campbell, 1977, and Triaenophoridae Lönnberg, 1889 (see Bray et al., 1994; Kuchta et al., 2008a). Taxa considered to validly belong to these families varied greatly among authors: Wardle and McLeod (1952) recognized a total of 22 genera with 44 valid species, Yamaguti (1959) 28 genera with 132 valid species, Protasova (1977) 32 genera with 96 valid species (and another 31 species designated as *species inquirendae*), and Schmidt (1986) listed 41 genera with 170 valid species. Following extensive review of specimens and the literature, Kuchta and Scholz (2007) critically re-evaluated bothriocephalidean membership. In that work they recognized 31 genera and only 125 valid species out of total of 305 nominal taxa (135 synonymized and 45 *species inquirendae* or of unclear status—predominant among these were the numerous insufficiently described species of *Senga* Dollfus, 1934 from snakeheads [*Channa* spp.] and the zig-zag eel, *Mastacembelus armatus* [Lacepède] in India and its neighboring countries).

Morphology. The last detailed taxonomic revision of the order (as the suborder Bothriocephalata), examining morphology at the species level, was that of Protasova (1977); however, as this monograph was published in Russian, its results were not widely accessible. Bray et al. (1994) presented a critical account of the order Pseudophyllidea, which included keys and very brief updated diagnoses of both bothriocephalidean and diphyllobothriidean genera.

When, informed by the earlier molecular work of Mariaux (1998), Kodedová et al. (2000), and Brabec et al. (2006), Kuchta et al. (2008a) formally dismantled the order Pseudophyllidea, they differentiated the Bothriocephalidea and Diphyllobothriidea from one another on the basis of the following characteristics: (i) the position of the genital pore, which is on the dorsal, dorsolateral, or lateral side of the proglottid, posterior to the ventral uterine pore in the Bothriocephalidea, but is located on the ventral surface anterior to the uterine pore in the Diphyllobothriidea; (ii) external seminal vesicle, which is lacking in the Bothriocephalidea, but present as a well-developed, muscular structure in the Diphyllobothriidea; (iii) enlarged distal part of the uterus in gravid proglottids, which is present in the Bothriocephalidea, but

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[1] Corresponding author (krtek@paru.cas.cz)

Kuchta, R. and T. Scholz. 2017. Bothriocephalidea Kuchta, Scholz, Brabec & Bray, 2008. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 29–45.

absent in the Diphyllobothriidea; and (iv) range of definitive hosts, which are mainly teleosts and never homeothermic vertebrates in the Bothriocephalidea, but are tetrapods and most frequently mammals in the Diphyllobothriidea.

The four families recognized prior to the PBI project are generally distinguished from one another (see Bray et al., 1994; Kuchta et al., 2008b) by genital pore position (median, sublateral, or lateral). The two families with a lateral gonopore (i.e., Philobythiidae and Triaenophoridae) differ in vitellarium shape (i.e., compact in the former and follicular in the latter) (see Bray et al., 1994). Because of uniformity in strobilar morphology, scolex morphology is one of the key diagnostic features for distinguishing among genera and their species. Developmental features, such as whether eggs embryonate while in utero (or not) and presence (or absence) of an egg operculum, are also informative (see Bray et al., 1994; Kuchta et al., 2008b).

HOST ASSOCIATIONS. Kuchta and Scholz (2007) nicely summarized the specturm of definitive hosts used by bothriocephalideans as follows. In total, 96% of the 125 valid species they recognized use Actinopterygii (ray-finned fishes) as definitive hosts, although three species of *Bothriocephalus* Rudolphi, 1808 parasitize North American lungless salamanders (Caudata: Plethodontidae Gray). Among Actinopterygii, teleosts serve as definitive hosts for the majority of bothriocephalideans. There are, however, five species that are interesting exceptions in that they parasitize more archaic actinopterygian groups. Specifically *Marsipometra hastata* (Linton, 1897) Cooper, 1917 and *M. parva* Simer, 1930 infect paddlefish, and *Eubothrium acipenserium* (Cholodkovsky, 1918) Dogiel & Bychowsky, 1939 infects sturgeons, both in the order Acipenseriformes, *Polyonchobothrium polypteri* (Leydig, 1853) Lühe, 1900 which is found in Polypteriformes (bichirs), and *Senga scleropagis* (Blair, 1978) Kuchta & Scholz, 2007 which has been reported from Osteoglossiformes (bony tongues).

As noted by Kuchta and Scholz (2007), approximately 65% of all species in the order parasitize marine fishes, while only 32% are found in freshwater fishes. Three species (i.e., *Eubothrium acipenserium*, *E. crassum* [Bloch, 1779] Nybelin, 1922, and *E. salvelini* [Schrank, 1790] Nybelin, 1922) infect migratory fishes (i.e., sturgeons and salmonids) and thus may live in both types of environments. Among teleosts, the group that most commonly serves as definitive host for bothriocephalideans are the Perciformes, with 45 species parasitizing fishes of this order—15 of these cestodes specifically parasitize centrolophids. In some cases (e.g., the Japanese butterfish, *Psenopsis anomala* [Temminck & Schlegel] or the rudderfish, *Centrolophus niger* [Gmelin]), up to four species may co-occur in the same host species.

The prevalence of bothriocephalideans in their definitive hosts is usually low—rarely exceeding 10%. However, instances of prevalences reaching 100% with infection intensities of up to 1,000 individuals per host have been reported in the triaenophorid *Eubothrium crassum* in brown trout, *Salmo trutta* L. (see Kennedy, 1996) and in the echinophallid *Neobothriocephalus aspinosus* Mateo & Bullock, 1930 in the palm ruff, *Serioella violacea* Guichenot (see Mateo and Bullock, 1966). In fact, the most prevalent bothriocephalideans are generally echinophallids of the genera *Bothriocotyle* Ariola, 1900, *Echinophallus* Schumacher, 1914, *Neobothriocephalus* Mateo & Bullock, 1966, *Parabothriocephaloides* Yamaguti, 1934, *Parabothriocephalus* Yamaguti, 1934, and *Paraechinophallus* Protasova, 1975. There may also be marked differences in infection parameters within adjacent marine ecosystems. For example, the coastal waters off the mainland of Scotland seem to be poor for bothriocephalidean cestodes. Kuchta and Scholz (2007) reported finding only four cestode individuals in two fish species infected with either *Abothrium gadi* van Beneden, 1871 or *Bothriocephalus scorpii* (Müller, 1776) Cooper, 1917 out of the approximately 500 individuals of 37 fish species from 11 localities throughout coastal Scotland surveyed in the autumn of 2004. In contrast, during an investigation of the helminth fauna of deep-sea fishes off the Outer Hebrides, Scotland, carried out in the fall of 2005, Kuchta and Scholz (2007) found 20 of the 286 fish individuals representing a total of 42 fish species infected with five species of bothriocephalideans. Host specificity of bothriocephalideans is usually strict, with about 95% of species being at least stenoxenous (*sensu* Caira et al. [2003]; i.e., restricted to a single host genus), and approximately 70% of species being oioxenous (*sensu* Euzet and Combes [1980]; i.e., known from 1 host species only). As few as seven species of bothriocephalideans are euryxenous (*sensu* Caira et al. [2003]; i.e., occur in hosts of different families). For example, *Clestobothrium crassiceps* (Rudolphi, 1819) Lühe, 1899 and *B. scorpii* have been reported from as many as 30 species belonging to six families of marine fishes each, although the latter taxon probably represents a species complex (Cooper, 1918; Protasova, 1977; Škeříková et al., 2004). However, the species of the *B. scorpii* complex, namely *B. barbatus* Renaud, Gabrion & Pasteur, 1983, *B. gregarius* Renaud, Gabrion & Pasteur, 1983, and *B. funiculus* Renaud & Gabrion, 1984, represent *nomina nuda* because their original description did not comply with requirements of the International Code of Zoological Nomenclature (1999; Article 13) (see Renaud et al., 1983; Renaud and Gabrion, 1984; Kuchta and Scholz, 2007). Moreover, phylogenetic analyses revealed a close relationship among these species and *B. andresi* Porta, 1911 and *B. clavibothrium* Ariola, 1899; their status as valid species thus requires verification (see Škeříková et al., 2004). By far the most extreme example of euryxeny is *Bothriocephalus acheilognathi* Yamaguti, 1934 (now *Schyzocotyle acheilognathi* [Yamaguti, 1934] Brabec, Waeschenbach, Scholz, Littlewood, & Kuchta, 2015), which has been reported from approximately 200 species of freshwater fishes, representing 10 orders, and 19 families (Scholz et al., 2011). It should, however, be noted that the range of definitive hosts of many bothriocephalidean species and thus, their actual degree of host specificity, is not clearly understood because of the insufficiently resolved taxonomy not only of many of the bothriocephalidean genera, but also of their hosts.

GEOGRAPHIC DISTRIBUTION. The majority of bothriocephalidean species have been reported from the Atlantic (45 species) and Pacific (31 species) Oceans, with only 18 species known from the Indian Ocean (Kuchta and Scholz, 2007). The number of freshwater bothriocephalidean species occurring in Eurasia (27 species) is higher than that reported from North America (18 species). In contrast, the species richness of freshwater bothriocephalideans on other continents is very low; they are particularly rare in the freshwaters of South America, including the Amazon River basin. *Galaxitaenia toloi* Gil de Pertierra & Semenas, 2005 and *Ailinella mirabilis* Gil de Pertierra, 2006 were described from Argentinian Patagonia (Kuchta and Scholz, 2007). There are only four records, probably all of conspecific *Senga*-like bothriocephalideans, from unrelated freshwater teleosts representing four orders (Characiformes, Cyprinidontiformes, Perciformes, and Pleuronectiformes) in Brazil (Woodland, 1935; Rego, 1997; Kuchta and Scholz, 2007).

The occurence of marine bothriocephalideans varies also among ocean ecosystems. The shelf and epipelagic ocean faunas (down to a depth of 200 m) are relatively depauperate, represented solely by species of *Bothriocephalus*, *Clestobothrium* Lühe, 1899, and *Abothrium* van Beneden, 1871. The mesopelagic fauna (200 to 1,000 m) is also very species poor, typically consisting of *Bothriocephalus manubriformis* (Linton, 1889) Ariola, 1900 and *Fistulicola plicatus* (Rudolphi, 1819) Lühe, 1899 in xiphiid fishes (swordfish), and *Anchistrocephalus microcephalus* (Rudolphi, 1819) Monticelli, 1890 in sunfish (Molidae Bonaparte). In contrast, bathypelagic (1,000 to 4,000 m) fishes harbor a relatively rich fauna of bothriocephalidean cestodes. Species of nine genera, namely *Andycestus* Kuchta, Scholz & Bray, 2008; *Australicola* Kuchta & Scholz, 2006; *Bathycestus* Kuchta & Scholz, 2004; *Kimocestus* Kuchta, Scholz & Bray, 2008; *Milanella*

Kuchta & Scholz, 2008; *Philobythoides* Campbell, 1977; *Philobythos* Campbell, 1979; *Pistana* Campbell & Gartner, 1982; and *Probothriocephalus* Campbell, 1979 are known only from deep-sea fishes (Kuchta et al., 2008b). The deepest record of a bothriocephalidean cestode is that of *Pistana eurypharyngis* Campbell & Gartner, 1982 from the pelican eel, *Eurypharynx pelecanoides* Vaillant, collected from 3,083 m (Campbell and Gartner, 1982). In general, the bothriocephalids are more common in benthic than in pelagic fishes.

PHYLOGENETIC RELATIONSHIPS. Dubinina (1980) and Yurakhno (1992) discussed possible relationships of pseudophyllidean cestodes, but the first cladistic assessment of the phylogenetic relationships of bothriocephalidean families was that of Bray et al. (1999) as part of a larger analysis of the, at that time, Pseudophyllidea overall. That study was based on morphological characters of the type genera of each of the 14 families recognized by Yurakhno (1992). Brabec et al. (2006) presented the first molecular phylogenetic analysis of pseudophyllidean cestodes, based on 18S and 28S rDNA sequence data for 17 bothriocephalidean species, including five species for which data were obtained from GenBank, and 12 species for which new data were generated. Their analyses confirmed the paraphyly of the order "Pseudophyllidea," which they found to consist of two unrelated clades, then informally designated as the "Bothriocephalidea" and "Diphyllobothriidea." Although Brabec et al. (2006) found the "Bothriocephalidea" to be monophyletic, two of its families (i.e., the Echinophallidae and the Triaenophoridae) were not. As noted above, the orders Bothriocephalidea and Diphyllobothriidea were formally proposed two years later once sufficient morphological and ecological (host range) evidence had been accumulated to support these molecular results (Kuchta et al., 2008a). In their analysis of the group in the context of cestodes overall, Waeschenbach et al. (2007) found their bothriocephalidean exemplar to group as the sister to the clade of all acetabulate orders (incl. *Litobothrium* Dailey, 1969), well away from the diphyllobothriidean exemplar included in their analyses.

CURRENT STATUS OF THE BOTHRIOCEPHALIDEA

DIVERSITY AND CLASSIFICATION. As a result of PBI project efforts, three new species were described (Kuchta et al., 2009a, 2012) and five new genera were erected, while another three genera were resurrected (Kuchta et al., 2008b, 2012; Brabec et al., 2015). In total, the order now houses 132 species in 48 genera (Table 1). It is of note that only 38% of the 350 nominal species are valid. In addition, our work revealed at least ten undescribed species, the novelty of which is supported by both morphological and molecular data (Brabec et al., 2015).

Since 2008, more than 40 allegedly new species have been described by authors outside of the PBI project. However, with the exception of two species of *Clestobothrium* described by Gil de Pertierra et al. (2011) and a species of *Bothriocephalus* described by Gil de Pertierra et al. (2015), species were described in the "catch-all" genus *Senga* or in the invalid genus *Circumoncobothrium* Shinde, 1968, all from India and its neighboring countries. No less than 26 species were described from *Mastacembelus armatus*, despite the fact that this notoriously repeatedly examined teleost has already been reported to host as many as 60 of the 100 nominal species of *Senga* described. The remainder of the allegedly new species were described from the snakehead *Channa striata* (Bloch), which is another teleost that has been reported to host dozens of invalid, insufficiently described species of tapeworms (see Kuchta and Scholz [2007], Kuchta et al. [2008b], and Ash et al. [2011, 2015] for detailed treatments of the problems associated with the taxonomy of fish cestodes from India and its neighboring countries). Provisionally, 14 species of *Senga*, based on their type host, have been retained as valid (Table 1). Of particular note are the two new species of *Circumoncobothrium* (*C. clariasi* Kadam & Dhole, 2011 and *C. jadhavi* Shinde, 2013) described from the walking catfish *Clarias batrachus* (Linnaeus), which is not known to host bothriocephalideans, but harbors a number of caryophyllidean cestodes (see Ash et al., 2011). We believe these records are in error because on several collecting trips to India and Bangladesh over the course of the PBI project, more than 100 specimens of this fish were dissected and no bothriocephalidean tapeworms were found (Ash et al., 2011). The recently described species *Parabothriocephaloides magnus* Sedova & Gulyaev, 2012 is considered herein to be a junior synonym of the type species of the genus, *P. segmentatus* Yamaguti, 1934, because, beyond a slight difference in testis number, these species in fact do not differ morphologically from one another.

The validity of both genera erected by non-PBI personnel is highly suspect. In fact, *Aitodiscus* Srivastav & Narayan, 2012 is a synonym of *Senga*. It was proposed to accommodate *A. jalaunensis* Srivastav & Narayan, 2012 from *Channa punctata* (Bloch) in India, which is here identified as a junior synonym of *Senga visakhapatnamensis* Ramadevi & Hanumantha Rao, 1973, described from the same fish host. *Indobothrium* Sedova & Gulyaev, 2009 was proposed to accommodate two species originally assigned to *Bothriocephalus* (i.e., *I. bengalensis* [Devil, 1975] Sedova & Gulyaev, 2009 and *I. branchiostegus* [Yamaguti, 1952] Sedova & Gulyaev, 2009). The new genus was characterized mainly by the markedly craspedote nature of the proglottids, but this character is present in several other species of *Bothriocephalus*, including *B. carangis* Yamaguti, 1968, *B. gadellus* Blend & Dronen, 2003, and *B. timii* Gil de Pertierra, Arredondo, Kuchta & Incorvaia, 2015. As a result, *Indobothrium* was considered to be a junior synonym of *Bothriocephalus* by Gil de Pertierra et al. (2015).

Regarding the overall species richness of bothriocephalideans (i.e., both described and undescribed), it is impossible to provide a reliable estimate because so many host groups, especially from marine environments, have not yet been examined. In freshwater, our molecular work suggests that a number of undescribed species of *Bothriocephalus* and *Ichthybothrium* Khalil, 1971 certainly exist in North America and Africa, respectively, and detailed study of bothriocephalideans in the Indomalayan biogeographic realm are also likely to reveal additional, undescribed species (see Brabec et al., 2015). However, most urgent is a revision of the infamous genus *Senga* with its more than 100 nominal species. Preliminary molecular data generated from well-fixed specimens from Cambodia, India, and Vietnam, collected over the course of the PBI project, lead us to believe that the actual number of species of *Senga* may be as low as five to ten.

MORPHOLOGY. In addition to revising the order, Kuchta et al. (2008b) and Brabec et al. (2015) provided emended generic diagnoses of all 48 genera based on a critical examination of a comprehensive selection of museum and newly collected material. They also presented the first scanning electron micrographs (SEM) of the scoleces of numerous taxa, which exhibited microtriches and tumuli-like globular surface structures, and they studied the surface ultrastructure of the eggs of several taxa for the first time. Beyond confirming that SEM micrographs of the scolex of specimens fixed with a standardized protocol (i.e., hot formalin fixation) are key for future comparative studies and species descriptions, as suggested by Kuchta and Scholz (2007) and Kuchta et al. (2008b), no new morphological characters were observed during the PBI project.

Although superficially the scoleces of different bothriocephalidean cestodes may look quite uniform because most taxa possess only two simple elongated bothria (e.g., Fig. 1M), in fact, the morphology of the scolex plays a crucial role mainly in generic identification. Across taxa, there is a high amount of variation in the shape of the scolex (e.g., Fig. 1); it may or may not bear an apical disc (but its presence may be influenced by fixation method) or hooks; the musculature of the bothria may be weakly developed, strong, or hypertrophied. When hooks are present, they can vary in size, shape, and number, and are not necessarily found in related taxa (e.g., Figs. 1B, F, O, and Q). In a few bothriocephalideans, the whole scolex or at least the bothria have been reduced (e.g., Fig. 1K), or the scolex including bothria has been strongly modified as in *Onchodiscus sauridae* Yamaguti, 1934 and *Ptychobothrium belones* (Dujardin, 1845) Lönnberg, 1889 (see Kuchta et al., 2008b, 2009b).

In contrast, the morphology of the strobila is rather uniform across bothriocephalideans, although some unique characters are present in species of the Echinophallidae. For example, the strobila can be folded along the longitudinal axis (convex dorsally and concave ventrally) as in *Bothriocotyle solinosomum* Ariola, 1900 (see Kuchta et al., 2008c). The cirrus of many echinophallids (e.g., *Paraechinophallus japonicus* [Yamaguti, 1934] Protasova, 1975; see Levron et al., 2008) is usually large and armed with massive spinitriches. All echinophallids, including *Echinophallus wageneri* (Monticelli, 1890) Schumacher, 1914 and *P. japonicus*, possess large, gladiate spinitriches on the posterior margins of their proglottids (Fig. 1R, S; see also Poddubnaya et al., 2007; Kuchta et al., 2008c; Levron et al., 2008).

HOST ASSOCIATIONS. Over the course of the PBI project, more than 8,000 host specimens of a total of over 500 species, the great majority from freshwater, were examined but only ten host species were found to be new hosts for bothriocephalideans (see Table 2). The Lepisosteiformes (gars), represented by *Lepisosteus oculatus* Winchell, from the USA, is a new host order; new host families are the Achiridae Rafinesque (American soles), represented by *Trinectes maculatus* (Bloch & Schneider) from the USA, the Bovichtidae Gill (thornfishes), represented by *Cottoperca gobio* (Günther) from Argentina (Brabec et al., 2015; Gil de Pertierra et al., 2015), the Platycephalidae Gill (flatheads), represented by *Platycephalus bassensis* Cuvier and *P. aurimaculatus* Knapp from Australia, and the Serranidae Swainson (sea basses and groupers), represented by *Cephalopholis aurantia* × *spiloparaea* (Valenciennes) from New Caledonia (Brabec et al., 2015). The serranids represent the first records of reef fish hosting adult bothriocephalideans (Kuchta et al., 2009a). New host species records are *Bagrus meridionalis* Günther (Bagridae) from Lake Malawi in Africa (Kuchta et al., 2012), *Mastacembelus favus* Hora (Mastacembelidae Bleeker) from Vietnam, and *Mesoborus crocodilus* Pellegrin (Distichodontidae Günther) from the Central African Republic (Brabec et al., 2015). Except for *T. maculatus* and *L. oculatus*, which represent new host records for the known cestodes, *Bothriocephalus claviceps* (Goeze, 1782) Rudolphi, 1810 and *B. cuspidatus* Cooper, 1917, respectively, the fish hosts listed above all harbor new species of bothriocephalideans.

Bothriocephalideans are most commonly found in fishes of the families Centrolophidae Bonaparte and Synodontidae Gill. However, only nine out of 31 species of centrolophids and 20 of 73 species of synodontids have been studied for parasites and thus new sampling of other members of these families may reveal additional new bothriocephalidean species.

Bothriocephalideans are conspicuously absent from siluriforms in South America and Eurasia (around 150 species examined), but were relatively diverse in families of this order in the Ethiopian (in Clariidae Bonaparte) and Australia (Ariidae Berg); our preliminary molecular work suggests that members of the latter family host what is likely to be a new genus.

GEOGRAPHIC DISTRIBUTION. PBI project bothriocephalidean collecting efforts were focused mainly on insufficiently known freshwater fishes from the following four poorly sampled regions: sub-Saharan Africa (i.e., the Central African Republic, the Democratic Republic of the

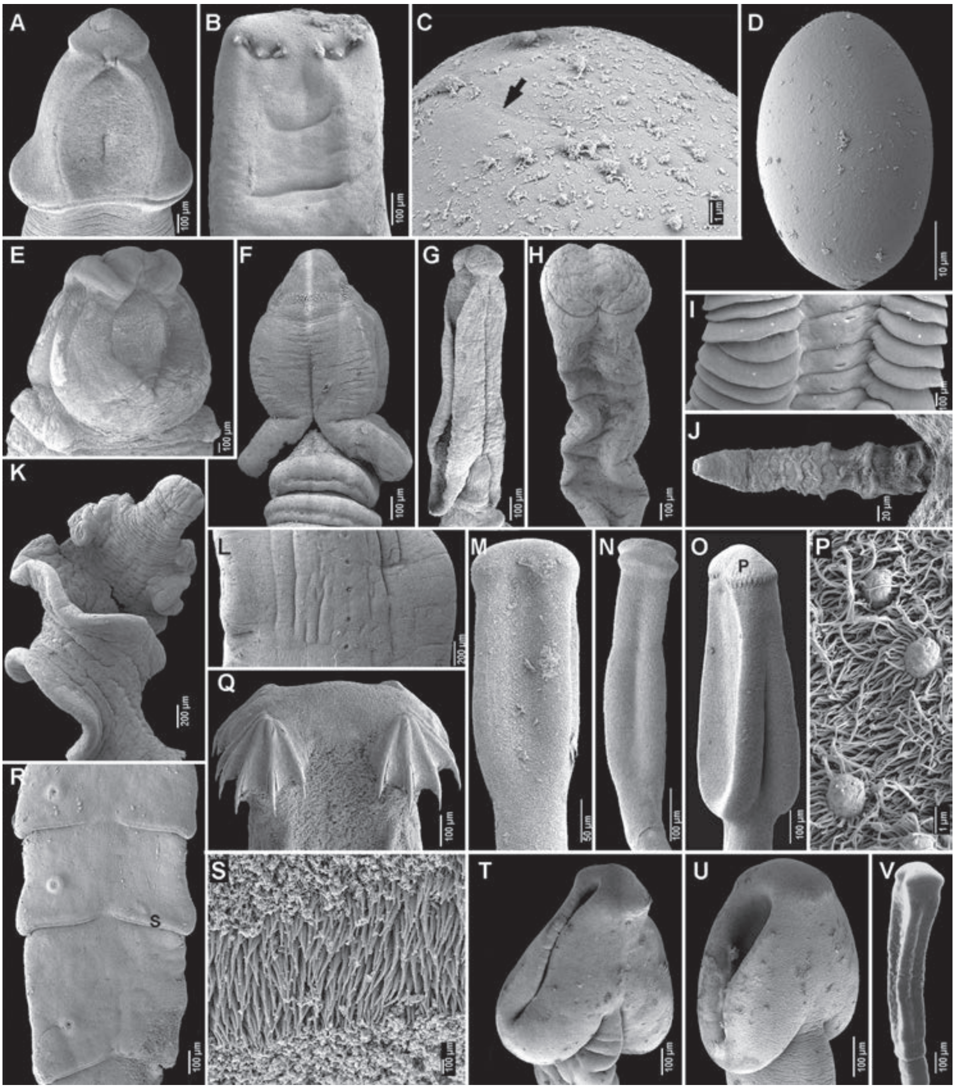

FIGURE 1. Scanning electron micrographs of selected bothriocephalideans. **(A)** Scolex of *Marsipometra hastata* ex *Polyodon spathula*, USA. **(B, C)** Scolex (B) and egg (C) with operculum (arrow) of *Triaenophorus nodulosus* ex *Esox lucius*, UK **(D)** Unoperculate egg of *Eubothrium salvelini* ex *Salvelinus alpinus*, UK. **(E)** Scolex of *Anchistrocephalus* n. sp. ex *Masturus lanceolatus*, Portugal. **(F)** Scolex of *A. microcephalus* ex *Mola mola*, USA. **(G, J)** Scolex (G) and cirrus (J) with tegumental bumps of Triaenophoridae n. gen. n. sp. ex *Hyperoglyphe antarctica*, Australia. **(H)** Scolex of Bothriocephalidae n. gen. n. sp. ex *Epinephelus coioides*, Indonesia. **(I)** Strobila of *Penetrocephalus ganapattii* ex *Saurida tumbil*, Indonesia. **(K, L)** Anterior region of body (K) and detail of strobila (L) of *Anantrum tortum* ex *Synodus foetens*, USA. **(M)** Scolex of *Bothriocephalus celinae* ex *Cephalopholis aurantia* × *spiloparaea*, New Caledonia. **(N)** Scolex of *Bothriocephalus scorpii* ex *Myoxocephalus scorpius*, UK. **(O, P)** Scolex (O) and tumuliform globular structures on scolex (P) of *Senga visakhapatnamensis* ex *Channa punctata*, India. **(Q)** Apical region of scolex of *Polyonchobothrium polypteri* ex *Polypterus senegalus*, Sudan. **(R, S)** Strobila with submedian genital pores (R) and posterior margin of proglottid armed with large gladiate spinitriches (S) of *Neobothriocephalus aspinosus* ex *Seriolella violacea*, Peru. **(T, U)** Scolex of *Schyzocotyle nayarensis* ex *Raiamas bola*, India. **(V)** Scolex of *Bothriocephalus claviceps* ex *Anguilla anguilla*, Czech Republic. Note: Small letters in (O) and (R) correspond to figure letters showing higher magnification images of these surfaces. Modified from Brabec et al. (2015).

Congo, Gabon, Kenya) and the Sudan, Southeast Asia (i.e., Bangladesh, Cambodia, India, and Vietnam), South America (i.e., Brazil and Peru), Canada (i.e., Manitoba), and the USA (i.e., Alaska, Connecticut, Mississippi, Nebraska, South Carolina, Texas, and Wisconsin) (Table 2). Also examined were marine fishes from South America (i.e., Argentina and Peru), Southeast Asia (i.e., Vietnam), Europe (i.e, Norway, incl. Svalbard), and Oceania (i.e., Australia and New Caledonia).

In combination with pre-PBI project data, the following summary of the geographic distribution of bothriocephalideans is provided, with a focus on freshwater taxa, which represent about one third of all valid species as they were more intensively studied over the course of the PBI project.

Almost 3,400 freshwater teleosts of approximately 80 species were examined in the Palaearctic realm, with most of the specimens from Europe, followed by China and the Far East of Russia (Primorsky region). However, only six already known species (out of 12 known) of five genera were found. In the Nearctic realm, we found nine species in four genera including three putatively new species of *Bothriocephalus*.

In the Afrotropic realm, only eight species of five genera (1 new species and 1 new genus erected by the present authors—see Kuchta et al., 2012) are currently known. This total number of bothriocephalideans is rather low and most of these species are widely distributed throughout sub-Saharan Africa (Kuchta et al., 2012).

The cestode fauna of the Indomalayan realm is least known and may be relatively species-poor, even though the literature is littered with dozens of "species" of *Senga* and *Senga*-like genera described inadequately. Based on a critical review of the literature (see also Kuchta and Scholz [2007] and Kuchta et al. [2008b]) and examination of almost 1,600 freshwater teleosts of approximately 50 species from Bangladesh, Cambodia, India, Indonesia, and Vietnam, only 14 species of bothriocephalideans are tentatively recognized, including presumably five distinct species of *Senga* (the number indicated by the number of different fish hosts and genetic differences revealed by preliminary molecular data).

The most depauparate faunas of bothriocephalidean cestodes are those of the Australasian and Neotropical realms, with only two and four species reported, respectively. In addition, the prevalence of infection of freshwater teleosts with these species seems to be quite low, especially in South America, which corresponds to the fact that only one bothriocephalidean, which represents a new species of a new genus (Scholz and Kuchta, unpubl. data) was found in only one of more than 1,100 fishes of approximately 150 species examined from Amazonia (Table 2; de Chambrier et al., 2015).

In the case of marine bothriocephalidean species, data on their geographic distribution largely depend on sampling effort and may not fully correspond with the actual distribution of individual species, which are probably much larger than currently recognized. Some of the widely distributed species such *Anchistrocephalus microcephalus*, *Bothriocephalus manubriformis*, *Fistulicola plicatus*, *Plicatobothrium cypseluri* (Rao, 1959) Khalil, 1971, *Plicocestus janickii* (Markowski, 1971) Kuchta, Scholz & Bray, 2008, and *Ptychobothrium belones* occur, at a minimum, in two Oceans (i.e., the Atlantic and Pacific Oceans). *Abothrium gadi*, *Australicola platycephalus* (Monticelli, 1889) Kuchta & Scholz, 2007, and *Kimocestus ceratias* (Tkachev, 1979) Kuchta, Scholz & Bray, 2008 have been reported from almost all regions in Arctic and temperate regions, whereas *Bothriocephalus carangis* is known to occur in most tropical regions (Kuchta et al., 2008b; unpubl. data).

Overall, no conspicuous changes in distributional patterns compared to those outlined by Kuchta and Scholz (2007) have been detected over the course of the PBI project. The Atlantic

Ocean hosts the most diverse fauna, with as many as 51 species reported (i.e., about 38% of all bothriocephalidean known diversity), whereas 39 species (29%) are known from the Pacific Ocean, largely as a result of pioneer studies of Satyu Yamaguti in Japan and Hawaii; only 23 species (17%) have been reported from the Indian Ocean.

As mentioned above, the parasite fauna of deep-sea fishes is characterized by the presence of bothriocephalidean cestodes, with 14 species in nine genera known only from teleosts living at depths greater than 1,000 m in the Atlantic, Indian and Pacific Oceans (see above and Kuchta et al., 2008b). In addition, one new taxon, possibly a new species of a new genus, was found in the roundnose grenadier, *Coryphaenoides rupestris* Gunnerus, off the coast of Norway and Scotland, but only immature specimens are available.

PHYLOGENETIC RELATIONSHIPS. Collecting trips conducted over the course of the PBI project (Table 2) considerably expanded the original dataset of Brabec et al. (2006) to include an additional 41 species in 18 genera for molecular phylogenetic analysis. The project's resulting multi-gene-based phylogenetic inferences (Fig. 2; Brabec et al., 2015) included sequence data for 59 species of 31 genera of bothriocephalideans (i.e., approx. 45% of valid species and approx. 72% genera in the order). This comprehensive dataset allowed for a relatively robust assessment of the phylogenetic relationships among the bothriocephalideans and the monophyly of individual families and genera. Some of Brabec et al.'s (2015) key conclusions are briefly summarized as follows:

(1) The earliest diverging lineages of the order represent species of the paraphyletic Triaenophoridae. It remains to be determined whether bothriocephalideans parasitizing freshwater (i.e., species of *Marsipometra* or *Bathybothrium*) or marine (i.e., species of *Abothrium* or *Parabothrium*) teleosts represent the earliest diverging lineages (Fig. 2). *Philobythoides* sp., the only representative of this family of parasites of bathypelagic fishes, which had previously been assigned to the Philobythiidae, was deeply nested among the paraphyletic triaenophorids as the sister lineage to a clade consisting of species of *Eubothrium*. The family Philobythiidae was thus suppressed.

(2) The Echinophallidae, essentially all of which exclusively parasitize pelagic fishes, are also paraphyletic.

(3) The Bothriocephalidae are monophyletic and consist of a single freshwater and several marine clades, which collectively represent the most derived clade in the order. Biogeographic patterns within the freshwater clade are indicative of rapid radiations having occurred in Africa and North America.

(4) The genus *Bothriocephalus*, as traditionally recognized, contains by far the greatest number of nominal species in the order. However, it represents an artificial assemblage of at least one marine and three unrelated freshwater clades/lineages. Thus, the genus *Bothriocephalus sensu stricto* will be limited to only marine species comprising a clade that includes the type species, *B. scorpii*. For the remaining species, new genera will have to be proposed, but they are provisionally kept in *Bothriocephalus* until these genera are sufficiently circumscribed.

(5) Two species previously assigned to *Bothriocephalus*, namely the Asian fish tapeworm *B. acheilognathi*, which is a widely distributed invasive parasite of numerous teleosts (Scholz et al., 2011) and *Ptychobothrium nayarensis* Malhotra, 1983 from India, were transferred to the resurrected genus *Schyzocotyle* Akhmerov, 1960. Both taxa differ from species of *Bothriocephalus* in their possession of a heart-shaped scolex with narrow, deep bothria.

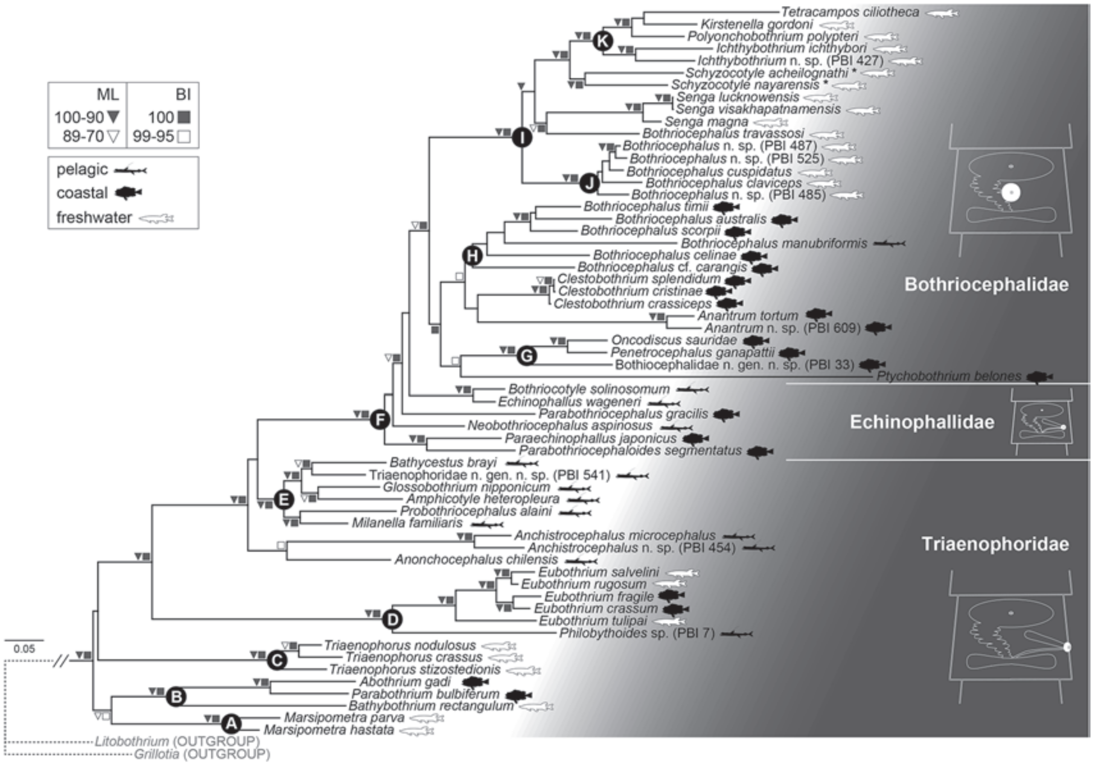

FIGURE 2. Phylogenetic tree of bothriocephalidean interrelationships resulting from maximum likelihood (ML) analysis of the concatenated, four-gene dataset with model parameters estimated separately for each partition. Partitions and models of nucleotide evolution implemented in the ML analysis were as follows: SSU rDNA (GTR+I+Γ), LSU rDNA (GTR+I+Γ), COI codon position 1 (TrN+I+Γ), COI codon position 2 (TVM+I+Γ), COI codon position 3 (TIM+I+Γ), 16S rRNA (GTR+I+Γ). Branch length scale bar indicates number of substitutions per site. Silhouettes indicate definitive host habitat. Current familial placements and corresponding genital pore positions (indicated by sold white circles) are presented to the right of the tree. Modified from Brabec et al. (2015).

CONCLUSIONS

The period just prior to the PBI was a very active period in the taxonomic history of this group. The order Bothriocephalidea was erected by Kuchta et al. (2008a) and was revised based on morphological characters that same year (Kuchta et al., 2008b). Over the course of the PBI project, relatively few major taxonomic changes have been made, and the amount of new morphological, host association, and distribution data for the order was relatively limited, especially considering the extraordinarily high number of potential hosts examined over that period. In contrast, considerable progress has been made during the PBI project on assessment of the phylogenetic interrelationships of bothriocephalidean cestodes. This came largely from the phylogenetic analyses of data generated for multiple genes for an unprecedented number of bothriocephalidean taxa, which provided a robust phylogenetic framework of the evolutionary history of this relatively small, but ecologically quite heterogeneous group of bothriate cestodes. Considering the obstacles associated with collecting from poorly known marine fishes, especially those living in deep seas that typically exhibit low prevalences of infection, it is difficult to predict reliably how many bothriocephalidean species remain to be discovered and formally described.

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TABLE 1. List of valid and *incertae sedis* bothriocephalidean taxa with their type hosts. New taxa and taxonomic actions resulting from PBI project activities indicated in bold.

VALID TAXA

- FAMILY BOTHRIOCEPHALIDAE BLANCHARD, 1849
  - *Anantrum* Overstreet, 1968
    - *Anantrum tortum* (Linton, 1904) Overstreet, 1968 (type) ex *Synodus foetens*
    - *Anantrum histocephalum* Jensen & Heckmann, 1977 ex *Synodus lucioceps*
  - ***Andycestus* Kuchta, Scholz & Bray, 2008**
    - *Andycestus abyssmus* (Thomas, 1953) **Kuchta, Scholz & Bray, 2008** (type) ex *Eulophias tanneri*
  - *Bothriocephalus* Rudolphi, 1808 (syn. *Indobothrium* Sedova & Gulyaev, 2009)
    - *Bothriocephalus scorpii* (Müller, 1776) Cooper, 1917 (type) ex *Myoxocephalus scorpius*
    - *Bothriocephalus andresi* Porta, 1911 ex *Citharus linguatula*
    - *Bothriocephalus antarcticus* Wojciechowska, Pisano & Zdzitowiecki, 1995 ex *Champsocephalus gunnari*
    - *Bothriocephalus apogonis* Yamaguti, 1952 ex *Apogon lineatus*
    - *Bothriocephalus atherinae* Chernyshenko, 1949 ex *Atherina boyeri*
    - ***Bothriocephalus australis* Kuchta, Scholz & Justine, 2009** ex *Platycephalus bassensis*
    - *Bothriocephalus bengalensis* Devi, 1975 ex *Carangoides plagiotaenia*
    - *Bothriocephalus branchiostegi* Yamaguti, 1952 ex *Branchiostegus japonicus*
    - *Bothriocephalus brotulae* Yamaguti, 1952 ex *Brotula multibarbata*
    - *Bothriocephalus carangis* Yamaguti, 1968 ex *Uraspis helfla*
    - ***Bothriocephalus celinae* Kuchta, Scholz & Justine, 2009** ex *Cephalopholis aurantia* x *spiloparaea*
    - *Bothriocephalus cepolae* Rudolphi, 1819 ex *Cepola macrophthalma*
    - *Bothriocephalus clavibothrium* Ariola, 1899 ex *Arnoglossus laterna*
    - *Bothriocephalus claviceps* (Goeze, 1782) Rudolphi, 1810 ex *Anguilla anguilla*
    - *Bothriocephalus cuspidatus* Cooper, 1917 ex *Sander vitreus*
    - *Bothriocephalus euryciensis* Schaeffer & Self, 1978 ex *Eurycea longicauda*
    - *Bothriocephalus fluviatilis* Yamaguti, 1952 ex *Leptobotia curta*
    - *Bothriocephalus formosus* Mueller & Van Cleave, 1932 ex *Percopsis omiscomaycus*
    - *Bothriocephalus gadellus* Blend & Dronen, 2003 ex *Gadella imberbis*
    - *Bothriocephalus japonicus* Yamaguti, 1934 ex *Anguilla japonica*
    - *Bothriocephalus kerguelensis* Prudhoe, 1969 ex *Notothenia cyanobrancha*
    - *Bothriocephalus lateolabracis* Yamaguti, 1952 ex *Lateolabrax japonicus*
    - *Bothriocephalus manubriformis* (Linton, 1889) Ariola, 1900 ex *Kajikia albida*
    - *Bothriocephalus monticelli* Ariola, 1899 ex *Trachypterus iris*
    - *Bothriocephalus nigropunctatus* von Linstow, 1901 ex *Sebastes norvegicus*
    - *Bothriocephalus occidentalis* (Linton, 1897) Lühe, 1899 ex *Sebastes* sp.
    - *Bothriocephalus pearsei* Scholz, Vargas-Vázquez & Moravec, 1996 ex *Cichlasoma urophthalmus*
    - *Bothriocephalus rarus* Thomas, 1937 ex *Triturus viridiscens*
    - *Bothriocephalus sciaenae* Yamaguti, 1934 ex *Pennahia argentata*
    - *Bothriocephalus tetragonus* Ariola, 1899 ex *Anarhichas minor*

  - *Bothriocephalus timii* Gil de Pertierra, Arredondo, Kuchta & Incorvaia, 2015 ex *Cottoperca gobio*
  - *Bothriocephalus travassosi* Tubangui, 1938 ex *Anguilla marmorata*
  - *Bothriocephalus typhlotritonis* Reeves, 1949 ex *Typhlotriton spelaeus*
- *Clestobothrium* Lühe, 1899
  - *Clestobothrium crassiceps* (Rudolphi, 1819) Lühe, 1899 (type) ex *Merluccius merluccius*
  - *Clestobothrium cristinae* Gil de Pertierra, Incorvaia & Arredondo, 2011 ex *Merluccius hubbsi*
  - *Clestobothrium gibsoni* Dronen & Blend, 2005 ex *Bathygadus macrops*
  - *Clestobothrium neglectum* (Lönnberg, 1893) Dronen & Blend, 2003 ex *Raniceps raninus*
  - *Clestobothrium splendidum* Gil de Pertierra, Incorvaia & Arredondo, 2011 ex *Merluccius australis*
- *Ichthybothrium* Khalil, 1971
  - *Ichthybothrium ichthybori* Khalil, 1971 (type) ex *Ichthyborus besse*
- ***Kirstenella* Kuchta, 2012 (in Kuchta et al., 2012)**
  - *Kirstenella gordoni* (Woodland, 1937) **Kuchta, 2012 (in Kuchta et al., 2012)** (type) ex *Heterobranchus bidorsalis*
- *Oncodiscus* Yamaguti, 1934 (syn. *Tetrapapillocephalus* Protasova & Mordvinova, 1986) **(new synonymy: Kuchta et al. [2009]**)
  - *Oncodiscus sauridae* Yamaguti, 1934 (type) ex *Saurida tumbil*
- *Penetrocephalus* Hanumantha Rao, 1960 **(resurrected: Kuchta et al. [2009])**
  - *Penetrocephalus ganapattii* (Hanumantha Rao, 1954) Hanumantha Rao, 1960 (type) ex *Saurida tumbil*
- *Plicatobothrium* Cable & Michaelis, 1967 (syn. *Alloptychobothrium* Yamaguti, 1968) **(new synonymy: Kuchta et al. [2008b]**)
  - *Plicatobothrium cypseluri* (Rao, 1959) Khalil, 1971 (type) ex *Cypselurus poecilopterus*
- ***Plicocestus* Kuchta, Scholz & Bray, 2008**
  - *Plicocestus janickii* (Markowski, 1971) **Kuchta, Scholz & Bray, 2008** (type) ex *Coryphaena* sp.
- *Polyonchobothrium* Diesing, 1854
  - *Polyonchobothrium polypteri* (Leydig, 1853) Lühe, 1900 (type) ex *Polypterus bichir*
- *Ptychobothrium* Lönnberg, 1889
  - *Ptychobothrium belones* (Dujardin, 1845) Lönnberg, 1889 (type) ex *Belone belone*
  - *Ptychobothrium ratnagiriensis* Deshmukh & Shinde, 1975 ex *Chelipogon cyanopterus*
- *Schyzocotyle* Akhmerov, 1960 (syns. *Capooria* Malhotra, 1985, *Coelobothrium* Dollfus, 1970) **(new synonymy: Brabec et al. [2015])**
  - *Schyzocotyle acheilognathi* (Yamaguti, 1934) **Brabec, Waeschenbach, Scholz, Littlewood, & Kuchta, 2015** (type) ex *Acheilognathus rhombea*
  - *Schyzocotyle nayarensis* (Malhotra, 1983) **Brabec, Waeschenbach, Scholz, Littlewood, & Kuchta, 2015** ex *Raiamas bola*
- *Senga* Dollfus, 1934 (syn. *Aitodiscus* Srivastav & Narayan, 2012) **(new synonymy: present study**)
  - *Senga besnardi* Dollfus, 1934 (type) ex *Betta splendens*
  - *Senga bagariusi* (Chincholikar & Shinde, 1977) Kuchta & Scholz, 2007 ex *Bagarius* sp.
  - *Senga filiformis* Fernando & Furtado, 1963 ex *Channa micropeltes*
  - *Senga gangesii* Gairola & Malhotra, 1986 ex *Mystus vittatus*
  - *Senga lucknowensis* Johri, 1956 ex *Mastacembelus armatus*
  - *Senga magna* (Zmeev, 1936) Protasova, 1977 ex *Siniperca chuatsi*
  - *Senga malayana* Fernando & Furtado, 1963 ex *Channa striata*
  - *Senga ophiocephalina* (Tseng, 1933) Kuchta & Scholz, 2007 ex *Channa argus*
  - *Senga pahangensis* Furtado & Chau-lan, 1971 ex *Channa micropeltes*
  - *Senga pathankotensis* Duggal & Bedi, 1989 ex *Labeo rohita*
  - *Senga pycnomera* (Woodland, 1924) Dollfus, 1934 ex *Channa marulius*
  - *Senga scleropagis* (Blair, 1978) Kuchta & Scholz, 2007 ex *Scleropages leichardti*
  - *Senga taunsaensis* Zaidi & Khan, 1976 ex *Channa gachua*
  - *Senga visakhapatnamensis* Ramadevi & Hanumantha Rao, 1973 ex *Channa punctata*
- *Taphrobothrium* Lühe, 1899
  - *Taphrobothrium japonense* Lühe, 1899 (type) ex *Muraenesox cinereus*
- *Tetracampos* Wedl, 1861 **(resurrected: Kuchta et al. [2008b])**
  - *Tetracampos ciliotheca* Wedl, 1861 (type) ex *Clarias anguillaris*
  - ***Tetracampos martinae* Kuchta, 2012 (in Kuchta et al., 2012)** ex *Bagrus meridionalis*

Family Echinophallidae Schumacher, 1914

- *Bothriocotyle* Ariola, 1900
  - *Bothriocotyle solinosomum* Ariola, 1900 (type) ex *Centrolophus niger*
- *Echinophallus* Schumacher, 1914
  - *Echinophallus wageneri* (Monticelli, 1890) Schumacher, 1914 (type) ex *Centrolophus niger*

Echinophallus lonchinobothrium (Monticelli, 1890) Kuchta & Scholz, 2007 ex *Coryphaena hippurus*
Echinophallus peltocephalus (Monticelli, 1893) Kuchta & Scholz, 2007 ex *Schedophilus ovalis*
Echinophallus seriolellae Korotaeva, 1975 ex *Seriolella brama*
Echinophallus stossichi (Ariola, 1896) Kuchta & Scholz, 2007 ex *Trachypterus trachypterus*
***Mesoechinophallus* Kuchta, Scholz & Bray, 2008**
Mesoechinophallus hyperogliphe (Tkachev, 1979) **Kuchta, Scholz & Bray, 2008** (type) ex *Hyperoglyphe japonica*
Mesoechinophallus major (Takao, 1986) **Kuchta, Scholz & Bray, 2008** ex *Pagrus major*
Neobothriocephalus Mateo & Bullock, 1966
Neobothriocephalus aspinosus Mateo & Bullock, 1966 (type) ex *Seriolella violacea*
Neobothriocephalus mamaevi (Tkachev, 1978) Kuchta & Scholz, 2007 ex *Seriolella tinro*
Parabothriocephaloides Yamaguti, 1934 (syn. *Paratelemerus* Gulyaev, Korotaeva & Kurochkin, 1989 **(resurrected: Kuchta et al. [2008b]**)
Parabothriocephaloides segmentatus Yamaguti, 1934 (type) ex *Psenopsis anomala*
Parabothriocephaloides psenopsis (Gulyeav, Korotaeva & Kurochkin, 1989) Kuchta & Scholz, 2007 ex *Psenopsis humerosa*
Parabothriocephaloides seriolella (Gulyeav, Korotaeva & Kurochkin, 1989) Kuchta & Scholz, 2007 ex *Seriolella brama*
Parabothriocephaloides wangi Kuchta, Scholz & Bray, 2008 ex *Psenopsis anomala* **(*nomen novum*: Kuchta et al. [2008b])**
Parabothriocephalus Yamaguti, 1934
Parabothriocephalus gracilis Yamaguti, 1934 (type) ex *Psenopsis anomala*
Parabothriocephalus johnstoni Prudhoe, 1969 ex *Macrourus whitsoni*
Parabothriocephalus macruri Campbell, Correia & Haedrich, 1982 ex *Macrourus berglax*
Parabothriocephalus sagitticeps (Sleggs, 1927) Jensen, 1976 ex *Sebastes paucispinis*
Paraechinophallus Protasova, 1975
Paraechinophallus japonicus (Yamaguti, 1934) Protasova, 1975 (type) ex *Psenopsis anomala*
Pseudamphicotyla Yamaguti, 1959 **(transferred from Triaenophoridae: Kuchta et al. [2008b])**
Pseudamphicotyla quinquarii (Yamaguti, 1952) Yamaguti, 1959 ex *Pentaceros japonicus*

Family Triaenophoridae Lönnberg, 1889 (syn. Philobythiidae Campbell, 1977) **(new synonymy: Brabec et al. [2015])**
Abothrium van Beneden, 1871
Abothrium gadi van Beneden, 1871 (type) ex *Gadus morhua*
Ailinella Gil de Pertierra & Semenas, 2006
Ailinella mirabilis Gil de Pertierra & Semenas, 2006 (type) ex *Galaxias maculatus*
Amphicotyle Diesing, 1863
Amphicotyle heteropleura (Diesing, 1850) Lühe, 1902 (type) ex *Centrolophus niger*
Anchistrocephalus Monticelli, 1890
Anchistrocephalus microcephalus (Rudolphi, 1819) Monticelli, 1890 (type) ex *Mola mola*
Anchistrocephalus aluterae (Linton, 1889) Linton, 1941 ex *Aluterus schoepfii*
Anonchocephalus Lühe, 1902
Anonchocephalus chilensis (Riggenbach, 1896) Lühe, 1902 (type) ex *Genypterus chilensis*
Anonchocephalus argentinensis Szidat, 1961 ex *Xystreurys rasile*
Anonchocephalus patagonicus Suriano et Labriola, 1998 ex *Paralichthys patagonicus*
Australicola Kuchta & Scholz, 2006
Australicola platycephalus (Monticelli, 1889) (type) Kuchta & Scholz, 2007 ex *Beryx decadactylus*
Bathybothrium Lühe, 1902 (syn. *Fissurobothrium* Roitman, 1965) **(new synonymy: Kuchta et al. [2008b])**
Bathybothrium rectangulum (Bloch, 1782) Lühe, 1902 (type) ex *Barbus barbus*
Bathybothrium unicum (Roitman, 1965) Kuchta & Scholz, 2007 ex *Gobio cynocephalus*
Bathycestus Kuchta & Scholz, 2004
Bathycestus brayi Kuchta & Scholz, 2004 (type) ex *Notacanthus bonaparte*
Eubothrioides Yamaguti, 1952
Eubothrioides lamellatus Yamaguti, 1952 (type) ex *Zenopsis nebulosa*
Eubothrium Nybelin, 1922
Eubothrium rugosum (Batsch, 1786) Nybelin, 1922 (type) ex *Lota lota*
Eubothrium acipenserinum (Cholodkovsky, 1918) Dogiel & Bychowsky, 1939 ex *Acipenser stellatus*
Eubothrium arcticum Nybelin, 1922 ex *Lycodes pallidus*
Eubothrium crassum (Bloch, 1779) Nybelin, 1922 ex *Salmo salar*
Eubothrium fragile (Rudolphi, 1802) Nybelin, 1922 ex *Alosa fallax*
Eubothrium parvum Nybelin, 1922 ex *Mallotus villosus*
Eubothrium salvelini (Schrank, 1790) Nybelin, 1922 ex *Salvelinus alpinus*
Eubothrium tulipai Ching & Andersen, 1983 ex *Ptychocheilus oregonensis*
Eubothrium vittevitellatus Mamaev, 1968 ex *Trichodon trichodon*

Fistulicola Lühe, 1899
  Fistulicola plicatus (Rudolphi, 1819) Lühe, 1899 (type) ex *Xiphias gladius*
Galaxitaenia Gil de Pertierra & Semenas, 2005
  Galaxitaenia toloi Gil de Pertierra & Semenas, 2005 (type) ex *Glaxias platei*
Glossobothrium Yamaguti, 1952 **(transferred from Echinophallidae: Kuchta et al. [2008b])**
  Glossobothrium nipponicum Yamaguti, 1952 (type) ex unknown marine fish related to *Psenopsis anomala*
***Kimocestus* Kuchta, Scholz & Bray, 2008**
  Kimocestus ceratias (Tkachev, 1979) **Kuchta, Scholz & Bray, 2008** (type) ex *Ceratias holboelli*
Marsipometra Cooper, 1917
  Marsipometra hastata (Linton, 1897) Cooper, 1917 (type) ex *Polyodon spathula*
  Marsipometra parva Simer, 1931 ex *Polyodon spathula*
Metabothriocephalus Yamaguti, 1968
  Metabothriocephalus menpachi Yamaguti, 1968 (type) ex *Myripristis amaena*
Milanella Kuchta & Scholz, 2008
  Milanella familiaris Kuchta & Scholz, 2008 (type) ex *Centrolophus niger*
Parabothrium Nybelin, 1922
  Parabothrium bulbiferum Nybelin, 1922 (type) ex *Pollachius pollachius*
Philobythoides Campbell, 1979
  Philobythoides stunkardi Campbell, 1979 (type) ex *Alepocephalus agassizii*
Philobythos Campbell, 1977
  Philobythos atlanticus Campbell, 1977 (type) ex *Acanthochaenus luetkenii*
Pistana Campbell & Gartner, 1982
  Pistana eurypharyngis Campbell & Gartner, 1982 (type) ex *Eurypharynx pelecanoides*
Probothriocephalus Campbell, 1979
  Probothriocephalus muelleri Campbell, 1979 (type) ex *Alepocephalus agassizii*
  Probothriocephalus alaini Scholz & Bray, 2001 ex *Xenodermichthys copei*
  Probothriocephalus atlanticus (Protasova & Parukhin, 1986) Bray, Jones, & Andersen, 1994 ex *Symbolophorus boops*
  Probothriocephalus berycis (Protasova & Parukhin, 1986) Bray, Jones, & Andersen, 1994 ex *Beryx splendens*
  Probothriocephalus electronus (Protasova & Parukhin, 1986) Bray, Jones, & Andersen, 1994 ex *Electrona paucirastra*
Pseudeubothrioides Yamaguti, 1968
  Pseudeubothrioides lepidocybii Yamaguti, 1968 (type) ex *Lepidocybium flavobrunneum*
Triaenophorus Rudolphi, 1793
  Triaenophorus nodulosus (Pallas, 1760) Rudolphi, 1793 (type) ex *Esox lucius*
  Triaenophorus crassus Forel, 1868 ex *Esox lucius*
  Triaenophorus stizostedionis Miller, 1945 ex *Sander vitreus*

TAXA *INCERTAE SEDIS*

Dactylobothrium choprai Srivastav, Khare & Jadhav, 2006 ex *Channa punctata—genus* and *species inquirenda*; *incertae sedis*

Table 2. Summary of fish and selected chondrichthyans examined for cestodes (by country) over the course of the PBI project by the authors and their colleagues.

Biogeographic realm Country	No. fish spcms. examined	No. fish species	No. of fish spcms. infected	No. fish species infected	No. of species of Bothriocephalidea	No. of species of Caryophyllidea	No. of species of Onchoproteocephalidea	No. of species of larval Cyclophyllidea (Gryporhynchidae)	No. of species of larval Diphyllobothriidea	Members of other cestode orders*	Collector(s)†	Collection date(s)
AFROTROPIC												
Central African Rep.	103	42	3	3	1	2	1	0	0		MJ	IX. 2012
Dem. Rep. Congo	38	16	15	3	1	2	2	0	0		MJ	VII. 2008
Gabon	59	21	0	0	0	0	0	0	0		AC	XI. 2010
Kenya	906	38	142	9	3	4	8	3	0		MJ, MO	2006–2010
Sudan	629	56	177	23	3	7	12	7	0		AC, MJ, TS	XI. 2008, III. 2009
Total (Afrotropic)	*1735*		*173*	*Prevalence: 19%*								
NEARCTIC												
Canada	77	15	32	12	1	4	2	0	0		MO	VII. 2013
USA (AK)	97	9	23	7	1	0	0	0	5	2 Phyll.	MO, RK	VII. 2013;
USA (MS, SC, TX)	196	30	77	20	4	21	7	0	0		MO, RK	III. 2012
Total (Nearctic)	*370*		*132*	*Prevalence: 36%*								
NEOTROPIC												
Brazil	242	57	44	17	0	0	30	0	0		AC, TS	IV–VI. 2013
Peru	897	130	210	31	0	0	63	1	0	1 Rhine.	AC, RK, TS	2005–2011
Total (Neotropic)	*1139*		*187*	*Prevalence: 22%*								
INDOMALAYA												
Bangladesh	242	35	25	8	1	7	2	0	1		AC, MO, TS	III. 2011
Cambodia	156	22	19	5	1	1	2	0	0		AC, RK, TS	X. 2010
India	915	38	115	21	3	11	5	0	0		AC, MO, TS	II. 2009, III. 2011
Vietnam	273	29	11	4	2	1	0	0	0		AC, RK, TS	X. 2010
Total (Indomalaya)	*1586*		*170*	*Prevalence: 11%*								
PALEARCTIC												
Bulgaria	450	31	35	10	1	3	2	0	1		VH	VI. 2009, 2010, 2012
China	1707	32	147	9	1	5	2	0	0		MO	III. 2009, III. 2010, IX. 2013
Italy	195	15	25	3	0	0	1	0	1		MO, RK	VIII. 2011; II. 2013
Norway	48	3	3	3	1	0	0	0	0	1 Gyro., 1 Tryp.	MO, RK, TS	V. 2010
Portugal	85	7	5	1	0	1	0	0	0		TS	IX. 2009
Russia (Far East)	302	22	73	13	3	4	7	0	0	1 Nippo.	AC, TS	VI. 2011
Russia (Volga)	256	12	69	7	0	3	2	0	1		VH	VII. 2009
Slovakia	305	32	34	11	2	6	1	1	1	1 Amphi., 1 Nippo.	MO, RK	2010–2013
Svalbard	48	7	5	2	0	0	0	0	1	2 Spathe.	RK	VII. 2008
Total (Palearctic)	*3396*		*396*	*Prevalence: 12%*								
TOTAL	**8226**		**1289**	**PREVALENCE: 16%**								

* *Abbreviations:* Amphi., Amphilinidea; Gyro., Gyrocotylidea; Nippo., Nippotaeniidea; Phyllo., Phyllobothriidea (larva); Rhine., Rhinebothriidea; Spathe., Spathebothriidea; Tryp., Trypanorhyncha.

† *Abbreviations:* AC, Alain de Chambrier (Switzerland); MJ, Miloslav Jirků (Czech Republic [CR]); MO, Mikuláš Oros (Slovakia); RK, Roman Kuchta (CR); TS, Tomáš Scholz (CR); VH, Vladimíra Hanzelová (Slovakia).

4

Caryophyllidea van Beneden in Carus, 1863

By
Tomáš Scholz[1] and Mikuláš Oros

CARYOPHYLLIDEA AS THEY WERE KNOWN PRIOR TO THE PBI PROJECT

Diversity and Classification. The Caryophyllidea was established in 1863 by van Beneden in Carus, but the order was not widely accepted until as late as 1952 (Wardle and McLeod, 1952). Prior to that, most authors (Nybelin, 1922; Fuhrmann, 1931; Joyeux and Baer, 1936) placed caryophyllideans either among the pseudophyllidean cestodes, or among the Cestodaria (e.g., Woodland, 1923). The first period of intensive systematic activity focused on caryophyllidean cestodes occurred between 1920 and 1940 followed by the second intensive period of taxonomic activity in the 1960s and 1970s. According to J. S. Mackiewicz (pers. com.), the principal contributors over the course of these two periods were Calentine, Fischthal, Hunter, Mackiewicz, and McCrae in North America; Kennedy and Woodland in England; Janiszewska in Poland; Szidat in Germany; Kulakovskaya in Ukraine; and Gupta in India (see Mackiewicz, 1972 for references). Based largely on the efforts of these authors, it became apparent that caryophyllideans are one of the principal cestode groups that parasitize freshwater fishes, especially in the Nearctic and Palaearctic biogeographic realms. Subsequently, Mackiewicz published a series of comprehensive synopses on the biology of caryophyllidean tapeworms (Mackiewicz, 1972, 1981a, 1982, 2003). Schmidt (1986) provided a comprehensive list of the species and their hosts then recognized in the order. Janiszewska (1954) reviewed the European and Russian species, Kulakovskaya (1961) and Protasova et al. (1990) provided a comprehensive survey of caryophyllideans from the former USSR, and a critical review of the fauna of the Indomalayan realm was published by Mackiewicz (1981b) and Hafeezullah (1993).

Higher-level classifications for the Caryophyllidea (originally recognized at the subfamily level, but later at the family level) were first proposed by Woodland (1923) and Hunter (1927). These familial classifications were generally accepted (e.g., see Yamaguti, 1959; Mackiewicz, 1972, 1994; Schmidt, 1986; Protasova et al., 1990). Prior to 2008, the order was considered to comprise 41 genera and approximately 190 species, arranged in four families, namely the Balanotaeniidae Mackiewicz & Blair, 1978, the Capingentidae Hunter, 1930, the Caryophyllaeidae Leuckart, 1878, and the Lytocestidae Hunter, 1927. In his comprehensive treatment of the order in 1994, Mackiewicz also provided keys to the families and genera.

Morphology. Prior to the inception of the PBI project in 2008, largely as a result of the seminal works of Mackiewicz (e.g., 1972, 1981a) in North America, the morphology of caryophyllidean cestodes was relatively well understood. The first monograph focused on caryophyllideans was that of Hunter (1930), who provided detailed descriptions of the morphology of the North American taxa known at that time. Mackiewicz (1972) subsequently

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[1] Corresponding author (tscholz@paru.cas.cz)

Scholz, T. and M. Oros. 2017. Caryophyllidea van Beneden in Carus, 1863. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 47–64.

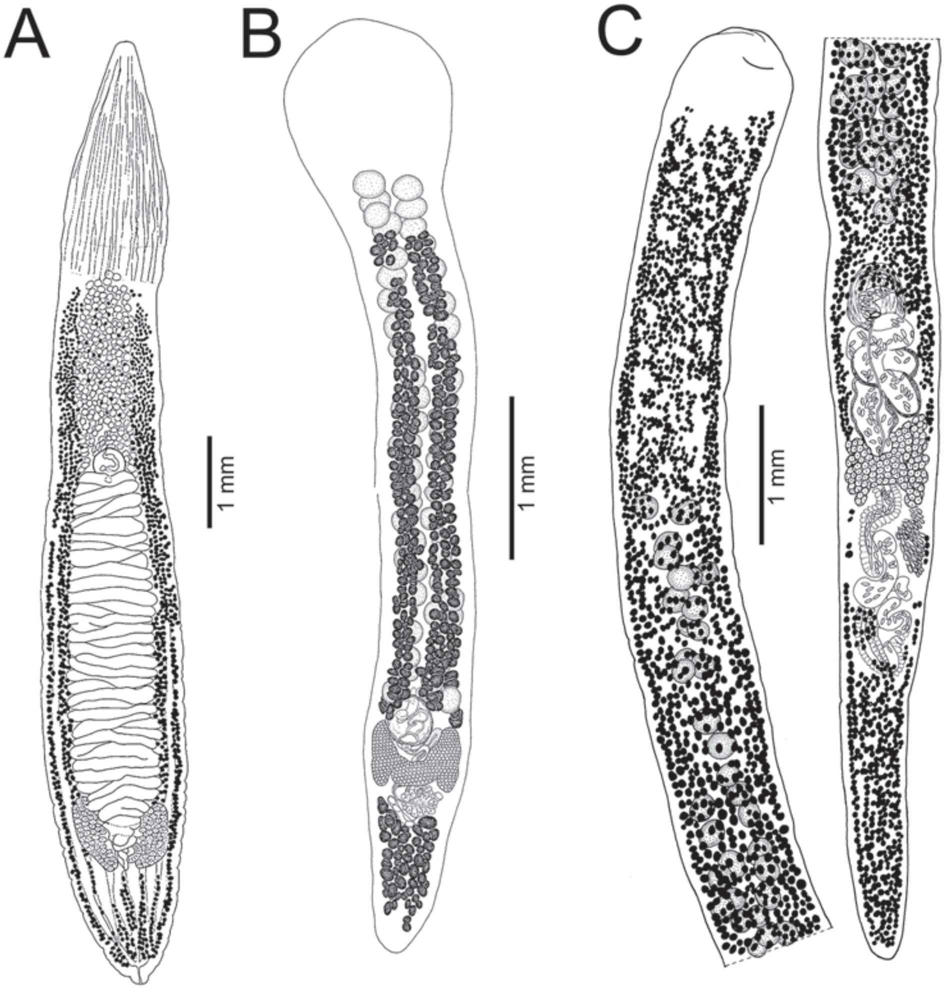

FIGURE 1. Line drawings of whole worms of representatives of caryophyllidean cestodes. **(A)** From the Afrotropic realm (*Wenyonia minuta* ex *Synodontis schall*) (modified from Schaeffner et al. [2011]). **(B)** From the Palaearctic realm (*Paracaryophyllaeus vladkae* ex *Cobitis bilseli*) (modified from Scholz et al. [2014]). **(C)** From the Indomalayan realm (*Lobulovarium longiovatum* ex *Puntius sophore*) (modified from Oros et al., [2012]).

synthesized information on the morphology of caryophyllideans globally, and Protasova et al. (1990) provided an exhaustive treatment of the morphology and ultrastructure studied using transmission electron microscopy of species occurring in the former Soviet Union.

Caryophyllideans are monozoic. Thus, they lack segmentation and are unique among eucestodes in that they also lack proglottization (Fig. 1). Among cestodes overall, they share their monozoic nature with the Amphilinidea and Gyrocotylidea. However, unlike both of the latter orders, caryophyllideans possess, rather than lack, a scolex. In addition, their first-stage larva, like that of all other eucestode groups, is an oncosphere (containing a hexacanth) with three pairs of embryonic hooks, whereas the first-stage larva of amphilinideans and gyrocotylideans is a lycophora with five pairs of hooks (i.e., a decacanth). Relative to that of other eucestode orders, the scolex of caryophyllideans is simple (Figs. 2B, 3B), often bearing shallow grooves (Figs. 2A, 3A) or loculi (Figs. 2D, 3D), or, in rare cases, frills (Figs. 2C, 3C). Their anatomy is fairly uniform across the order. The testes are pre-ovarian. The ovary is usually H-shaped in frontal view and posterior in position. The vitellarium is follicular and the vitelline follicles are circumcortical or form two lateral bands in the cortex. The genital pores are ventral and a common utero-vaginal pore opens posterior to, or together with, the male genital pore (Fig. 4).

Classification at the family level is based on the position (cortical or medullary) of the testes and vitelline follicles in relation to the inner longitudinal musculature (Mackiewicz, 1972, 1994). Genera are distinguished by morphological features such as body and scolex shape (e.g., Figs. 2, 3), and anatomical features such as shape and extent of the uterus, vitelline follicle arrangement, and presence or absence of an external seminal vesicle (e.g., Fig. 4). Mackiewicz (1994) provided a detailed treatment of the key features for distinguishing among the 41 genera recognized at that time.

Host Associations. The caryophyllideans are intestinal parasites of freshwater teleosts. They are most commonly associated with cypriniform and siluriform fishes. About one half of all nominal caryophyllidean species have been described from fishes of the family Cyprinidae Rafinesque, with most records from the genera *Abramis* Cuvier, *Alburnus* Rafinesque, *Ballerus* Heckel, *Barbus* Cuvier, *Blicca* Heckel, *Carassius* Nilsson, *Cyprinus* Linnaeus, *Chondrostoma* Agassiz, *Gobio* Cuvier, *Hemibarbus* Bleeker, *Leuciscus* Cuvier, *Rutilus* Rafinesque, *Tinca*

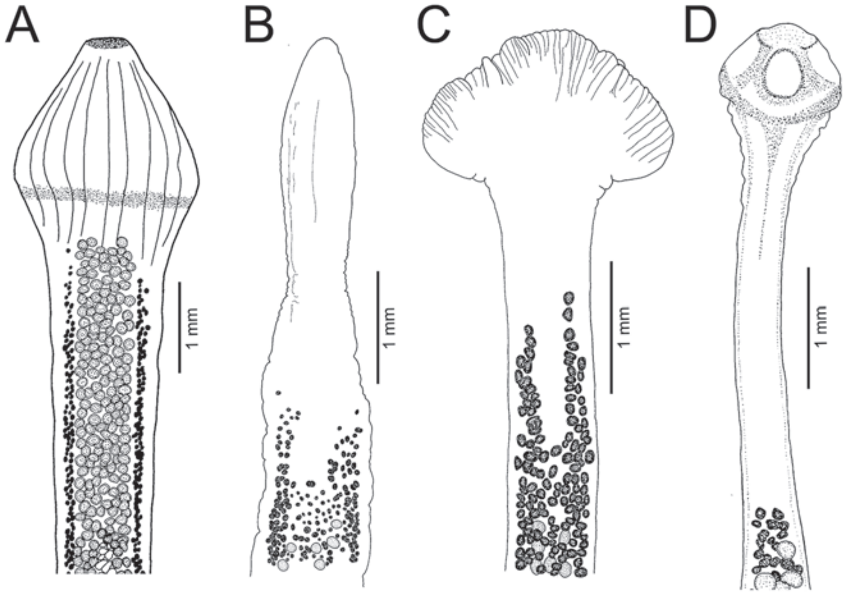

Figure 2. Line drawings of anterior regions of representatives of caryophyllidean cestodes. **(A)** From the Afrotropic realm (*Wenyonia virilis* ex *Synodontis schall*) (modified from Schaeffner et al. [2011]). **(B)** From the Indomalayan realm (*Lytocestus indicus* ex *Clarias batrachus*) (modified from Ash et al. [2011a]). **(C)** From the Palaearctic realm (*Caryophyllaeus brachycollis* ex *Abramis brama*) (modified from Barčák et al. [2014]). **(D)** From the Nearctic realm (*Biacetabulum* sp. ex *Moxostoma poecilurum*).

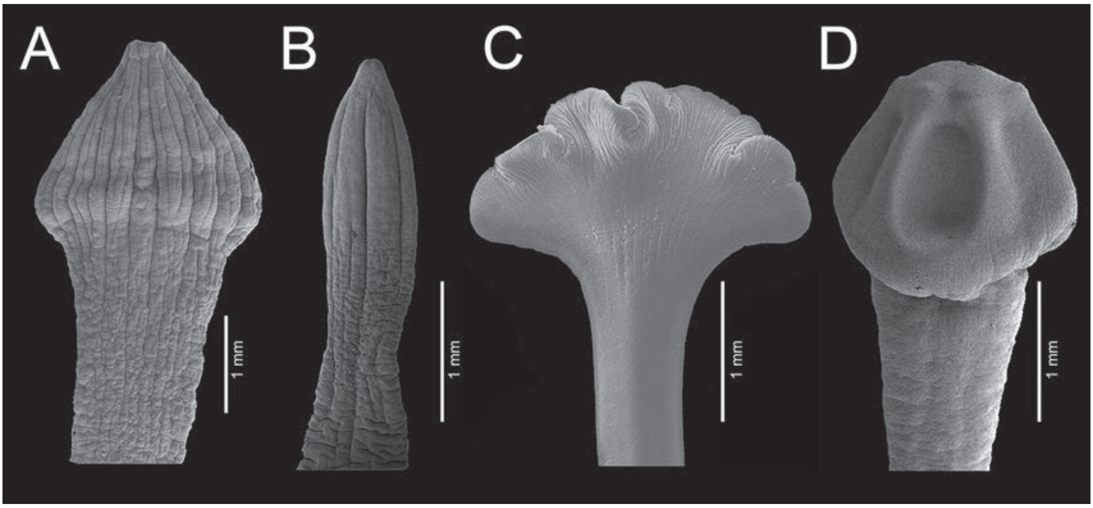

FIGURE 3. Scanning electron micrographs of scoleces of representatives of caryophyllidean cestodes illustrated in Figure 2. **(A)** From the Afrotropic realm (*Wenyonia virilis* ex *Synodontis schall*) (modified from Schaeffner et al. [2011]). **(B)** From the Indomalayan realm (*Lytocestus indicus* ex *Clarias batrachus*) (modified from Ash et al. [2011a]). **(C)** From the Palaearctic realm (*Caryophyllaeus laticeps* ex *Abramis brama*) (modified from Hanzelová et al. [2015]). **(D)** From the Nearctic realm (*Biacetabulum* sp. ex *Moxostoma poecilurum*).

Cuvier, and *Vimba* Fitzinger. Approximately one quarter of caryophyllideans have been described from fishes of the family Catostomidae Agassiz (suckers), with most records from *Carpiodes* Rafinesque, *Catostomus* Lesueur, *Erimyzon* Jordan, *Hypentelium* Rafinesque, *Ictiobus* Rafinesque, *Minytrema* Jordan, and *Moxostoma* Rafinesque. The majority of the remaining caryophyllidean species parasitize Cobitidae Swainson (loaches) or Siluriformes (catfishes). The latter are the dominant hosts of caryophyllideans in the Afrotropic, Indomalayan, and Australasian biogeographic realms, where they have been reported from five families, namely the Bagridae Bleeker (naked catfishes), Clariidae Bonaparte (airbreathing catfishes), Heteropneustidae Hora (airsac catfishes), Mochokidae Regan (upside down catfishes), and Plotosidae Bleeker (eeltail catfishes) (Mackiewicz, 1972).

Caryophyllideans exclusively use freshwater annelids (formerly placed in the Oligochaeta) of the family Naididae Ehrenberg, and specifically the Tubificinae Vejdovský and Naidinae Ehrenberg, as intermediate hosts. Mackiewicz (1972) listed 27 species of oligochaetes in 13 genera as suitable intermediate hosts. Among these, the most common were members of the genera *Limnodrilus* Claparède and *Tubifex* Lamarck (both members of the Tubificinae).

GEOGRAPHIC DISTRIBUTION. Prior to 2008, caryophyllideans had been reported from almost all biogeographic realms (Mackiewicz, 1972), with the exception of Antarctica and the Neotropics. The lack of appropriate hosts in Antarctica likely explains their absence from that continent. However, their absence from the Neotropics is more puzzling. *Archigetes* Leuckart, 1878 has been reported from tubificins in South America (Mackiewicz, 1972), but no records from fish definitive hosts in that region exist, despite the fact that the siluriformes in particular are exceptionally diverse in that region.

Within each biogeographic realm certain families tend to predominate. For example, the Balanotaeniidae are predominant in the Australasian realm, the Capingentidae and Lytocestidae in the Indomalayan realm, and the Caryophyllaeidae in the Nearctic realm.

Based on the works of Mackiewicz (1982, 1994), Schmidt (1986), Protasova et al. (1990), Hafeezullah (1993), and Hoffman (1999), the following summaries of caryophyllidean species distributions within individual biogeographic realms can be made. Australasian realm: six species, all of which are endemic to this realm, in four genera of two families (Balanotaeniidae and Lytocestidae). Afrotropic realm: 18 species in six genera of two families (Caryophyllaeidae and Lytocestidae). Nearctic realm: approximately 60 species, almost all of which are endemic to the region, in 22 genera of three families (Capingentidae, Caryophyllaeidae, and Lytocestidae). Indomalayan realm: approximately 80 species in ten genera of two families (Capingentidae and Lytocestidae). Palaearctic realm: approximately 25 species in ten genera of three families (Capingentidae, Caryophyllaeidae, and Lytocestidae).

PHYLOGENETIC RELATIONSHIPS. The interrelationships of all 41 caryophyllidean genera considered valid by Mackiewicz (1994) were assessed by Oros et al. (2008), based on a phylogenetic analysis of 30 morphological characters coded from the type species of all but four caryophyllidean genera. The monogeneric Balanotaeniidae aside, their results call into question the monophyly of caryophyllidean families as they were circumscribed at that time.

Prior to 2008, only a few species of caryophyllideans had been included in molecular phylogenetic works (Mariaux, 1998; Olson and Caira, 1999; Kodedová et al., 2000; Olson et al., 2001; Waeschenbach et al., 2007). The most comprehensive analysis conducted prior to the PBI was that of Olson et al. (2008). Their combined analyses of complete 18S rDNA and partial (D1–D3) 28S rDNA gene sequence data for ten caryophyllidean species in a total of nine genera representing all four families confirmed the non-monophyly of the caryophyllidean families

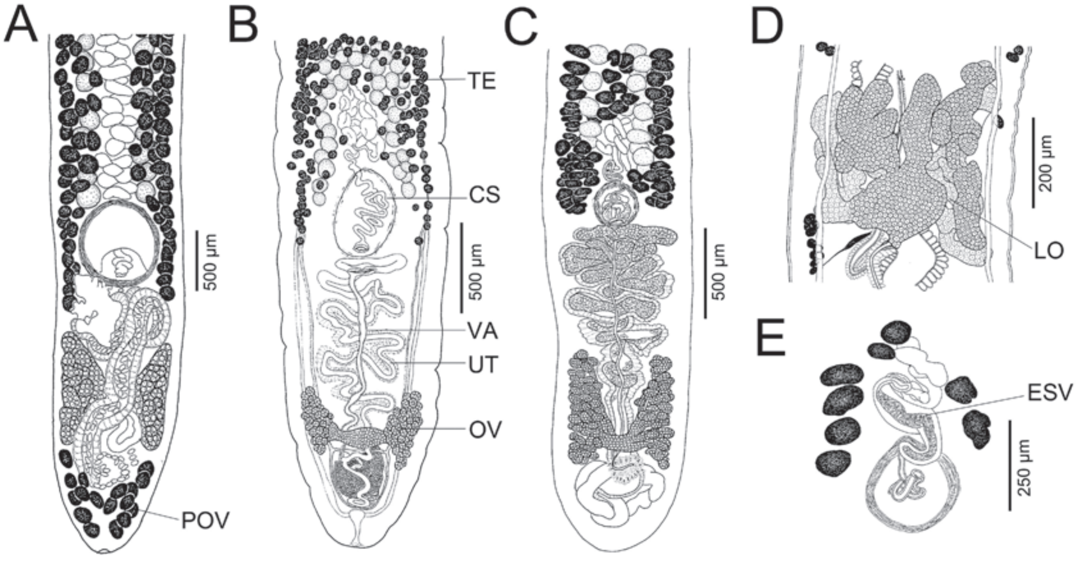

FIGURE 4. Line drawings of posterior regions of representatives of caryophyllidean cestodes. **(A)** From the Palaearctic realm (*Caryophyllaeus laticeps* ex *Abramis brama*) (modified from Hanzelová et al. [2015]). **(B)** From the Indomalayan realm (*Lytocestus indicus* ex *Clarias batrachus*) (modified from Ash et al. [2011a]). **(C)** From the Nearctic realm (*Promonobothrium papiliovarium* ex *Erimyzon oblongus* [Mitchill]) (modified from Oros et al. [2016]). **(D)** Detail of the multilobulate ovary of *Lobulovarium longiovatum* ex *Puntius sophore* (modified from Oros et al. [2012]). **(E)** Detail of external seminal vesicle of *P. papiliovarium* ex *Erimyzon oblongus* (original). *Abbreviations*: CS, cirrus-sac; ESV, external seminal vesicle; LO, lobes of ovary; OV, ovary; POV, postovarian vitelline follicles; TE, testis; UT, uterus; VA, vagina.

as they were configured at that time. Prior to the PBI, the most serious obstacle for more comprehensive phylogenetic work was the lack of specimens of representative taxa preserved for molecular work; especially lacking was representation of monotypic genera from North America and genera from the Afrotropic and Indomalayan realms.

CURRENT STATUS OF THE CARYOPHYLLIDEA

Diversity and Classification. Over the course of the PBI project, a total of nine new species of caryophyllideans in five genera were described from newly collected material. However, we note that taxa described from India by other authors since 2008 are not included in this total because they are synonyms of already known species (see Ash et al., 2011a, b; Protasova et al., 2014). The new species considered to be valid came from the Nearctic (*Homeomorpha mackiewiczi* Dutton & Barger, 2014, *Promonobothrium currani* Oros, Brabec, Kuchta, Choudhury & Scholz, 2016, and *P. papiliovarium* Oros, Brabec, Kuchta, Choudhury & Scholz, 2016), Palaearctic (*Khawia abbottinae* Xi, Oros, Wang, Scholz & Xie, 2013, *K. saurogobii* Xi, Oros, Wang, Wu, Gao & Nie, 2009, *Paracaryophyllaeus vladkae* Scholz, Oros & Aydogdu, 2014, *P. kulakowskae* Protasova, Sokolov, Kalmykov & Zhokov, 2014, and *P. misgurni* Protasova, Sokolov, Kalmykov & Zhokov, 2014), and Indomalayan (*Lobulovarium longiovatum* Oros, Ash, Brabec, Kar & Scholz, 2012) realms (Xi et al., 2009, 2013; Dutton and Barger, 2014; Protasova et al., 2014; Scholz et al., 2014; Oros et al., 2012, 2016). In addition, two new genera, *Homeomorpha* Dutton & Barger, 2014 from the Nearctic realm and *Lobulovarium* Oros, Ash, Brabec, Kar & Scholz, 2012 from the Indomalayan realm were erected since 2008, the latter as part of the PBI project. Fieldwork funded by the PBI project also yielded specimens of novel species that have not yet been described. These include a new species from the naked catfish genus *Mystus* sp. in India, two new species from the naked catfish genus *Auchenoglanis* Günther in Africa, and several putative new species from catostomid fish hosts in North America.

By far the most important aspect of PBI work on the caryophyllideans, again mostly made possible through the collection of new material fixed properly for both morphological and molecular work, were the taxonomic revisions made. A total of 12 new combinations were proposed and 86 nominal species were synonymized. The latter were largely from taxa in the Indomalayan realm (Ash et al., 2011a, b; Schaeffner et al., 2011; Scholz et al., 2011, 2015a; Oros et al., 2012; see also Table 1). Four caryophyllidean genera from the Holarctic (*Khawia* Hsü, 1935, *Monobothrium* Diesing, 1863, and *Promonobothrium* Mackiewicz, 1968) and Afrotropic (*Wenyonia* Woodland, 1923) realms were revised and their diagnoses amended (see Schaeffner et al. [2011], Scholz et al. [2011], Scholz et al. [2015a], and Oros et al. [2016], respectively). A total of 22 species in seven genera from the Holarctic, Afrotropic, and Indomalayan regions were redescribed based on the examination of types, if available, and newly collected specimens. The number of valid species in the order has decreased to 122 in 42 genera (see Table 1).

The two most notable achievements of the PBI project relative to the accurate assessment of diversity and classification of the caryophyllideans are as follows. First, the horrendous taxonomic situation in the Indomayalan realm with dozens of inadequately described taxa has largely been resolved. For example, such serious issues as the extremely high number of caryophyllidean species reported from two common catfishes of economic importance in India and neighboring countries (i.e., *Clarias batrachus* [Linnaeus] with over 80 species and *Heteropneustes fossilis* [Bloch] with over 15 species) have been formally addressed with establishment of numerous synonymies (see Ash et al., 2011a, b). Second, the spectrum of caryophyllideans for which tissue samples are now available for molecular work was substantially increased. This has facilitated assessments of conspecificity and has made the generation of the first robust phylogenetic hypotheses of caryophyllidean interrelationships possible. As a consequence, species diversity and the degree to which the current classification reflects phylogenetic relationships have been critically evaluated (see, e.g., Brabec et al., 2012; Bazsalovicsová et al., 2014; Scholz et al., 2014, 2015a).

Although much of PBI work on the caryophyllideans resulted in a reduction, rather than increase, in the diversity in the order, it is interesting that three of the six new species described came from the Palaearctic realm where the parasite fauna of freshwater fishes was considered to be fairly well known (Dubinina, 1987; Protasova et al., 1990). Several fish species, including those found to host the three new species, had not been examined previously. Clearly, many novel taxa remain to be discovered. In addition to the existence of cryptic species, for example, as detected in *Paracaryophyllaeus* Kulakovskaya, 1961 by Scholz et al. (2014), the low prevalences seen in the caryophyllideans (e.g., Oros et al., 2008) would suggest that species richness may currently be underestimated if an insufficient number of fish host individuals is examined. This may be especially true in the eastern part of the Palaearctic realm as was documented by the description of two new species of *Khawia* from the Yangtze River basin in eastern China within the last six years (Xi et al., 2009, 2013). Our preliminary work in the Nearctic (e.g., Oros et al., 2016) leads us to believe that caryophyllidean species richness in this region is currently highly underestimated. The caryophyllidean faunas of many of its endemic cyprinids and suckers have yet to be examined, particularly in the western and southern parts of North America. It is also possible that even the common and widely distributed catostomid hosts still have undescribed caryophyllideans because these fishes are among the least attractive for anglers, and sport and commercial fishermen, and have thus too been poorly sampled in this region. It is obvious that a better understanding of the caryophyllidean diversity will require further studies, in particular in North America, with a focus on poorly known or not yet studied fish hosts.

As described in more detail below, despite results from molecular phylogenetic work, the higher-level classification of the order has not yet been reconfigured to reflect monophyletic family groups. This awaits work to circumscribe morphological and associated features to support the primary monophyletic lineages emerging from molecular work.

Morphology. Almost no major novelties in caryophyllidean morphology were discovered over the course of the PBI project. The exception is the unique ovary seen in *Lobulovarium longiovatum*, described from small cyprinids (*Puntius* spp.) in the Indomayalan realm (Oros et al., 2012). Although roughly H-shaped overall, the ovary of this species consists of asymmetrical, irregular lobes on both ventral and dorsal sides (Fig. 4D; see also Oros et al., 2012). An apparently unusual feature that has been eliminated from the repertoire of caryophyllidean morphology, was the report of testis numbers as high as 5,800–6,000 in *Lytocestus clariasae* from *C. batrachus* (in fact homonym of *Lytocestus clariasae* Jadav & Gavahne, 1991, syn. of *Lytocestus indicus* [Moghe, 1925]) by Pawar and Shinde (2002). Ash et al. (2011a) provided evidence that these authors were likely counting vitelline follicles rather than testes.

Detailed study of species of *Caryophyllaeus* Gmelin, 1790 from cyprinid fishes in the Palaearctic realm did, however, reveal plasticity in morphological and anatomical features including scolex morphology, body shape and size, and anterior and posterior extent of vitelline follicles in two of the most common species of the genus. The highly polymorphic nature of *C. laticeps* (Pallas, 1781) Lühe, 1910, which exhibits euryxenous specificity (*sensu* Caira et al. [2003]) for its fish hosts from multiple subfamilies of cyprinids, was confirmed (Barčák et al., 2014; Bazsalovicsová et al., 2014; Hanzelová et al., 2015). Such morphological variability, some of which may be host-induced, represents a serious obstacle for the reliable identification of species of *Caryophyllaeus* as well as for defining species boundaries in the caryophyllidean taxa from the Palaearctic realm using morphological criteria alone. However, this issue can be remediated in part by proper fixation using standardized methods. In contrast, features of the terminal genitalia, and especially those of the cirrus-sac and vas deferens, seem to be more stable and thus more suitable for the differentiation of species of *Caryophyllaeus*. In the African genus *Wenyonia*, considerable intraspecific variability was also documented including the existence of several morphotypes of *W. virilis* Woodland, 1923 (see Schaeffner et al., 2011).

Spermiogenesis, vitellogenesis, and ultrastructure of spermatozoa and vitellocytes of several caryophyllidean species from different biogeographic realms were characterized based on material largely collected as part of the PBI project (see, e.g., Bruňanská et al., 2009; Levron et al., 2010; Yoneva et al., 2012a, b).

Fixation of live worms in hot fixative, preferrably near boiling 4% formalin, gives the best results for morphological work involving preparation of whole mounts and histological sections (see Oros et al., 2010). This procedure ensures that the specimens are not artificially deformed or contracted and thus provides standardized material suitable for comparable light microscopic and scanning electron microscopic observations (see Ash et al., 2011a, b). The lack of high quality specimens, especially from the Indomalayan and Afrotropic realms, was one of the main reasons for the many incomplete or even erroneous descriptions in the past; in some cases, artifacts and deformities, caused by strong flattening or tissue decomposition in dead worms, had been used as species- or even genus-specific differential characters (see Ash et al., 2011a, b).

The monozoic body plan of the caryophyllideans presents a methodological obstacle for proper molecular vouchering, particularly if the goal is to retain a hologenophore (*sensu* Pleijel et al. [2008]) of the specimen sequenced as a voucher. The strategy employed in caryophyllideans is to divide the specimen into three portions. The scolex and posterior portion containing taxonomically important structures is fixed in hot fixative for morphological studies including histology and scanning electron microscopy (SEM; see Oros et al., 2010). The middle portion, containing only testes and vitelline follicles, is fixed in molecular-grade 99% ethanol for molecular work.

HOST ASSOCIATIONS. Fieldwork aimed at collections of caryophyllideans conducted over the course of the PBI project was focused on the re-collection of inadequately described taxa from well-known fish hosts such as catfishes (*Auchenoglanis*, *Clarias* Scopoli, *Heteropneustes* Müller, *Synodontis* Cuvier) in the Afrotropic and Indomalayan realms in order to resolve the taxonomic morass in these regions, but also from cyprinids (e.g., *Abramis*, *Ballerus*, *Cyprinus*) and cobitids (*Cobitis* Linnaeus, *Misgurnus* Lacepède) in the Palaearctic. More specifically, these collections included re-sampling of known species from the Indomalayan realm, especially India and Bangladesh, the Afrotropic, and the eastern-most Palaearctic. Effort was focussed on collections in regions in which the caryophyllidean fauna was incompletely known; these included North America, with an emphasis on southern localities, and part of the Afrotropic realm (the Central African Republic and the Democratic Republic of the Congo). Efforts to discover novel taxa were focused on regions with particularly low known caryophyllidean diversity, such as Cambodia, Thailand, and Vietnam in Southeast Asia, as well as the Neotropics. As a consequence, relatively few new fish hosts were examined and those that were examined yielded no new caryophyllideans. The new collections allowed for the actual host specificity of numerous species to be critically evaluated. Many incidental or even erroneous fish host records have now been corrected for a diversity of caryophyllidean species (e.g., Ash et al., 2011a, b).

Variation in the degree of host specificity of caryophyllidean species for their teleost hosts, even within genera, has now been observed. For example, the recent revision of the primarily Palaearctic genus *Khawia* Hsü, 1935 by Scholz et al. (2011) confirmed that while most species exhibit narrow (stenoxenous or even oioxenous) specificity for their fish hosts, host specificity in *K. armeniaca* (Cholodkovsky, 1915) Kulakovskaya, 1961 is euryxenous. Similarly, some species of the Afrotropic caryophyllaeid genus *Wenyonia* parasitize only one or a few species of mochokid catfishes of the genus *Synodontis*, but *W. virilis* Woodland, 1923 has been reported from as many as 12 species of this genus of catfish (Schaeffner et al., 2011). It can thus be concluded that while host specificity may vary from oioxenous to euryxenous, most caryophyllideans seem to be specific at least to a single host genus (Ash et al., 2011a, b; Schaeffner et al., 2011; Scholz et al., 2011). Future collecting activities should focus on critically assessing host associations and host specificity of individual caryophyllidean species, especially in closely related hosts and particularly in the cases of the Nearctic taxa for which a number of doubtful fish hosts have been reported (Hoffman, 1999).

Caryophyllideans appear to exhibit substantial variation in prevalence and intensity, but comparable, reliable data are rare. Data that are available suggest that caryophyllideans generally occur in low prevalences (see, e.g., Oros et al., 2012), often with conspicuous seasonal fluctuations (e.g., Scholz et al., 2014). In contrast, *Lytocestus indicus* (Moghe, 1925) Woodland, 1926 occurs with a prevalence of 74% in *C. batrachus* in West Bengal, with a mean intensity of seven worms per infected fish and a range of 1–42 (Ash et al., 2011a).

Two histological studies describing the strong pathological effects of the caryophyllidean *Monobothrium wageneri* Nybelin, 1922 on its cyprinid fish host, the tench (*Tinca tinca* [Linnaeus]), have been published (Dezfuli et al., 2011; Williams et al., 2011). These parasites were found attached in tight clusters of up to 109 specimens in individual hosts. These infections were associated with the degeneration of the mucosal layer and the formation of inflammatory swellings surrounding the worm clusters. Furthermore, the lesions associated with attachment of *M. wageneri* were found to be more severe than those recorded for any other tapeworm in European freshwater fishes.

Geographic Distribution. Caryophyllideans were collected from previously unsampled localities in Africa including the Central African Republic and the lower Congo River in the Democratic Republic of the Congo, as well as from India. However, none of these records substantially expanded the known distribution of the order.

PBI work served to confirm the fact that the lack of records of caryophyllideans from the Neotropics may reflect their absence from the region rather than an artifact of lack of sampling. Even though a large number of potential hosts, which included numerous catfishes (Siluriformes), was examined from the Neotropics (see table 2 in Chapter 3 this volume, Kuchta and Scholz, 2017; and table 2 in de Chambrier et al. [2015]), no caryophyllideans were found. Their absence from this realm, like their absence from Antarctica, may be a result of the absence of appropriate hosts from that realm. Not only are native cyprinid and catostomid fishes absent from the Neotropics, but also the siluriforms that do occur in that region are phylogenetically only distantly related to the lineages of siluriforms that host caryophyllideans in the Old World (i.e., Bagriidae, Clariidae, Heteropneustidae, Mochokidae, and Plotosidae) (see Sullivan et al., 2006).

It is of note that caryophyllideans (e.g., *Atractolytocestus huronensis* Anthony, 1957, *Khawia japonensis* [Yamaguti, 1934] Hsü, 1935, and *Khawia sinensis* Hsü, 1935) have been introduced with their carp hosts into new areas. In such cases, these invasive parasites may have a negative effect on populations of their hosts (Oros et al., 2009, 2011, 2015; Scholz et al., 2011, 2015b).

Phylogenetic Relationships. In terms of the phylogenetic relationships of caryophyllideans relative to the other cestode orders, in contrast to previous molecular phylogenetic works (e.g., Olson and Caira, 1999; Waeschenbach et al., 2007; Olson et al., 2008), there is some consensus that the Caryophyllidea represent the earliest diverging group of eucestodes (e.g., Waeschenbach et al., 2012). A series of molecular phylogenetic studies focused on specific caryophyllidean groups were conducted over the course of the PBI project. Brabec et al. (2012) examined the utility of 28S rDNA, 18S rDNA, NAD3, and COI for assessing generic boundaries based on phylogenetic relationships within the order. In addition to determining that the signal from these four markers was insufficient to fully resolve the intraordinal relationships, they demonstrated the paralogous structure of nuclear ribosomal spacers and nuclear copies of mitochondrial genes in tapeworms for the first time. Scholz et al. (2014) discovered cryptic species in the genus *Paracaryophyllaeus* parasitizing loach in East Asia using sequence data from 28S rDNA, 18S rDNA, and 16S rDNA. Most recently, Scholz et al. (2015a) used phylogenetic analyses of 28S rDNA and 18S rDNA sequence data in combination with morphological data to re-align the membership of three caryophyllidean genera.

Moreover, recent molecular and cytogenetic studies on selected caryophyllideans such as *A. huronensis* and *Caryophyllaeides fennica* (Schneider, 1902) Nybelin, 1922 have revealed unusual molecular phenomena, which were not previously reported for caryophyllideans, such as divergent intragenomic ribosomal internal transcribed spacers along with multiple rDNA loci (Králová-Hromadová et al., 2010; Orosová et al., 2012). Also confirmed was the existence of triploidy in Palaearctic species (Špakulová et al., 2011)—a phenomenon previously reported only for Nearctic species (see Mackiewicz, 1972, 1981a). A comprehensive molecular phylogenetic analysis of caryophyllidean cestodes for the PBI project is currently being carried out by A. Waeschenbach at the Natural History Museum in London in the laboratory of D. T. J. Littlewood. The dataset consists of 83 samples representing 58 species, in 30 genera, and all four caryophyllidean families. This sample represents most genera from all but the Nearctic region, with an emphasis on multiple species from particularly species-rich genera; type species were included whenever possible. Sequence data were or are in the process of being generated for the nuclear genes 28S rDNA and 18S rDNA, as well as for the mitochondrial genes 16S rDNA and COI. Voucher specimens for most have been deposited in the Helminthological Collection of the Institute of Parasitology of the Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic (www.paru.cas.cz/en/collections/).

Although preliminary, results to date confirm the conclusions of previous phylogenetic studies focused on selected caryophyllidean taxa (Olson et al., 2008; Oros et al., 2008; Brabec et al., 2012; Scholz et al., 2014, 2015a). Based on these preliminary results, the following observations can be made. None of the three non-monogeneric families (i.e., the Capingentidae, the Caryophyllaeidae, and the Lytocestidae) is monophyletic as currently circumscribed. *Balanotaenia bancrofti* Johnston, 1924 from the plotosid catfish *Tandanus tandanus* (Mitchell) in Australia, a member of the monogeneric family Balanotaenidae, appears to be the earliest diverging lineage of caryophyllideans. The remaining caryophyllideans comprise two major groups. One of these groups includes the species that parasitize catfishes in the Afrotropic and Indomalayan realms, most of which possess post-ovarian vitelline follicles. The second group includes all of the Holarctic taxa. The Holarctic group comprises two subgroups. One of these subgroups includes Palaearctic taxa parasitizing cyprinids and cobitids; these taxa have well-developed post-ovarian vitelline follicles (Fig. 4A) and lack an external seminal vesicle. The second subgroup includes the Nearctic species that parasitize suckers (Catostomidae); many of these species possess an external seminal vesicle (Fig. 4E), and many also lack post-ovarian vitelline follicles (Fig. 4C).

Preliminary results support the monophyly of many of the genera represented in the analyses by multiple species (e.g., *Biacetabulum* Hunter, 1930, *Promonobothrium* Mackiewicz, 1968, and *Wenyonia*). Other genera were clearly polyphyletic. For example, species of *Glaridacris* Lamont, 1920 clustered in two distantly related groups, suggesting that the genus, as currently configured, comprises at least two distinct groups of unrelated species.

CONCLUSIONS

The PBI project has considerably advanced knowledge of the diversity and interrelationships of caryophyllidean cestodes. This was largely the result of the collection of substantial new material, fixed properly for both morphological and molecular work, from across the globe. Substantial taxonomic revision was carried out, particularly of many of the taxonomically problematic or poorly known groups. Only six new species and one new genus were established, but tens of species were synonymized. As a consequence, the number of valid species in the order has declined from 190 to 122. The order appears to represent the earliest diverging order of "true" cestodes (i.e., Eucestoda). Although the comprehensive molecular phylogenetic analyses are not yet complete, the present family-level classification will require substantial revision if monophyletic families are to be recognized. In contrast, most existing caryophyllidean genera appear to be monophyletic, thus supporting their current delimitation based largely on morphological characteristics. In many other respects our understanding of the order has not substantially changed. The order remains known primarily from freshwater fishes of the orders Cypriniformes and Siluriformes. Despite substantial collecting effort in the Neotropics, the absence of the order from the region was confirmed, possibly because that region lacks appropriate hosts. Except for a peculiar (multilobulate) ovary in the new species of the newly erected genus, little additional novelty was discovered in these monozoic cestodes. Surprisingly, the most substantial gap in the global picture of caryophyllidean diversity is in the fauna of suckers and cyprinids in North America, especially in western and southern regions. Most Nearctic caryophyllideans were described many decades ago (mainly in the 1960s and 1970s) and thus should be reviewed in the light of modern integrative taxonomy and molecular phylogenetics.

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Table 1. List of valid caryophyllidean taxa with their type hosts. New taxa and taxonomic actions resulting from PBI project activities indicated in bold. * Names of fish hosts following Froese and Pauly (2016).

VALID TAXA

- Family Balanotaeniidae Mackiewicz & Blair, 1978
  - *Balanotaenia* Johnston, 1924
    - *Balanotaenia bancrofti* Johnston, 1924 (type) ex *Tandanus tandanus*
    - *Balanotaenia newguinensis* Mackiewicz & Blair, 1978 ex *Neosilurus brevidorsalis*
- Family Capingentidae Hunter, 1927
  - *Adenoscolex* Fotedar, 1958
    - *Adenoscolex oreini* Fotedar, 1958 (type) ex *Schizothorax richardsonii**
  - *Breviscolex* Kulakovskaya, 1962
    - *Breviscolex orientalis* Kulakovskaya, 1962 (type) ex *Hemibarbus maculatus*
  - *Capingens* Hunter, 1927
    - *Capingens singularis* Hunter, 1927 (type) ex *Carpiodes carpio*
  - *Edlintonia* Mackiewicz, 1970
    - *Edlintonia ptychocheila* Mackiewicz, 1970 (type) ex *Ptychocheilus oregonensis*
  - *Pseudolytocestus* Hunter, 1929
    - *Pseudolytocestus differtus* Hunter, 1929 (type) ex *Ictiobus bubalus*
  - *Spartoides* Hunter, 1929
    - *Spartoides wardi* Hunter, 1929 (type) ex *Carpiodes carpio*
- Family Caryophyllaeidae Leuckart, 1878
  - *Archigetes* Leuckart, 1878
    - *Archigetes sieboldi* Leuckart, 1878 (type) ex *Limnodrilus hoffmeisteri*
    - *Archigetes brachyurus* Mrázek, 1908 ex *Limnodrilus hoffmeisteri*
    - *Archigetes cryptobothrius* Wisniewski, 1928 ex *Limnodrilus hoffmeisteri*
    - *Archigetes iowensis* Calentine, 1962 ex *Cyprinus carpio*
    - *Archigetes limnodrili* (Yamaguti, 1934) Kennedy, 1965 ex *Limnodrilus hoffmeisteri*
  - *Biacetabulum* Hunter, 1927
    - *Biacetabulum infrequens* Hunter, 1927 (type) ex *Moxostoma anisurum*
    - *Biacetabulum banghami* Mackiewicz, 1968 ex *Minytrema melanops*
    - *Biacetabulum biloculoides* Mackiewicz & McCrae, 1965 ex *Catostomus commersonii*
    - *Biacetabulum carpiodi* Mackiewicz, 1969 ex *Carpiodes carpio*
    - *Biacetabulum giganteum* Hunter, 1929 ex *Ictiobus bubalus*
    - *Biacetabulum hoffmani* Mackiewicz, 1972 ex *Hypentelium etowanum*
    - *Biacetabulum macrocephalum* McCrae, 1962 ex *Catostomus commersonii*
    - *Biacetabulum meridianum* Hunter, 1929 ex *Erimyzon sucetta*
    - *Biacetabulum oregoni* Williams, 1978 ex *Catostomus macrocheilus*
    - *Biacetabulum tandani* Johnston & Muirhead, 1950 ex *Tandanus tandanus*
  - *Bialovarium* Fischthal, 1953
    - *Bialovarium nocomis* Fischthal 1953 (type) ex *Nocomis biguttatus*
  - *Calentinella* Mackiewicz, 1974
    - *Calentinella etnieri* Mackiewicz, 1974 (type) ex *Erimyzon oblongus*
  - *Caryophyllaeus* Gmelin, 1790
    - *Caryophyllaeus laticeps* (Pallas, 1781) Lühe, 1910 (type) ex *Abramis brama* **(redescription: Hanzelová et al. [2015])**
    - *Caryophyllaeus auriculatus* (Kulakovskaya, 1961) **Scholz, Oros, Choudhury, Brabec & Waeschenbach, 2015** ex *Leuciscus danilewskii*
    - *Caryophyllaeus brachycollis* Janiszewska, 1953 ex *Barbus barbus*
    - *Caryophyllaeus fimbriceps* Annenkova-Khlopina, 1919 ex *Cyprinus carpio* **(redescription: Barčák et al. [2016])**
    - *Caryophyllaeus syrdarjensis* Skrjabin, 1913 ex *Schizothorax curvifrons*
  - *Diefluvium* Williams, 1978
    - *Diefluvium unipapillatum* Williams, 1978 (type) ex *Moxostoma carinatum*
  - *Glaridacris* Cooper, 1920
    - *Glaridacris catostomi* Cooper, 1920 (type) ex *Catostomus commersonii*
    - *Glaridacris confusus* Hunter, 1929 ex *Ictiobus bubalus*
    - *Glaridacris intermedius* Lyster, 1940 ex *Catostomus commersonii*
    - *Glaridacris laruei* (Lamont, 1921) Hunter, 1927 ex *Catostomus commersonii*

  - *Glaridacris oligorchis* Haderlie, 1953 ex *Catostomus tahoensis*
  - *Glaridacris terebrans* (Linton, 1893) Mackiewicz, 1974 ex *Catostomus* sp.
  - *Glaridacris vogei* Mackiewicz, 1976 ex *Catostomus macrocheilus*
- *Homeomorpha* Dutton & Barger, 2014
  - *Homeomorpha mackiewiczi* Dutton & Barger, 2014 (type) ex *Minytrema melanops*
- *Hunterella* Mackiewicz & McCrae, 1962
  - *Hunterella nodulosa* Mackiewicz & McCrae, 1962 (type) ex *Catostomus commersonii*
- *Hypocaryophyllaeus* Hunter, 1927
  - *Hypocaryophyllaeus paratarius* Hunter, 1927 (type) ex *Carpiodes carpio*
  - *Hypocaryophyllaeus gilae* Fischthal, 1953 ex *Gila atraria*
- *Isoglaridacris* Mackiewicz, 1965
  - *Isoglaridacris bulbocirrus* Mackiewicz, 1965 (type) ex *Catostomus commersonii*
  - *Isoglaridacris agminis* Williams & Rogers, 1972 ex *Erimyzon sucetta*
  - *Isoglaridacris calentinei* Mackiewicz, 1974 ex *Catostomus columbianus*
  - *Isoglaridacris chetekensis* Williams, 1972 ex *Moxostoma macrolepidotum*
  - *Isoglaridacris folius* Fredericson & Ulmer, 1965 ex *Moxostoma erythrurum*
  - *Isoglaridacris hexacotyle* (Linton, 1897) Mackiewicz, 1968 ex *Catostomus* sp.
  - *Isoglaridacris jonesi* Mackiewicz, 1972 ex *Moxostoma duquesnii*
  - *Isoglaridacris longus* Fredericson & Ulmer, 1965 ex *Moxostoma macrolepidotum*
  - *Isoglaridacris multivitellaria* Amin, 1986 ex *Erimyzon sucetta*
  - *Isoglaridacris wisconsinensis* Williams, 1977 ex *Hypentelium nigricans*
- *Janiszewskella* Mackiewicz & Deutsch, 1976
  - *Janiszewskella fortobothria* Mackiewicz & Deutsch, 1976 (type) ex *Carpiodes cyprinus*
- *Monobothrium* Diesing, 1863 **(revised diagnosis: Scholz et al. [2015])**
  - *Monobothrium wageneri* Nybelin, 1922 (type) ex *Tinca tinca*
- *Paracaryophyllaeus* Kulakovskaya, 1961
  - *Paracaryophyllaeus gotoi* (Motomura, 1928) Dubinina, 1971 (type) ex *Misgurnus anguillicaudatus*
  - *Paracaryophyllaeus kulakowskae* Protasova, Sokolov, Kalmykov & Zhokov, 2014 ex *Cobitis lutheri*
  - *Paracaryophyllaeus lepidocephali* (Kundu, 1985) Hafeezullah, 1993 ex *Lepidocephalichthys guntea*
  - *Paracaryophyllaeus misgurni* Protasova, Sokolov, Kalmykov & Zhokov, 2014 ex *Misgurnus nikolskyi*
  - ***Paracaryophyllaeus vladkae*** **Scholz, Oros & Aydogdu, 2014** ex *Cobitis bilseli*
- *Paraglaridacris* Janiszewska, 1950
  - *Paraglaridacris silesiacus* Janiszewska, 1950 (type) ex *Abramis brama*
  - *Paraglaridacris gobii* (Szidat, 1938) Mackiewicz, 1994 ex *Gobio gobio*
  - *Paraglaridacris limnodrili* (Yamaguti, 1934) Mackiewicz, 1994 ex *Pseudogobio esocinus*
- *Penarchigetes* Mackiewicz, 1969
  - *Penarchigetes oklensis* Mackiewicz, 1969 (type) ex *Minytrema melanops*
  - *Penarchigetes fessus* Williams, 1979 ex *Erimyzon sucetta*
  - *Penarchigetes macrorchis* Christensen & Calentine, 1983 ex *Erimyzon sucetta*
- *Pliovitellaria* Fischthal, 1951
  - *Pliovitellaria wisconsinensis* Fischthal, 1951 (type) ex *Notemigonus crysoleucas*
- *Promonobothrium* Mackiewicz, 1968 **(revised diagnosis & species synonymies: Scholz et al. [2015], Oros et al. [2016])**
  - *Promonobothrium minytremi* Mackiewicz, 1968 (type) ex *Minytrema melanops*
  - ***Promonobothrium currani*** **Oros, Brabec, Kuchta, Choudhury & Scholz, 2016** ex *Ictiobus bubalus*
  - *Promonobothrium fossae* (Williams, 1974) **Scholz, Oros, Choudhury, Brabec & Waeschenbach, 2015** ex *Moxostoma poecilurum*
  - *Promonobothrium hunteri* (Mackiewicz, 1963) **Scholz, Oros, Choudhury, Brabec & Waeschenbach, 2015** ex *Catostomus commersonii*
  - *Promonobothrium ingens* (Hunter, 1927) **Scholz, Oros, Choudhury, Brabec & Waeschenbach, 2015** ex *Ictiobus cyprinellus*
  - *Promonobothrium mackiewiczi* (Williams, 1974) **Scholz, Oros, Choudhury, Brabec & Waeschenbach, 2015** ex *Hypentelium etowanum*
  - ***Promonobothrium papiliovarium*** **Oros, Brabec, Kuchta, Choudhury & Scholz, 2016** ex *Erimyzon oblongus*
  - *Promonobothrium rogersi* (Williams, 1980) **Oros, Brabec, Kuchta, Choudhury & Scholz, 2016** ex *Moxostoma poecilurum*
  - *Promonobothrium ulmeri* (Calentine & Mackiewicz, 1966) **Scholz, Oros, Choudhury, Brabec & Waeschenbach, 2015** ex *Hypentelium nigricans*
- *Rowardleus* Mackiewicz & Deutsch, 1976
  - *Rowardleus pennensis* Mackiewicz & Deutsch, 1976 (type) ex *Carpiodes cyprinus*

- *Wenyonia* Woodland, 1923 **(revised diagnosis & 2 species synonymies: Schaeffner et al. [2011])**
  - *Wenyonia virilis* Woodland, 1923 (type) ex *Synodontis schall* **(redescription: Schaeffner et al. [2011])**
  - *Wenyonia acuminata* Woodland, 1923 ex *Synodontis membranaceus* **(redescription: Schaeffner et al. [2011])**
  - *Wenyonia longicauda* Woodland, 1937 ex *Synodontis schall* **(redescription: Schaeffner et al. [2011])**
  - *Wenyonia minuta* Woodland, 1923 ex *Chrysichthys auratus* **(redescription: Schaeffner et al. [2011])**
  - *Wenyonia synodontis* Ukoli, 1972 ex *Synodontis sorex* **(redescription: Schaeffner et al. [2011])**
  - *Wenyonia youdeoweii* Ukoli, 1972 ex *Synodontis gobroni* **(redescription: Schaeffner et al. [2011])**

- Family Lytocestidae Hunter, 1927
  - *Atractolytocestus* Anthony, 1958
    - *Atractolytocestus huronensis* Anthony, 1958 (type) ex *Cyprinus carpio*
    - *Atractolytocestus sagittatus* (Kulakovskaya & Akhmerov, 1965) Mackiewicz, 1994 ex *Cyprinus carpio*
    - *Atractolytocestus tenuicollis* (Li, 1964) Xi, Wang, Wu, Gao & Nie, 2009 ex *Cyprinus carpio*
  - *Bovienia* Fuhrmann, 1931 **(new generic & 11 new species synonymies: Ash et al. [2011a])**
    - *Bovienia serialis* (Bovien, 1926) Fuhrmann, 1931 (type) ex *Clarias batrachus* **(redescription: Ash et al. [2011a])**
    - *Bovienia indica* (Niyogi, Gupta & Agarwal, 1982) **Ash, Scholz, Oros & Kar, 2011** ex *Clarias batrachus* **(redescription: Ash et al. [2011a])**
    - *Bovienia raipurensis* (Satpute & Agarwal, 1980) **Ash, Scholz, Oros & Kar, 2011** ex *Clarias batrachus* **(redescription: Ash et al. [2011a])**
  - *Caryoaustralus* Mackiewicz & Blair, 1980
    - *Caryoaustralus sprenti* Mackiewicz & Blair, 1980 (type) ex *Neosilurus ater*
  - *Caryophyllaeides* Nybelin, 1922
    - *Caryophyllaeides fennica* (Schneider, 1902) Nybelin, 1922 (type) ex *Scardinius erythrophthalmus*
    - *Caryophyllaeides ergensi* Scholz, 1990 ex *Leuciscus baicalensis*
  - *Djombangia* Bovien, 1926
    - *Djombangia penetrans* Bovien, 1926 (type) ex *Clarias batrachus* **(redescription: Ash et al. [2011a])**
  - *Khawia* Hsü, 1935 **(revised diagnosis & 7 species synonymies: Scholz et al. [2011])**
    - *Khawia sinensis* Hsü, 1935 (type) ex *Cyprinus carpio* **(redescription: Scholz et al. [2011])**
    - ***Khawia abbottinae*** **Xi, Oros, Wang, Scholz & Xie, 2013** ex *Abbottina rivularis*
    - *Khawia armeniaca* (Cholodkovsky, 1915) Shulman, 1958 ex *Capoeta capoeta sevangi* **(redescription: Scholz et al. [2011])**
    - *Khawia baltica* Szidat, 1942 ex *Tinca tinca* **(redescription: Scholz et al. [2011])**
    - *Khawia japonensis* (Yamaguti, 1934) Hsü, 1935 ex *Cyprinus carpio* **(redescription: Scholz et al. [2011])**
    - *Khawia parva* (Zmeev, 1936) Kulakovskaya, 1961 ex *Carassius carassius* **(redescription: Scholz et al. [2011])**
    - *Khawia prussica* (Szidat, 1937) Markevich, 1951 ex *Carassius carassius*
    - *Khawia rossittensis* (Szidat, 1937) Markevich, 1951 ex *Carassius carassius* **(redescription: Scholz et al. [2011])**
    - ***Khawia saurogobii*** **Xi, Oros, Wang, Wu, Gao & Nie, 2009** ex *Saurogobio dabryi* **(redescription: Scholz et al. [2011])**
  - ***Lobulovarium*** **Oros, Ash, Brabec, Kar & Scholz, 2012**
    - ***Lobulovarium longiovatum*** **Oros, Ash, Brabec, Kar & Scholz, 2012** (type) ex *Puntius sophore*
    - *Lobulovarium osteobramense* (Gupta & Sinha, 1984) **Oros, Ash, Brabec, Kar & Scholz, 2012** ex *Osteobrama cotio*
  - *Lucknowia* Gupta, 1961 (syns. *Crescentovitus* Murhar, 1963, *Pseudoadenoscolex* Mathur & Srivastav, 1994, *Pseudoheteroinverta* Srivastav & Sahu, 2008, *Sukhpatae* Srivastav, Khare & Sahu, 2007) **(4 new generic & 23 new species synonymies: Ash et al. [2011a, b])**
    - *Lucknowia fossilisi* Gupta, 1961 (type) ex *Heteropneustes fossilis* **(redescription: Ash et al. [2011b])**
    - *Lucknowia microcephala* (Bovien, 1926) **Ash, Scholz, Oros & Kar, 2011** ex *Clarias batrachus* (**redescription: Ash et al. [2011a])**
  - *Lytocestoides* Baylis, 1928
    - *Lytocestoides tanganyikae* Baylis, 1928 (type) ex a cichlid fish (probably *Alestes* sp.)
  - *Lytocestus* Cohn, 1908 **(1 generic & 26 species synonymies: Ash et al. [2011a])**
    - *Lytocestus adhaerens* Cohn, 1908 (type) ex *Clarias fuscus*
    - *Lytocestus filiformis* (Woodland, 1923) Fuhrmann & Baer, 1925 ex *Mormyrus caschive*
    - *Lytocestus indicus* (Moghe, 1925) Woodland, 1926 ex *Clarias batrachus* **(redescription: Ash et al. [2011a])**
    - *Lytocestus marcuseni* Troncy, 1978 ex *Hippopotamyrus harringtoni*
    - *Lytocestus puylaerti* Khalil, 1973 ex *Clarias buettikoferi*
  - *Monobothrioides* Fuhrmann & Baer, 1925
    - *Monobothrioides cunningtoni* Fuhrmann & Baer, 1925 (type) ex *Auchenoglanis occidentalis*
    - *Monobothrioides chalmersius* (Woodland, 1924) ex *Clarias anguillaris*
    - *Monobothrioides tchadensis* Troncy, 1978 ex *Auchenoglanis biscutatus*
    - *Monobothrioides woodlandi* Mackiewicz & Beverly-Burton, 1967 ex *Clarias ngamensis*

Notolytocestus Johnston & Muirhead, 1950
  Notolytocestus major Johnston & Muirhead, 1950 (type) ex *Tandanus tandanus*
  Notolytocestus minor Johnston & Muirhead, 1950 ex *Tandanus tandanus*
Pseudocaryophyllaeus Gupta, 1961 **(1 generic & 17 species synonymies: Ash et al. [2011a])**
  Pseudocaryophyllaeus tenuicollis (Bovien, 1926) **Ash, Scholz, Oros & Kar, 2011** ex *Clarias batrachus*
    (syn. *Pseudocaryophyllaeus indica* Gupta, 1961 [type]) **(redescription: Ash et al. [2011a])**
  Pseudocaryophyllaeus ritai Gupta & Singh, 1983 ex *Clarias batrachus* **(redescription: Ash et al. [2011a])**
Stocksia Woodland, 1937
  Stocksia pujehuni Woodland, 1937 (type) ex *Clarias gariepinus*
Tholophyllaeus Mackiewicz & Blair, 1980
  Tholophyllaeus johnstoni Mackiewicz & Blair, 1980 (type) ex *Neosilurus hyrtlii*

5

Cathetocephalidea Schmidt & Beveridge, 1990

By
Janine N. Caira[1], Veronica M. Bueno, and Kirsten Jensen

CATHETOCEPHALIDEA AS THEY WERE KNOWN PRIOR TO THE PBI PROJECT

Diversity and Classification. In 1961, Thatcher reported finding specimens he identified as *Pillersium owenium* Southwell, 1927 from the blacktip shark (*Carcharhinus limbatus* [Müller & Henle]) in the Gulf of Mexico, USA. These specimens were later determined to belong to the unusual genus *Cathetocephalus* Dailey & Overstreet, 1973, established by Dailey and Overstreet (1973) to house specimens they considered were conspecific with those of Thatcher (1961), but which they had collected from the bull shark (*Carcharhinus leucas* [Müller & Henle]) in the Gulf of Mexico off Texas, USA. In addition to erecting the genus to house their new species, *Cathetocephalus thatcheri* Dailey & Overstreet, 1973—so named in recognition of Thatcher's earlier (1961) discovery—these authors established the family Cathetocephalidae Dailey & Overstreet, 1973 for these atypical worms. The unusual features of these worms included a scolex without bothridia or suckers but with a "transverse organ; anterior surface highly rugose, with fleshy papilliform projections on leading and trailing edges; posterior surface of organ smooth with a central longitudinal fold extending entire length" (Dailey and Overstreet, 1973; pg. 469) (e.g., Fig. 1A). Even more peculiar was their discovery of a number of multistrobilate individuals of the species. *Cathetocephalus australis* Schmidt & Beveridge, 1990 was subsequently described by Schmidt and Beveridge (1990) from the bronze whaler shark (*Carcharhinus brachyurus* [Günther]), among other shark species, in Australia. In that same publication, Schmidt and Beveridge (1990) formally established the order Cathetocephalidea to house the Cathetocephalidae and the single genus *Cathetocephalus*; the authors cited the transversely elongated form of the scolex and lack of bothridia, suckers, and armature, as grounds for that action. *Cathetocephalus resendezi* Caira, Mega & Ruhnke, 2005, a second species from the bull shark, was described from the Gulf of California, Mexico by Caira et al. (2005). Schmidt and Beveridge (1990) also reported an additional species of *Cathetocephalus*, which they were unfortunately unable to describe owing to the condition of their material, from the graceful shark (*Carcharhinus amblyrhynchoides* [Whitley]), again, in Australia. Similarly, an undescribed species of *Cathetocephalus* was reported by Caira et al. (2005) from the pigeye shark (*Carcharhinus amboinensis* [Müller & Henle]), also in Australia.

Pillersium owenium remains a species *incertae sedis*. It was originally described by Southwell (1927) from the porcupine ray (*Urogymnus asperrimus* [Bloch & Schneider]) in Sri Lanka (as Ceylon). However, our collections from this host species in Australia in 1999 (J. N. Caira and K. Jensen, unpubl. data) yielded material consistent with *Pillersium* Southwell, 1927, leading us to believe that this monotypic genus may be valid, but likely as a member of the Rhinebothriidea—a placement that is also more consistent with its parasitizing a stingray,

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[1] Corresponding author (janine.caira@uconn.edu)

Caira, J. N., V. M. Bueno, and K. Jensen. 2017. Cathetocephalidea Schmidt & Beveridge, 1990. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 65–76.

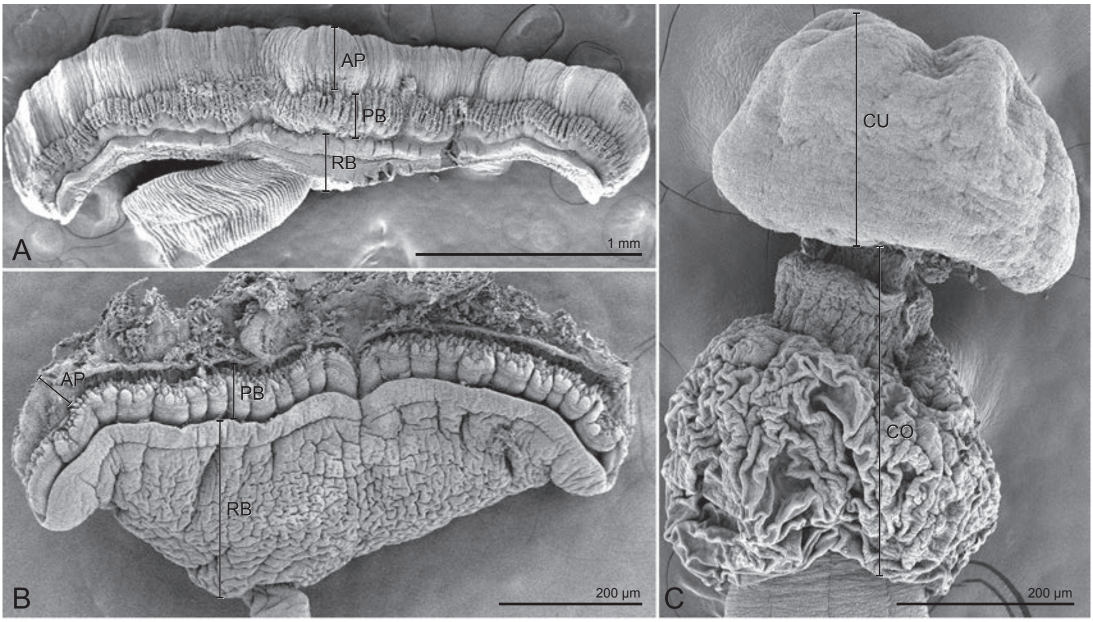

FIGURE 1. Scanning electron micrographs of cathetocephalideans. **(A)** Scolex of *Cathetocephalus resendezi* from *Carcharhinus leucas* from the Gulf of California. **(B)** Scolex of *Sanguilevator yearsleyi* from *Lamiopsis tephrodes* from Malaysian Borneo. **(C)** Scolex of *Disculiceps* sp. from *Carcharhinus brevipinna* from the Gulf of Mexico. *Abbreviations*: AP, apical pad; CO, collar; CU; cushion; PB, papillate base; RB, rugose base.

rather than a shark. Thus, while the genus may ultimately be determined to be valid, it does not belong in the Cathetocephalidea.

Sanguilevator Caira, Mega & Ruhnke, 2005 was established in the order and also in the family Cathetocephalidae by Caira et al. (2005) for peculiar tapeworms collected from the broadfin shark (*Lamiopsis tephrodes* [Fowler]; as *Lamiopsis temmincki* [Müller & Henle]) in Malaysian Borneo. The scolex (Fig. 1B) of these specimens resembles that of species of *Cathetocephalus* in overall morphology, but differs in bearing internal chambers and channels that appear to sequester host white and red blood cells, respectively. Only the single species *Sanguilevator yearsleyi* Caira, Mega & Ruhnke, 2005 has been formally described. However, the illustrations of *Cathetocephalus limbatus* Pramanik & Manna, 2006 provided by Pramanik and Manna (2006) suggest that a second species exists. Unfortunately, because type material was not designated by Pramanik and Manna (2006), their description violates Article 16.4 of the International Code of Zoological Nomenclature (ICZN, 1999) and thus this name is unavailable.

Although *Disculiceps* Joyeux & Baer, 1936 was formally transferred to the order as a result of PBI work, the elements of its history that predate the PBI project are treated here. *Discocephalum* Linton, 1890 was established by Linton (1890) for *Discocephalum pileatum* Linton, 1890—an unusual cestode collected from the dusky shark, *Carcharhinus obscurus* (Lesueur) (as *Carcharias obscurus* [Lesueur]), in Woods Hole, Massachusetts, USA. The species was unusual in that its scolex appeared to lack both bothridia ("bothria are united into a globe or disc;" Linton, 1890; pg. 720) and suckers (referred to as "supplemental disks;" Linton, 1890; pg. 781), and instead consisted of, what Linton (1890) described as an anterior, muscular disc and a posterior, globose, corrugated region. Although he provisionally placed his new genus in the then predominantly tetraphyllidean family Tetrabothriidae Linton, 1889, Linton (1890) noted that if his interpretation of the homologies of *Discocephalum* were correct, this form should be placed in the new, although undefined, family Gamobothriidae Linton, 1890 along with the lecanicephalidean genera *Lecanicephalum* Linton, 1890 and *Tylocephalum* Linton, 1890, both of which also lacked bothridia. In 1928, Pintner did a wonderful job of describing the scolex morphology and proglottid anatomy of *Discocephalum pileatum* in great detail. Unfortunately, in that paper he also erected the family Discocephalidae Pintner, 1928 to accommodate *Discocephalum*, unwittingly creating a family-group name homonym with the insect family-group name Discocephalinae Fieber, 1861. The replacement name *Disculiceps* Joyeux & Baer, 1936 was suggested by Joyeux and Baer (1936) to address this issue; thereby also providing a replacement name for the family. However, because the nominotypical generic name (i.e., *Discocephalum* Linton, 1890) of the cestode family Discocephalidae Pintner, 1928 antedates the replacement name suggested by Joyeux and Baer (1936) (i.e., *Disculiceps* Joyeux & Baer, 1936), a petition to the International Commission of Zoological Nomenclature (ICZN) was required to formally suppress the former name. In the meantime, Wardle and McLeod (1952) established the order Disculicepitidea for the Disculicepitidae and *Disculiceps pileatus* (Linton, 1890) Joyeux & Baer, 1936—an action, which because the ICZN had not yet been petitioned, at that time was not valid. The required petition was ultimately submitted by Caira in 1987 (Caira, 1987) and was approved by the ICZN in 1989 (ICZN, 1989), thereby establishing Disculicepitidae Joyeux & Baer, 1936 as the replacement name for Discocephalidae Pintner, 1928, and concomitantly *Disculiceps* Joyeux & Baer, 1936 as the replacement name for *Discocephalum* Linton, 1890. Although the Disculicepitidea Wardle & McLeod, 1989 pre-dates the Cathetocephalidea Schmidt & Beveridge, 1990, the latter ordinal name was in common use and has thus been retained. This action did not require approval of the ICZN because it is an ordinal name and is thus beyond the jurisdiction of the Code.

To our knowledge, only two additional species in this genus were discovered prior to PBI work. In 1988, Nock and Caira described *Disculiceps galapagoensis* Nock & Caira, 1988 for specimens collected from the oceanic whitetip shark (*Carcharhinus longimanus* [Poey]) in the Galapagos Rift off Ecuador. Thatcher (1961) reported specimens he identified as *Disculiceps pileatus* from *Carcharhinus limbatus* in the Gulf of Mexico, but, as discussed below, we believe these represent an undescribed species. Similarly, *Disculiceps* sp. (fig. 21 of Caira et al., 2001; Fig. 1C) was collected from the spinner shark (*Carcharhinus brevipinna* [Müller & Henle]) in the Gulf of Mexico off Louisiana and also appears to represent an undescribed species.

Phylogenetic Relationships. The status of the Cathetocephalidea as an order independent of the Tetraphyllidea (e.g., Euzet, 1994) or Lecanicephalidea (e.g., Nock and Caira, 1988; Brooks and McLennan, 1993) was initially not universally embraced. Phylogenetic analyses that included representation of the order did much to strengthen the case for its validity. The first comprehensive morphological phylogenetic analyses to include representation of the group were conducted by Caira et al. (1999). Their results not only revealed close affinities between the single species of *Cathetocephalus* and *Disculiceps* included in their analyses, but also suggested that, together these genera represent the sister taxon of the large clade of acetabulate cestodes. Results of their more extensive analyses (Caira et al., 2001), which included replicates of most elasmobranch-hosted cestode genera, were less definitive because the phylogenetic positions of *Cathetocephalus* and *Disculiceps* were labile across analyses.

Caira et al. (2005) conducted the first molecular phylogenetic analyses with representation of the order. Their study included both *Cathetocephalus thatcheri* and *Sanguilevator yearsleyi*; unfortunately *Disculiceps* was not represented. In the trees resulting from their analyses, *C. thatcheri* and *S. yearsleyi* were highly supported as sister taxa. This clade nested robustly among acetabulate cestode groups, as the sister of a clade comprising representatives of what are now the Onchoproteocephalidea + the Phyllobothriidea + the terrestrial cestode taxa (including the Cyclophyllidea).

MORPHOLOGY. Members of this order are relatively large worms (23–530 mm in total length) that possess tens to hundreds of proglottids. The divergent nature of the scolex of members of the order relative to that of typical tetraphyllidean and lecanicephalidean taxa has been apparent since Linton's description of the first species in 1890. The scolex of species in all three genera lack bothridia, suckers, and armature, and consist instead of a bipartite fleshy organ. The anterior portion of the scolex is cushion-like, while the posterior portion is corrugated or rugose. In some cases, a band of papillae is found between the anterior and posterior portions. In *Disculiceps*, both the cushion and posterior portion (Fig. 1C) are essentially round in cross-section (see Pintner, 1928); in *Cathetocephalus* (Figs. 1A, 2A) and *Sanguilevator* (Figs. 1B, 2B), both regions of the scolex are laterally expanded. As noted above, in *Sanguilevator* the center of the scolex proper bears chambers and channels (Fig. 2B, C) that appear to house host white and red blood cells, respectively (see Caira et al., 2005). In contrast, the proglottid anatomy of the three genera is generally consistent with that seen in some members of the Lecanicephalidea and Trypanorhyncha, and some members of genera assigned to the Tetraphyllidea prior to PBI work. The proglottids are acraspedote, bear lateral genital pores, numerous testes, a large, bilobed (Fig. 2G) ovary that is posterior in position, and a vagina that opens anterior to the cirrus-sac (Fig. 2D, E, and H). While the mature proglottids of species of *Cathetocephalus* and *Sanguilevator* are much longer than wide (Fig. 2D, E, respectively), those of *Disculiceps* are wider than long, or square (Fig. 2H). Unlike most other groups of cestodes parasitizing elasmobranchs, however, the vitelline follicles are circummedullary (Fig. 2F, G). Multistrobilate specimens have been reported in at least one species of *Cathetocephalus* (see Dailey and Overstreet, 1973).

HOST ASSOCIATIONS. Collectively, the *Cathetocephalus*, *Sanguilevator*, and *Disculiceps* are somewhat restricted in their host associations relative to other elasmobranch-hosted cestode orders in that they parasitize only sharks of the order Carcharhiniformes. Among the eight families in that order, they parasitize only requiem sharks (Carcharhinidae Jordan & Evermann) and hammerhead sharks (Sphyrnidae Gill). Among requiem sharks, they predominantly parasitize species of *Carcharhinus* Blainville. These generalizations come in part from information on the type hosts of the six described species, but also from published data of undescribed material. *Cathetocephalus thatcheri* and *Cat. resendezi* both parasitize *Car. leucas* (see Dailey and Overstreet, 1973; Caira et al., 2005, respectively). In addition to *Car. brachyurus*, *Cat. australis* was reported from *Carcharhinus* cf. *sorrah sensu* Naylor et al. (2012a) (as *Car. sorrah* [Müller & Henle] = *Carcharhinus spallanzani* Péron & Lesueur; see Eschmeyer et al., 2016), and *Carcharhinus* cf. *limbatus sensu* Naylor et al. (2012a) (as *Car. limbatus* [Müller & Henle]) by Schmidt and Beveridge (1990). Suriano and Labriola (2001) reported *Cat. australis* from hosts that were likely *Carcharhinus* cf. *brachyurus sensu* Naylor et al. (2012a) (i.e., the Atlantic Ocean member of the *Car. brachyurus* complex) rather than *Car. brachyurus* (i.e., the Pacific Ocean member of the *Car. brachyurus* complex; see Naylor et al., 2012a), given the collecting locality was Argentina. The material originally collected by Thatcher (1961) and subsequently identified as *Cat. thatcheri* by Dailey and Overstreet (1973) was collected from *Carcharhinus limbatus*. Schmidt and Beveridge (1990) and Caira et al.'s (2005) report of undescribed species of *Cathetocephalus* from *Car. amblyrhynchoides* and *Car. amboinensis*, respectively, add two species of *Carcharhinus* to the repertoire of hosts for this genus. The

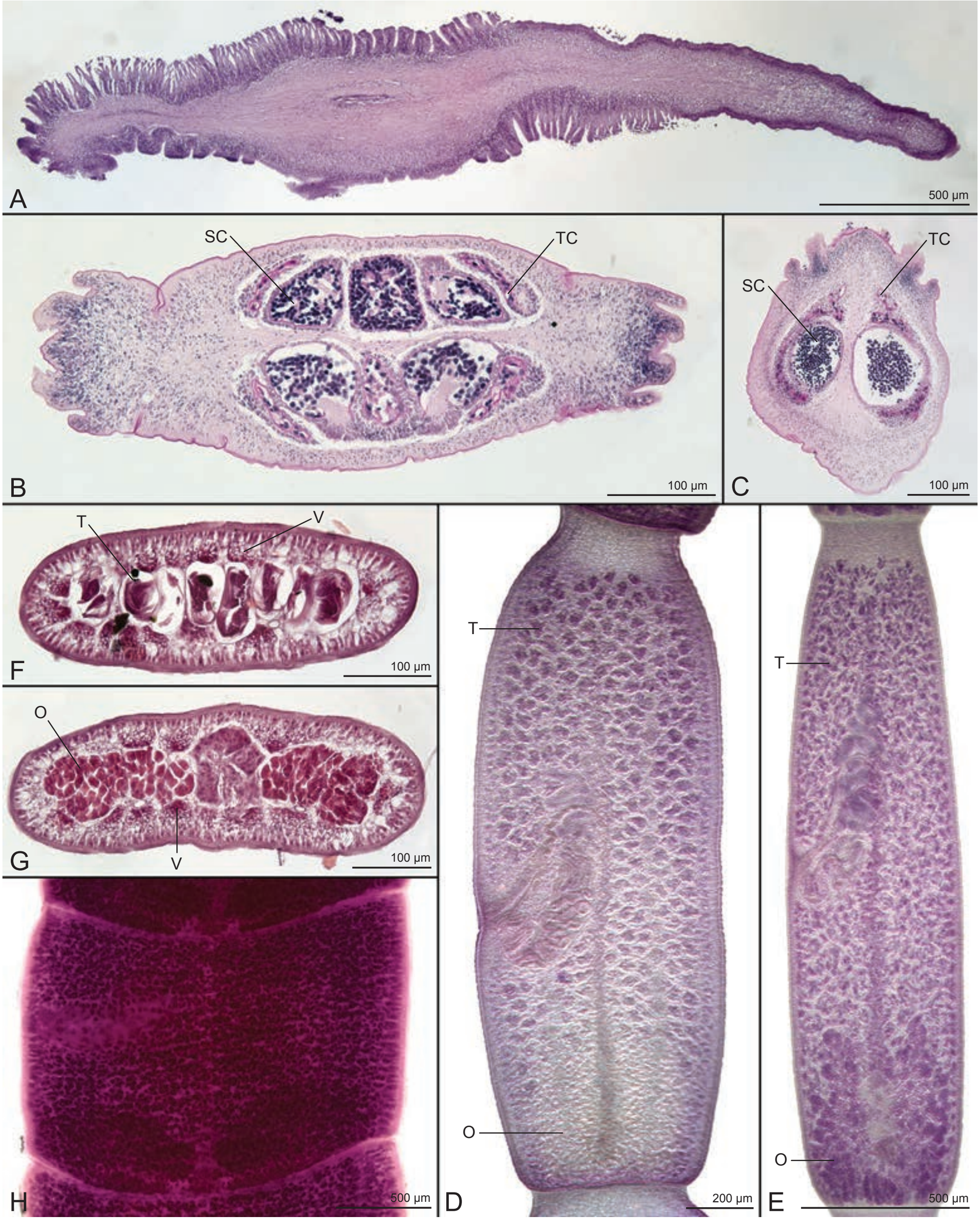

FIGURE 2. Light micrographs of cathetocephalideans. **(A)** Cross-section through apical pad of scolex of *Cathetocephalus resendezi* (LRP No. 3722) from *Carcharhinus leucas* from the Gulf of California. **(B)** Cross-section through rugose base of scolex of *Sanguilevator yearsleyi* (LRP No. 3732) from *Lamiopsis tephrodes* from Malaysian Borneo. **(C)** Longitudinal section through scolex of *Sanguilevator yearsleyi* (LRP No. 3731). **(D)** Whole mount of mature proglottid of *C. resendezi* (LRP No. 3720). **(E)** Whole mount of mature proglottid of *S. yearsleyi* (LRP No. 3723). **(F)** Cross-section through mature proglottid of *S. yearsleyi* anterior to cirrus-sac (LRP No. 3728). **(G)** Cross-section through mature proglottid of *S. yearsleyi* at level of ovary (LRP No. 3728). **(H)** Mature proglottid of undescribed species of *Disculiceps* from *Carcharhinus limbatus* from the Gulf of Mexico (LRP No. 8328). *Abbreviations*: O, ovary; SC, spherical chambers; T, testis; TC, transverse channels; V, vitelline follicle.

issues surrounding the identity of the type host of *D. pileatus* were discussed by Linton (1908). Although he originally described this tapeworm from *Car. obscurus* in 1890, he provided evidence in 1908 to suggest the identity of that host may have been *Car. leucas* (as *Car. platyodon* [Poey]). The type host of *Disculiceps galapagoensis* is *Car. longimanus* (see Nock and Caira, 1988). Caira et al. (2001) provided a scanning electron micrograph of the scolex of a species of *Disculiceps* from *Car. brevipinna*. Beyond species of *Carcharhinus*, Schmidt and Beveridge (1990) also reported *Cat. australis* from the great hammerhead, *Sphyrna mokarran* (Rüppell). The monotypic *Sanguilevator* is somewhat exceptional in that *S. yearsleyi* was reported from one of only two species in the carcharhinid genus *Lamiopsis* Gill (see Caira et al., 2005).

Some host records, however, require confirmation. Linton (1924; pg. 47) reported *D. pileatum* from a shark 150 cm in total length that he identified as "*Scoliodon terrae-novae*." We believe the identity of this host is in error. The accepted name for this shark is *Rhizoprionodon terraenovae* (Richardson) (Eschmeyer et al., 2016). This is a small shark that reaches a total length of only 110 cm (see Ebert et al., 2013), and thus it seems unlikely that Linton had a specimen of this species that was over 150 cm in total length. Also potentially erroneous is the identity of the sharks from the *Valdivia* expedition on which Pintner (1928) based his morphological work. The name given by Pintner was *Carcharias lamia*; the accepted name of this species is *Carcharodon carcharias* (L.) (see Eschmeyer et al., 2016). Not only is this a lamniform, rather than a carcharhiniform, shark but also we have examined a number of specimens of that species and have found no evidence of cathetocephalideans.

GEOGRAPHIC DISTRIBUTION. Prior to the PBI project, candidate members of the order had been reported from the eastern Pacific Ocean in the Gulf of California (Caira et al., 2005) and the Galapagos Rift off Ecuador (Nock and Caira, 1988), the western Atlantic Ocean off the coast of Massachusetts, USA (Linton, 1890, 1924), the Gulf of Mexico (Thatcher, 1961; Dailey and Overstreet, 1973; Conn et al., 2004), the Dry Tortuga Islands (Linton, 1908), Bermuda (Linton, 1907), Lake Nicaragua (Watson and Thorson, 1976), Argentina (Suriano and Labriola, 2001), South China Sea off Malaysian Borneo (Caira et al., 2005), India (Pramanik and Manna, 2006), and a diversity of localities off Australia (Butler, 1987; Schmidt and Beveridge, 1990; Caira et al., 2005). Based on reports of the voyage of the *Valdivia* (Chun, 1903), Pintner's material was collected from the Indian Ocean off the western Seychelles (Station 228) and the coast of Somalia (Station 268).

CURRENT STATUS OF THE CATHETOCEPHALIDEA

DIVERSITY, CLASSIFICATION, AND HOST ASSOCIATIONS. The only taxonomic action involving the members of this order made over the course of the PBI project was the formal transfer of *Disculiceps* to the Cathetocephalidea. Although an undescribed species of *Disculiceps* was found among specimens in the Lawrence R. Penner Parasitology collection (LRP Nos. 8657–8660) from blue sharks (*Prionace glauca* [L.]) collected from the Gulf of California in 1993, no new species were described. As a consequence, known diversity in the order remains essentially as it was at the inception of the PBI project. However, the multiple reports of what likely represent undescribed members of the order bear further investigation. These include: the specimens originally identified as *D. pileatus* by Thatcher (1961) and which we believe are conspecific with those identified as *Disculiceps* sp. 1 by Caira et al. (2014) from *Car. limbatus* in the Gulf of Mexico, an image of the scolex of which appears in Caira and Jensen (2014); *Disculiceps* sp. of Caira et al. (2001) from *Car. brevipinna* (Fig. 1C); the specimens of *Cathetocephalus* from *Car. amblyrhynchoides* in Australia noted by Schmidt and Beveridge (1990) to represent an undescribed taxon; specimens identified as an undescribed species of *Cathetocephalus* from *Car. amboinensis* in Australia by Caira et al. (2005). In addition, the specimens identified as *Cat. australis* from *Car.* cf. *sorrah*, *Car.* cf. *limbatus*, and *Sphyrna mokarran* in Australia by Schmidt and Beveridge (1990) would be interesting to examine given the oioxenous specificity (*sensu* Euzet and Combes [1980]) observed in members of this order to date. Also potentially novel are the specimens identified as *Cat. australis* from *Car.* cf. *brachyurus* off Argentina by Suriano and Labriola (2001). As noted above, the specimens referred to by the unavailable name *Cat. limbatus* by Pramanik and Manna (2006) likely represent an undescribed species of *Sanguilevator*. We believe the correct identity of the host from which this material was collected is likely *Lamiopsis temmincki*.

Our estimate of cathetocephalidean diversity globally (Table 1) is guided by our prediction that species of *Cathetocephalus* and *Disculiceps* generally parasitize only larger species of sharks. Based on maximum size data from Ebert et al. (2013), existing host records indicate that shark size is >160 cm for species of *Cathetocephalus* (i.e., *Car.* cf. *sorrah*) and >255 cm (i.e., *Car.* cf. *limbatus*) for species of *Disculiceps*. In terms of carcharhinid sharks, this eliminates all but species of *Galeocerdo* Müller & Henle, *Carcharhinus*, *Prionace* Cantor, and *Glyphis* Agassiz as candidate hosts. Extensive collections from the first of these genera (e.g., Linton, 1889, 1908; Southwell, 1912; J. N. Caira, unpubl. data) has never yielded a cathetocephalidean, thus we do not believe *Galeocerdo* is an appropriate host of the order. In terms of the 29 species of *Carcharhinus* with maximum sizes of >160 cm, seven are already known to host one or more species of *Cathetocephalus*; we predict that at least half (i.e., 11) of the 22 remaining species will each be found to host their own species of *Cathetocephalus*. Of the 19 species of *Carcharhinus* with maximum sizes greater than 255 cm, three of which are known to host *Disculiceps*, we predict that one-third (i.e., 5) of the 16 remaining species will each be found to host their own species of *Disculiceps*. As noted by numerous authors (e.g., Compagno, 1988; Dosay-Akbulut, 2008; Naylor et al., 2012b) the monotypic *Prionace* clusters among *Carcharhinus* species and thus the blue shark (*P. glauca*) should be considered a member of the former genus. To date, we have examined hundreds of specimens of blue sharks and the only cathetocephalidean we have discovered is the undescribed species of *Disculiceps* noted above. We do not anticipate additional cathetocephalidean diversity in that host species. According to Ebert et al. (2013), all six known species of *Glyphis* have maximum recorded total lengths greater than 160 cm; we have no data for members of this genus to date, but predict that half (i.e., 3) will be found to host its own species of cathetocephalidean. If the association with larger sharks also holds true for hammerhead sharks—a prediction supported by Schmidt and Beveridge's (1990) report of a species of *Cathetocephalus* from *Sphyrna mokarran*—we predict that among the 11 other species of *Sphyrna* only the largest that remain to be examined (i.e., *S. lewini* [Griffith & Smith] and *S. zygaena* [L.]) will be found to host cathetocephalideans, but likely only a single species each. Our work on the monotypic *Eusphyra* Gill has yet to yield a cathetocephalidean and thus we do not anticipate this will change in the future. If we are correct in terms of the host of Pramanik and Manna's (2006) material, no new species of *Sanguilevator* will be found as potentially one each is now known from each of the two species of *Lamiopsis*.

The number of known (described and undescribed) species of cathetocephalideans likely totals 15 and we predict the order will ultimately be found to include an additional 21, for a global tally of 36 species. Our global collections of carcharhinid and sphyrnid sharks have been sufficiently extensive for us to be relatively confident that the number of genera in the order will remain stable at three: *Cathetocephalus*, *Disculiceps*, and *Sanguilevator*.

PHYLOGENETIC RELATIONSHIPS. The first phylogenetic work to include representation of all three genera of cathetocephalideans was the molecular phylogenetic study of Caira et al.

(2014). Although, each genus was represented by only a single species, the trees resulting from their analyses provided strong support for the monophyly of *Cathetocephalus* + *Sanguilevator* + *Disuliceps*, and thus also for the Cathetocephalidea as an independent order of cestodes. This led Caira et al. (2014) to formally transfer *Disculiceps* and the Disculicepitidae to the Cathetocephalidea. The species of *Sanguilevator* was found to be sister to the species of *Cathetocephalus*, supporting placement of both genera in the Cathetocephalidae. The trees resulting from their analyses also provided support for the affinities suggested by Caira et al. (2005) relative to other cestode orders. The Cathetocephalidea grouped robustly among the acetabulum-bearing orders, as sister taxon to a group composed of the Cyclophyllidea and their kin + the "Tetraphyllidea" relics, and the orders Phyllobothriidea and Onchoproteocephalidea—to the exclusion of the Lecanicephalidea and the Rhinebothriidea. This result suggests that the unusual configuration of the scolex of members of the order (see Morphology section below) is a derived configuration in this group.

Morphology. No new features of note were discovered in cathetocephalideans over the course of the PBI project. However, the results of the phylogenetic analyses of Caira et al. (2014) provide insight for the interpretation of scolex homologies across the three cathetocephalidean genera (Fig. 1A–C). The anterior region of the scolex is homologous in all three genera; this region is referred to as an apical pad in *Cathetocephalus* and *Sanguilevator*, and as a cushion in *Disculiceps*. Both of the former genera bear a band of papillae at the posterior margin of the pad; this feature is lacking in *Disculiceps*. We believe the rugose region comprising the posterior-most portion of the scolex is homologous across all three genera. In *Cathetocephalus* and *Sanguilevator* this region is referred to as a rugose base; in *Disculiceps* it is referred to as a collar.

Geographic Distribution. Our knowledge of the geographic distribution of the order has changed little over the course of the PBI project. The order is essentially cosmopolitan in distribution. In terms of Spalding et al.'s (2007) Marine Ecoregions of the World, the order is known from the Temperate Northern Pacific, Tropical Eastern Pacific, Temperate Northern Atlantic, Tropical Atlantic, Temperate South Atlantic, Temperate Australasia, Central Indo-Pacific, and the Western Indo-Pacific marine realms. It is currently not known from the Arctic, Southern Ocean, Temperate Southern Africa, or Eastern Indo-Pacific marine realms. We anticipate collections from the latter two marine realms are most likely to yield new records because they are home to a diversity of relatively large species of carcharhinid sharks (Ebert et al., 2013). The dearth of records from the Arctic and Southern Ocean marine realms is likely to reflect a true lack of this order from these regions.

CONCLUSIONS

Despite intensive collecting efforts focused on elasmobranchs over the course of the PBI project, the Cathetocephalidea were only rarely encountered and thus our knowledge of most elements of the biology of the order has not substantially changed since 2008. The order houses three genera in two families, and six described species. Evidence of an additional nine undescribed species exists. The paucity of records from elasmobranchs of the waters of the far north and south of the globe likely reflect the absence of the order from these regions. The paucity of records from Temperate South Africa and the Eastern Indo-Pacific likely reflect a lack of sampling. The order has an affinity for sharks of the order Carcharhiniformes, and specifically of the family Carcharhinidae, although one species has been described from a sphyrnid shark. Within these families, *Sanguilevator* is restricted to species of *Lamiopsis*; *Disculiceps* and *Cathetocephalus* are most common in species of *Carcharhinus*. The order is generally associated with larger members of these shark groups. This leads us to predict the final total number of species globally is unlikely to exceed 36 species.

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Table 1. Expected global elasmobranch associations of cathetocephalidean species (in yellow). Number of shark species per genus given in parentheses (includes known undescribed shark species). First column: number of cathetocephalidean species parasitizing each shark taxon as of 2017 (includes known undescribed cestode species); second column: predicted total number of cathetocephalidean species parasitizing each shark taxon globally. Quotes indicate non-monophyletic taxa (Naylor et al., 2012b). Question marks indicate genera not yet examined for cestodes. * Designation New genus D is for *Scyliorhinus torazame* (Tanaka). Estimated total number of cathetocephalidean species parasitizing elasmobranchs globally given at bottom of table.

	Cathetocephalidean spp.			Cathetocephalidean spp.			Cathetocephalidean spp.	
	2017	**ESTIM.**		**2017**	**ESTIM.**		**2017**	**ESTIM.**
SELACHOIDEA								
Carcharhiniformes	**15**	**36**	Proscylliidae	**0**	**0**	**Heterodontiformes**	**0**	**0**
Carcharhinidae	**14**	**33**	*Ctenacis* (1 sp.)	?	0	**Hexanchiformes**	**0**	**0**
Carcharhinus (44 spp.)	11	27	*Eridacnis* (3 spp.)	0	0	**Lamniformes**	**0**	**0**
Galeocerdo (2 spp.)	0	0	*Proscyllium* (3 spp.)	?	0	**Orectolobiformes**	**0**	**0**
Glyphis (6 spp.)	0	3	Pseudotriakidae	0	0	**Pristiophoriformes**	**0**	**0**
Isogomophodon (1 sp.)	?	0	*Gollum* (2 spp.)	?	0	**Squaliformes**	**0**	**0**
Lamiopsis (2 spp.)	2	2	*Planonasus* (1 sp.)	?	0	**Squatiniformes**	**0**	**0**
Loxodon (2 spp.)	0	0	*Pseudotriakis* (1 sp.)	0	0			
Nasolamia (1 sp.)	?	0	"Scyliorhinidae"	**0**	**0**	**SHARK TOTAL**	**15**	**36**
Negaprion (2 spp.)	0	0	*Atelomycterus* (6 spp.)	0	0	**BATOID TOTAL**	**0**	**0**
Prionace (1 sp.)	1	1	*Aulohalaelurus* (2 spp.)	?	0			
Rhizoprionodon (10 spp.)	0	0	*Bythaelurus* (11 spp.)	?	0	**ELASMOBRANCH TOTAL**	**15**	**36**
Scoliodon (3 spp.)	0	0	*Cephaloscyllium* (18 spp.)	0	0			
Triaenodon (1 sp.)	0	0	*Figaro* (3 spp.)	?	0			
Hemigaleidae	**0**	**0**	New genus D* (1 sp.)	0	0			
Chaenogaleus (2 spp.)	?	0	*Poroderma* (2 spp.)	0	0			
Hemigaleus (2 spp.)	0	0	*Schroederichthys* (5 spp.)	?	0			
Hemipristis (1 sp.)	0	0	*Scyliorhinus* (15 spp.)	0	0			
Paragaleus (4 spp.)	0	0	Sphyrnidae	**1**	**3**			
Leptochariidae	**0**	**0**	*Eusphyra* (1 sp.)	0	0			
Leptocharias (1 sp.)	0	0	*Sphyrna* (12 spp.)	1	3			
Pentanchidae	**0**	**0**	Triakidae	**0**	**0**			
Apristurus (46 spp.)	0	0	*Furgaleus* (1 sp.)	0	0			
Asymbolus (9 spp.)	0	0	*Galeorhinus* (1 sp.)	0	0			
Cephalurus (1 sp.)	?	0	*Gogolia* (1 sp.)	?	0			
Galeus (18 spp.)	0	0	*Hemitriakis* (8 spp.)	0	0			
Halaelurus (7 spp.)	0	0	*Hypoglaeus* (1 sp.)	?	0			
Haploblepharus (4 spp.)	0	0	*Iago* (5 spp.)	0	0			
Holohalaelurus (5 spp.)	0	0	*Mustelus* (30 spp.)	0	0			
Parmaturus (11 spp.)	?	0	*Scylliogaleus* (1 sp.)	?	0			
Pentanchus (1 sp.)	?	0	*Triakis* (5 spp.)	0	0			

TABLE 2. List of valid cathetocephalidean taxa with type hosts.

VALID TAXA

FAMILY CATHETOCEPHALIDAE DAILEY & OVERSTREET, 1973
- *Cathetocephalus* Dailey & Overstreet, 1973
  - *Cathetocephalus thatcheri* Dailey & Overstreet, 1973 (type) ex *Carcharhinus leucas*
  - *Cathetocephalus australis* Schmidt & Beveridge, 1990 ex *Carcharhinus brachyurus*
  - *Cathetocephalus resendezi* Caira, Mega & Ruhnke, 2005 ex *Carcharhinus* cf. *leucas sensu* Naylor et al. (2012a) (as *Carcharhinus leucas*)
- *Sanguilevator* Caira, Mega & Ruhnke, 2005
  - *Sanguilevator yearsleyi* Caira, Mega & Ruhnke, 2005 (type) ex *Lamiopsis tephrodes* (as *Lamiopsis temmincki*)

FAMILY DISCULICEPITIDAE JOYEUX & BAER, 1936
- *Disculiceps* Joyeux & Baer, 1936
  - *Disculiceps pileatus* (Linton, 1890) Joyeux & Baer, 1936 (type) as *Carcharhinus obscurus*
  - *Disculiceps galapagoensis* Nock & Caira, 1988 ex *Carcharhinus longimanus*

UNAVAILABLE NAMES & *NOMINA NUDA*

- *Cathetocephalus leucas* Vankara, Vijaya Lakshmi & Gangadharam, 2007 (unavailable name as type material not designated)
- *Cathetocephalus limbatus* Pramanik & Manna, 2006 (unavailable name as type material not designated); evidence of *Sanguilevator* in India
- *Disculiceps chowpaatiensis* Chincholikar & Shinde, 1975 (*nomen nudum*)
- *Disculiceps tandoni* Pramanik & Manna, 2005 (unavailable name as type material not designated)
- *Disculiceps trygonis* Shinde & Chincholikar, 1975 (*nomen nudum*)

6

Cyclophyllidea van Beneden in Braun, 1900

By
Jean Mariaux[1], Vasyl V. Tkach, Gergana P. Vasileva, Andrea Waeschenbach,
Ian Beveridge, Yana D. Dimitrova, Voitto Haukisalmi, Stephen E. Greiman,
D. Timothy J. Littlewood, Arseny A. Makarikov, Anna J. Phillips,
Tantely Razafiarisolo, Vincent Widmer, and Boyko B. Georgiev

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    5.6. Dilepididae Fuhrmann, 1907
    5.7. Dioicocestidae Southwell, 1930
    5.8. Dipylidiidae Railliet, 1896
    5.9. Gryporhynchidae Spasskii & Spasskaya, 1973
    5.10. Hymenolepididae Perrier, 1897
    5.11. Mesocestoididae Perrier, 1897
    5.12. Metadilepididae Spasskii, 1959
    5.13. Nematotaeniidae Lühe, 1910
    5.14. Paruterinidae Fuhrmann, 1907
    5.15. Progynotaeniidae Fuhrmann, 1936
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[1] Corresponding author (jean.mariaux@ville-ge.ch)

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1. INTRODUCTION

The Cyclophyllidea are the largest order of cestodes with over 3,000 known species in 437 genera and 16 families (Georgiev, 2003; Caira and Littlewood, 2013; Table 1). Besides their high diversity, cyclophyllideans are also the quintessential cestodes because they are the most commonly known and the most pathogenic in humans and domestic animals. With rare exceptions, they are parasites of homeotherms and are particularly diverse in birds and mammals, although a few species also parasitize amphibians and "reptiles." Their known life-cycles include one or two, typically invertebrate, intermediate hosts; vertebrates rarely act as intermediate hosts.

Although cyclophyllideans are found on all continents, they have chiefly been studied in regions known to be home to strong schools of parasitology (i.e., Europe, North America, the territories of the former Soviet Union, and Japan). Data from other parts of the world, especially the tropics, remain patchy. Important biodiversity contributions focusing on the Cyclophyllidea are few and have predominantly concentrated on aquatic birds in eastern Europe, northern Asia, and the Far East. Synthetic studies covering a large diversity of hosts include Southwell and Lake (1939a, b), Mahon (1954), Baer (1959), Spasskaya and Spasskii (1971), Petrova (1977, 1978), Illescas-Gomez and Lopez-Roman (1979), Brglez (1981), Zhuk et al. (1982), Maksimova (1989), and Mariaux (1994) for birds, and Skrjabin and Matevosyan (1948), Gvozdev et al. (1970), Vaucher (1971), Hunkeler (1974), Kozlov (1977), Ryzhikov et al. (1978), Genov (1984), and Sawada (1997) for mammals. Most of these contributions were, however, geographically restricted.

One of the goals of the PBI project was to provide a more comprehensive global assessment of overall cestode diversity. Unfortunately, compared with the diversity of this order, the number of researchers who worked specifically on cyclophyllideans over the course of this project was limited. This meant that not all host groups could be targeted with equal effort. Furthermore, many birds and mammals are protected; therefore, opportunities to examine their parasite faunas are severely restricted in many areas. Despite these limitations, significant progress has been made in characterizing the cyclophyllidean fauna of a number of host groups from all continents (except Antarctica). These include terrestrial birds (mostly Passeriformes), and, among mammals, the Soricomorpha and Rodentia. Altogether, almost 3,500 bird specimens across more than 120 families, representing close to 10% of extant bird species, as well as over 1,000 mammal specimens across 32 families and 143 species were examined, making the present effort the largest cyclophyllidean diversity research program to date.

2. CYCLOPHYLLIDEA OVERVIEW

2.1. Morphological characteristics

Members of the Cyclophyllidea are variable in size (from less than 1 mm to several meters in length) but are usually easily recognizable by the presence of four circular suckers, a compact posterior vitellarium, and lateral genital pores. They are hermaphroditic (with rare exceptions). Furthermore a rostellum, armed or not, is usually present. The uterus may be persistent, or replaced by egg capsules or associated with one, or several, paruterine organs. However, all of these characters are variable and there are known deviations from these traits.

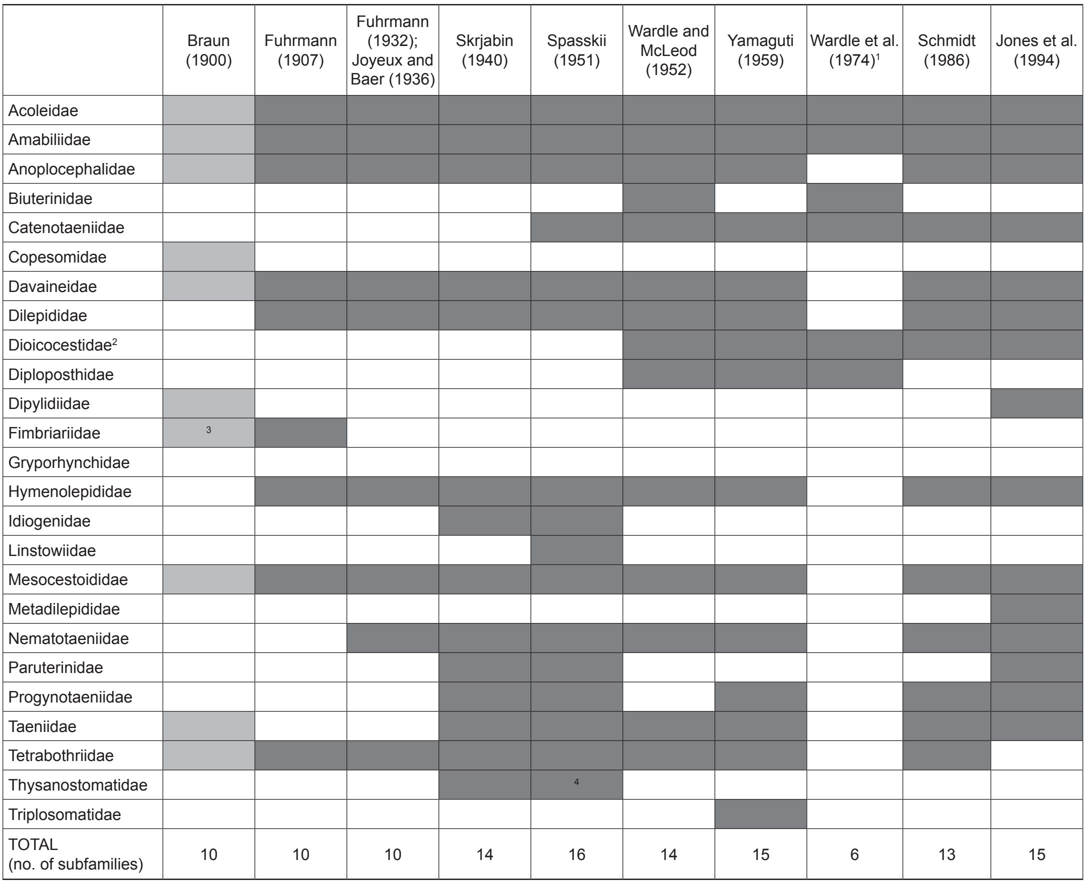
Within the order, the main differentiating characters are linked to the scolex (presence/absence/structure/retractibility of the rostellum; presence/absence/shape/organization of hooks, and presence of spine-like microtriches on tegument of scolex, especially of suckers and rhynchus, sometimes of proglottids); the genital organs (present in 1 or 2 sets per proglottid); number and disposition of testes; presence of internal and/or external seminal vesicles; shape and position of ovary; relative position of genital ducts to osmoregulatory canals; alternation of genital pores along the length of the strobila; presence of accessory structures to the copulatory organs (e.g., glands, sphincters, or spines); and development of gravid proglottids (shape and development of uterus, presence of paruterine organs, shape and peculiarities of eggs, nature of embryonic envelopes). Other characters, such as the shape and number of proglottids, the conspicuousness of proglottization, the shape of suckers are also used to discrimate among taxa.

2.2. Higher-level classification

The original establishment of the order remains a matter of controversy (see Wardle and McLeod [1952] and Hoberg et al. [1999] for short summaries). Jones et al. (1994) attributed the order to van Beneden (in Braun, 1900), although Braun (1900) himself is more often credited because it was one of the five orders of cestodes he recognized. Since then, the higher-level classification of the group has gone through numerous changes. Braun (1900) considered the order to include only the single family Taeniidae Ludwig, 1886, which he subdivided into ten subfamilies and 33 genera. The rapid discovery of numerous new taxa at the beginning of the 20th century prompted a number of refinements to that classification system (Fig. 1). Fuhrmann (1907) proposed a more complex scheme comprising ten families and 66 genera. A few years later, the Nematotaeniidae Lühe, 1910 were added to this scheme and the Fimbriariidae Wolffhügel, 1899 were reduced to subfamily level (Fuhrmann, 1932; Joyeux and Baer, 1936). Skrjabin (1940) proposed the order be subdivided into seven suborders, each with between one and four families. He believed that the presence of a paruterine organ was sufficiently distinct to justify erection of the family Idiogenidae Skrjabin, 1940 within the suborder Davaineata. He also recognized the Thysanosomatidae Skrjabin, 1933 as valid within the suborder Anoplocephalata and elevated the Paruterininae Fuhrmann, 1907 to the family level. Within families, he considered features of the uterus (sac-like or breaking down into egg capsules) as appropriate for recognizing subfamilies. Spasskii (1951) essentially followed Skrjabin (1940), but with some modifications in the membership of suborders and superfamilies. Most notably, he placed the Catenotaeniidae Spasskii, 1950, a family he had erected the previous year (Spasskii, 1950), in the suborder Anoplocephalata.

In their comprehensive book on cestodes, Wardle and McLeod (1952) included the Catenotaeniidae, Biuterinidae Meggitt, 1927, and Diploposthidae Poche, 1926 in Fuhrmann's classification scheme, thus recognizing 14 families. However, in the update of that book, Wardle et al. (1974) drastically reorganized the order, technically retaining only the families Catenotaeniidae, Biuterinidae, Acoleidae Fuhrmann, 1899, Amabiliidae Braun, 1900, Dioicocestidae Southwell, 1930, and Diploposthidae in the Cyclophyllidea *sensu stricto*. They elevated most of the other generally recognized families to ordinal level and further divided them into a total of 26 families, many of which had been recognized as subfamilies in other systems. However, Wardle et al.'s (1974) classification scheme was not generally accepted.

In his book, Yamaguti (1959) accepted the 15 families recognized by Wardle and McLeod (1952), to which he added the Triplotaeniidae Yamaguti, 1959. Freeman (1973) based his concept of cestode classification on ontogeny, proposing four lineages within the traditional Cyclophyllidea, with some traditionally recognized families split among them. However, he refrained from formally reorganizing the order. His proposals were summarized by Hoberg et al. (1999). Schmidt (1986) followed Yamaguti (1959) but treated the Diploposthidae as a synonym



	Braun (1900)	Fuhrmann (1907)	Fuhrmann (1932); Joyeux and Baer (1936)	Skrjabin (1940)	Spasskii (1951)	Wardle and McLeod (1952)	Yamaguti (1959)	Wardle et al. (1974)[1]	Schmidt (1986)	Jones et al. (1994)
Acoleidae	░	▓	▓	▓	▓	▓	▓	▓	▓	▓
Amabiliidae	░	▓	▓	▓	▓	▓	▓	▓	▓	▓
Anoplocephalidae	░	▓	▓	▓	▓	▓	▓		▓	▓
Biuterinidae						▓		▓		
Catenotaeniidae					▓	▓	▓	▓	▓	▓
Copesomidae	░									
Davaineidae	░	▓	▓	▓	▓	▓	▓		▓	▓
Dilepididae		▓	▓	▓	▓	▓	▓		▓	▓
Dioicocestidae[2]						▓	▓	▓	▓	▓
Diploposthidae						▓	▓	▓		
Dipylidiidae	░									▓
Fimbriariidae	░ 3	▓								
Gryporhynchidae										
Hymenolepididae		▓	▓	▓	▓	▓	▓		▓	▓
Idiogenidae				▓	▓					
Linstowiidae					▓					
Mesocestoididae	░	▓	▓	▓	▓	▓	▓		▓	▓
Metadilepididae										▓
Nematotaeniidae			▓	▓	▓	▓	▓		▓	▓
Paruterinidae				▓	▓					▓
Progynotaeniidae				▓	▓		▓		▓	▓
Taeniidae	░			▓	▓	▓	▓		▓	▓
Tetrabothriidae	░	▓	▓	▓	▓	▓	▓		▓	
Thysanostomatidae				▓	▓ 4					
Triplosomatidae							▓			
TOTAL (no. of subfamilies)	10	10	10	14	16	14	15	6	13	15

FIGURE 1. Higher cyclophyllidean classification through time. Braun's (1900) original subfamilies are in lighter gray.
[1] For comments on Wardle et al.'s (1974) families see Section 2.2.
[2] Sometimes spelled Dioecocestidae, see Section 5.7 for clarification.
[3] An "Annex" in Braun's system.
[4] Avitellinidae in Spasskii (1951).

of the Acoleidae and considered the Triplotaeniidae as a subfamily of the Anoplocephalidae Cholodkowsky, 1902, reducing the number of families to 13.

In the most recent authoritative treatment of the group, Jones et al. (1994) recognized 15 families. They transferred the Tetrabothriidae Linton, 1991 to their own order, and added the Metadilepididae Spasskii, 1959, Dipylidiidae Railliet, 1896, and Paruterinidae, to the order, the latter two of which had been treated as subfamilies in Schmidt's (1986) system. The current classification (see Table 1) also includes the Gryporhynchidae Spasskii & Spasskaya, 1973. Although doubts remain as to the status of the Mesocestoididae Perrier, 1897, which have repeatedly been proposed to be treated as a separate order, (e.g., Wardle et al., 1974; Brooks et al., 1991; Mariaux, 1998), they are treated as a family in the taxonomic framework presented here pending their ordinal status be more formally assessed in the context of the Cyclophyllidea overall.

3. PBI PROJECT RESULTS

3.1. Geographic sampling

This project resulted in the sampling of avian and mammalian hosts from areas of the planet that were among the most poorly known from the standpoint of cyclophyllidean diversity. Although we aimed to cover as many different regions as possible, the localities ultimately sampled were biased to some extent by logistical considerations. These included local administrative regulations, weather at the time of the scheduled expeditions, safety, as well as the participation of local academic counterparts. Thirty dedicated field trips (as well as a few more opportunistic smaller collecting trips) were organized between 2008 and 2015. These consisted of three to Australia, five to Africa, one to Europe, one to the Middle East, two to Madagascar, eight to Asia, three to North America, one to Central America, and six to South America. With the notable exceptions of Australia, the USA, the Ivory Coast, the Ukraine, Russia, and some South American countries, beyond some occasional mostly ancient reports, the cyclophyllidean fauna of all of these locations was very poorly known. A summary of our PBI expeditions is provided by country below. As noted above, owing to the limited number of individuals with taxonomic expertise in this, the largest cestode order, PBI project efforts emphasized collecting over the description of novelty in the hope of developing a resource for future taxonomic work.

Mist nets (and occasionally guns) were used to capture birds in the field. Mammals were trapped using Sherman live traps or pit fall traps. Birds were euthanized using chloroform or by thoracic compression, and mammals by exposure to isoflurane. All animals were dissected as soon as possible after their death. Cestodes were removed from the digestive tract, washed and relaxed in water, fixed with hot 4% formaldehyde, and preserved in 70% ethanol. Separate tissue fragments were kept in 95% ethanol for DNA extraction and sequencing. The worms were stained following various protocols; stains used included iron acetocarmine, hydrochloric carmine, aqueous alum carmine, Ehrlich's hematoxylin, and Mayer's hematoxylin. Some scoleces and fragments of strobila were mounted in Berlese's medium to facilitate detailed examination of the rostellar hooks, cirrus armature, and structure of the eggs (see Dubinina, 1971; Ivashkin et al., 1971; Georgiev et al., 1986; Miller et al., 2010).

Parasite specimens examined over the course of this project have been deposited in the collections of the HWML (Harold W. Manter Laboratory of the University of Nebraska, Lincoln, NE, USA); IBER-BAS (Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria); ISEA (Institute of Systematics and Ecology of Animals, Novosibirsk, Russia); MHNG (Natural History Museum of Geneva, Geneva, Switzerland); MZUSP (Museum of Zoology of the University of São Paulo, São Paulo, Brazil); NMNH (Smithsonian's National Museum of Natural History—Invertebrate Zoology Collection, Washington, D.C., USA); SAMA (South Australian Museum, Adelaide, Australia). Associated genomic DNA and ethanol-preserved tissue samples were deposited in the NHM (Natural History Museum, London, UK). Host vouchers (note that not all hosts specimens were preserved) have been deposited in the ISEA, MHNG, as well as the FMNH (Field Museum of Natural History, Chicago, IL, USA), KU (Biodiversity Institute, University of Kansas, Lawrence, KS, USA), NMPh (National Museum of the Philippines, Manila), and MPEG (Museu Paraense Emílio Goeldi, Belém, Brazil).

Host taxonomy follows Avibase (Lepage, 2014; Lepage et al., 2014) for birds and the online version of the Mammals Species of the World, 3rd edition (Wilson and Reeder, 2005) for mammals. Public databases ("Host-parasite database" [Gibson et al., 2005; http://www.nhm.ac.uk/research-curation/scientific-resources/taxonomy-systematics/host-parasites/

database/index.jsp]; "Zoological Records®" [Thompson Reuters]) were queried for known host-parasite associations. Molecular specimens collected over the course of the PBI project were assigned PBI-codes that are available from the corresponding author upon request.

AUSTRALIA (3 expeditions). **June 2010:** Arid pastoral lands, Western Australia; elevation 20 m. June 2011: Central desert, Northern Territory; elevation 650 m. **May 2013:** tropical coastal rainforest, Queensland; elevation 0–300 m. *Base camps:* Karratha (-20.74; 116.84), Mulga Park Station (-26.00; 131.59), and Cairns (-16.92; 145.77).

Vertebrates examined: 89 mammal specimens representing 13 species in seven families.

Cyclophyllideans encountered: Ten species; 40% overall prevalence.

Remarks: Cestodes of Australian mammals have been relatively well studied (see, e.g., Beveridge, 1976, 1985; Beveridge and Jones, 2002; Beveridge and Johnson, 2004) and no new species were collected. However, these new expeditions yielded material usable for molecular studies. For example, several species of *Bertiella* Stiles & Hassall, 1902 were preserved for the first time in ethanol and included in our molecular phylogenetic studies. In addition, collection of specimens of the anoplocephalids *Progamotaenia macropodis* Beveridge, 1976 and *Wallabicestus ewersi* Schmidt, 1975 from kangaroos will facilitate future analysis of both species complexes. A review of the cyclophyllidean holdings at the South Australian Museum in Adelaide did, however, yield taxa new to science.

BRAZIL (2 expeditions). **November 2011:** Atlantic rainforests in protected catchment areas, coastal massifs south of Salesopolis; elevation 800–900 m. Agricultural landscapes, north of Tremembe; elevation 500–600 m; both São Paulo Region. **July 2013:** Lowland tropical forest within Reserva Biologic do Gurupi, Maranhao State; elevation 0–100 m. *Base camps:* Estação Biológica de Boracéia, University of São Paulo (-23.65; -45.89), Fazenda Nabor (-22.92; -45.57), and Reserva Biológica do Gurupi (-3.70; -46.76).

Vertebrates examined: 413 bird specimens representing 173 species in 38 families.

Cyclophyllideans encountered: 57 species; 17% overall prevalence.

Remarks: The Neotropics, and specifically Brazil as its largest country, harbor one of the richest avifaunas in the world. Among other areas, we had excellent access to well-preserved patches of primary Atlantic coastal rainforests, in which few parasitological studies had been carried out previously. In the São Paulo Region, about one third of the species collected are likely new to science; the specimens belonging to known species are also important, since most of the species described from Brazil were based on poorly preserved specimens collected in the first half of 19th century by the Austrian naturalist and explorer J. Natterer. We have also examined birds in the southeastern-most area of the southern Amazon where helminths of birds had never been studied. Prevalence of cestode infections in the Amazonian Belem area of endemism (Gurupi) was lower (only 13%) than that in the Atlantic forest, which is considered a generally more disturbed habitat. The sources of these differences are yet to be determined. This region also yielded cestode taxa new to science.

CHILE (2 expeditions). **November 2008:** "Cathedral forests" on slopes of Andes and open land around estuaries in Fjord Comau, northern Patagonia, south of Puerto Montt, Los Lagos Region; elevation 0–100 m. **June 2015:** Lowland savannah, cattle pastures, and temperate deciduous forest outside of Chillán and wetland outside of Los Angeles, Biobio Region; elevation 100–200 m. *Base camps:* Huinay Scientific Field Station (-42.38; -72.41) and Universidad de Concepción, Chillán (-36.59; -72.08).

Vertebrates examined: 121 bird specimens of 27 species in 19 families, including some marine taxa, as well as ten mammal specimens of two species in two families.

Cyclophyllideans encountered in birds: Approximately 26 species, including at least ten which are new to science; 53% overall prevalence.

Cyclophyllideans encountered in mammals: One species; 10% prevalence.

Remarks: Cestode data are extremely limited for the birds and mammals of Chile, although a few localized contributions have been published (e.g., Babero et al., 1981; Torres et al., 1991; González-Acuña et al., 2000, 2011). In fact, in general, data on bird and mammal cestode diversity in the temperate latitudes of South America are not available. The late F. Bona collected extensively in Chile, including the Valdivia region, however most of his specimens have not yet been examined. Even though our collections in Chile were restricted to a very small area and the diversity of hosts examined was low, we obtained the highest relative diversity and proportion of new cestode taxa in terrestrial birds, including new genera from that country, than from any other country represented by our other expeditions. The second expedition to Chile targeted waterfowl and small mammals. The cestode fauna of three species of ducks and two species of coots turned out to be extremely depauperate. Morphological and molecular analyses have demonstrated that previous identification of mammalian hymenolepidids in Chile were likely incorrect. This locality yielded a member of a new cestode genus most closely related to another new cestode that we discovered in Central America (Guatemala; see below) found in the Chilean small mammals examined.

CHINA (1 expedition): **July 2011:** Mountainous area around Lanzhou City and in mixed forested, shrublands, and agricultural areas south of Yuzhong City, Xinglong Mountain; river valley and adjacent slopes, Lanzhou Shifogou National Forest Park; vicinities of the village of Dagoucun, Lanshan Forest Park; mountain slopes west of the city campus of the Northwest University for Nationalities (NWUN), as well as parks and grasslands on the new campus of NWUN and adjacent fields. Gansu Province; elevation 1,700–2,500 m. *Base camp:* Yuzhong campus of NWUN (35.93; 104.15).

Vertebrates examined: 129 bird specimens of 32 species in 16 families.

Cyclophyllideans encountered: 17 species; 33% overall prevalence.

Remarks: China's cyclophyllidean fauna remains extremely poorly known. Most previous data on the avian cestodes of China come from eastern parts of the country (e.g., Hsü, 1935). We explored some localities in the central parts of the country with relatively rich avifaunas—typical high altitude regions with continental climate. We mostly collected known Palaearctic species, which have been used widely in molecular phylogenetic analyses and ultrastructural studies. Furthermore, these specimens will be used for the redescription of species for which most of the morphology is poorly known.

ETHIOPIA (1 expedition): **November 2012:** Secondary open forests in Wondo Genet area; Southern Nations, Nationalities, and Peoples' Region; elevation 1,900–2,100 m. Shore of Lake Ziway in Ziway town; Oromia Region; elevation 1,650 m. *Base camps:* Wondo Genet (7.08; 38.63) and Ziway Fishery Resource Research Center (7.92; 38.73).

Cyclophyllideans encountered: 13 species; 19% overall prevalence.

Remarks: The only previous detailed taxonomic study of the cyclophyllideans of Ethiopia (Fuhrmann and Baer, 1943) was based on samples from the southern-most parts of the country, more specifically the region of the Sagan and Omo rivers. Over the course of the PBI project, we were able to examine areas in the Rift Valley that were home to a considerable diversity of birds. We found new species of the families Hymenolepididae, Dilepididae, and Paruterinidae as well as described species with poorly known morphology requiring the preparation of contemporary redescriptions.

GABON (1 expedition). **November 2009:** Mosaic savannah and river shores. Southeastern region, Franceville area, Haut-Ogooué Province; elevation 300–400 m. *Base camp:* Centre International de Recherches Médicales de Franceville (CIRMF) (-1.61; 13.58).

Cyclophyllideans encountered: 31 species; 24% overall prevalence.

Remarks: Although some neighboring countries, especially the Democratic Republic of Congo, had been explored for tapeworms in the first half of the 20th century (e.g., Baer, 1925, 1959; Southwell and Lake, 1939a, b; Mahon, 1954), basically nothing was known about cyclophyllideans from Gabon at the initiation of the project. The diverse landscapes of the Haut-Ogooué Province make it the richest part of the country for its avian diversity and allowed for the collection of cestodes that are representative of equatorial parts of Africa. Cestodes found included both new and described species of cyclophyllideans that were subsequently widely used in molecular and morphological studies carried out as part of the PBI project.

GUATEMALA (1 expedition). **January 2015:** Remnant, isolated, mixed-hardwood cloud forest in Cerro Cucurucho, Sacatepéquez Department; elevation 2,640 m. *Base camp:* Finca El Pilar, Cerro Cucurucho 11 km SE of Antigua Guatemala, Sacatepéquez, Guatemala (14.52; -90.69).

Vertebrates examined: 58 mammal specimens of ten species in four families.

Cyclophyllideans encountered: Approximately ten species with a combined overall prevalence of 43%.

Remarks: Almost all mammalian species collected on this trip had never been examined for helminths, including cyclophyllidean cestodes. All cyclophyllidean species appear to be new to science, including a member of a new genus in rodents that appears to be closely related to a new species from Chile. Cestodes parasitic in shrews belonged to several genera and besides being new, provided invaluable resource for phylogenetic studies of this group. This expedition provided the southern-most records of shrew-hosted cestodes so far in the Western Hemisphere. This material significantly complements material from higher latitudes in North America and Eurasia, and provides opportunities to obtain a more complete picture of several genera (e.g., *Skrjabinacanthus* Spasskii & Morosov, 1959, *Lineolepis* Spasskii, 1959, *Staphylocystoides* Yamaguti, 1959, *Cryptocotylepis* Skrjabin & Matevosyan, 1948) and also to inform historical biogeography (Hope et al., 2016; Cook et al., in press).

GUYANA (1 expedition). **April 2014:** Lowland savannah, cattle pastures, and deciduous tropical forest on the foothills of the Pakaraima Mts.; gallery forest on Ireng River near Karasabai; Region 9, Upper Takutu-Upper Essequibo; elevation 200–400 m. *Base camp:* Karasabai Amerindian Village (4.00; -59.53).

Vertebrates examined: 82 bird specimens of 47 species in 19 families.

Cyclophyllideans encountered: Approximately ten species with 15% overall prevalence.

Remarks: Collections focused on terrestrial birds. This work built on the knowledge gained during the Smithsonian sponsored program "Biological Diversity of the Guiana Shield", started in 1983, that included an extensive survey of the plants, insects, and vertebrates of Guyana (see http://botany.si.edu/bdg/index.html). While there have been a handful of studies on the helminths of amphibians and "reptiles" from Guyana, the cestodes of the country remain poorly known. The cyclophyllidean specimens collected during this trip were fixed appropriately for morphological and molecular work and represent several families.

IRAN (1 expedition). **December 2010:** Persian Gulf shore and Sea of Oman, intertidal areas, mangroves, area of the town of Minab, South of the city of Bandar Abbas, Hormozgan Province; elevation 0–20 m. *Base camp:* State Environmental Agency Office, Minab (27.13; 57.07).

Vertebrates examined: 54 bird specimens of 18 species in 11 families.

Cyclophyllideans encountered: Approximately 18 species; 50% overall prevalence.

Remarks: We studied mostly aquatic (shore and marine) birds. This resulted in a representative collection of cestode families that are specific to these hosts, which is of great value for both future morphological and molecular phylogenetic studies. Tetrabothriideans were also collected.

IVORY COAST (1 expedition). **April–June 2010:** Coastal lagoons near and east of Abidjan and southern Savannah. Grands Ponts, Belier and Sud Comoe Regions; elevation 10–150 m. *Base camps:* Centre Suisse de Recherches Scientifiques CSRS (5.33; -4.13) and its Bringakro field station (6.41; -5.09).

Vertebrates examined: 120 bird specimens of 31 species in 16 families.

Cyclophyllideans encountered: Six species; 13% overall prevalence.

Remarks: The Ivory Coast, and particularly the Adiopodoumé region, was extensively explored in the middle of the 20th century (Baer, 1972; Hunkeler, 1974) and again in the 1980s and 1990s (see Mariaux [1994] for a synthesis). This field trip allowed for some complementary collecting in the coastal and southern parts of the country and resulted in the collection of specimens of many taxa fixed appropriately for molecular work (see, e.g., Widmer et al., 2013).

MADAGASCAR (2 expeditions). **October 2013:** Secondary humid forests, east of Antananarivo; Toamasina Region; elevation 900–1,000 m. **December 2014:** Dry forests, Menabe region and Sofia region; elevation 20–50 m. *Base camps:* Sahambaky (-19.07; 48.34), Mahatsara (-18.85; 48.42), Maromizaha (-18.96; 48.47), Ankaraobato (-20.13; 44.64), and Ampombibe III (-15.54; 47.55).

Vertebrates examined: 132 bird specimens of 34 species in 22 families.

Cyclophyllideans encountered: 13 species; 15% overall prevalence.

Remarks: Despite the country's high bird diversity and the well-known high level of endemicity, Malagasy cyclophyllideans have barely been explored and only a dozen species, including some from domestic birds, have been recorded (i.e., Deblock et al., 1962; Rosé and Broussart, 1962; Quentin, 1963; Bona, 1975). Most of the collected specimens represent new taxa, probably endemic to the island.

MALAWI (1 expedition). **October 2009:** Vwaza Marsh Reserve (lowland marsh and plain); elevation 1,100–1,200 m Nyika National Park (highlands); elevation 1,800–2,000 m; both Rumphi District, northern Malawi. *Base camps:* Vwaza Marsh Reserve (-10.88; 33.46) and Nyika National Park (-10.79; 33.80).

Vertebrates examined: 438 bird specimens of 134 species in 28 families; 67 mammal specimens of 16 species in five families.

Cyclophyllideans encountered in birds: Approximately 50 species; 17% overall prevalence.

Cyclophyllideans encountered in mammals: Approximately ten species; 34% overall prevalence.

Remarks: This was the first major study of helminths (including cestodes) of birds and small mammals in Malawi. Rather little knowledge is available on the neighboring countries as well. Avian cestodes included a number of taxa known elsewhere in Africa as well as several putative new taxa. However, new, properly collected specimens of even previously described species provide material for redescriptions needed for many avian cestodes described from Africa. Mammalian cestodes, although not very diverse, have yielded a high level of novelty with one species from shrews already described (Greiman and Tkach, 2012) and additional new species descriptions from shrews and rodents (e.g., *Lophurolepis* sp.) underway. Some known species (e.g., a member of the anoplocephalid genus *Afrobaeria* Haukisalmi, 2008) will be very useful for broader phylogenetic analyses.

MALAYSIA (1 expedition). **August 2010:** Rainforest, including primary patches in northern vicinities of Kuala Lumpur, Selangor; elevation 200–500 m. *Base camp:* Gombak Field Station of the University of Malaya (3.32; 101.75).

Vertebrates examined: 90 bird specimens of 36 species in 14 families.

Cyclophyllideans encountered: 16 species; 19% overall prevalence.

Remarks: This expedition yielded specimens of avian cestodes from Peninsular Malaysia for the first time, which is of key importance due to the current lack of data on this group from Southeast Asian countries in general, the few exceptions being rather ancient (e.g., Burt, 1940a, b).

PERU (1 expedition). **November 2013:** Tropical lowland forests.

Vertebrates examined: 234 bird specimens of 104 species in 26 families.

Cyclophyllideans encountered: Approximately 25 species; 18% overall prevalence.

Remarks: This was the first significant collecting effort targeting cestodes of birds in that region of Peru and essentially in the whole country, especially considering the quality of collected material. Prevalence of cestode infections in birds inhabiting western slopes of the Andes was lower than that in Chile, but somewhat higher than in the Brazilian Amazonian forest obtained during the Gurupi collecting trip. This material includes several new species as well as interesting records of known species (e.g., only the second record of the dilepidid cestode *Arostellina reticulata* Neiland, 1955 in humming birds).

PHILIPPINES (3 expeditions). **May–July 2009:** Luzon Island, Aurora Province. Mostly mountain forests. Aurora Memorial National Park, near Sitio Dimani, elevation 400–600 m (15.70; 121.32); Barangay Casapsipan, Municipality of Casiguran, elevation 1–50 m (16.29; 122.19); Sitio Minoli, Barangay Real, Municipality of San Luis, elevation 600 m (15.68; 121.53); Barangay Lipimental, Municipality of San Luis; elevation 543 m (15.39; 122.19). **July 2011:** Luzon Island. Mostly mountain forests. Mt. Cagua, Barangay Magrafil, Gonzaga City, Cagayan Province, elevation 680 m (18.24; 122.10); Mt. Pao, Ilocos Norte Province, elevation 750 m (18.44; 120.88); Mt. Cabacan, Ilocos Norte Province, elevation 475 m (18.45; 120.90). **August 2013:** Mindoro Island, Sablayan Municipality, Occidental Province. Lowland rain forest and open land around Libuao Lake, elevation 100–200 m (Sablayan Prison and Penal Farm [12.79; 120.92] and Libuao Lake [12.82; 120.90]).

Vertebrates examined: 601 bird specimens of 96 species in 42 families; 324 mammal specimens of 40 species in 12 families.

Cyclophyllideans encountered in birds: Approximately 35 species; 17% overall prevalence.

Cyclophyllideans encountered in mammals: Approximately 20 species; 13% overall prevalence.

Remarks: Specimens collected in the Philippines represent a broad range of cyclophyllidean families. Cestodes of birds include several new species and rare findings of cestodes from doves and sunbirds, which will provide insight into their phylogenetic relationships, evolution, and systematics. Cestodes of small mammals were systematically studied in the Philippines for the first time as previous records contained only reports of *Hymenolepis diminuta* (Rudolphi, 1819) Weinland, 1858 (likely a misidentification) from the Norwegian rat, *Rattus norvegicus* (Berkenhout). We have discovered a rich, highly endemic fauna of cestodes in both rodents and insectivores. The cestode fauna of small mammals was represented by members of the families Hymenolepididae and Davaineidae. All collected cestodes from these hosts turned out to be new species. Remarkably, the Philippines (essentially, two islands of Luzon and Mindanao) yielded greater diversity of *Hymenolepis* Weinland, 1858, a well-known genus with cosmopolitan distribution, than the whole Palearctic and the whole Nearctic biogeographic realms (Makarikov et al., 2013a, b, 2015a). This can be attributed to the highly endemic fauna of hosts, complex landscape, and numerous colonization events due to the appearance of land bridges during periods of low sea level, coincident with glaciation at higher latitudes (Hopkins, 1973). There is no doubt that exploration of additional Philippine islands will allow for discovery of additional, yet unknown, species, and a better understanding of the island biogeography of parasites, as well as complex evolutionary trajectories of cestodes of small mammals in this part of the world.

RUSSIA/KAZAKHSTAN (3 expeditions). **Russian Federation August 2012:** Deciduous forest, Arkharinskiy Raion, Khinganskiy State Nature Reserve; Amurskaya Oblast'; elevation 100 m. **May 2014:** Steppe, Karasukskiy Raion, Novosibirskaya Oblast'; elevation 110 m. **Kazakhstan May 2012:** Semidesert, Ili River, Altyn-Emel State National Natural Park, Almaty Province; elevation 495 m. *Base camps:* Lake Dolgoe (49.37; 129.69); Karasuk Scientific Field Station (53.73; 77.87), Kalkan field station (43.85, 78.74).

Main results: Over 175 mammals, 14 species in four families; 5–25% prevalence; 12 cestode species and larval stages of four species.

Remarks: Collections targeted small mammals. Parts of our investigations were also based on previously collected cyclophyllidean specimens from the East Kazakhstan region and Russia (Novosibirskaya Oblast', Amurskaya Oblast' and south of Primorskiy Kray). Even though these localities had been documented by previous authors (e.g., Nadtochii, 1970; Fedorov, 1975, 1986; Shaikenov, 1981) the knowledge of the cestode fauna of mammals from Siberia and RussianFar East needed to be revised. Since many widespread species reported from this area are currently recognized as complexes of cryptic species, the existing data on cestodes do not reflect the actual species diversity. We found at least four species previously not reported from these regions and, at a minimum, three new species.

UGANDA (1 expedition). **March 2013:** Secondary forest and scrub and Dura River forest, Mainaro. Kibale National Park, Western Region, Kamwenge District; elevation 1,200–1,400 m. *Base camp:* Ngogo Research Camp (0.50; 30.43) and (0.36; 30.39).

Vertebrates examined: 224 bird specimens of 59 species in 28 families; 106 mammal specimens of 30 species in six families.

Cyclophyllideans encountered in birds: Approximately 25 species; 22% overall prevalence.

Cyclophyllideans encountered in mammals: Approximately 15 cestode species; 44% overall prevalence.

Remarks: Cestodes of birds were represented by members of several families, while the vast majority of cestodes parasitic in mammals belonged to the Hymenolepididae and the Davaineidae. Some previously unknown species, especially those collected from bats, provided unique morphological and molecular materials. They will significantly improve our understanding of the evolution of these cestode lineages and especially multiple host switching events recently demonstrated in several groups of mammalian cestodes, for instance, within the so-called *Rodentolepis* Spasskii, 1954 clade (Hymenolepididae) (Greiman and Tkach, 2012; Makarikov et al., 2015b)

UKRAINE (1 expedition). **August 2011.**

Vertebrates examined: 109 bird specimens of 52 species in 18 families.

Cyclophyllideans encountered: Approximately 35 species; 41% overall prevalence.

Remarks: These collections were focused on several groups of water birds (mostly Anseriformes, Charadriiformes, Ralliformes) as well as some passerine birds living near water. The Ukraine is a country in which the diversity of avian cestodes was already quite well known. Thus, collecting efforts were focused on taking advantage of the unique opportunity for obtaining of a broad diversity of avian cestodes from European avian hosts. This is important because, historically, a number of cestode genera were initially discovered in Europe but lack molecular vouchers. These taxa are thus important from a phylogenetic standpoint.

USA (Contiguous states). This dataset includes results from several smaller collections in various US states (California, Mississippi, Montana, North Dakota, Oklahoma, and Oregon) and more extensive collections in Texas (2 trips). Details for the trips to Texas are as follows: **September 2014:** Dry scrub forest, cattle pastures near Brackettville, Kinney County, elevation 300–430 m. Plains grassland and pinyon-juniper-oak woodlands near Fort Davis and Sky Mountains, Jeff Davis County, elevation 1,380–1,560 m. *Base camp:* Fort Clark Springs (29.30; -100.42) and Calamity Creek Ranch (30.53; -103.82). **May 2015:** Plains grassland, cattle pastures. Riparian and oak-mesquite-juniper hills near Brackettville, Kinney County, elevation 300–430 m. *Base camp:* Fort Clark Springs (29.30; -100.42) and Tularosa Nueces Ranch (29.48; -100.24).

Main results (Texas): 192 bird specimens of 70 species in 22 families; approximately 20 cestode species, 13% overall prevalence,

Main results (various states): 175 bird specimens of 67 species in 24 families; probably about 40 cestode species, greater than 55% overall prevalence. 144 mammal specimens of 20 species in ten families; approximately 25 cestode species including eight new to science; greater than 41% overall prevalence.

Remarks: In Texas, terrestrial birds were targeted; in the other states, targeted birds mostly belong to aquatic groups. Among the mammals, shrews of the genus *Sorex* L. (Soricidae Fischer) constitute the large majority of this material. Soricid hosts proved to be highly productive from the viewpoint of cestode prevalence, taxonomic diversity, and the number of the new species found. Several new species were found in the cestode genera *Skrjabinacanthus* Spasskii & Morozov, 1959, *Staphylocystoides* Yamaguti, 1952, *Soricinia* Spasskii & Spasskaya, 1954, *Urocystis* Villot, 1880, and *Staphylocystis* Villot, 1877 (see Tkach et al., 2013). All cyclophyllideans of *Sorex* shrews have been brought to North America with shrew hosts that colonized the continent over the Beringian land bridge that existed and disappeared several times in relatively recent geological history (Repenning, 1967; Prost et al., 2013). Despite the overall high similarity between the North American shrew cestodes and their counterparts in the eastern Palearctic at the level of cestode genera, the North American shrews are parasitized by an almost completely endemic cestode fauna at the level of species. This provides a unique opportunity to assess the timing and trends of the process formation of cestode fauna in North American shrews and possibly extrapolate these findings to other regions.

USA (Alaska). June 2011: Arctic tundra and boreal forest, north of Fairbanks, along the Dalton Highway, across the Brooks Range and beyond the Arctic Circle, elevation 100–300 m.

Main results: 17 bird specimens of nine spp. in two families; approximately ten cestode species, 53% overall prevalence. 124 mammal specimens of six species in four families; nine cestode species, 37% overall prevalence.

Remarks: Although all bird cestode species found during this expedition are known species, they constitute important comparative material. On the other hand, cestodes of small mammals, particularly shrews, proved to be highly diverse and little studied. Several new species were found in Alaskan shrews including members of the genera *Staphylocystoides* (e.g., Greiman et al., 2013), *Soricinia*, and a new as-of-yet undescribed genus. We have also found at least one trans-Beringian species of shrew cestodes belonging to the Dilepididae.

VIETNAM (2 expeditions). **June 2014:** Humid tropical forest in Tam Dao National Park. Vin Phuc Province; elevation 900–1,100 m. Dryer tropical forest in Xuan Son National Park. Phu Tho Province; elevation 400–500 m. Humid tropical forest in Cat Ba National Park, Cat Ba Island. Hai Phong Province; elevation 30–100 m. **October–November 2014:** Rainforest in Ba Be National Park, Bac Kan Province elevation 300–800 m. *Base camps:* Tam Dao (21.46; 105.64), Xuan Son (21.12; 104.96), Cat Ba Park headquarters (20.79; 106.99), and Quang Ke Commune (22.35; 105.71).

Vertebrates examined: 67 bird specimens of 22 species in nine families; 51 mammal specimens of ten species in six families.

Cyclophyllideans encountered in birds: Eight species; 21% overall prevalence.

Cyclophyllideans encountered in mammals: Approximately four species; 8% overall prevalence.

Remarks: Our collections focused on various types of protected tropical forests in the north of the country. Early data on the cyclophyllidean diversity of Vietnam were provided by foreign researchers (e.g., Joyeux and Baer, 1935, 1937; Oshmarin and Demshin, 1972). These, and the results of subsequent studies by Vietnamese authors, were provided in two monographic works by Nguyen (1994, 1995). Nevertheless, the knowledge of the cyclophyllidean fauna of the country remains incomplete, and includes much fewer cyclophyllidean taxa than expected given the rich vertebrate fauna of the country. This mostly reflects insufficient taxonomic and geographic coverage of collecting efforts. Nevertheless, several species of cestodes of small mammals were found for the first time in Vietnam. Several cestode species from bats and members of the shrew genus *Suncus* Ehrenberg are very important for phylogenetic inferences linking our richer materials from the Philippines with taxa distributed on continental Eurasia

3.2. Host groups and prevalences

The vast majority of cyclophyllideans use birds and mammals as definitive hosts. Exceptions to this include the Nematotaeniidae, which parasitize amphibians and "reptiles" (see Jones, 1987, 1994), the linstowiine anoplocephalids, some of which parasitize "reptiles" (see Beveridge, 1994), and a small number of records of Gryporhynchidae and Paruterinidae from amphibians and "reptiles" (Georgiev and Kornyushin, 1994; Pichelin et al., 1998). Nonetheless, our PBI project cyclophyllidean collecting efforts focused on birds and mammals, and within both groups we targeted specific taxa.

3.2.1. Birds

With respect to birds, we focused our collecting efforts almost exclusively on terrestrial taxa, mostly Passeriformes; however, some shore and marine birds were collected in Iran, Chile, the Ukraine, and some parts of the USA. All collections were opportunistic and were limited by logistical constraints and the various restrictions imposed by our collecting permits in each country visited. A total of 3,473 specimens consisting of 989 species (or 10% of the known bird diversity) in 122 families and 23 orders was examined across the more than 30 field expeditions conducted. A few additional isolated specimens were obtained opportunistically or through exchanges. Among the bird species examined, 417 (over 40%) were represented by only a single individual; only 41 or 4% were represented by samples of greater than ten specimens (Table 2). With the exception of the ratites and marine bird orders such as the Sphenisciformes and Procellariiformes, at least a few representatives of most terrestrial orders were examined. Among the Passeriformes, only a few important families were not represented, mostly because of their Australasian distribution (e.g., Acanthizidae Bonaparte, Meliphagidae Vigors, Paradisaeidae Vigors, and Petroicidae Mathews). The extent of our sampling in each order and family was, however, highly variable.

Concerning prevalences, in total, 749 individuals (21.6%) of 397 species were parasitized by at least one cyclophyllidean species. Among those, 234 bird species (58.9%) had never been reported to host cestodes prior to the start of the PBI project. These birds are distributed across most orders and about half of the families sampled in this project; the newly recorded hosts are especially numerous in the large Neotropical families Thamnophilidae Swainson (antbirds) and Tyrannidae Vigors (tryrant flycatchers) as well as in the Old World Pycnonotidae Gray (bulbuls) and Muscicapidae Fleming (Old World flycatchers). Other avian families with relatively numerous new host species records include the Cuculidae Vigors (cuckoos), Picidae Vigors (woodpeckers), Hirundinidae Vigors (swallows), Motacillidae Horsfield (wagtails and pipits), and Turdidae Rafinesque (thrushes) (Table 2). Of particular note are the six species of Trochilidae Vigors (hummingbirds) and four species of Nectariniidae Vigors (sunbirds) that were found to host cyclophyllideans, because they confirm that these birds harbor a diverse fauna of cyclophyllideans, despite their nectarivorous diet. Also of note was the single kingfisher (Alcedinidae Rafinesque) in Malaysia found to host cestodes, since the only previous record from this family was from Australia (Johnston, 1909). As expected, the new host records included very few aquatic birds. This is likely because not only are such species broadly distributed, but they have also been more frequently examined. Also not unexpected, was the higher infection prevalence seen in aquatic (Anseriformes, Charadriiformes [except Turnicidae], Gaviiformes, Gruiformes, Pelecaniformes, Podicipediformes, and Suliformes) than in terrestrial (especially Passeriformes) orders of birds (Table 2).

Although the following numbers may differ slightly once our newly collected material is fully identified, it is clear that most parasitized birds (76% in total; 79% in terrestrial birds; 66% in aquatic birds) were infected with a single species of cestode. Infections with two (16%, 15%, 21%), three (4%, 4%, 7%), or four or more cestode species (3%, 3%, 6%) were relatively rare. The latter category comprised two species each of Hirundinidae, Pycnonotidae, and Turdidae as well as one each of Apodidae Hartert (swifts) and Phasianidae Horsfield for terrestrial birds. Most aquatic birds harboring four or more cestode species belonged to the Charadriiformes.

The likelihood of detecting cestodes in a given host species is clearly linked to the number of individuals of that species examined. In terrestrial birds, a plateau of 60–70% of species parasitized (by 1 or more species of cestodes) was reached when over seven individuals of each species were examined. Below that threshold the chance of finding cestodes begins at 28% for a single specimen and increases almost linearly from there. These figures are higher for aquatic birds; the chance of finding cestodes begins at 55% for a single specimen and reaches 90–100% when six or more birds are examined. These data suggest that, globally, it is worth examining a minimum of five to seven specimens of each bird species in any locality in order to maximize the number of infected host species recovered in that area. While four to five specimens may be sufficient for each species of aquatic bird, six to eight specimens per species of terrestrial bird is needed. Larger sample sizes remain preferable in order to detect rare species of tapeworms.

3.2.2. Mammals

With the exception of marsupials (*sensu lato*) in Australia, among mammal hosts, no particular species were targeted. However, for practical reasons, rodents (Rodentia), bats (Chiroptera), and shrews (Soricomorpha) were the most abundant mammals captured during our PBI expeditions. Among the 143 species sampled, 56 (39%) were represented by only a single specimen—a percentage similar to that encountered in birds. However 29 (20%) species were relatively well sampled, with more than ten specimens necropsied of each.

A total of 1,160 mammal specimens belonging to 143 species in 32 families and 14 orders was necropsied over the course of the PBI project (Table 2). In addition, a few isolated specimens were obtained opportunistically or through exchanges. A total of 356 individuals (30.7%) representing 85 mammal species was found to be parasitized by at least one cyclophyllidean species. Among these, 36 (42.4%) were mammal species from which cestodes had not previously been reported. Half of the new host species belong to the Soricidae, while the majority of the others are rodents, mostly Muridae Illiger. Only three of the 40 bat species examined are new hosts of cestodes.

Most infected mammal species (70%) hosted only a single cestode species; infections with two (16%) or three (3%) species were similarly rare as compared to values observed in birds. In contrast, at 11%, infections with four or more species of cestodes were notably higher than seen in birds. This is mostly due to the extremely diverse hymenolepidid fauna found in the Soricidae, especially in the genera *Sorex* and *Crocidura* Wagler, 1832.

Not unexpectedly, as seen in birds, the probability of detecting cestodes in a given species of mammal increases with the number of specimens examined. At 37%, when only a single host specimen was necropsied, the prevalence of overall cestode infection observed was higher in

Table 2. Summary of collections for birds and mammals.

	No. of orders	No. of families	No. of species	No. of specimens	No. of species infected	No. of individuals infected	No. of new hosts for cestodes
BIRDS							
Terrestrial	16	104	866	3,131	307 (35.5%)	577 (17.8%)	229
Aquatic	7	19	123	342	90 (73.1%)	192 (56.1%)	5
Total	23	123	989	3,473	397 (40.1%)	749 (21.6%)	234
MAMMALS							
Total	14	32	143	1,160	85 (59.4%)	356 (30.7%)	36

mammals than in birds. However interordinal variation is high. The Chiroptera, for example, were conspicuously less parasitized than other mammal orders examined. When bats are removed from our calculation, almost all mammal species were found to be parasitized by one or more cyclophyllidean species when six specimens or more were studied.

3.3. Faunal composition and new taxa

3.3.1. Birds

Of all the cyclophyllideans collected over the course of the PBI project, approximately 70% were identified at least to family (Fig. 2A). The Hymenolepididae were the most frequently encountered family comprising 157 (38%) of the 415 identified records (Fig. 2B)—making them the most important family in many country datasets, with a tendency to be more abundant in Africa (Fig. 3B). At present, 17 new species and four new genera have been identified from among our hymenolepidid material (Fig. 3A). The Dilepididae are almost as numerous globally representing 115 (28%) of our identified records (Fig. 2B); that material likely includes six new genera and 18 new species (Fig. 3A). Dilepidids are particularly abundant in the Brazilian sample. Both the Paruterinidae and the Davaineidae are also well represented, although members of the latter family are clearly less abundant in the New World. The Metadilepididae are present in Africa and South America, but were notably absent from our Asian samples and were far less abundant than expected in our identified material overall. Taken together, all seven other cyclophyllidean families encountered represent only 8% of our identified records (Fig. 2B). This was, however, expected given the terrestrial emphasis of our collecting activities because most of these other families are specific to aquatic birds. In contrast, the surprisingly low prevalence of the Anoplocephalidae and the relatively common occurrence of the Mesocestoididae should be noted. In total, our newly collected material includes a minimum of 50 new species from birds (Fig. 3A) that have not yet been described; this figure is likely to increase substantially once all of this material has been examined in detail.

Previous studies in which family faunal compositions have been estimated have focused on particular geographic regions or countries and are thus far more limited than the present work. For example, in Bulgaria, Petrova (1977, 1978) found the Dilepididae to be more numerous than the Hymenolepididae (47% vs. 18% in 1,124 birds, and 44% vs. 22% in 1,200 birds, respectively). A similar result was obtained by Mariaux (1994) from the Ivory Coast with the relative proportion of Dilepididae and Hymenolepididae in the 1,252 bird specimens examined at 36% and 30%, respectively. However, that author also found an unusually high proportion of Metadilepididae (5%). In all three studies, the Paruterinidae, with 11–21%, was the third- or second-most commonly encountered family, and the Davaineidae (8–18%) was the fourth most common family. In contrast, in the 500 birds they examined in the Belgian Congo, Southwell and Lake (1939a, b) found the majority of cestodes to be Hymenolepididae (30%); they also found higher proportions of Paruterinidae and Davaineidae (27% each), and a relatively surprising low proportion of Dilepididae (2%). Most other significant faunal studies have concentrated on aquatic birds and are thus not directly comparable to ours.

3.3.2. Mammals

Representing over 75% of our records, the Hymenolepididae comprised an overwhelming majority of the cyclophyllideans found in mammals over the course of the PBI project (Fig. 4A). It is important to note, however, that this is likely due in part to the high proportion of shrews examined, as well as the fact that shrews host a diversity of hymenolepidids, and the mammal cestode taxonomists involved in the project (i.e., V. V. Tkach and A. Makarikov),

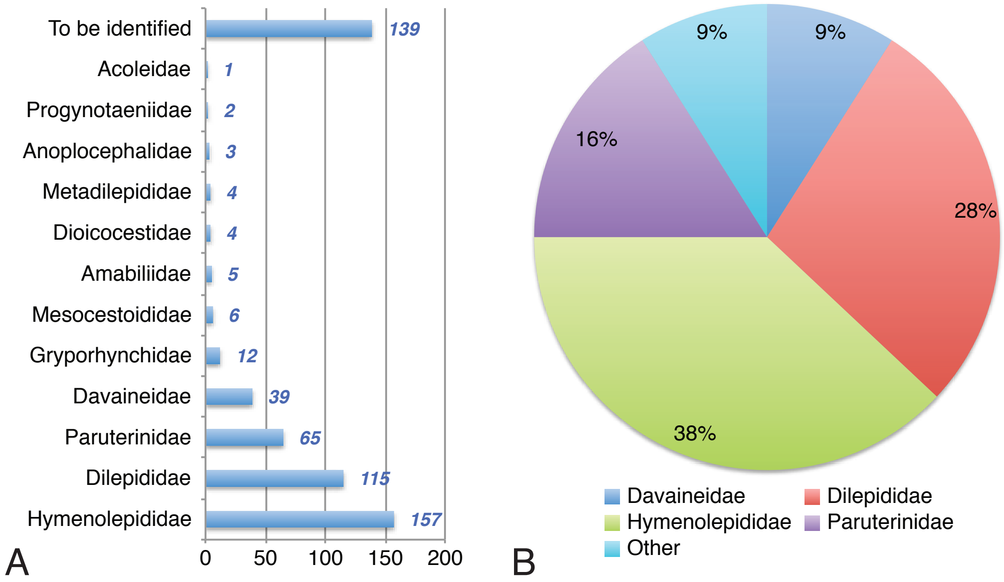


FIGURE 2. Bird cestodes encountered in PBI project collections. **(A)** Number of occurrences per family. **(B)** Relative proportion of cyclophyllidean families.

both have extensive expertise in that family. It is also party due to the fact that some samples of other families have not yet been fully identified. Nevertheless, previous studies have also demonstrated that the species-rich family Hymenolepididae is the primary groups of cestode parasitizing not only the Soricomorpha (see Vaucher, 1971; Genov, 1984), but also, together with the Anoplocephalidae and Catenotaeniidae, rodents overall (Ryzhikov et al., 1978; Genov, 1984; Haukisalmi et al., 2010a, 2014). In the present study, the greatest number of new cestode species discovered in mammals (i.e., more than 50 new species) were hymenolepidids (Fig. 4B). The Anoplocephalidae were also well represented in our material, but were mostly restricted to our samples from Australian marsupials, in which they were already known to dominate the cestode fauna (Beveridge and Jones, 2002). In combination, all other cyclophyllidean families composed only 14% of our records from mammals (Fig. 4A). Although higher numbers of Catenotaeniidae and Davaineidae might have been expected, the poor representation of other families is likely the result of the biased nature of the host taxa targeted here, particularly given the absence and/or underrepresentation of Carnivora and Lagomorpha in our sample.

4. PHYLOGENY

4.1. Overview

Hoberg et al. (1999) provided the first comprehensive family-level phylogenetic analyses of cyclophyllideans in a study based on 42 morphological, ultrastructural, and ontogenetic characters. The resulting trees supported the following affinities. The Mesocestoididae and Nematotaeniidae were sister taxa and together represented the earliest diverging lineage, followed by the Catenotaeniidae. The Metadilepididae and Paruterinidae, as well as the Taeniidae and *Dasyurotaenia* Beddard, 1912 were sister groups, respectively, and together composed a clade. The individual representatives of the four subfamilies of Davaineidae

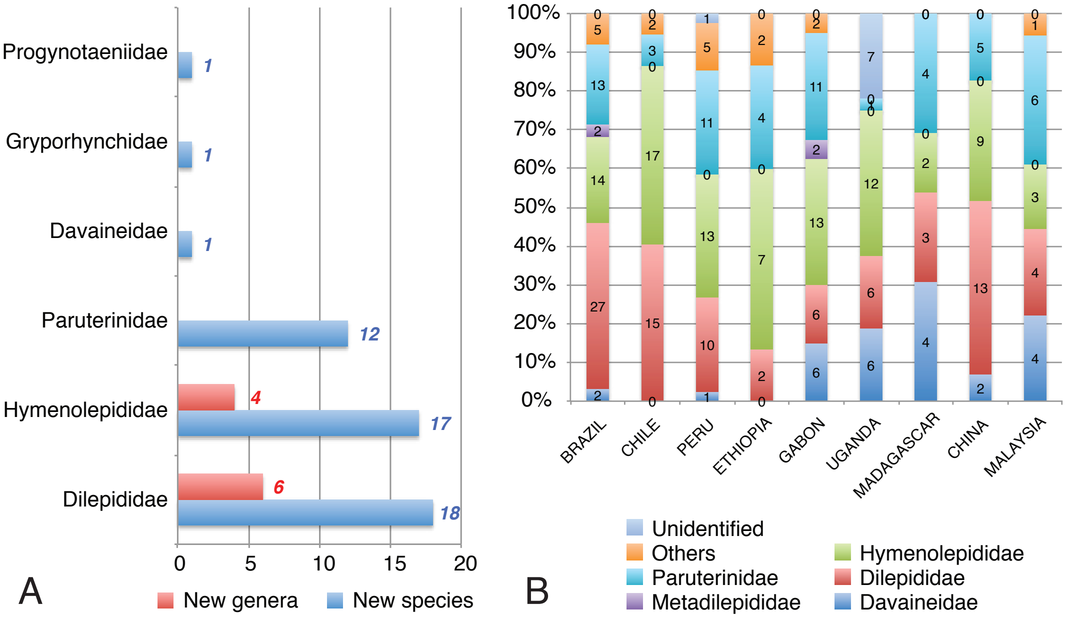


Figure 3. Bird cestodes encountered in PBI project collections. **(A)** Number of new species and genera by family. **(B)** Relative proportion of cyclophyllidean families by country (only countries from which a high proportion of cestodes collected were identified are shown).

were recovered as monophyletic. The Hymenolepididae, Amabiliidae, Dioicocestidae, Acoleidae, and Progynotaeniidae represented a clade, in which the latter three families composed a subclade. The Gryporhynchidae and Dipylidiidae were shown to represent independent families. The Anoplocephalidae grouped as two separate, non-related clades (i.e., the Linstowiinae Fuhrmann, 1907 + the Inermicapsiferinae Lopez-Neyra, 1943 and the Anoplocephalinae Blanchard, 1891 + the Thysanosomatinae Skrjabin, 1988). In a subsequent total evidence analysis, Hoberg et al. (2001) found a sister-group relationship between the Dilepididae and the Davaineidae (+ the Amabiliidae), and also between the Hymenolepididae and the Anoplocephalidae. They too found the Catenotaeniidae to be among the earliest diverging cyclophyllidean families. However, as their study was primarily aimed at resolving ordinal-level relationships among cestodes, their taxon sampling only partially covered cyclophyllidean diversity. It is of note that some of these phylogenetic relationships had been predicted by earlier authors on the basis of comparative morphology alone. For example, Spasskii (1951) combined Skrjabin's (1940) suborders Anoplocephalata and Hymenolepidata into a single suborder, and Spasskaya and Spasskii (1971) proposed the superfamily Paruterinoidea, which consisted of the families Paruterinidae and Metadilepididae.

Very few attempts had been made to resolve the phylogenetic relationships within the Cyclophyllidea using molecular sequence data prior to PBI project efforts (see Mariaux and Olson, 2001 for a summary)—a fact that is at least partly due to a lack of suitable molecular markers (Littlewood et al., 2008). Von Nickisch-Rosenegk et al. (1999) were the first to generate a molecular phylogenetic hypothesis specifically for the order. Their taxon sampling was, however, very limited and highly biased towards the Taeniidae. Furthermore, their analysis was based on only a very short fragment (314 bp) of the small mitochondrial

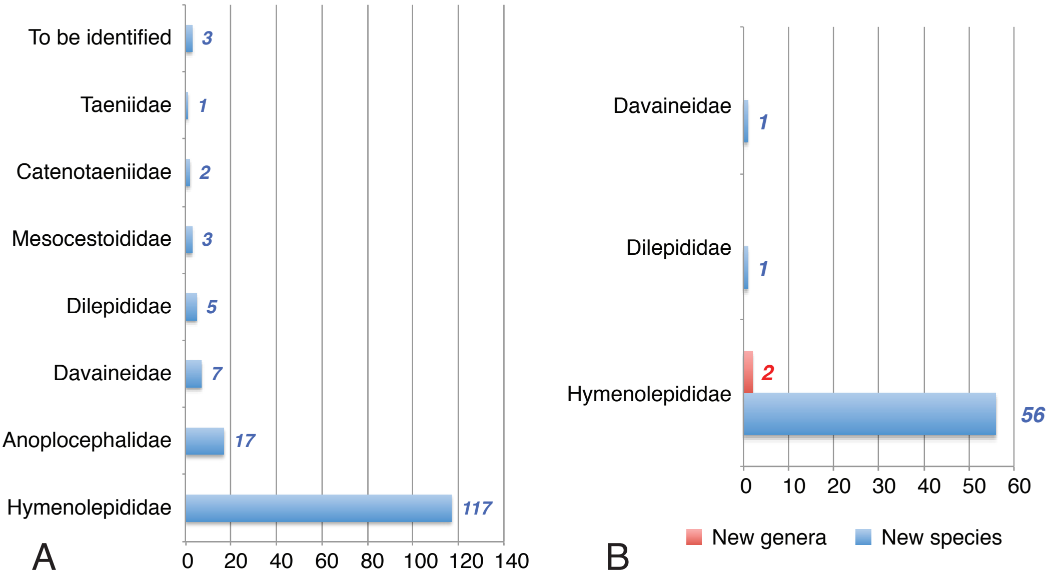


Figure 4. Mammal cestodes encountered in PBI project collections. **(A)** Number of occurrences by family. **(B)** Number of new species and genera by family.

ribosomal RNA subunit (12S rRNA), which may explain why most nodes in the resulting tree were not strongly supported. Mariaux's (1998) phylogeny, which was based on sequence data generated for the small subunit nuclear ribosomal RNA gene (18S rDNA), included a variety of cyclophyllideans, but was designed to study the phylogenetic structure of the class, and thus it too included representation of only a subset of cyclophyllidean families. Nonetheless, the monophyly of all families represented, including the Gryporhynchidae, and the sister-group relationship of Hymenolepididae and Anoplocephalidae were supported in that work. Subsequent major efforts in the field (e.g., Olson and Caira, 1999; Waeschenbach et al., 2007) also included limited representation of cyclophyllidean diversity and thus provide little insight into the phylogenetic relationships in the order overall.

4.2. PBI taxon coverage

Largely as a result of PBI-funded collecting expeditions, which were complemented by a few additional specimens obtained from various other sources, molecular data were generated for a total of 318 cyclophyllidean specimens from across the globe (i.e., Australia, Brazil, Bulgaria, Chile, China, Czech Republic, Ethiopia, France, Gabon, Guyana, Iran, Jordan, Malawi, Malaysia, Philippines, Russia, Slovakia, Sudan, Taiwan, Ukraine, USA, and Vietnam; see Section 3). The following four genes were targeted: small subunit nuclear ribosomal RNA (18S rDNA), partial large subunit nuclear ribosomal RNA (28S rDNA), partial large mitochondrial ribosomal RNA subunit (16S rDNA), and partial cytochrome *c* oxidase subunit I (COI). Sequence data for these genes were generated for 300, 296, 286, and 291 specimens, respectively (see Chapter 22 this volume). The concatenated alignment included representatives of the following 15 cyclophyllidean families (numbers in parentheses indicate the number of specimens and percent of known species diversity per family represented by these specimens): Acoleidae (1; 10%), Amabiliidae (2; 8%), Anoplocephalidae (12; 3%), Catenotaeniidae (4; 13%), Davaineidae

(39; 8%), Dilepididae (73; 10%), Dioicocestidae (9; 43%), Dipylidiidae (1; 7%), Gryporhynchidae (14; 16%), Hymenolepididae (111; 13%), Mesocestoididae (3; 10–20%), Metadilepididae (2; 13%), Paruterinidae (34; 28%), Progynotaeniidae (5; 14%), and Taeniidae (4; 8%).

4.3. PBI phylogenetic hypotheses

The molecular phylogeny generated as a result of the PBI project (see Fig. 5 for a schematic) is the most comprehensively sampled phylogeny of cyclophyllidean tapeworms to date. Unfortunately, the data from the four genes employed here do not provide sufficient signal to offer a well-resolved backbone to the phylogeny, nor do they unambiguously support the monophyly of the Davaineidae, the Paruterinidae + Metadilepididae + Taeniidae, the Dilepididae, and the Hymenolepididae + Anoplocephalidae. However, close relationships between the Progynotaeniidae + Acoleidae + Gyrocoeliinae Yamaguti, 1959, as well as between the Amabiliidae + Dioicocestinae were supported. Subfamilial components of the Anoplocephalidae (i.e., Linstowiinae vs. Anoplocephalinae) were shown to be unrelated confirming the non-monophyly of the family. In general, relationships towards the tips (not shown) of the phylogeny are more well-resolved than those of the deeper nodes. These relationships will be the subject of a later publication in which the backbone of the phylogeny will be based on almost complete mitochondrial genome sequences from 38 lineages across the Cyclophyllidea.

5. FAMILY SUMMARIES AND DISCOVERIES RESULTING FROM THE PBI PROJECT

This section outlines the history and diagnostic features of each of the 16 currently recognized cyclophyllidean families. In each case, novel insights gained over the course of the PBI project are also summarized. Information on life-cycles was retrieved from the literature and from the Cestode Life Cycle database of Lefebvre et al. (2009a) (see Lefebvre et al., 2009b).

5.1. Acoleidae Fuhrmann, 1899

Fuhrmann (1899) proposed the family Acoleidae for two newly erected genera, *Acoleus* Fuhrmann, 1899 and *Gyrocoelia* Fuhrmann, 1899; he based this decision mostly on the absence of a vagina and presence of the strobilar musculature consisting of two longitudinal and three transverse muscle layers. In a subsequent paper, Fuhrmann (1900) added the genera *Dioicocestus* Fuhrmann, 1900 and *Diplophallus* Fuhrmann, 1900 and demoted the group to a subfamily within the Taeniidae. He later reinstated family status for this taxon (Fuhrmann, 1907). In 1932, the same author considered eight genera to be part of the family, adding *Leptotaenia* Cohn, 1901, *Progynotaenia* Fuhrmann, 1909, *Proterogynotaenia* Fuhrmann, 1911, and *Shipleyia* Fuhrmann, 1907. Southwell (1930) erected the Dioicocestidae Southwell, 1930 for dioecious forms. After further study, Fuhrmann (1936) erected the Progynotaeniidae for the proterogynous forms. The validity of the Acoleidae is now generally accepted (Skrjabin, 1940; Yamaguti, 1959; Ryzhikov and Tolkacheva, 1981; Schmidt, 1986; Khalil et al., 1994).

The Acoleidae is one of the families of the suborder Acoleata Skrjabin, 1940 (together with the Progynotaeniidae, Amabiliidae, and Dioicocestidae) and includes cestodes that lack a vaginal pore (and vagina altogether) and reproduce by traumatic copulation (i.e., the cirrus penetrates through the body surface and strobilar parenchyma, and ejaculates sperm directly into the seminal receptacle). The current concept of the Acoleidae is that it includes cestodes that lack a vagina, are hermaphroditic (vs. Dioicocestidae), protandrous (vs. Progynotaeniidae), and that lack canals connecting the seminal receptacles of neighboring

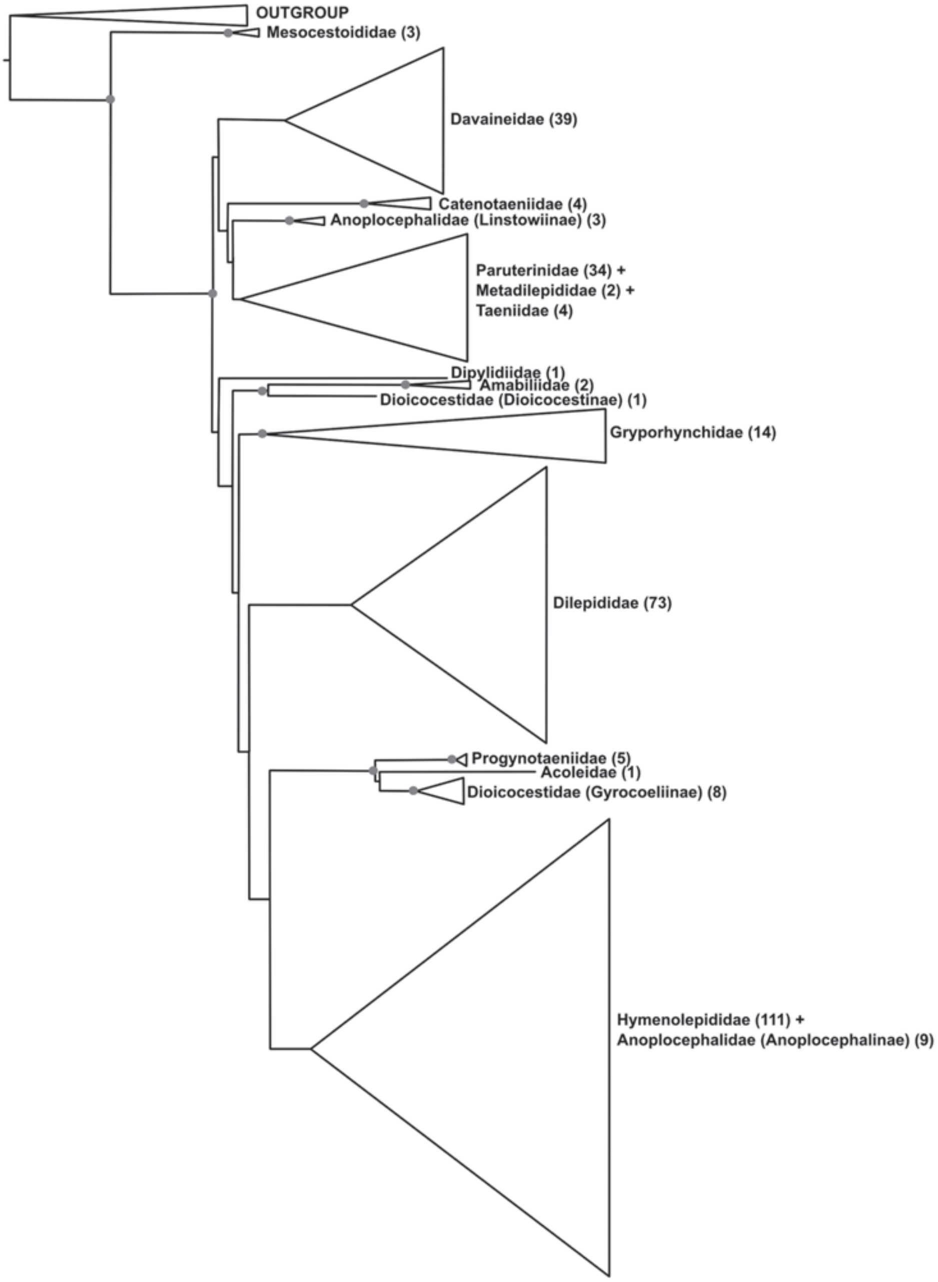


FIGURE 5. Diagrammatic representation of the PBI project cyclophyllidean phylogeny based on a concatenated dataset of small and large subunits nuclear ribosomal RNA (18S rDNA and 28S rDNA), large mitochondrial ribosomal RNA subunit (16S rRNA), and cytochrome c oxidase subunit I (COI) (number of terminals are given in parentheses for each family). Nodal support (≥ 0.95 posterior probability), as inferred from a Bayesian inference analysis using MrBayes 3.2.1 using the GTR+I+Γ model of nucleotide evolution, is indicated with gray dots.

proglottids (vs. Amabiliidae). Acoleids have strong, heavily armed cirri (Fig. 6B), and their scolex bears an armed or unarmed (Fig. 6A) rostellum. Only two genera, *Acoleus* (with a single set of male genital organs per proglottid; 3 species) and *Diplophallus* (with 2 sets of male genital organs per proglottid; 2 species) are now recognized in the family (Ryzhikov and Tolkacheva, 1981; Khalil, 1994a). Their host associations include charadriiform and, rarely, gruiform (rallid) birds (Ryzhikov and Tolkacheva, 1981). Both genera are cosmopolitan in distribution (Khalil, 1994a). No life-cycle is known (Beveridge, 2001).

Discoveries over the course of the PBI project. Only a single species of this group—an unidentified species of *Diplophallus* from *Recurvirostra americana* Gmelin in the USA—was collected over the course of PBI expeditions. A specimen of *Diplophallus polymorphus* (Rudolphi, 1819) Fuhrmann, 1900 from *R. americana*, collected from the USA on a pre-PBI expedition, was included in the molecular phylogenetic analyses. These analyses revealed a close relationship between acoleids, progynotaeniids, and the Gyrocoeliinae (all parasitic in Charadriiformes). However, our results indicate that this clade is only distantly related to a clade of grebe cestodes (i.e., Dioicocestinae plus several amabiliids), suggesting that the suborder Acoleata is polyphyletic.

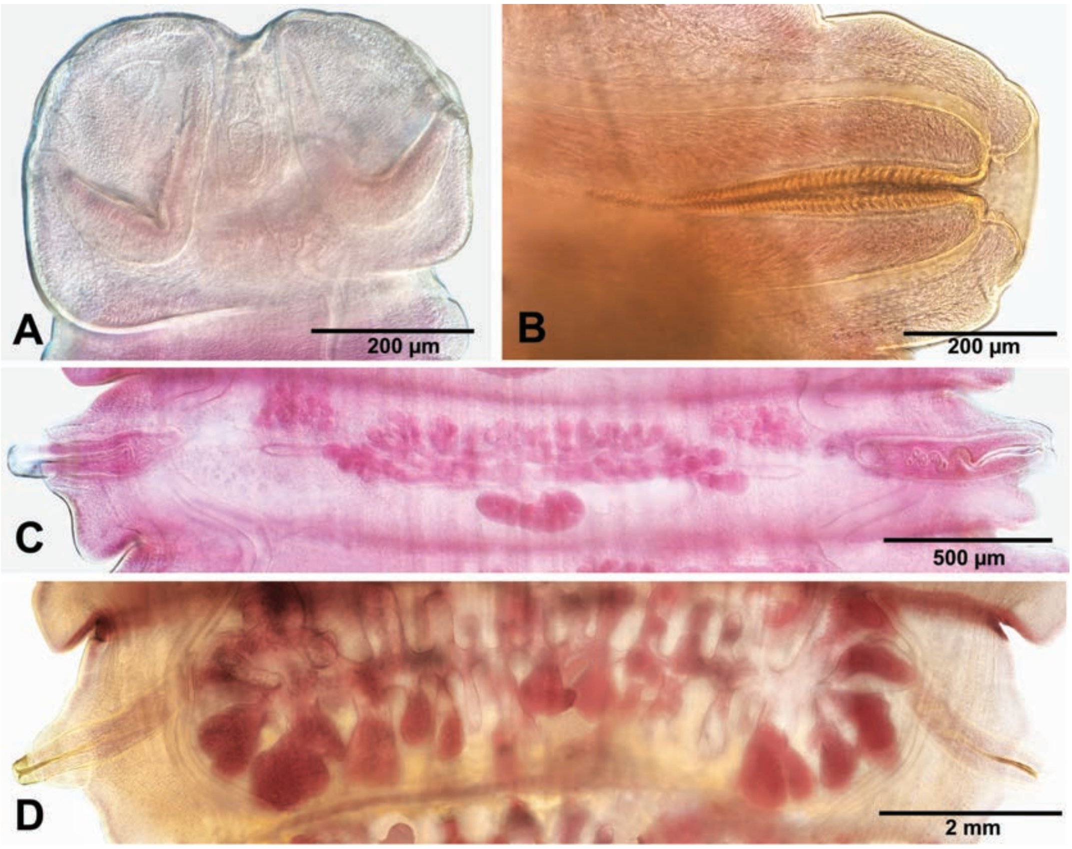


Figure 6. ACOLEIDAE: *Diplophallus andinus* from *Himantopus himantopus* from Paraguay. **(A)** Scolex. **(B)** Partly evaginated cirrus. **(C)** Mature proglottid. **(D)** Pre-gravid proglottid.

5.2. Amabiliidae Braun, 1900

This group was originally erected as a subfamily within the Taeniidae by Braun (1900). Fuhrmann (1907) subsequently raised it to the rank of family. Two subfamilies were erected by Johri (1959)—the Amabiliinae Braun, 1900 for *Amabilia* Diamare, 1893 and the Schistotaeniinae Johri, 1959 for *Schistotaenia* Cohn, 1900 and *Tatria* Kowalewski, 1904. Ryzhikov and Tolkacheva (1975) added a third subfamily, the Diporotaeniinae Ryzhikov & Tolkacheva, 1975, for *Diporotaenia* Spasskaya, Spasskii & Borgarenko, 1971. These three subfamilies were recognized by Ryzhikov and Tolkacheva (1981) but were not considered valid by Schmidt (1986) or Jones (1994a). The monophyly of the family has been called into question (Spasskii, 1992a; Gulyaev et al., 2010). In the taxonomic revision proposed by Spasskii (1992a), the family Amabiliidae included only *Amabilia*, a parasite of flamingos because he transferred all of the remaining genera, which parasitize grebes, to the family Schistotaeniidae, with the two subfamilies Schistotaeniinae and Diporotaeniinae. Spasskii (1992a) regarded the Amabiliidae and the Schistotaeniidae as sister taxa within the superfamily Amabilioidea. However, his rearrangement of the Amabiliidae has not been tested in a phylogenetic context and has not been generally accepted.

The main morphological characters of importance for identification of members of this family are the lack of a true vagina, the lack of a vaginal pore, the presence of an external seminal vesicle, and the presence of accessory or supplementary seminal ducts associated with the female reproductive organs (Fig. 7D). Copulation is traumatic and the cirrus is often destroyed in the process of copulation. A common accessory vaginal duct is not present in *Amabilia* and its presence in the Schistotaeniinae and the Diporotaeniinae (Gulyaev et al., 2010) appears to be a synapomorphy supporting the sister taxon status of these two subfamilies, as suggested by Spasskii (1992a). Amabiliids share the presence of an external seminal vesicle with the Hymenolepididae. They also typically have a scolex with a sac-like rostellar apparatus armed with a single row of rostellar hooks (Fig. 7A).

The host associations of the Amabiliidae, as adults, include aquatic birds of the order Phoenicopteriformes (*Amabilia*) and Podicipediformes (all 10 remaining amabiliid genera) (Ryzhikov and Tolkacheva, 1981; Jones, 1994a; Vasileva et al., 2003a, b; Gulyaev et al., 2010).

Life-cycles are known for seven amabiliid species parasitic in grebes. All seven have two-host life-cycles that include insect intermediate hosts of the orders Odonata, Ephemeroptera, or Hemiptera. The larval stage found in the intermediate host is a modification of the cysticercoid referred to as an "ascocercus" by some authors (e.g., Gulyaev, 1989). Chervy (2002), however, considered the "ascocercus" to be a synonym of the diplocysticercoid stage.

The geographical distribution of the family is cosmopolitan, coinciding with those of flamingos and grebes (Ryzhikov and Tolkacheva, 1981; Jones, 1994a).

Currently, the family houses 11 genera and 32 species. Major taxonomic works dealing with this family are those by Ryzhikov and Tolkacheva (1981) and Jones (1994a). Several papers present taxonomic revisions of the genera *Tatria* and *Joyeuxilepis* Spasskii, 1947 (see Gulyaev and Tolkacheva, 1987; Borgarenko and Gulyaev, 1990; Gulyaev, 1990, 1992; Vasileva et al., 2003a–d).

Discoveries over the course of the PBI project. Specimens of this family were collected in the USA from five species of grebes (Podicipedidae Bonaparte). These represented three genera and six species of cestodes. Two species from other sources (i.e., *Ryjikovilepis* sp. from *Podiceps nigricollis* Brehm, 1831 in the USA and *Schistotaenia colymba* Schell, 1955 from the same host species in the Ukraine) were incorporated into our molecular phylogenetic analyses. This allowed assessment of the position of the Schistotaeniinae and the Diporotaeniinae within the

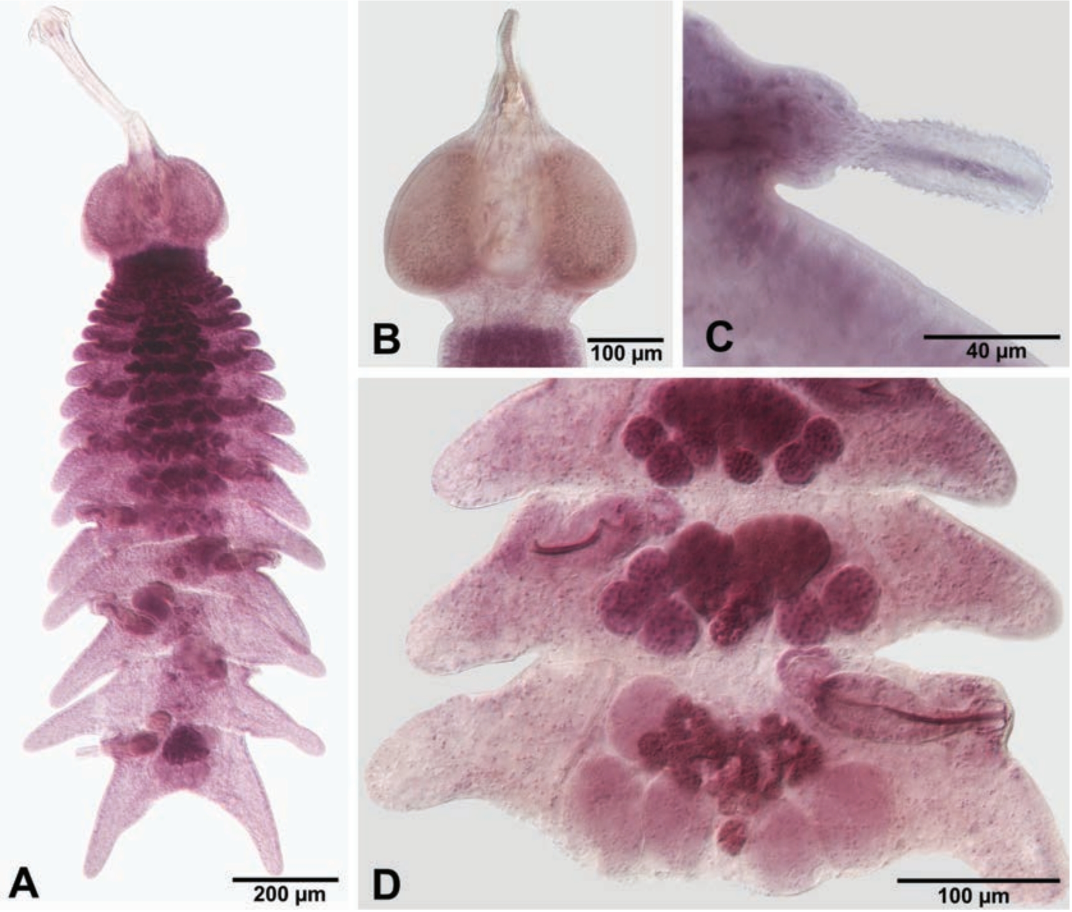


FIGURE 7. AMABILIIDAE: *Tatria biremis* from *Podiceps nigricollis* from Bulgaria. **(A)** Whole worm. **(B)** Scolex. **(C)** Evaginated cirrus. **(D)** Mature proglottids.

phylogeny of the Cyclophyllidea for the first time. In the context of our limited sampling of amabiliid genera, our results support a sister taxon relationship between these two genera. Furthermore, the sister group to the Amabiliidae appears to be the Dioicocestinae, while the Progynotaeniidae, Acoleidae, and Gyrocoeliinae grouped away from this clade.

5.3. Anoplocephalidae Blanchard, 1891

This family was erected by Blanchard (1891) (not Cholodkowsky, 1902 as erroneously reported by Spasskii [1951] and Beveridge [1994]) for cestodes lacking a rostellum, although species lacking such an organ also exist in the Davaineidae, Dilepididae, and Hymenolepididae. Because this character is obviously homoplasious, it has been recognized for some time that the family is almost certainly a polyphyletic assemblage. This view is reinforced by differences in proglottid anatomy (i.e., uterine structure) and life-cycles (Beveridge, 1994; Chervy, 2002).

Four subfamilies are currently recognized. The main morphological characters of importance for distinguishing among them are the single or double set of reproductive organs per proglottid (Fig. 8B), the structure of the uterus (with a paruterine organ in the

Thysanosomatinae), the presence of eggs in the uterine (Linstowiinae) or fibrous capsules (Inermicapsiferinae), and the unique modification of the egg envelopes into a pyriform apparatus (most Anoplocephalinae).

Anoplocephalids are primarily parasites of mammals (all 4 anoplocephalid subfamilies), birds (subset of Anoplocephalinae) and "reptiles" (subset of Linstowiinae). With the exception of the Inermicapsiferinae, which are restricted to Asia and Africa (Beveridge, 1994), the family is cosmopolitan. All known life-cycles involve two hosts. The intermediate host of the cysticercoids of anoplocephalines is usually an oribatid mite, whereas the linstowiines usual develop as precysticerci in coleopterans. Insects of the order Psocoptera (booklice or barklice) have been identified as intermediate hosts of the Thysanosomatinae (Chervy, 2002).

Major taxonomic works treating representatives of this family are those by Baer (1927), Spasskii (1951), and Beveridge (1994). Two principal systems of classification have been proposed. Spasskii (1951) utilized the suborder Anoplocephalata Skrjabin, 1933 with the families Anoplocephalidae (subfamilies Anoplocephalinae and Monieziinae Spasskii, 1951), Avitellinidae Spasskii, 1950 (subfamilies Avitellininae Gough, 1911 and Thysanosomatinae Fuhrmann, 1907), Linstowiidae Mola, 1929 (subfamilies Linstowiinae and Inermicapsiferinae), and Catenotaeniidae Spasskii, 1950. Yamaguti (1959), basing his classification on that of Fuhrmann (1907), recognized the single family, Anoplocephalidae, with five subfamilies: the Anoplocephalinae, Linstowiinae, Inermicapsiferinae, Thysanosomatinae (which included the Avitellininae), and the Rajotaeniinae Yamaguti, 1959. Beveridge (1994) recognized only the first four of the above subfamilies: the Anoplocephalinae, with a tubular uterus and a pyriform apparatus surrounding the embryo; the Linstowiinae with eggs surrounded by uterine capsules and scattered in the parenchyma; the Thysanosomatinae with paruterine organs; and the Inermicapsiferinae with fibrous egg capsules resembling those of davaineids. Beveridge (1994) also noted that the family Anoplocephalidae was clearly a non-monophyletic assemblage based not only on morphological but also on known life-cycle data, however molecular support was lacking. The Rajotaeniinae are now considered a synonym of the Skrjabinotaeniinae Genov & Tenora, 1979 within the Catenotaeniidae.

Discoveries over the course of the PBI project. Only three anoplocephalid species from birds, all in Africa, were found over the course of the PBI project expeditions. One of these has not yet been identified to species. In mammals, four species were collected from African rodents and one species from dermopteran mammals in the Philippines. Most of the newly collected material of this family came from Australian marsupials (10 cestode species); all of these specimens represent known species. In addition, a single species of the Linstowiinae, *Oochoristica fibrata* Meggitt, 1927, was collected from the colubrid snake *Boiga trigonata melanocephala* (Annandale) in the vicinity of Minab, southern Iran.

The most significant development of the PBI project has been the first molecular evidence confirming the non-monophyly of the Anoplocephalidae—more specifically, our phylogenetic results show that the Linstowiinae (represented by 3 species) and the Anoplocephalinae (represented by 9 species) are phylogenetically only distantly related (see Fig. 5). The Anoplocephalinae, as expected on the basis of larval development and the presence of true seminal vesicles, cluster with the Hymenolepididae (albeit with low nodal support), while the Linstowiinae cluster with the Paruterinidae, Metadilepididae, and Taeniidae (also with low nodal support). Although these results conform to those of previous morphological and life history work, the poorly supported nodes require resolution from mitogenome and other additional molecular data. No representatives of the Thysanosomatinae or Inermicapsiferinae were available for these analyses.

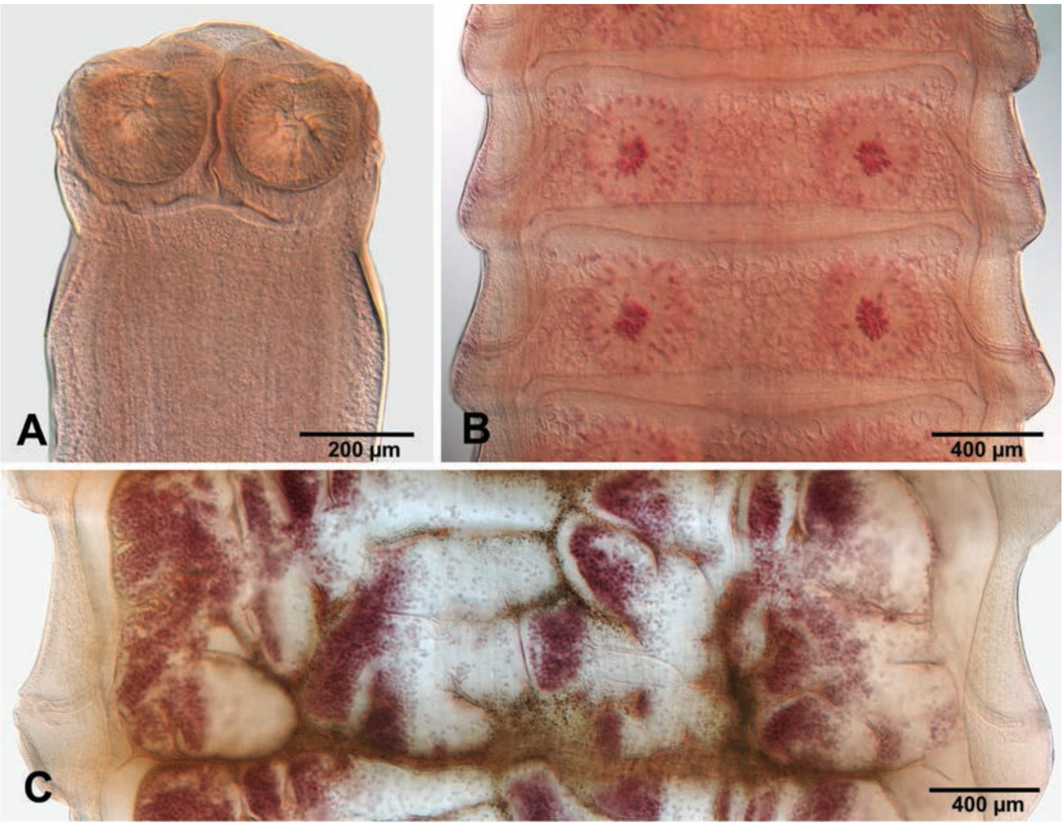


FIGURE 8. ANOPLOCEPHALIDAE: *Bulbultaenia calcaruterina* from *Pycnonotus tricolor* from Gabon. **(A)** Scolex. **(B)** Mature proglottids. **(C)** Pre-gravid proglottid.

Also resulting from the PBI project was the molecular phylogenetic study of Australian anoplocephalines by Hardman et al. (2012), which provided a firm molecular basis for a slightly revised generic arrangement of the subfamily. *Progamotaenia* Nybelin, 1917 was shown to be polyphyletic, resulting in the resurrection of *Wallabicestus* Schmidt, 1975; the other genera into which species of *Progamotaenia* had variously been placed (i.e., *Hepatotaenia* Nybelin, 1917, *Fuhrmannodes* Strand, 1942, and *Adelataenia* Schmidt, 1986) were not supported and are retained as synonyms. This study also showed that the single species in each genus occurring in wombats (Diprotodontia: Vombatidae) (i.e., *Phascolotaenia* Beveridge, 1976 and *Paramoniezia* Maplestone & Southwell, 1923) comprised a monophyletic group, prompting a review of *Paramoniezia* in general. In this review, Beveridge (2014) erected the new genus *Phascolocestus* Beveridge, 2014 for the only species formerly assigned to *Paramoniezia* found in wombats. The remaining valid species, *Paramoniezia phacochoeri* Baylis, 1927, found in African warthogs, was transferred to *Moniezia* Blanchard, 1891.

Haukisalmi and colleagues contributed substantially to the generic diversity of the anoplocephalids over the course of the PBI. In 2013, Haukisalmi erected two new genera (*Afrojoyeuxia* Haukisalmi, 2013 and *Hunkeleriella* Haukisalmi, 2013) for cestodes parasitizing African rodents and proposed two new combinations. Furthermore, he led a revision of the rather diverse and heterogeneous genus *Paranoplocephala* Lühe, 1910 from rodents based on morphological and molecular analyses (Haukisalmi et al., 2014). In that work, 12 additional new genera (i.e., *Arctocestus*, *Beringitaenia*, *Chionocestus*, *Cookiella*, *Douthittia*, *Eurotaenia*, *Gulyaevia*, *Lemminia*, *Microticola*, *Rauschoides*, *Rodentocestus*, and *Tenoraia*, all with authorship by Haukisalmi, Hardman, Hoberg & Henttonen, 2014) were erected and 23 new combinations were proposed. In addition, the new species *Beringitaenia nanushukensis* Haukisalmi, Hardman, Hoberg & Henttonen, 2014 from the singing vole, *Microtus miurus* Osgood was described. Several additional lineages, likely representing yet other independent species and genera, were identified, but not formally described because of the lack of good-quality specimens and/or absence of reliable morphological differences. Most recently, Haukisalmi et al. (2016) presented the results of phylogenetic and phygeographic analyses focused on members of the genus *Anoplocephaloides* from lemmings in the Holarctic.

At present, about 480 species in 81 genera are known in the family (Table 2); these consist of 258 species in 59 genera of Anoplocephalinae, 171 species in 13 genera of Linstowiinae, 27 species in four genera of Inermicapsiferinae, and 21 species in five genera of Thysanosomatinae.

5.4. Catenotaeniidae Spasskii, 1950

Spasskii (1950) erected the Catenotaeniidae for two genera previously assigned to the Anoplocephalidae (i.e., *Catenotaenia* Janicki, 1904 and *Skrjabinotaenia* Akhumyan, 1946) and confirmed this action in the first monographic treatment of the family (Spasskii, 1951). Subsequent studies added further species and genera. Currently, the family is subdivided into two subfamilies, the Catenotaeniinae Spasskii, 1950, characterized by two pairs of lateral osmoregulatory canals and testes situated posteriorly to the ovary, and the Skrjabinotaeniinae Genov & Tenora, 1979, characterized by numerous osmoregulatory canals and testes surrounding, at least posteriorly, the ovary (Genov and Tenora, 1979). Quentin (1994) recognized four genera in the Catenotaeniinae and two genera in the Skrjabinotaeniinae and provided emended diagnoses for each. Haukisalmi et al. (2010a) added one further genus to the former subfamily. Currently, the family consists of six genera and 36 species, 20 of which are members of the Catenotaeniinae (see Schmidt, 1986; Haukisalmi and Tenora, 1993; Haukisalmi et al., 2010a; Jrijer and Neifar, 2014).

Morphologically, catenotaeniids are diagnosed by their possession of a uterus consisting of a longitudinal stem with lateral branches (Fig. 9C), similar to that seen in the Taeniidae. Their scolex bears only suckers (Fig. 9A)—a rostellar apparatus is lacking, but adults occasionally have a vestigial "apical sucker" that appears to be a remnant of the apical organ of the metacestode.

Catenotaeniids are parasites of rodents, and specifically the families Sciuridae, Muridae, Heteromyidae Gray, Geomyidae Bonaparte, Dipodidae Fischer de Waldheim, and Caviidae Fischer de Waldheim. The geographic distribution of the family includes all continents except Australia (Quentin, 1994). Species diversity in the Catenotaeniinae peaks in cricetid rodents in the Holarctic region; species diversity in the Skrjabinotaeniinae peaks in murid rodents in Africa. The only South American species, *Quentinia mesovitellinica* (Rego, 1967) Quentin, 1994, from caviids, is morphologically divergent and its taxonomic position should be reconsidered.

The life-cycle of only one species, *Catenotaenia pusilla* (Goeze, 1782) Janicki, 1904, a common parasite of the house mouse, was described by Joyeux and Baer (1945). Tyroglyphid mites were reported to serve as intermediate hosts for its metacestode, which is a merocercoid that bears a large apical organ ("apical sucker") but no true suckers. The final stage of scolex development, which involves degeneration of the apical organ and differentiation of four suckers, is completed in the mouse definitive host.

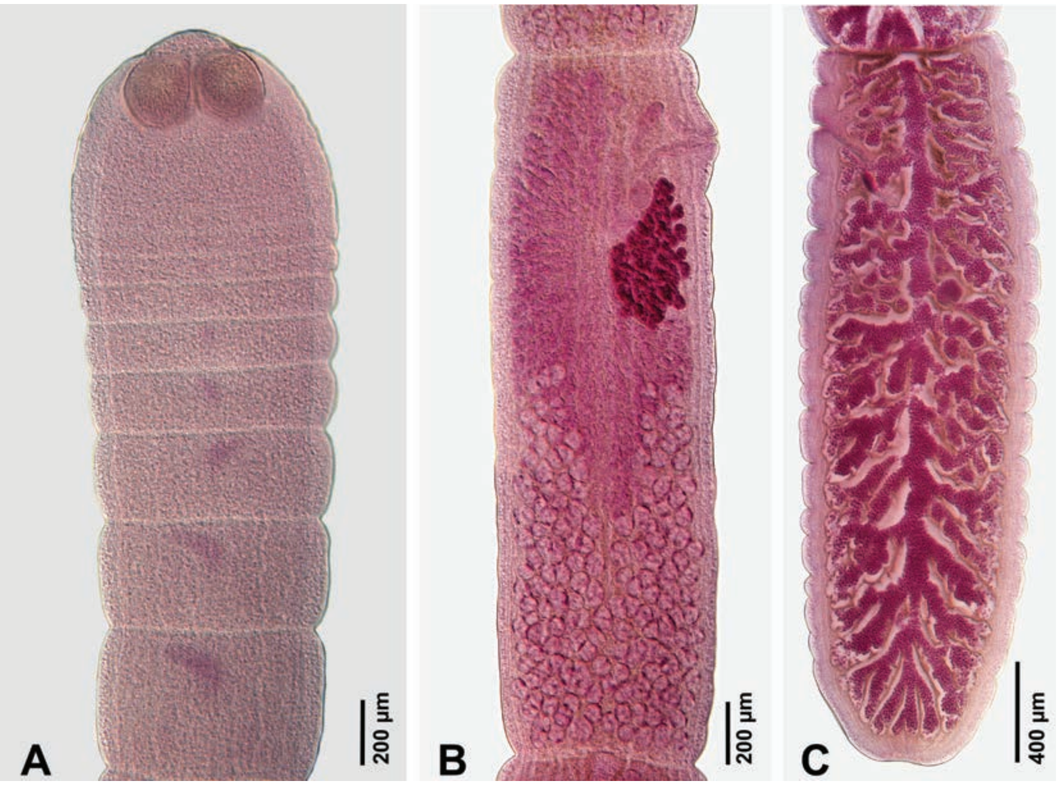


FIGURE 9. CATENOTAENIIDAE: *Catenotaenia indica* from *Tatera indica* from Iran. **(A)** Scolex. **(B)** Mature proglottid. **(C)** Gravid proglottid with branched uterus.

Discoveries over the course of the PBI project. One species of catenotaeniid (i.e., *Catenotaenia indica* Parihar & Nama, 1977) was collected from *Tatera indica* (Hardwicke) (Muridae: Gerbillinae) in Iran. Additional members of this family may be present in our unsorted samples of cestodes from rodents. A total of three species was included in our molecular phylogenetic analyses. The resulting tree supports the monophyly of the family as the sister of a clade composed of the Taeniidae, Paruterinidae, Metadilepididae, and Linstowiidae (albeit with low nodal support). However, these results require confirmation given the limited nature of our taxon sampling across the family.

5.5. Davaineidae Braun, 1900

This taxon was originally erected by Braun (1900) as a subfamily of the Taeniidae and then elevated to family status by Fuhrmann (1907) for those cyclophyllideans with a rostellum bearing numerous small hammer-shaped rostellar hooks, armed or unarmed suckers, and single or double genital systems per proglottid. Fuhrmann (1907) subdivided the family into three subfamilies: the Ophryocotylinae Fuhrmann, 1907 (for cestodes with a sac-like uterus), the Davaineinae Braun, 1900 (for cestodes with a uterus that, with maturity, breaks down into parenchymatous capsules, each containing 1 or several eggs), and the Idiogeninae Fuhrmann, 1907 (for cestodes with a uterus in the form of a paruterine organ). Additional key morphological features for identification of the Davaineidae include the number of rostellar hook rows, the duplication (or not) of genitalia, the position of the genital pores (unilateral or alternating), the number and position of the testes, the number of osmoregulatory canals, and the structure of gravid proglottids (Jones and Bray, 1994). Davaineids have a unique rostellar apparatus (Fig. 10A) consisting of a discoidal rostellum and a protrusible thick ring encircling the apical part of the scolex immediately posterior to the rostellum, termed the "pseudoproboscis" (see Stoitsova et al., 2001). Scale-like spines (considered to be spinitriches by Chervy et al. [2009]) on the pseudoproboscis (Fig. 10B) may be a synapomorphy for the family (Bâ et al., 1995).

Davaineids parasitize most bird orders (especially terrestrial birds) and many mammals, including marsupials, rodents, bats, primates, and others (Jones and Bray, 1994). Life-cycles are known for approximately 30 species (Artyukh, 1966; O'Callaghan et al., 2003). Davaineids have a single intermediate host that is typically an annelid, gastropod, or insect. Ants have been identified as intermediate hosts of davaineids parasitizing poultry. The larval stage is a cysticercoid (Chervy, 2002). The geographic distribution of the family is cosmopolitan; they are found mostly in terrestrial habitats, rarely in freshwater, or marine environments (Artyukh, 1966; Jones and Bray, 1994).

Major taxonomic works treating this family were published by Artyukh (1966), Schmidt (1986), Jones and Bray (1994), and Movsesyan (2003a, b). Subdivision of the family in two subfamilies is currently widely accepted; these are the Davaineinae (without a paruterine organ) and the Idiogeninae (with a paruterine organ). Some (e.g., Schmidt, 1986), but not all (e.g., Jones and Bray, 1994) authors also recognize the Ophryocotylinae, which differ from the Davaineinae in the presence of a persistent uterus, rather than a uterus that is replaced by a paruterine organ. Alternative classification schemes have been proposed by Russian authors. Artyukh (1966) recognized the Davaineidae and the Idiogenidae as distinct families; the former being subdivided into the Davaineinae and the Ophryocotylinae. Movsesyan (2003a, b) recognized three distinct families, all in the suborder Davaineata Skrjabin, 1940: the Davaineidae, with the subfamilies Davaineinae (for cestodes bearing a single set of genital organs per proglottid) and the Cotugniinae Movsesyan, 1969 (for cestodes with double sets of genital organs per proglottid), the Ophryocotylidae (using a much wider concept than previous authors), and the Idiogenidae. At present, 37 genera and 450 species are recognized in the family (Jones and Bray, 1994; Movsesyan, 2003a, b) (Table 1).

Jones and Bray (1994) considered the family, in its present form, to be polyphyletic. This was not supported by the work of Hoberg et al. (1999) who reached the opposite conclusion and favored its monophyly.

Discoveries over the course of the PBI. Davaineids were collected from 16 bird families from 12 countries, on all continents. They were notably absent from our Ethiopian and Chilean samples. The Pycnonotidae were found to host the highest diversity of davaineids, but davaineids were also well represented in the Piciformes (Picidae and Rhamphastidae Vigors) and Columbiformes. No members of the Idiogeninae were collected. Nine of the bird species hosting davaineids represent new host records for cestodes overall.

Our new collections included seven records of davaineids from mammals; six of these were from the Muridae and one was from the sciurid *Funisciurus pyrrhopus* (Cuvier) (a new host for cestodes) in Uganda. In total, over 30 species of at least four genera were collected. Our preliminary taxonomic work indicates the presence of at least two new species of *Raillietina*, one in birds and one in mammals.

Thirty-nine davaineid specimens were included in PBI project phylogenetic analyses; our preliminary results highly support the monophyly of the family to the exclusion of

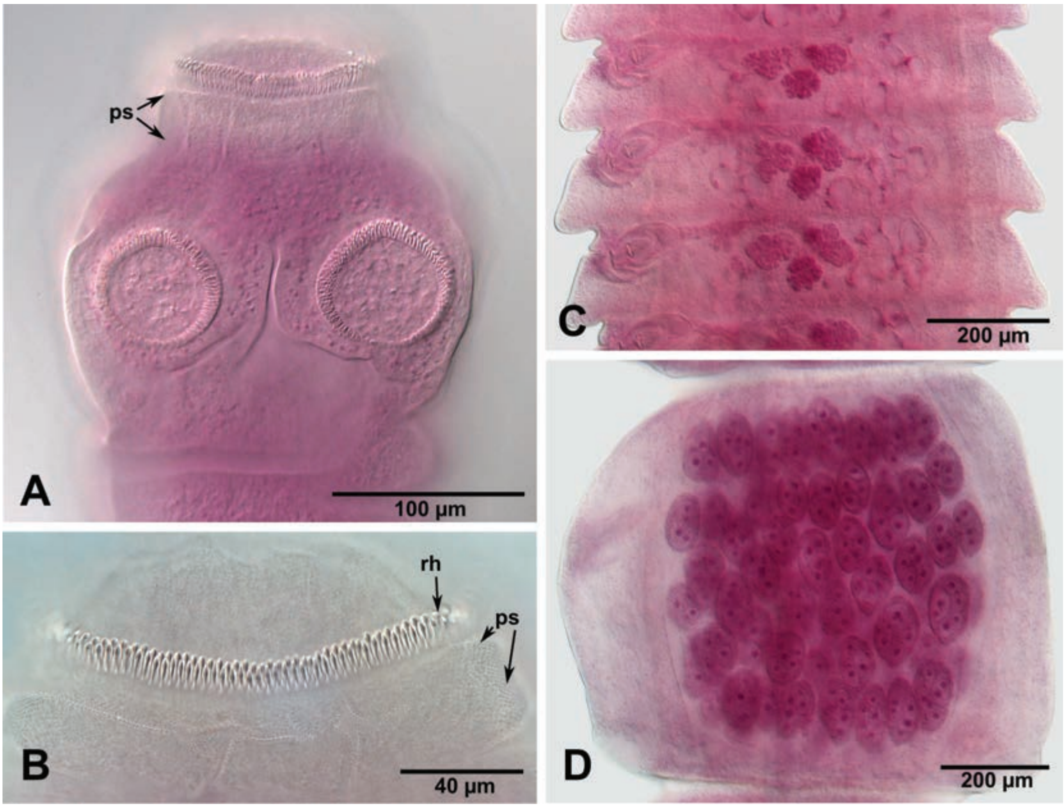


FIGURE 10. DAVAINEIDAE: *Raillietina* from *Colius striatus* from Gabon. **(A)** Scolex. **(B)** Armature of rostellum and pseudoproboscis. **(C)** Mature proglottids. **(D)** Gravid proglottid with parenchymatous multiovular capsules. *Abbreviations:* ps, pseudoproboscis; rh, rostellar hooks.

Ophryocotyle Friis, 1870 (result not shown in Fig. 5). However nodal support for the entire group (i.e., including *Ophryocotyle*) is currently weak (Fig. 5). Our results suggest the Davaineidae are a relatively early diverging group within the Cyclophyllidea, and are most closely related to the Catenotaeniidae, Linstowiinae, and a group consisting of the Paruterinidae, Metadilepididae, and Taeniidae (Fig. 5). However nodal support for this grouping is also weak.

5.6. Dilepididae Fuhrmann, 1907

This family was erected (under the incorrect spelling "Dilepinidae") by Fuhrmann (1907), who, nonetheless, must be credited as the authority of this taxon (ICZN, 1999, Article 19.2). Railliet and Henry (1909) used the correct spelling and thus these authors have since, albeit erroneously, been used as the authority of the family name, including by, for example, Schmidt (1986) and Khalil et al. (1994), but not, for example, by Matevosyan (1963) or Spasskaya and Spasskii (1977, 1978). This family is widely accepted as one of the most speciose cyclophyllidean families but its membership and classification have varied considerably throughout the last century (e.g., Ransom, 1909; Fuhrmann, 1932; Freeman, 1973). The most recent overview of the group was by Bona (1994), whose definition of the family (i.e., as excluding the Dipylidiinae, Paruterininae, and Metadilepididae) has been widely accepted. The exceptions are a number of genera with a three-host life-cycle that parasitize piscivorous birds and bear a unique rostellar configuration; these taxa are now considered members of the family Gryporhynchidae (see section 5.9.).

The main morphological characters of importance for identification of the Dilepididae include the structure of the (usually) armed rostellum (Fig. 11A), rostellar hooks (Fig. 11B), post-ovarian position of the compact vitellarium, bilobed ovary, single set of reproductive organs per proglottid, lack of seminal vesicles, numerous testes, and ventral position of the uterus. It should be noted, however, that most of these features are found in many states within the family and thus the Dilepididae are presently defined by a set of semi-exclusive characters rather than by one or more unambiguous morphological synapomorphies.

The Dilepididae are found in most orders of birds; they are particularly diverse in the Passeriformes, and to a lesser extent, in the Ciconiiformes and the Charadriiformes. They are also known from various mammal groups, primarily the Soricomorpha and Rodentia, but also marsupials (Bona, 1994). "Reptiles" are no longer considered among their potential hosts, given the single species reported from Australian turtles (Pichelin et al., 1998) now belongs to the Gryporhynchidae.

Life-cycles are known for approximately 25 species (Matevosyan, 1963; Spasskaya and Spasskii, 1977, 1978). Dilepidids use only one intermediate host, which is generally an arthropod, but annelids or molluscs are also known to serve as intermediate hosts. The larval stage is a cysticercoid (existing in several variants, but generally a monocysticercoid, see Chervy, 2002). Their geographic distribution is cosmopolitan, including Antarctica (Bona, 1994).

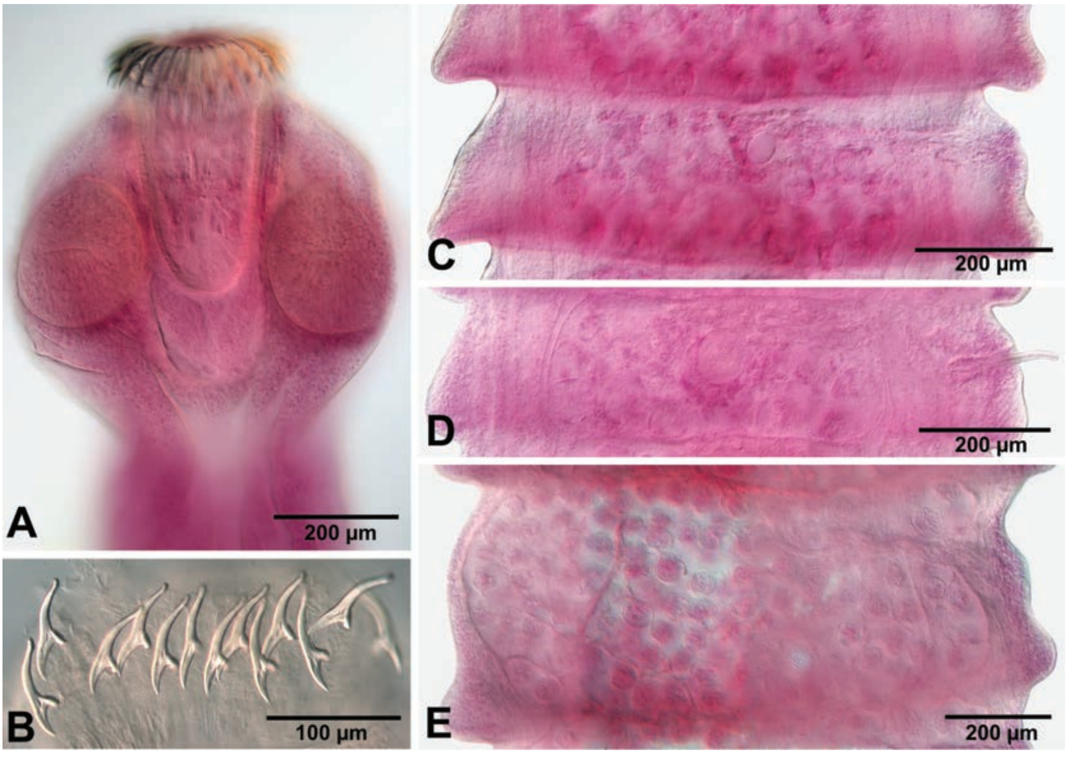


FIGURE 11. DILEPIDIDAE: *Dilepis undula* from *Turdus mupinensis* from China. **(A)** Scolex. **(B)** Rostellar hooks. **(C, D)** Mature proglottids. **(E)** Gravid proglottid.

Major taxonomic works dealing with representatives of this family are those by Matevosyan (1963), Spasskaya and Spasskii (1977, 1978), and Bona (1994). Although the family has historically been divided into a number of subfamilies, these are no longer recognized. The family currently includes 90 valid genera (Table 1) and about 750 species.

Discoveries over the course of the PBI. Specimens of this family were collected from all countries visited, from a total of 44 bird families. This material yielded approximately 107 species and at least 36 genera. In all countries except Ethiopia, dilepidids represented over 20% of the avian cyclophyllidean fauna collected. The Dilepididae were particularly well represented in the Turdidae and Hirundinidae. One new genus (*Gibsonilepis* Dimitrova, Mariaux & Georgiev, 2013) was erected and one new species (*Pseudangularia gonzalezi* Dimitrova, Mariaux & Georgiev, 2013) was described (Dimitrova et al., 2013). The descriptions of an additional two new genera and species from Chile as well as one new species from the Philippines are in preparation. An additional two new genera and approximately 18 new species are represented among the material that has been sorted, but not formally described. In mammals, four known species of *Monocercus* Villot, 1882 were collected from North American shrews of the genus *Sorex*, and one new species was collected from the eastern mole, *Scalopus aquaticus* (L.) (Talpidae).

Although Bona (1994) suggested that the family was not monophyletic, even once genera belonging to the Gryporhynchidae were removed, the results of our preliminary molecular analyses, which included 73 dilepidid specimens, tend to support the monophyly of the family. The highly nested position of the Dilepididae within the order Cyclophyllidea and its position as sister taxon to a clade composed of the Progynotaeniidae, Acoleidae, Gyrocoeliinae, and Hymenolepididae + Anoplocephalinae is, however, not strongly supported (Fig. 5). The results of our molecular analyses confirm the Gryporhynchidae as a taxon distinct from the Dilepididae.

5.7. Dioicocestidae Southwell, 1930

Southwell (1930) proposed the family Dioicocestidae (erroneously spelled Dioecocestidae) for the single genus *Dioicocestus* Fuhrmann, 1900 (erroneously spelled *Dioecocestus*) on the basis of the separation of sexes (i.e., some individuals have proglottids with only male genital organs, and others have proglottids with only female organs). The spelling *Dioecocestus* [sic] is recognized here as an unjustified emendation of this generic name (ICZN, 1999, Article 33.2.3) and, therefore, the spelling Dioicocestidae is adopted as a derivate of the generic name originally proposed by Fuhrmann (1900) and as used in the only monograph on the family (Ryzhikov and Tolkacheva, 1981).

Fuhrmann (1932) rejected the validity of the Dioicocestidae, transferring all of its species to the Acoleidae. In a subsequent paper (Fuhrmann, 1936), he accepted the group as a subfamily within the acoleids. Burt (1939) recognized the family and added three additional genera. Yamaguti (1959) divided the Dioicocestidae into two subfamilies: the Dioicocestinae (for *Dioicocestus*) with female individuals without male copulatory apparatus and possessing a transverse tubular uterus, and male individuals with two reproductive systems per proglottid; and the Gyrocoeliinae Yamaguti, 1959 (for *Gyrocoelia* Fuhrmann, 1899, *Shipleya* Fuhrmann, 1908, and *Infula* Burt, 1939) with female individuals possessing vestigial (non-functional) male copulatory apparatus and a ring-shaped uterus, and male individuals with one set of reproductive systems per proglottid. Ryzhikov and Tolkacheva (1981) elevated both subfamilies to family level, expanding existing recognized morphological differences between them to include the fact that, while the dioicocestids are specific to grebes and ibises, the gyrocoeliids parasitize only charadriiform hosts. Schmidt (1986) recognized the single family Dioicocestidae (including gyrocoeliids) without subfamilies. In contrast, Jones (1994b) recognized the two subfamilies (Dioicocestinae with 1 genus, and Gyrocoeliinae with 4 genera) and followed the generic assignments of Yamaguti (1959), placing *Echinoshipleya* Tolkacheva, 1979 in the Gyrocoeliinae. The main characteristics used for distinguishing among genera are the presence (Fig. 12A) or absence of a rostellum, and the presence and arrangement of rostellar hooks (e.g., in festoons [Fig. 12A] or many rows). In total, 21 species in five genera are currently considered members of the family (Ryzhikov and Tolkacheva, 1981; Schmidt, 1986).

Host associations of the family include grebes (Podicipedidae) and ibises (Threskiornithidae Poche) for the Dioicocestinae, and charadriiform birds for *Gyrocoelia*, *Shipleya*, *Infula*, and *Echinoshipleya* (Ryzhikov and Tolkacheva, 1981; Jones, 1994b). The geographic distribution is cosmopolitan (Jones, 1994b). No life-cycle is known for any member of the family.

Discoveries over the course of the PBI. Specimens of this family were collected from Brazil, Iran, and the USA, in numerous host species of the Charadriidae and one species of the Podicipedidae. These consisted of two species of *Gyrocoelia* and one species of *Dioicocestus*, none of which were new.

Dioicocestids were included in a molecular phylogenetic study for the first time. Five of the eight specimens analyzed were collected during PBI project expeditions. Our results (Fig. 5) do not support the monophyly of the family, instead they suggest that *Dioicocestus* is closely related to amabiliid genera from grebes and that the gyrocoeliines belong to a clade that also includes the acoleids and progynotaeniids (Fig. 5). These relationships are in agreement with the taxonomic concept of Ryzhikov and Tolkacheva (1981) who recognized the Dioicocestidae and Gyrocoeliidae as distinct families.

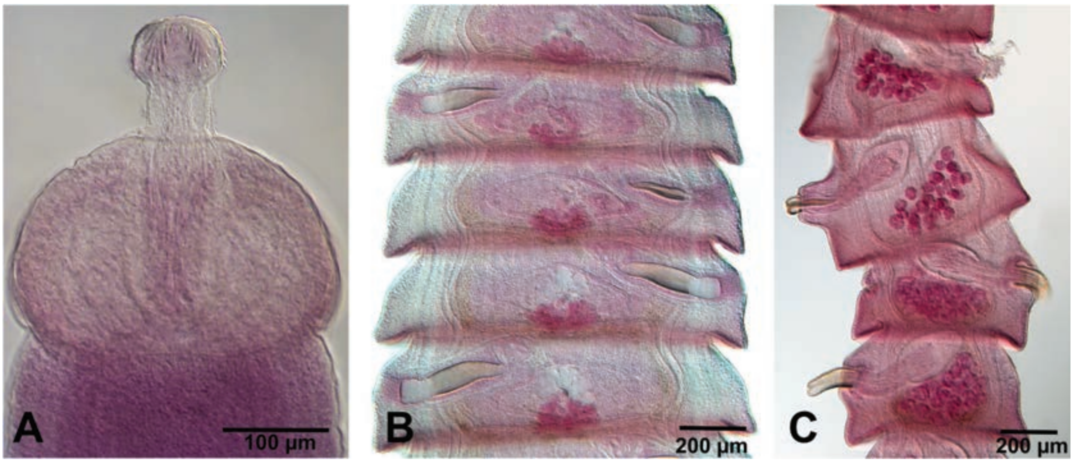


FIGURE 12. DIOICOCESTIDAE: *Gyrocoelia perversa* from *Charadrius alexandrinus* from Iran. **(A)** Scolex. **(B)** Mature proglottids of female strobila. **(C)** Mature proglottids of male strobila.

5.8. Dipylidiidae Railliet, 1896

The taxonomic history of the Dipylidiidae is among the most complex of all cyclophyllidean families. The name was first proposed by Railliet (1896) (and not Stiles [1896] as is frequently reported) as a subfamily of the Taeniidae (as Taeniadae). Although periodically considered as a family (e.g., Matevosyan, 1963; Wardle et al., 1974), its subfamilial status in the Dilepididae was adopted by the majority of earlier authors, including Schmidt (1986). However, Khalil et al. (1994) subdivided the Dilepididae *sensu lato* into several families, including the Dipylidiidae, which were thus treated in that same volume as a separate family by Jones (1994c). The subsequent morphology-based phylogenetic analysis of Hoberg et al. (1999) supported the status of the group as an independent family.

The main character differentiating the Dipylidiidae from the Dilepididae, and other cyclophyllideans, is the replacement of the uterus by mono- or multi-ovular egg capsules. Other characters of importance are the armature of the rostellum, which consists of several (3 or more) rows of hooks (Fig. 13A), the lack of a rostellar pouch, and the presence of a double set of genital organs in each proglottid (Fig. 13B). However, Hoberg et al. (1999) noted the homoplasious nature of all of these characters.

Membership in, and thus the concept of, the family have varied substantially over time. This is largely due to its imprecise original definition, with up to 20 genera parasitic in mammals and birds having been assigned to the group. Taxonomic treatments over time have progressively led to the assignment of most of these genera to other families, keeping only eight (Meggitt, 1924), five (Matevosyan, 1963), and only three (Witenberg, 1932) genera in the Dipylidiidae. Jones (1994c) followed the latter scheme, recognizing only *Dipylidium* Leuckart, 1863, *Diplopylidium* Beddard, 1913, and *Joyeuxiella* Fuhrmann, 1935 (reviewed by Jones, 1983) as valid members of the family. Collectively these three genera are considered to house a total of 15 valid species today.

The definitive hosts of the Dipylidiidae consist of carnivorous mammals (Jones, 1994c), mostly Canidae and Felidae. The life-cycle appears to include two hosts, with an insect, "reptile," or small mammal serving as the intermediate host. However, vertebrate paratenic hosts are common. *Dipylidium caninum* (L.), a common species in domestic dogs, uses fleas (Siphonaptera) and lice (Phthiraptera) as intermediate hosts. A list of both definitive

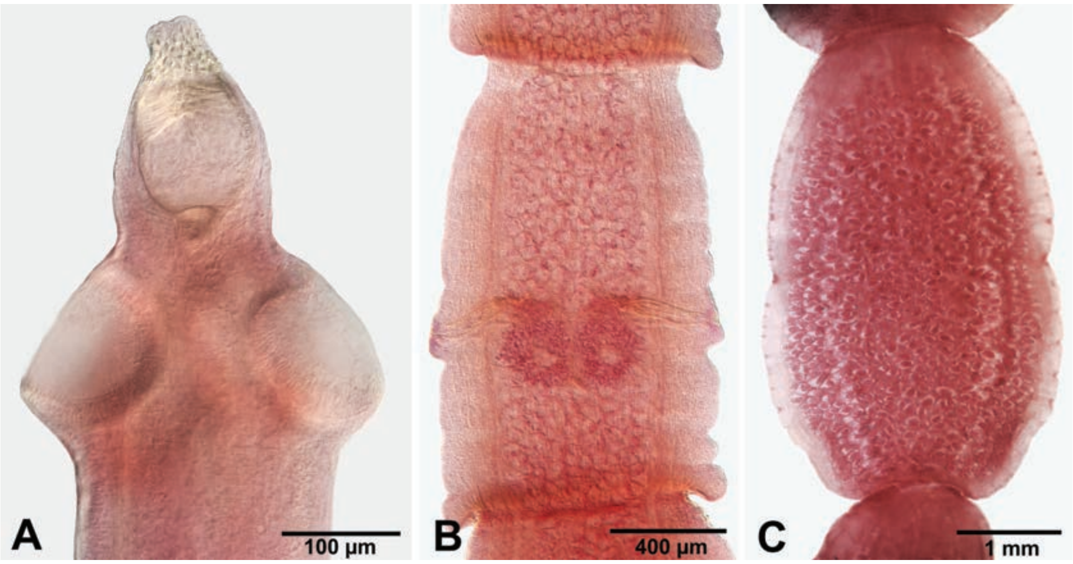


Figure 13. DIPYLIDIIDAE: *Dipylidium caninum* from *Canis familiaris* from Bulgaria. **(A)** Scolex. **(B)** Mature proglottid. **(C)** Gravid proglottid with multiovular egg capsules.

and intermediate hosts can be found in Matevosyan (1963). The larval stage is a modified cysticercus termed a cryptocysticercus (Chervy, 2002). Dipylidiids have a cosmopolitan distribution (Jones, 1994c).

The phylogenetic position of the family has been studied by Hoberg et al. (1999). Their morphological analysis placed the group as the sister to a large clade composed of seven families, including the Davaineidae, but clearly showed the Dipylidiidae to represent a lineage independent from the latter family.

Discoveries over the course of the PBI. Although no members of this family were collected during any of the PBI field trips, a specimen that had been obtained from a previous collecting trip in Werribee, Victoria, Australia was included in our molecular phylogenetic analyses. That specimen grouped as the sister taxon to a large clade including all the families with a sac-like rostellar apparatus (Fig. 5), albeit with low nodal support.

5.9. Gryporhynchidae Spasskii & Spasskaya, 1973

This taxon was originally erected by Spasskii and Spasskaya (1973) as a subfamily within the Dilepididae, primarily on the basis of the three-host life-cycle. In 1980, these authors elevated it to the family level. Its genera were treated as members of the Dilepididae (see Bona, 1994) in the most recent comprehensive treatment of the order by Khalil et al. (1994). However, the phylogenetic analyses of the Cyclophyllidea of Mariaux (1998) and Hoberg et al. (1999) supported its validity as an independent family.

Although similar to dilepidids in overall morphology, gryporhynchids can be distinguished from them in that their rostellar apparatus bears a rostellar sheath with strong muscular walls consisting of longitudinal and oblique fibers. As a consequence, when the rostellum is retracted, the tips of the rostellar hooks are directed anteriorly (Fig. 14A). Furthermore, the hooks of gryporhynchids are typically robust and large and are arranged in two concentric circles (Bona, 1975, 1994).

Definitive hosts of gryporhynchids are fish-eating birds, mostly belonging to the Ciconiiformes, although they are also found in other aquatic bird orders including the Pelecaniformes, Anseriformes, Gruiformes (Rallidae Vigors), and Accipitriformes (Bona, 1975, 1994). One species has been reported to use Australian turtles as definitive hosts (Pichelin et al., 1998).

The gryporhynchids have a three-host life-cycle which, as noted earlier, is a key biological character differentiating them from the dilepidids with their two-host life-cycles. Only a few life-cycles are completely known. It appears that crustaceans (copepods, experimentally) serve as first intermediate hosts and freshwater (rarely brackish) fish, and especially the Perciformes, serve as second intermediate hosts (reviewed by Scholz et al. [2004]). The larval stage found in the second intermediate host is a merocercoid (Chervy, 2002). The family is cosmopolitan in distribution with the majority of known species occurring in the Holarctic region (Bona, 1975, 1994).

Major taxonomic works dealing with representatives of this family are those by Bona (1975, 1994) and Scholz et al. (2004). Presently, 16 genera and approximately 76 species are recognized (Matevosyan, 1963; Bona, 1975, 1994; Schmidt, 1986; Pichelin et al., 1998; Scholz et al., 2004; Kornyushin and Greben, 2014).

Discoveries over the course of the PBI project. Specimens of this family were collected from Gabon (1 species), Brazil (4 species), Chile (1 species), and the USA (6 species). Brazil as "an unending source" of cestodes of ciconiiforms was already noted by Bona (1975; p. 11) as a major center of diversification for the group. The majority of gryporhynchid

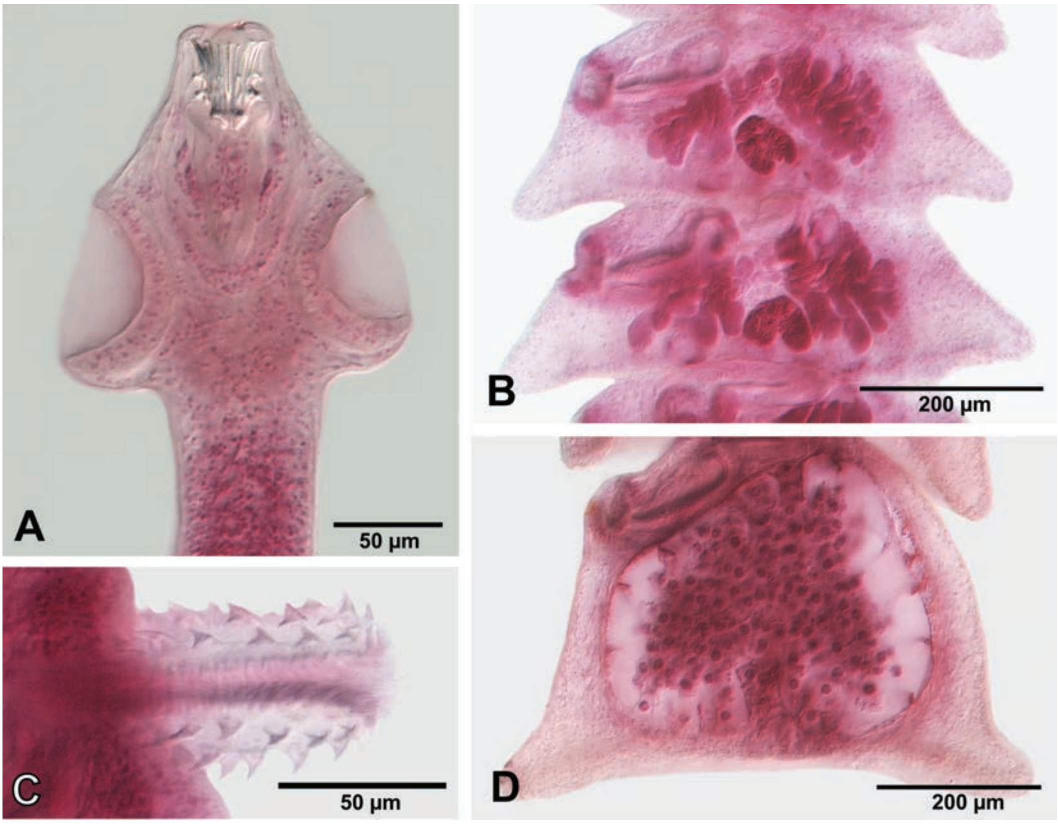


FIGURE 14. GRYPORHYNCHIDAE: *Parvitaenia macropeos* from *Nycticorax nycticorax* from Bulgaria. **(A)** Scolex. **(B)** Mature proglottids. **(C)** Evaginated cirrus. **(D)** Pre-gravid proglottid.

specimens collected over the course of the PBI project were from the Ardeidae (herons) and the Threskiornithidae (ibises and spoonbills)—both of which were already known to host a diversity of gryporhynchids. Our Gabonese sample from *Ixobrychus sturmii* (Wagler) appears to be a new species of *Valipora* Linton, 1927. Other records of this genus from Africa are limited (Bona, 1975); the closest in terms of greographic proximity are those of Mettrick (1967) in Zambia and Zimbabwe, and Mariaux (1994) in the Ivory Coast. Other preliminary identifications are of a species of *Dendrouterina* Fuhrmann, 1912 in Brazil and of *Paradilepis* Hsü, 1935 in Chile. The latter is a new locality record for this genus.

In total, 14 specimens of this family were included in our phylogenetic analyses. The monophyly of the family Gryporhynchidae is well supported (Fig. 5), however, their relationships within the Cyclophyllidea remain uncertain. The family appears to represent the sister-group of a large clade consisting of the Dilepididae, Hymenolepididae, Anoplocephalinae, and a well-supported subclade consisting of the Progynotaeniidae + Acoleidae + Gyrocoeliinae.

5.10. Hymenolepididae Perrier, 1897

This family was erected as the tribe Hymenolepinae within the Taeniidae by Perrier (1897) and elevated to family rank as the Hymenolepidae by Ariola (1899). Fuhrmann (1907) provided the first detailed diagnosis of the family Hymenolepinidae (later emended to Hymenolepididae by Railliet and Henry [1909]), including four genera within the family. Fuhrmann (1932) subdivided the family into the two subfamilies, Hymenolepidinae Perrier, 1897 and Fimbriariinae Wolffhügel, 1898. Joyeux and Baer (1936) and later Skrjabin and Matevosyan (1945) recognized four subfamilies on the basis of the structure of the uterus and the number of the sets of genital organs per proglottid. The latter classification was essentially the one followed by Wardle and McLeod (1952) and Yamaguti (1959).

Spasskii (1954) and Spasskii and Spasskaya (1954) proposed significant changes to the systematics of hymenolepidids at the generic level, employing many characters that had not previously been applied, such as peculiarities of life-cycles and associations with specific host groups. Over the next 40 years, Spasskii and his colleagues modified the classification of hymenolepidids further following that same approach (e.g., Spasskii, 1963; Spasskaya, 1966; Kornyushin, 1983, 1995; Bondarenko and Kontrimavichus, 2004).

Skrjabin (1940) erected the suborder Hymenolepidata Skrjabin, 1940, to which he attributed four families, one of which was the Hymenolepididae. However, Spasskii (1992b, 2003a–c, 2004) proposed a new higher-level classification dividing the suborder Hymenolepidata into three superfamilies in which he collectively recognized more than 25 family-group taxa. This classification resulted in an inefficient dismantling of the Hymenolepididae and although it has not been generally accepted, subsequently some authors have followed this scheme in part (e.g., Bondarenko and Kontrimavichus, 2006).

In the latest taxonomic revision of the family, Czapliński and Vaucher (1994) recognized four subfamilies within the Hymenolepididae of birds. In contrast, no subfamilies have been recognized within the hymenolepidids of mammals. Czapliński and Vaucher (1994) also proposed numerous new generic synonymies, which included the suppression of a number of well-defined genera, especially from birds. Their concepts of avian hymenolepidid genera were based on few morphological criteria and ignored numerous distinguishing morphological and life-cycle characteristics. This approach was in stark contrast to the criteria they used to define hymenolepid genera from mammals employed in the same publication.

The validity of the family Hymenolepididae is now generally accepted. However, despite numerous attempts to develop an effective classification at the subfamily level, a generally accepted unified scheme has yet to emerge. In addition, until now, a comprehensive phylogenetic analysis of the family, based on either morphological or molecular data, has not been conducted and, as a consequence, the interrelationships among the genera remain unclear.

This is the most speciose cestode family—currently containing at least 923 valid species (565 species from birds and 358 species from mammals) and 130 valid genera (Schmidt, 1986; Czapliński and Vaucher, 1994; McLaughlin, 2003; Gibson et al., 2014) (see Table 1). The most important morphological traits characterizing the family include the sac-like rostellar apparatus (Fig. 15A), typically with one, or exceptionally two, rows of rostellar hooks (although a rostellum may be lacking [Fig. 15C] or present in only rudimentary form), proglottids that are usually wider than long (Figs. 15B, D, E), genital pores that are typically unilateral (Fig. 15B), a single or rarely double set of reproductive organs per proglottid, small number of testes (typically 1 to 4, rarely up to 32), and the presence of both external and internal seminal vesicles. Additional diagnostic characters at the generic level include the number of longitudinal osmoregulatory canals, the number of the inner longitudinal muscle bundles, the presence of a pseudoscolex, the presence of an accessory sac and stylet, and the structure and pattern of development of the uterus. Of key importance at the generic level, however, are the number and shape of the rostellar hooks (see Skrjabin and Matevosyan

[1945] for the generally accepted classification of hymenolepidid hook shapes) (e.g., Khalil et al., 1994). It is of note that the presence of an external seminal vesicle is a character the hymenolepidids share with both the Anoplocephalidae and the families placed in the, albeit controversial, suborder Acoleata.

The host associations of the Hymenolepididae include almost all orders of birds, both aquatic and terrestrial taxa (Schmidt, 1986; Czapliński and Vaucher, 1994), and many groups of mammals, with an emphasis on the orders Soricomorpha, Rodentia, Lagomorpha, Chiroptera, and Marsupialia (see Czapliński and Vaucher, 1994; Georgiev et al., 2006; Binkienė et al., 2011). Of note is the fact that humans are also among the hosts of hymenolepidids (which otherwise are mainly parasites of rodents) (Fan, 2005; Magalhaes et al., 2013; Nkouawa et al., 2016).

Life-cycles are known for 230 species of hymenolepidids (Lefebvre et al., 2009a, b). Most have a two-host life-cycle that involves an invertebrate intermediate host and a vertebrate definitive host. Intermediate host taxa differ depending on the habitat. Intermediate hosts of terrestrial taxa are generally arthropods (i.e., Insecta, Entognatha, Myriapoda, Arachnida) or annelids. Intermediate hosts of aquatic taxa are generally aquatic crustaceans, insects, or annelids (Skrjabin and Matevosyan, 1945; Lefebvre et al., 2009a, b). In exceptional cases, the life-cycles of aquatic taxa may have a snail paratenic host. The larval stage developing in the intermediate host is a cysticercoid, with eight recognized variants (Chervy, 2002). A notable exception to this scenario is the life-cycle of *Pararodentolepis fraterna* (Stiles, 1906) Tkach, Makarikov & Kinsella, 2013, which may be entirely completed within the mammalian definitive host alone—a strategy that is considered to represent a secondary simplification of the two-host life-cycle (Skrjabin and Matevosyan, 1948). The family is cosmopolitan (including Antarctica) in distribution (Czapliński and Vaucher, 1994).

Major taxonomic works treating this family are those of Mayhew (1925), Skrjabin and Matevosyan (1945, 1948), Spasskii and Spasskaya (1954), Spasskii (1954, 1963), Spasskaya (1966), Vaucher (1971), Czapliński and Vaucher (1994), Sawada (1997), and Bondarenko and Kontrimavichus (2006).

Discoveries over the course of the PBI project. Hymenolepidids from birds were collected from 17 countries and 49 bird families (10 families of aquatic and 39 of terrestrial birds). In total, 141 species of at least 30 genera of this cestode family were collected. In addition to taxa from aquatic birds (35 species), these collections revealed a substantial diversity in terrestrial birds (77 hymenolepidid species). The Hymenolepididae are particularly well represented in the Passeriformes, especially in the Turdidae (10 species) and Thamnophilidae (7 species). One new genus (*Colibrilepis* Widmer, Georgiev & Mariaux, 2013) and one new species from Chile (*Colibrilepis pusilla* Widmer, Georgiev & Mariaux, 2013) and one new species (*Diorchis thracica* Marinova, Georgiev & Vasileva, 2015) from Bulgaria were described (Widmer et al., 2013; Marinova et al., 2015). Preliminary taxonomic work on other newly collected material suggests it includes an additional three new genera and at least 17 new species, most of which are members of *Passerilepis* Spasskii & Spasskaya, 1954.

Hymenolepidids from mammals were collected from 12 countries and nine families representing four orders of hosts. In total, 106 species and 33 genera of Hymenolepididae were collected. Hymenolepidids are known to be very well represented in Soricidae, with more than 60 species parasitizing the family. One new genus (*Sawadalepis* Makarikova & Makarikov, 2013) and 22 new species were described: *Potorolepis gulyaevi* Makarikova & Makarikov, 2012 (see Makarikova and Makarikov, 2012), *Pararodentolepis gnoskei* (Greiman & Tkach, 2012) Tkach, Makarikov & Kinsella, 2013 (see Greiman and Tkach, 2012), *Sawadalepis prima* Makarikova

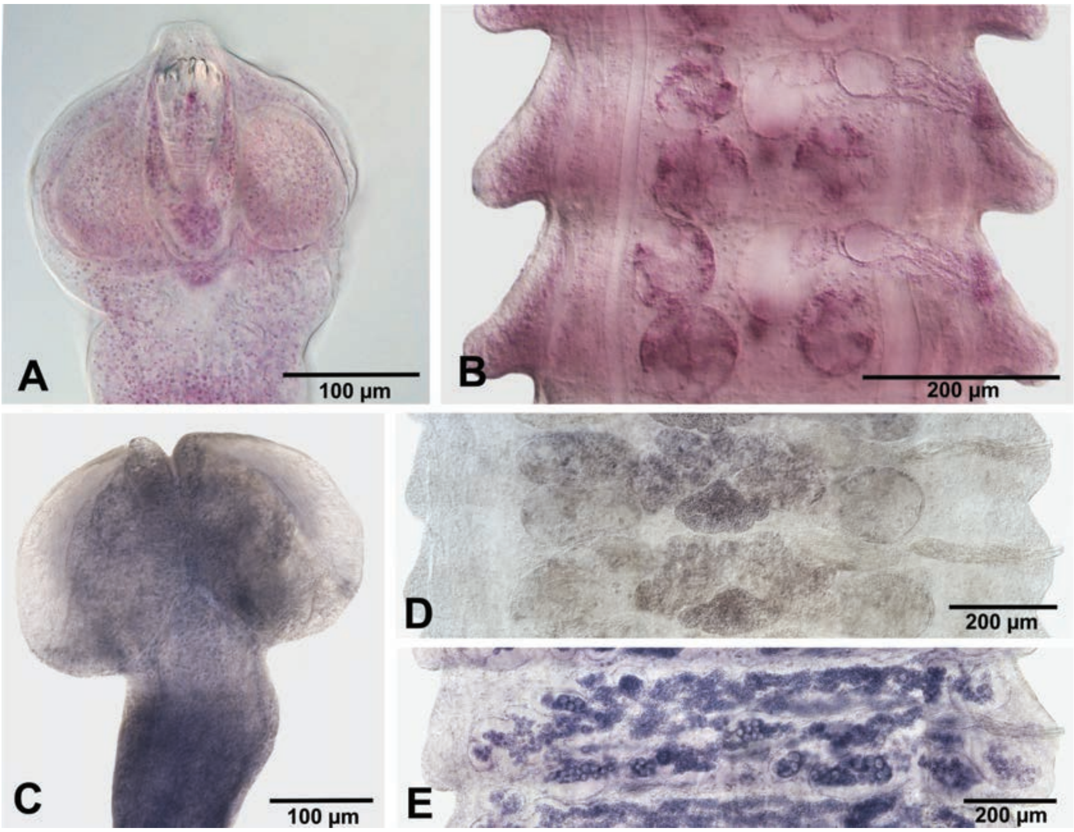


Figure 15. HYMENOLEPIDIDAE: **(A–B)** *Passerilepis crenata* from *Turdus mupinensis* from China. **(A)** Scolex. **(B)** 'Male' mature proglottids. **(C–E)** *Arostrilepis intermedia* from *Myodes rufocanus* from Russia. **(C)** Scolex. **(D)** Mature hermaphroditic proglottids. **(E)** Pre-gravid proglottid.

& Makarikov, 2013 (see Makarikova and Makarikov, 2013), *Staphylocystis clydesengeri* Tkach, Makarikov & Kinsella, 2013 (see Tkach et al., 2013), *Staphylocystoides gulyaevi* Greiman, Tkach & Cook, 2013 (see Greiman et al., 2013), *Arostrilepis intermedia* Makarikov & Kontrimavichus, 2011, *A. janickii* Makarikov & Kontrimavichus, 2011 (see Makarikov and Kontrimavichus, 2011), *A. mariettavogeae* Makarikov, Gardner & Hoberg, 2012, *A. schilleri* Makarikov, Gardner & Hoberg, 2012 (see Makarikov et al., 2012), *A. cooki* Makarikov, Galbreath & Hoberg, 2013, *A. gulyaevi* Makarikov, Galbreath & Hoberg, 2013, *A. rauschorum* Makarikov, Galbreath & Hoberg, 2013 (see Makarikov et al., 2013a), *Hymenolepis apodemi* Makarikov & Tkach, 2013, *H. rymzhanovi* Makarikov & Tkach, 2013 (see Makarikov and Tkach, 2013), *H. bicauda* Makarikov, Tkach & Bush, 2013, *H. haukisalmii* Makarikov, Tkach & Bush, 2013 (see Makarikov et al., 2013b), *H. folkertsi* Makarikov, Nims, Galbreath & Hoberg, 2015 (see Makarikov et al., 2015c), *H. alterna* Makarikov, Tkach, Villa & Bush, 2015, *H. bilaterala* Makarikov, Tkach, Villa & Bush, 2015 (see Makarikov et al., 2015a), *Soricinia genovi* Binkienė, Kornienko & Tkach, 2015 (see Binkienė et al., 2015), *Nomadolepis fareasta* Makarikov, Mel'nikova & Tkach, 2015, and *N. shiloi* Makarikov, Mel'nikova & Tkach, 2015 (see Makarikov et al., 2015b), and two species of *Armadolepis* Spassky, 1954 (Makarikov, 2017). In addition, albeit not as part of the PBI project, Makarikov and Hoberg (2016) recently described another new species of *Arostrilepis*, *A. kontrimavichusi* Makarikov & Hoberg, 2016. Preliminary taxonomic work on other material collected from mammals over the course of the PBI project leads us to believe it includes one additional new genus and 34 new species.

This family was the most well represented of all cyclophyllidean families in our molecular phylogenetic analyses. The sample consisted of a total of 111 specimens (41 of which were collected on PBI expeditions) of 91 identified species (66 species from birds and 25 from mammals) in at least 38 genera. The hymenolepidids were found to nest deeply among the cyclophyllideans, in a clade that also includes the anoplocephaline cestodes (Fig. 5). Although nodal support for this relationship was not high, it is interesting to note that all taxa in this clade have a sac-like rostellar apparatus. In terms of relationships to other families, our results suggest that the Hymenolepididae may be phylogenetically most related to Progynotaeniidae, Acoleidae, and the dioicocestid subfamily Gyrocoeliinae but nodal support for these relationships is also weak. One further molecular outcome from the PBI project was the examination of the distribution and genetic variation of three hymenolepidid species from rodents from the Canary Islands (Foronda et al., 2011).

5.11. Mesocestoididae Perrier, 1897

This family was erected by Perrier (1897) for the genus *Mesocestoides* Vaillant, 1863 and has been widely accepted as a monophyletic group by later authors. Skrjabin (1940) elevated it to subordinal status, as the Mesocestoidata Skrjabin, 1940 within the order Cyclophyllidea (see also Chertkova and Kosupko, 1978). Wardle et al. (1974) recognized it as the independent order Mesocestoididea on the basis of its lack of a rostellar apparatus, and its possession of median genital pores, a pair of vitelline glands, a paruterine organ, and vermiform oncospheres. However, the status of the group as an independent order has not generally been accepted by subsequent authors, most of whom considered the Mesocestoididae as a family within the Cyclophyllidea (e.g., Schmidt, 1986; Khalil et al., 1994). Nonetheless, discussion of the position of the group within or outside of the Cyclophyllidea has been revitalized by the wider application of molecular phylogenetic approaches to the classification of cestodes—a topic that is treated in more detail below.

The main morphological characters of importance for identification of this family include the lack of a rostellum (Fig. 16A) and the mid-ventral position of the genital atrium (Fig. 16C), as well as the presence of a paruterine organ (Fig. 16C) and typically also possession of a pair, rather than a single, vitelline gland (Fig. 16B). The exception is the monotypic *Mesogyna* Voge, 1952, which has a transversely elongated vitellarium and a saccular uterus without a paruterine organ.

Definitive hosts of the family are carnivorous mammals, and more rarely birds of prey (Rausch, 1994a). The geographic distribution is cosmopolitan with the exception of Australia (James, 1968). No complete life-cycle is known for the family. However, they are thought to have a three-host life-cycle. Mites have been suspected, but not proven, to serve as the first intermediate host because the first larval stage has never been found. The second larval stage, known as a tetrathyridium, is commonly found in a wide array of tetrapods, in which it can asexually reproduce, usually by longitudinal fission (Chertkova and Kosupko, 1978; Galan-Puchades et al., 2002).

Major taxonomic monographs dealing with representatives of this family are those of Witenberg (1934), Chertkova and Kosupko (1978), and Rausch (1994a). The family is typically subdivided into the subfamilies Mesocestoidinae and Mesogyninae, each with a single genus (Rausch, 1994a). Host-induced morphological variation makes the identification of species

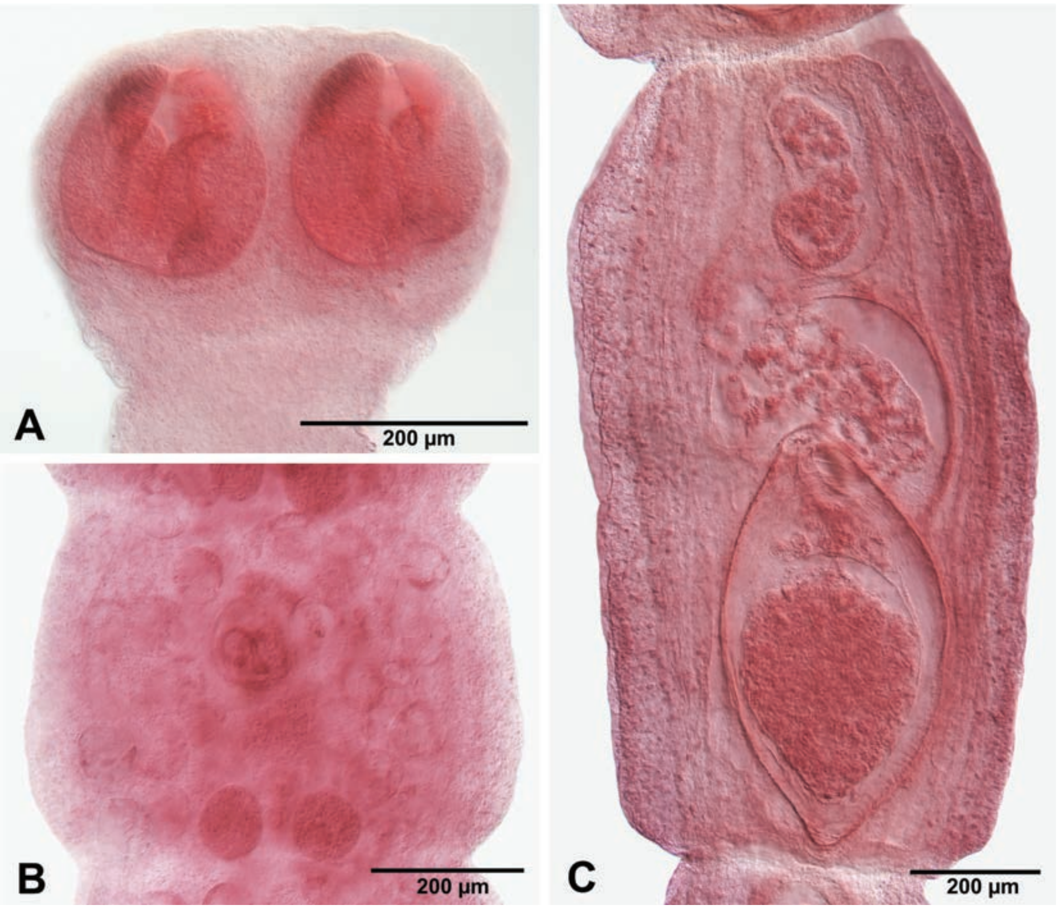


FIGURE 16. MESOCESTOIDIDAE: *Mesocestoides lineatus* from *Vulpes vulpes* from Bulgaria. **(A)** Scolex. **(B)** Mature proglottid (ventral view). **(C)** Pre-gravid proglottid with paruterine capsule formation.

difficult (Rausch, 1994a). To date, approximately 30 nominal species have been proposed in *Mesocestoides* but only a subset of these (i.e., 12 according to Chertkova and Kosupko [1978] and 17 according to Wardle et al. [1974]) can be distinguished with confidence. *Mesogyna* is monotypic.

Hoberg et al. (1999), as a result of their morphology-based phylogenetic analysis, believed the Mesocestoididae to be the earliest diverging group of cyclophyllideans. Molecular phylogenetic studies are almost unanimous in suggesting that the Mesocestoididae should be removed from the Cyclophyllidea and recognized as an indepentent order (Mariaux, 1998; Olson et al., 2001; Waeschenbach et al., 2007; Caira et al., 2014) although its exact phylogenetic affinities have never been strongly supported. The only divergent view is that of von Nickisch-Rosenegk et al. (1999) who found the Mesocestoididae to be highly nested within the cyclophyllidean evolutionary tree as the sister group to the most derived families or of the Anoplocephalidae, depending on the type of analysis employed. Their work was, however, based on data from only a very short fragment of a single gene (i.e., 12S rDNA) and thus support for this hypothesis is limited.

Discoveries over the course of the PBI project. Collections from PBI expeditions emphasized tetrathyridia of *Mesocestoides*. In birds, five occurrences were seen in Peru (including 3 in thamnophilid birds and 1 each in members of the Emberizidae Vigors and Formicariidae Gray), with one occurrence each in Ethiopia (in a turdid) and Malaysia (in a vangid). In mammals, two adults were found, one each in a procyonid and a didelphid in USA, and one tetrathyridium was collected from a soricid in Malawi. All eight of these represent new host and locality records. However, this is not surprising as tetrathyridia are known from a large variety of intermediate hosts, including passerine birds of various families (Witenberg, 1934; Chertkova and Kosupko, 1978) and nothing is known about their host specificity.

Recent molecular studies by Waeschenbach et al. (2007, 2012) and Caira et al. (2014) failed to resolve the phylogenetic position of this group among the acetabulate cestode taxa, although significant support was found for its exclusion from the Cyclophyllidea. Waeschenbach et al.'s (2012) 516 mitochondrial amino acid analysis provided strong support for a sister-group relationship between the Mesocestoididae and Cyclophyllidea (Waeschenbach et al., 2012). In a larger analysis of acetabulate taxa, although with limited sampling of cyclophyllideans, Caira et al. (2014) found the Mesocestoididae to group as sister to the order Tetrabothriidea, which in turn was sister to a clade consisting of the Cyclophyllidea + Nippotaeniidea.

Our molecular phylogenetic analyses included three specimens of tetrathyridia of *Mesocestoides*. They were indeed found to comprise a clade that grouped as the sister taxon of the remaining cyclophyllideans (Fig. 5). However, as the Nippotaeniidea and Tetrabothriidea were not represented in our analyses, the inferences about the position of the Mesocestoididae that can be drawn from these analyses are limited.

5.12. Metadilepididae Spasskii, 1959

This taxon was originally established as a subfamily within the family Dilepididae by Spasskii (1959) for three genera with a sucker-like rostellar apparatus, a sac-like uterus, and genital ducts that were usually located ventral to the osmoregulatory canals. It was elevated to family level by Spasskaya and Spasskii (1971) who considered it to be a close relative of the Paruterinidae and who proposed the superfamily Paruterinoidea to house the two families. For decades, the metadilepidids were recognized as a distinct family solely in the Russian-language literature (Borgarenko, 1981; Kornyushin, 1989). It was not until they were "rediscovered" through the description of several African metadilepidid taxa by Mariaux and his collaborators (e.g., Mariaux and Vaucher, 1989; Mariaux, 1991; Mariaux et al., 1992) that the group regained family-level status more globally. Kornyushin and Georgiev (1994) treated the family and the eight genera then recognized; Georgiev and Vaucher (2003) subsequently established two new genera in the family.

The main morphological features characterizing metadilepidids include a sucker-like rostellar apparatus, which is typically armed with triangular rostellar hooks with epiphyses (Figs. 17A, B). Based on these characters, metadilepidids are similar to paruterinids but can be distinguished from them by their possession of a sacciform uterus positioned dorsal to the ovary (Figs. 17 C, D), rather than paruterine organs.

The host associations of this family consist of terrestrial birds of the orders Caprimulgiformes, Coraciiformes, and Passeriformes (Kornyushin and Georgiev, 1994). No complete life-cycle is known for any metadilepidid cestode. Since the definitive hosts are insectivorous birds, it seems likely that arthropods serve as intermediate hosts of this group. The Metadilepididae exhibit the narrowest geographic distribution of any of the cyclophyllidean families. They are generally restricted to tropical regions, although a few

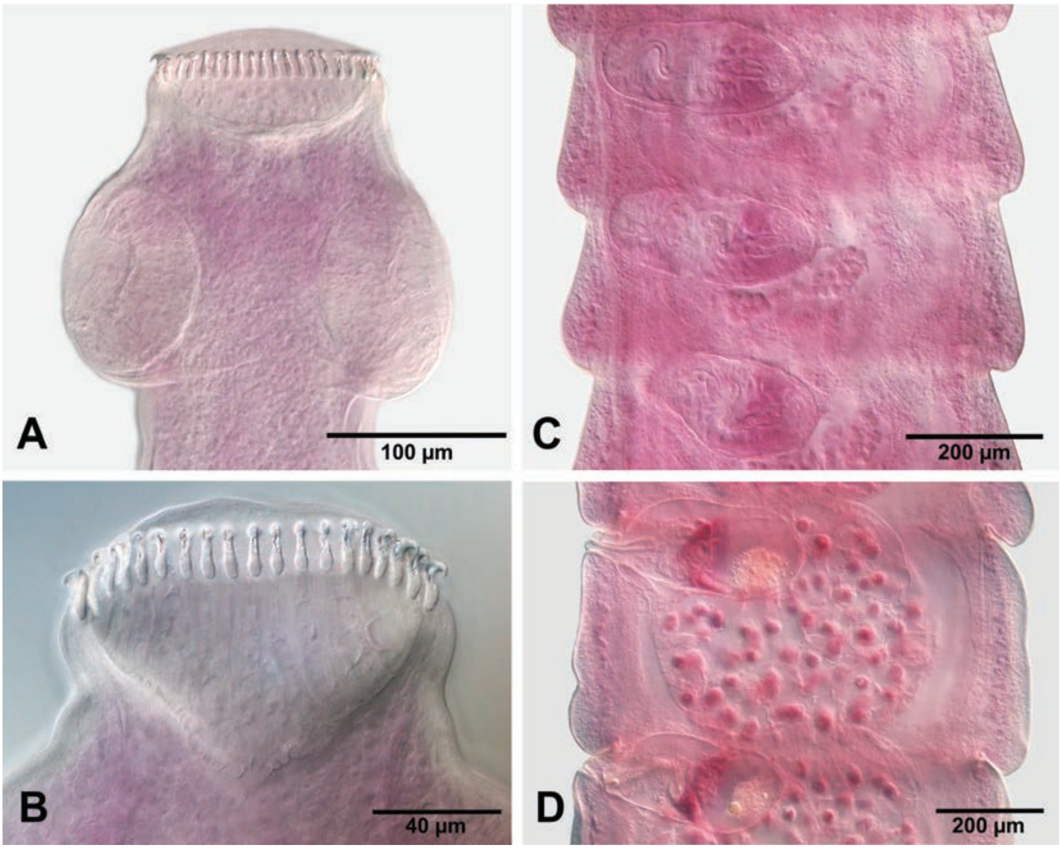


FIGURE 17. METADILEPIDIDAE: *Pseudadelphoscolex eburnensis* from *Terpsiphone rufiventer* from Gabon. **(A)** Scolex. **(B)** Sucker-like rostellar apparatus. **(C)** Mature proglottids. **(D)** Gravid proglottids.

species also occur in migrating birds in their summer nesting grounds in temperate latitudes (Kornyushin and Georgiev, 1994).

Currently, the family includes ten genera and 15 species (Kornyushin and Georgiev, 1994; Georgiev and Vaucher, 2003).

Discoveries over the course of the PBI project. Specimens of this family were collected from two countries and three bird families (2 passeriforms and 1 coraciiform). This material consisted of four species, only two of which (i.e., *Pseudadelphoscolex eburnensis* Mariaux, Bona & Vaucher, 1992 and *Skrjabinoporus merops* [Woodland, 1928] Spasskii & Borgarenko, 1960), both from Gabon, have been identified. Both of the latter species were included in our molecular phylogenetic analyses. They were found to be composed of a well-supported subclade within the Paruterinidae suggesting that the lack of the paruterine organ is likely the result of a secondary loss in the metadilepidids, but also calling into question the independence of the two families.

5.13. Nematotaeniidae Lühe, 1910

This family was erected by Lühe (1910) for *Nematotaenia dispar* (Goeze, 1782) Lühe, 1899. It is one of the least speciose families of the Cyclophyllidea with only about 20 valid species.

The main features characterizing nematotaeniids include the weakly segmented cylindrical strobila (Fig. 18C), the simple scolex devoid of apical structures (Fig. 18A), the reduced number of testes (2 or 3) and the presence of multiple paruterine organs in each gravid proglottid (Fig. 18C). A particularly useful list of characters for identifying nematoteniids was provided by Jones (1987).

Nematotaeniids are among the few cyclophyllidean groups that use amphibians as definitive hosts. Host groups include both Anura and Caudata, and "reptiles" (Sauria), mostly the Anguidae Gray, Gekkonidae Oppel, and Scincidae Gray. In addition, one species has been reported from a turtle (Jones, 1987). No life-cycle is known for the family (Beveridge, 2001). The geographic distribution is cosmopolitan (Jones, 1994).

Major taxonomic monographs dealing with representatives of this family are those by Douglas (1958) and Jones (1987, 1994). Jones (1987) recognized 18 species in four genera. Since that work, a few more species have been described (e.g., Buriola et al., 2005) and one genus (*Lanfrediella* Melo, Giese, Furtado, Soares, Gonçalves, Vallinoto & Santos, 2011; see Melo et al., 2011) has been erected. The group however remains very small. Jones (1987) provided a preliminary phylogeny and biogeographical history on the basis of morphological characters.

Mariaux (1998) included one nematotaeniid specimen in his analysis of 18S rDNA sequence data, but his results served only to confirm it as a member of the Cyclophyllidea. Beyond that work, the family has not been represented in other phylogenetic contributions based on molecular data.

Discoveries over the course of the PBI project. Only a few amphibians and "reptiles" were collected in our field trips and no nematotaeniids were found.

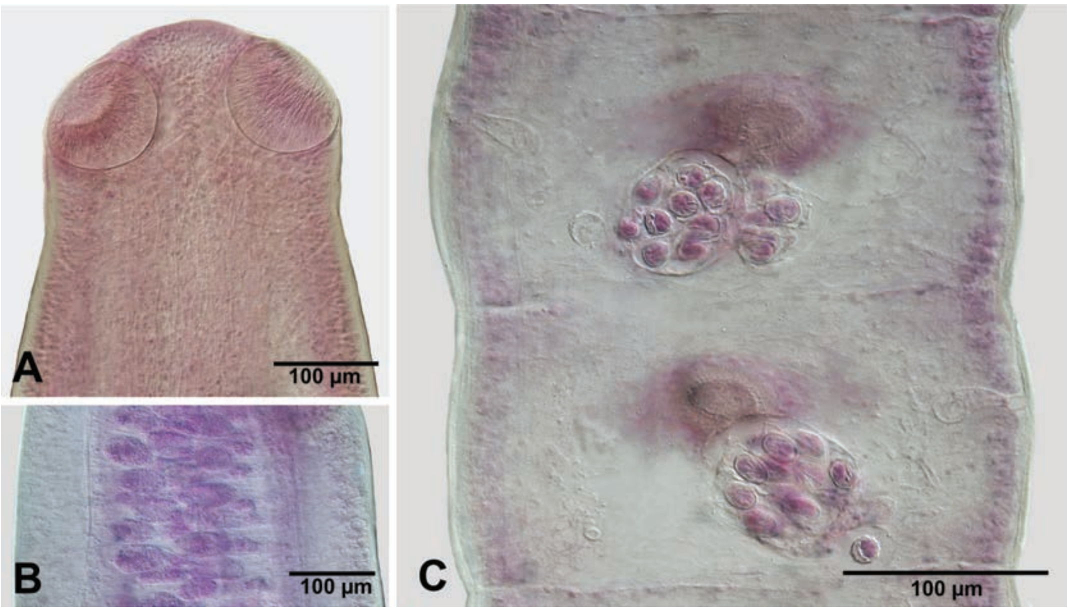


FIGURE 18. NEMATOTAENIIDAE: *Cylindrotaenia americana* from *Rhinella marina* from Peru. **(A)** Scolex. **(B)** Mature proglottids. **(C)** Pre-gravid proglottids with early paruterine capsule formation.

5.14. Paruterinidae Fuhrmann, 1907

This group was established as a subfamily within the family Dilepididae by Fuhrmann (1907). This concept was embraced by some subsequent authors (e.g., Yamaguti, 1959; Schmidt, 1986), however others have considered the group to represent a distinct family (e.g., Mola, 1929; Skrjabin, 1940; Spasskaya and Spasskii, 1971; Georgiev and Kornyushin, 1994). Yet other authors elevated it to superfamilial rank and included one or two other families (e.g., Matevosyan, 1969; Kornyushin, 1989).

A key morphological feature characterizing the paruterinids is the presence of a single paruterine organ in the form of a fibrous or granular appendage to the uterus that usually receives the eggs and retains them in a common capsule (Figs. 19B, C). This structure is believed to serve to protect against desiccation of eggs allowing them to be disseminated in terrestrial habitats, and/or to have a propagative function perhaps attracting intermediate hosts and thereby facilitating the simultaneous transmission of groups of eggs (Georgiev and Kornyushin, 1994). Another key character of the paruterinids is the position of the developing uterus dorsal to the ovary—a feature the group shares only with the family Metadilepididae (Kornyushin and Georgiev, 1994). The scolex of paruterinids typically bears a sucker-like rostellar apparatus (Fig. 19A) armed with two rows of rostellar hooks that usually bear epiphyseal thickenings on the handle and guard. However, some genera are characterized by either the presence of a rudimentary (unarmed) rostellum or by their lack of a rostellum entirely (see Georgiev and Kornyushin, 1994).

The host associations of members of this family, as adults, consist mostly of terrestrial birds of the orders Passeriformes, Coraciiformes, Piciformes, Trogoniformes, Strigiformes, Accipitriformes, Galliformes, Cuculiformes, and Apodiformes; a few species have been recorded from mammals and amphibians (Yamaguti, 1959; Matevosyan, 1969; Schmidt, 1986; Georgiev and Kornyushin, 1994). The few species for which life-cycles are known use two hosts. For species of the genera *Paruterina* Fuhrmann, 1906 (parasitic in owls) and *Cladotaenia* Cohn, 1901 (parasitic in eagles, hawks, and falcons), rodents and soricomorph mammals serve as intermediate hosts (Freeman, 1957, 1959). For species of *Metroliasthes* Ransom, 1900 and *Lyruterina* Spasskii & Spasskaya, 1971 (parasitic in galliform birds), insects serve as intermediate hosts (Jones, 1936; Smigunova, 1991). The larval stage developing in the intermediate host is a merocercoid (Chervy, 2002).

With the exception of the Antarctic, paruterinids are cosmopolitan in distribution, occurring in habitats spanning the range of tundra to equatorial forests (Yamaguti, 1959; Matevosyan, 1969; Schmidt, 1986).

The only taxonomic monograph on the Paruterinidae is that of Matevosyan (1969). The more recent work by Georgiev and Kornyushin (1994) considered the taxonomy of the family at the generic level. The family currently includes 24 genera (Georgiev and Kornyushin, 1994; Phillips et al., 2012) and 125 species, the majority of which were either listed by Matevosyan (1969) and Schmidt (1986) or described in subsequent publications (Bona et al., 1986; Kornyushin, 1989; Georgiev and Vaucher, 2001; Georgiev and Gibson, 2006; Georgiev and Mariaux, 2007; Phillips et al., 2012, 2014).

Discoveries over the course of the PBI project. Specimens of this family were collected from 12 countries and from 38 bird families. The Pycnonotidae and Thraupidae Cabanis (tanagers) were found to host the richest paruterinid faunas, with seven and five species, respectively. In total, 61 species of at least 12 genera were collected. Genera that were especially well represented in our collections are *Anonchotaenia* Cohn, 1900 (16 species), *Biuterina* Fuhrmann, 1902 (12 species), and *Sphaeruterina* Johnston, 1914 (5 species). Work on

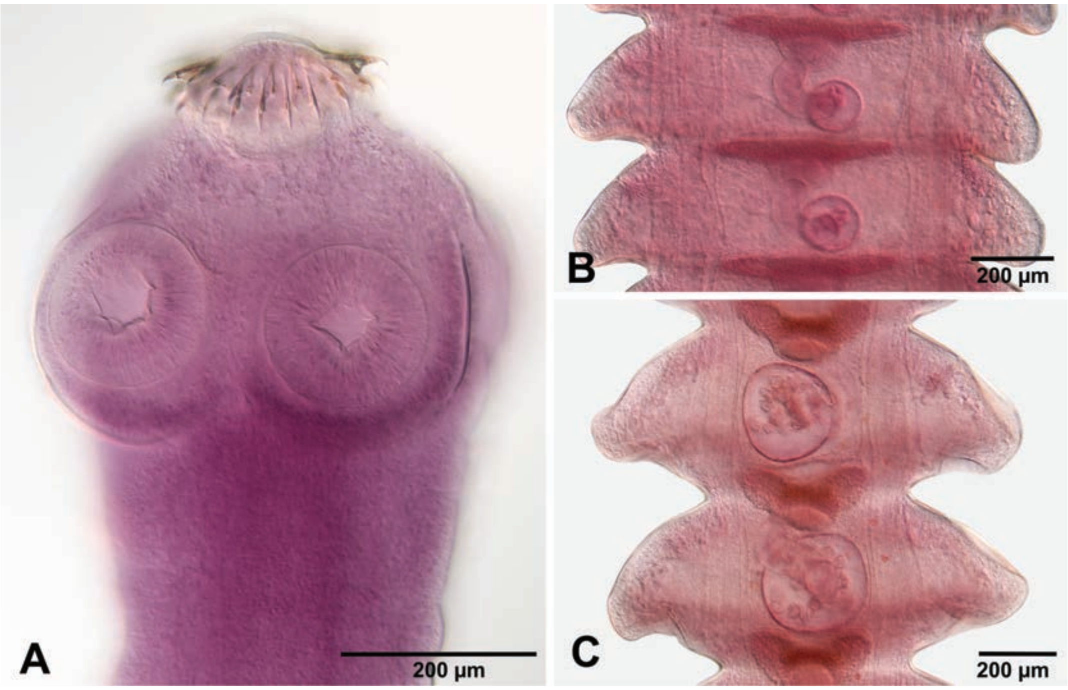


FIGURE 19. PARUTERINIDAE: *Sphaeruterina* sp. from *Mixornis gularis* from Vietnam. **(A)** Scolex. **(B)** Post-mature proglottids. **(C)** Pre-gravid proglottids.

this material continues. To date, the new genus *Cucolepis* Phillips, Mariaux & Georgiev, 2012 was erected (Phillips et al., 2012). Three new species have been described: *Cucolepis cincta* Phillips, Mariaux & Georgiev, 2012 from Paraguay, *Anonchotaenia vaslata* Phillips, Georgiev, Waeschenbach & Mariaux, 2014 also from Paraguay, and *A. prolixa* Phillips, Georgiev, Waeschenbach & Mariaux, 2014 from Chile (Phillips et al., 2012, 2014). Redescriptions of five species have also been published (Phillips et al., 2014; Dimitrova et al., in press). At least nine additional new species appear to be represented among this material. Additionally, specimens of *Dictyterina cholodkowskii* (Skrjabin, 1914) Spasskii in Spasskaya & Spasskii, 1971 collected in China were used to study the vitellogenesis of a paruterinid for the first time (Yoneva et al., 2016).

In total, 33 specimens of 25 species were included in our molecular phylogenetic analyses; 27 of these had been collected during PBI project expeditions. The paruterinids were found to group with the taeniids and metadilepidids, albeit in a clade with relatively poor nodal support (Fig. 5). As the metadilepidids grouped among the paruterinids, it is possible that, based on traditional concepts (i.e., Khalil et al., 1994), one or possibly both of these families may not be monophyletic, although nodal support for these inferences is currently weak.

5.15. Progynotaeniidae Fuhrmann, 1936

Fuhrmann (1936) erected the family Progynotaeniidae for four genera, three of which were initially considered to belong to the Acoleidae (see Khalil, 1994a). The criteria he applied to distinguish his new family from the acoleids included their proterogyny (i.e., maturation of the female gonads before the male genital system), small body size (strobila consisting of only few proglottids), and weak body musculature. Fuhrmann (1936) subdivided the family into the subfamilies Progynotaeniinae with hermaphroditic proglottids exhibiting proterogyny (i.e., with each proglottid initially functioning as female and later becoming simultaneously gravid and male) and Gynandrotaeniinae, characterized by a strobila with regularly alternating male and female proglottids. Skrjabin (1940), Yamaguti (1959), Ryzhikov and Tolkacheva (1981), Schmidt (1986), and Khalil et al. (1994) also recognized the family Progynotaeniidae as valid but the subfamilies were recognized only by a subset of these authors (i.e., Skrjabin, 1940; Yamaguti, 1959; Ryzhikov and Tolkacheva, 1981).

The only monograph on the Progynotaeniidae was that of Ryzhikov and Tolkacheva (1981), who recognized six genera and 15 valid species. Khalil (1994b) provided emended diagnoses and a key to the genera. More recent taxonomic developments include redescriptions of known and descriptions of new species (Macko and Špakulová, 1995, 1998; Nikolov and Georgiev, 2002; Nikolov et al., 2005) as well as revisions of the genera *Leptotaenia* Cohn, 1901 (see Nikolov et al., 2004) and *Paraprogynotaenia* Rysavy, 1966 (see Nikolov and Georgiev, 2008). Currently, 24 species are recognized in the family's six valid genera.

The diagnostic features of the family are the sac-like rostellar apparatus with a highly protrusible rhynchus that is armed with one or two rows of rostellar hooks (Fig. 20B), and the lack of a vaginal pore (Fig. 20D). Whereas the Progynotaeniinae exhibit monoecious proglottids and testes arranged in two groups positioned lateral to the uterus (Fig. 20D), the Gynandrotaeniinae bear dioecious proglottids, and an enormous, heavily armed cirrus.

The host associations of the family include flamingos for *Leptotaenia* and *Gynandrotaenia* Fuhrmann, 1936, and waders (Charadriiformes) for the remaining genera (Ryzhikov and Tolkacheva, 1981). *Gynandrotaenia stammeri* Fuhrmann, 1936 is the only species for which a complete life-cycle is known. This parasite of flamingos uses brine shrimp (*Artemia* spp.) as an intermediate host, with cysticercoids developing in the body cavity (Gvozdev and Maksimova, 1979; Georgiev et al., 2005). Progynotaeniids are generally distributed along seashores and wetlands, mostly in tropical areas, throughout the world, although some species occur in aquatic birds in temperate latitudes (Ryzhikov and Tolkacheva, 1981).

Discoveries over the course of the PBI project. A single undescribed species of *Proterogynotaenia* was collected from the American oystercatcher (*Haematopus palliatus* Temminck) in Chile, and an unidentified genus and species was obtained from *Charadrius vociferus* L. in the USA. The former is the first record of a progynotaeniid from South America, although a member of the family has been reported from Cuba (Rysavy, 1966).

For the first time, progynotaeniids were included in a molecular phylogenetic study (5 specimens representing 3 species). These specimens were found to compose a monophyletic group, which appears to be the sister group of a clade consisting of the Acoleidae and Gyrocoeliinae (all parasitic in Charadriiformes). Our results question the monophyly of the suborder Acoleata, for this clade appears to be only distantly related to the clade of grebe parasites (i.e., Dioicocestinae plus several amabiliid genera).

5.16. Taeniidae Ludwig, 1886

The family Taeniidae was erected by Ludwig (1886) for nine species of *Taenia* L., 1758, which then included the most common large tapeworms from humans and domestic animals, as well as a species that is now placed in the genus *Echinococcus* Rudolphi, 1801. The features he identified as characterizing the family were rostellar armature, proglottid shape, position of the genital pores, and lack of a uterine pore. Other typical characteristics of the group are the long ribbon-like strobila, the shape of the rostellar hooks (Fig. 21A) (when present), and

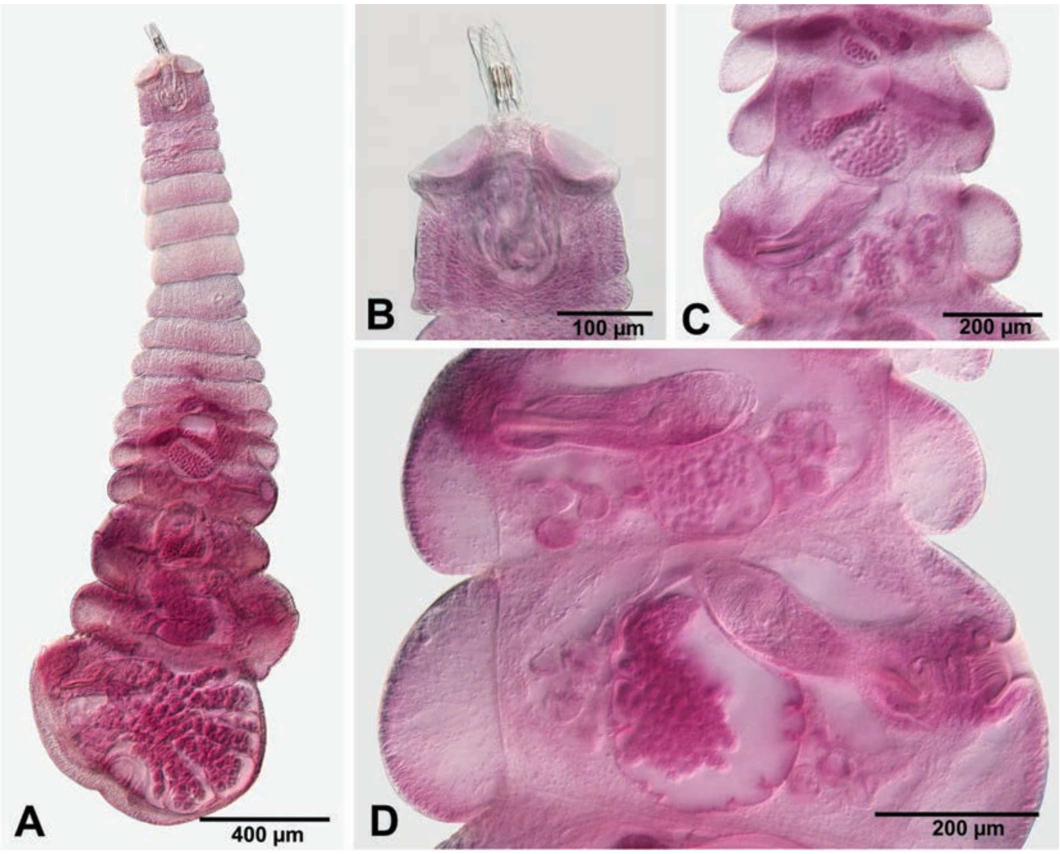


Figure 20. PROGYNOTAENIIDAE: *Proterogynotaenia* sp. from *Haematopus palliatus* from Chile. **(A)** Whole worm. **(B)** Scolex. **(C)** Mature proglottids. **(D)** Post-mature and pre-gravid proglottids. Note the functional male genitalia in the latter..

possession of numerous testes, a bilobed ovary (Fig. 21B), a sacciform uterus with lateral branches (Fig. 21C), and thick-walled eggs. The family includes both some of the largest tapeworms, with some species reaching several meters in length, and some of the smallest tapeworms, with adults of *Echinococcus* reaching only a few millimeters in length.

The family has been unanimously accepted since its erection. Skrjabin (1940) and Wardle et al. (1974) proposed elevating it to subordinal or ordinal status, respectively, however, neither proposal has been generally embraced. The number of genera attributed to the Taeniidae has varied widely. For example, Wardle and McLeod (1952) recognized seven, Abuladze (1964) recognized 13, Wardle et al. (1974) recognized 11, and Schmidt (1986) only five genera. The source of much of this confusion is the variation seen in the metacestode stage across the family, because a number of genera were originally erected on the basis of metacestode characters alone and have subsequently been synonymized or attributed to other families (see Rausch [1994b] for a review). In fact, in his major revision, Rausch (1994b) considered only *Taenia* and *Echinococcus* as valid genera, placing each in its own subfamily (i.e., Taeniinae Stiles, 1896 and Echinococcinae Abuladze, 1960). Nevertheless, the taxonomic position of a few genera formerly assigned to the Taeniidae, and *Dasyurotaenia* Beddard, 1912 in particular, remains doubtful. The most important taxonomic treatments of the family are those of Abuldaze (1964), Verster (1969), Rausch (1994b), and Loos-Frank (2000); Lavikainen (2014) provided a particularly detailed summary of the taxonomic history of the family.

Given their importance for humans, human activities, and domesticated animals, taeniids have been studied more intensely than any other group of tapeworms. This also applies to their diversity and systematics with what turn out to be a large number of synonyms, both at the generic and specific level, having been established over time. Quite unusual for tapeworms is the fact that many studies have led to the recognition of subspecies, "genotypes" or "strains," particularly for the most pathogenic taxa and especially within *Echinococcus* (see Lymbery, 2017).

The life-cycles of many taeniid species are known. In general, mammals serve both as herbivorous intermediate (Rodentia, Artiodactyla, and Lagomorpha) and carnivorous definitive (Carnivora, humans) hosts (Rausch, 1994b). Since the introduction of *Echinococcus* to Australia, the family is present on all continents, although it is poorly represented in South America (Rausch, 1994b; Jenkins and Macpherson, 2003). Several species have been dispersed by anthropogenic activities (Rausch, 1995).

The Taeniidae are largely considered to represent a monophyletic group and, in fact, most phyogenetic studies focused on either *Taenia* or *Echinococcus* use the other genus as an outgroup (Lavikainen, 2014). Hoberg et al. (1999) formally studied the phylogenetic position of the family based on analyses of morphological data. They found it to be the well-supported sister group to a clade consisting of the Paruterinidae plus Metadilepididae, with the "epiphyseal structure" of hooks serving as a synapomorphy for this three-family group. They also found these taxa (+ *Dasyurotaenia*) to be early diverging within the order and to represent the sister group of all other cyclophyllidean families, with the exception of the Catenotaeniidae, Mesocestoididae, and Nematotaeniidae. In contrast, the molecular analysis of von Nickisch-Rosenegk et al. (1999) placed the Taeniidae (+ Dipylidiidae) as the sister group to the Anoplocephalidae and Mesocestoididae, although with weak support.

Prior to the PBI project, the interrelationships among *Taenia* species based on morphological features have been examined in some detail (e.g., Verster, 1969; Hoberg et al., 2000; Hoberg, 2006). A number of molecular studies have also focused on the genus (e.g., Okamoto et al., 1995; Lavikainen et al., 2008). But, in general there has been poor congruence between results from morphological and molecular analyses (see Lavikainen [2014] for a summary). *Echinococcus* has received much less attention in terms of morphological contributions beyond that of Lymbery (1992), and also fewer molecular studies (e.g., Bowles et al., 1995; Le et al., 2002; Saarma et al., 2009) have examined the inter- and intraspecific relationships among species of *Echinococcus*. Nakao et al. (2013a) and Lymbery (2017) published recent comprehensive reviews of this topic.

Discoveries over the course of the PBI project. No new adult material of this family was collected during the PBI expeditions; this was largely because their definitive hosts are primarily Carnivora and are thus difficult to collect for obvious legal and logistical reasons. A single larva was collected from a cricetid rodent in Alaska as part of the PBI project. The bulk of the material examined came from other sources.

Recent molecular phylogenies (some unrelated to the PBI project) (e.g., Lavikainen et al., 2008; Knapp et al., 2011) confirmed the monophyly of *Echinococcus* and the paraphyly of *Taenia* as traditionally defined, leading to the latter genus being split by Nakao et al. (2013b). However, these studies did not consider the placement of the Taeniidae within the Cyclophyllidea. To clarify the interrelationships among species of *Taenia*, molecular phylogenies were constructed using nuclear and mitochondrial genes (Nakao et al., 2013a).

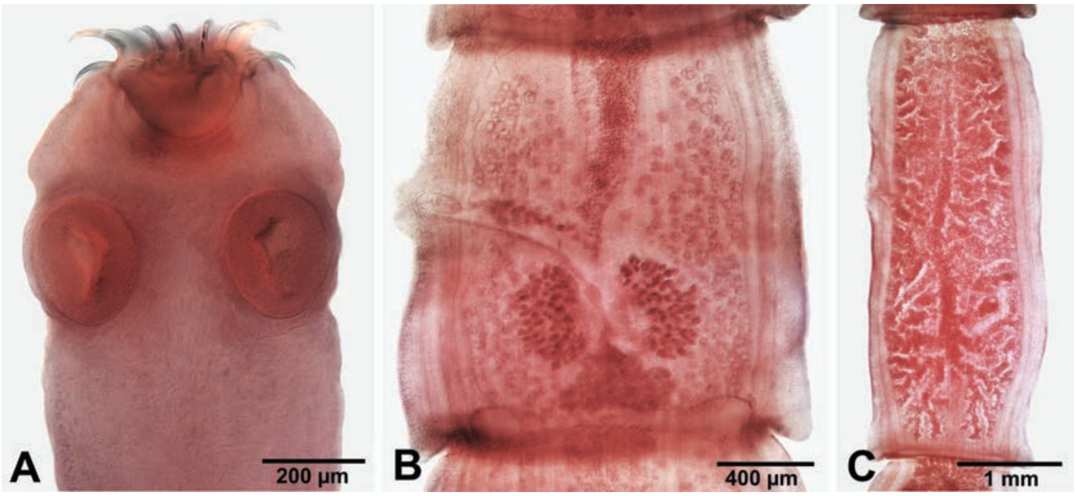


FIGURE 21. TAENIIDAE: *Taenia crassiceps* from *Vulpes vulpes* from Bulgaria. **(A)** Scolex. **(B)** Post-mature proglottid. **(C)** Gravid proglottid with branched uterus.

The resulting phylogenetic trees demonstrated that both *Taenia mustelae* Gmelin, 1790, and a clade consisting of *Taenia parva* Baer, 1924, *Taenia krepkogorski* (Schulz & Landa, 1934) Verster, 1969, and *Taenia taeniaeformis* (Batsch, 1786) Wolffügel, 1911 are only distantly related to the other species of *Taenia*. Based on these results, the resurrection of *Hydatigera* Lamarck, 1816 for *T. parva* Baer, 1924, *T. krepkogorski*, and *T. taeniaeformis* was proposed. They also erected a new genus, *Versteria* Nakao, Lavikainen, Iwaki, Haukisalmi, Konyaev, Oku, Okamoto & Ito, 2013 with *T. mustelae* Gmelin, 1790, thereby establishing the new combination *V. mustelae* (Gmelin, 1790) Nakao, Lavikainen, Iwaki, Haukisalmi, Konyaev, Oku, Okamoto & Ito, 2013. Due to obvious morphological and ecological similarities, *Taenia brachyacantha* Baer & Fain, 1951 was also included in *Versteria* (thus establishing *V. brachyacantha* [Baer & Fain, 1951] Nakao, Lavikainen, Iwaki, Haukisalmi, Konyaev, Oku, Okamoto & Ito, 2013), although molecular evidence was not available. Furthermore, although historically regarded as a single species, these authors clearly demonstrated that *Taenia taeniaeformis* comprises two cryptic species. One of these was described as the new species *Taenia arctos* Haukisalmi, Lavikainen, Laaksonen & Meri, 2011, from the brown bear *Ursus arctos* L., 1758 (definitive host) and moose/elk *Alces* spp. (intermediate hosts) from Finland (type locality) and Alaska by Haukisalmi et al. (2011). The independent status of this new species and the conspecificity of its adults and metacestodes had previously been confirmed with mitochondrial sequence data (Lavikainen et al., 2011). Haukisalmi et al. (2011) also identified potentially useful morphometric features that had not been previously applied to *Taenia* taxonomy.

Recently, molecular approaches have been used effectively to help with the detection of additional new species in this group (Haukisalmi et al., 2011; Lavikainen et al., 2011, 2013), as a consequence, at present a total of 56 species, including the recently described *Hydatigera kamiyai* Iwaki, 2016 (in Lavikainen et al. [2016]) and *Taenia lynciscapreoli* Haukisalmi, Konyaev, Lavikainen, Isomursu & Nakao, 2016, are recognized in four genera, with a few others awaiting formal description (Lavikainen, 2014; Haukisalmi et al, 2016a; Lavikainen et al., 2016).

Our more comprehensive phylogenetic analyses of the Cyclophyllidea overall, which included the above and other published sequences of taeniids, yielded topologies in which the taeniids grouped together in a clade with the paruterinids and metadilepidids, in which the taeniids formed the sister group of two paruterinid genera known to use vertebrates as intermediate hosts (results not shown in Fig. 5).

6. DISCUSSION AND CONCLUSIONS

The global collecting efforts of this project likely represent the largest such collective undertaking ever conducted for cyclophyllideans both in their magnitude and diversity, involving the examination of 4,633 host individuals from 1,132 host species (avian and mammalian) across 21 countries. Specimens of about 10% of all known bird species were examined; among those, 234 species of birds were reported to host cestodes for the first time. A smaller proportion of the mammalian fauna was studied but it nevertheless revealed 36 new cestode hosts. As expected, no new taxa at the familial level were found, which confirms that all of the primary evolutionary lineages of the order have likely already been discovered. Material of approximately 108 species and 12 genera of Cyclophyllidea that are new to science was collected, that is about 16% of all identified species found during the course of this project, and even close to 40% of those found in mammals. Globally, this represents an estimated 3% increase in the total number of species in Cyclophyllidea, which is a particularly significant contribution considering the size of the order. This indicates that the specific diversity in the Cyclophyllidea is still far from being fully documented.

Our results indicate that at least 40% of all studied bird species host cestodes. Approximately 75% of these host at least one cestode species while the remaining 25% host two or more species of cestode. Although higher species richness may have been present, our sampling methodology did not allow us to uncover it. As was already known (see, e.g., Fuhrmann, 1932), aquatic bird species generally host a relatively high diversity of cestodes, while terrestrial bird species mostly host a single and rarely a few species of cestodes. Most bird species that were not found to host cestodes were represented by only one to three individuals in our captures (81%); those for which no cestodes were found, despite the examination of five birds or more, were only few and mostly distributed in families that either have particular diets (Alcedinidae, Fringillidae Leach) or seem to represent exceptions (Cisticolidae Sundevall, Asian Muscicapidae). As expected (e.g., Fuhrmann, 1932; Bona, 1975), host-specificity was high and each cestode species was only rarely found in more than a single host species. This leads us to estimate that the total number of cyclophyllidean species parasitizing birds globally may be as high as 8,000.

The number of cyclophyllideans infecting mammals is even more difficult to estimate. However, our results lead us to predict that the highly-parasitized Soricomorpha alone, probably host a greater number of species of cyclophyllideans than are presently known for the entire class Mammalia. This is due to the strict nature of the specificity of their cestodes (Hunkeler, 1974; Genov, 1984; Vaucher, 1992; Haukisalmi et al., 2010b). However, as has been shown in recent studies, rodents also are likely to harbor a greater cestode diversity than currently appreciated (Haukisalmi et al., 2008, 2009, 2014, 2016b). The genus *Arostrilepis* has been recently shown to contain at least 13 genetically and morphologically distinguishable species in high latitudes of Eurasia and North America (Makarikov et al., 2012, 2013a; Makarikov and Hoberg, 2016).

New taxa were identified from all major geographic regions surveyed. In the case of birds, the Neotropics remain a important source of novel cestode taxa, largely because of the rich diversity of the candidate host taxa and comparatively limited number of previous survey work that has been done in this region. However non-tropical areas—even those with a cold climate and relatively low candidate host diversity—such as Chilean Patagonia, were found to be home to a surprisingly diverse and very poorly known cestode fauna. We thus recommend that such regions should not be overlooked in future avian cestode surveys.

The unknown diversity of cestodes of mammals is likely to be high in all areas of the world. For example, the single Luzon island of the Philippine archipelago sampled as part of the PBI project was found to be home to a remarkably high number of new species of *Hymenolepis* from rodents; in fact that number equals the total number of species of the genus known so far from whole continents like Eurasia or North America (Makarikov et al., 2013b, 2015a). Considering that large regions of the planet and a very large number of small mammals have yet to be examined for cestodes, we anticipate that the number of tapeworms described from these hosts to continue to grow steadily. This is true even in those regions where a strong parasitological tradition exists, as shown by our results from Russian and North American collections. However, further exploration in tropical regions where mammal parasite faunas remain poorly known, especially in Asia, is likely to yield substantial additional novelty.

Beyond the discovery of new taxa, specimens collected on our PBI expeditions facilitated the redescription and revision of numerous cyclophyllidean taxa. This was especially important because the descriptions of most of the species described in the 19th and the first half of the 20th century were based on single specimens, often collected by non-specialists, and improperly fixed and preserved. As consequence, descriptions based on these specimens are frequently vague and do not allow morphological interpretations according to current taxonomic standards. The newly collected material was of extremely high quality as it was fixed, preserved, and mounted according to a standardized protocol. It is of high scientific value, since taxonomic revisions and redescriptions are a substantial part of the work associated with understanding the global cestode diversity.

The majority of the samples collected and preserved for morphological studies was complemented by specimens preserved for molecular analyses. In combination, our collections yielded the most diverse molecular tissue collection of cyclophyllidean cestodes in existence, with over 340 specimens representing over 250 species. These specimens have been, and will continue to be, essential for confirming species identifications and identifying cryptic species. In a larger context, apart from the Gyrocoeliinae needing to be extracted from the Dioicocestidae, the paraphyly of the Anoplocephalidae, and possibly also of the Paruterinidae, our molecular results, to date, confirm the validity of the majority of the morphologically defined cyclophyllidean families, and preliminarily support a sister group relationship between the Mesocestoididae and all other Cyclophyllidea. The molecular data generated over the course of the PBI project, in conjunction with almost complete mitochondrial genome data for key lineages, will be crucial for strengthening the phylogenetic framework and enabling the study of cyclophyllidean evolution at a scale that was not possible before the implementation of this project.

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TABLE 1. List of 437 valid cyclophyllidean genera by family. New taxa resulting from PBI project activities indicated in bold.

VALID HIGHER TAXA

FAMILY ACOLEIDAE FUHRMANN, 1899 [2 GENERA]
- *Acoleus* Fuhrmann, 1899
- *Diplophallus* Fuhrmann, 1900

FAMILY AMABILIIDAE BRAUN, 1900 [11 GENERA]
- *Amabilia* Diamare, 1893
- *Decarabia* Konyaev & Gulyaev, 2005
- *Diporotaenia* Spasskaya, Spasskii & Borgarenko, 1971
- *Isezhia* Gulyaev & Koyaev, 2004
- *Joyeuxilepis* Spasskii, 1947
- *Laterorchites* Fuhrmann, 1932
- *Mircia* Konyaev & Gulyaev, 2006
- *Pseudoschistotaenia* Fotedar & Chishti, 1976
- *Ryjikovilepis* Gulyaev & Tolkacheva, 1987
- *Schistotaenia* Cohn, 1900
- *Tatria* Kowalewski, 1904

FAMILY ANOPLOCEPHALIDAE BLANCHARD, 1891 [81 GENERA]
- Subfamily Anoplocephalinae Blanchard, 1891
  - *Afrobaeria* Haukisalmi, 2008
  - ***Afrojoyeuxia* Haukisalmi, 2013**
  - *Andrya* Railliet, 1893
  - *Anoplocephala* Blanchard, 1848
  - *Anoplocephaloides* Baer, 1923
  - *Aporina* Fuhrmann, 1902
  - ***Arctocestus* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
  - ***Beringitaenia* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
  - *Bertiella* Stiles & Hassell, 1902
  - *Bulbutaenia* Beveridge, 1994
  - ***Chionocestus* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
  - *Cittotaenia* Riehm, 1881
  - ***Cookiella* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
  - *Crossotaenia* Mahon, 1954
  - *Ctenotaenia* Railliet, 1893

- *Diandrya* Darrah, 1930
- *Diuterinotaenia* Gvozdev, 1961
- ***Douthittia* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
- *Ectopocephalium* Rausch & Ohbayashi, 1974
- *Equinia* Haukisalmi, 2009
- ***Eurotaenia* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
- *Flabelloskrjabinia* Spasskii, 1951
- *Gallegoides* Tenora & Mas-Coma, 1978
- *Genovia* Haukisalmi, 2009
- ***Gulyaevia* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
- *Hemiparonia* Baer, 1925
- *Hokkaidocephala* Tenora, Gulyaev & Kamiya, 1999
- ***Hunkeleriella* Haukisalmi, 2013**
- *Killigrewia* Meggitt, 1927
- ***Lemminia* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
- *Leporidotaenia* Genov, Murai, Georgiev & Harris, 1990
- *Marmotocephala* Gvozdev, Zhigileva & Gulyaev, 2004
- *Microcephaloides* Haukisalmi, Hardman, Hardman, Rausch & Henttonen, 2008
- ***Microticola* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
- *Moniezia* Blanchard, 1891
- *Moniezoides* Fuhrmann, 1918
- *Monoecocestus* Beddard, 1914
- *Mosgovoyia* Spasskii, 1951
- *Neandrya* Haukisalmi & Wickström, 2005
- *Neoctenotaenia* Tenora, 1976
- *Parandrya* Gulyaev & Chechulin, 1996
- *Paranoplocephala* Lühe, 1910 (syn. *Aprostatandrya* Kirshenblat, 1938)
- *Paranoplocephaloides* Gulyaev, 1996
- *Parasciurotaenia* Haukisalmi, 2009
- *Paronia* Diamare, 1900
- ***Phascolocestus* Beveridge, 2014**
- *Phascolotaenia* Beveridge, 1976
- *Progamotaenia* Nybelin, 1917
- *Pseudocittotaenia* Tenora, 1976
- *Pulluterina* Smithers, 1954
- ***Rauschoides* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
- ***Rodentocestus* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
- *Schizorchis* Hansen, 1948
- *Stringopotaenia* Beveridge, 1978
- ***Tenoraia* Haukisalmi, Hardman, Hoberg & Henttonen, 2014**
- *Triplotaenia* Boas, 1902
- *Triuterina* Fuhrmann, 1922
- *Viscachataenia* Denegri, Dophic, Elissondo & Beveridge, 2003
- *Wallabicestus* Schmidt, 1975

Subfamily Linstowiinae Fuhrmann, 1907

- *Atriotaenia* Sandground, 1926
- *Cycloskrjabinia* Spasskii, 1951
- *Echidnotaenia* Beveridge, 1980
- *Gekkotaenia* Bursey, Goldberg & Kraus, 2005
- *Linstowia* Zschokke, 1899
- *Mathevotaenia* Akhumyan, 1946
- *Oochoristica* Lühe, 1898
- *Panceriella* Stunkard, 1969
- *Paralinstowia* Baer, 1927
- *Pritchardia* Gardner, Agustín Jimenez & Campbell, 2013
- *Sinaiotaenia* Wertheim & Greenberg, 1971
- *Tupaiataenia* Schmidt & File, 1977
- *Witenbergitaenia* Wertheim, Schmidt & Greenberg, 1986

- Subfamily Inermicapsiferinae Lopez-Neyra, 1943
  - *Inermicapsiper* Janicki, 1910
  - *Metacapsifer* Spasskii, 1951
  - *Pericpasifer* Spasskii, 1951
  - *Thysanotaenia* Beddard, 1911
- Subfamily Thysanosomatinae Fuhrmann, 1907
  - *Avitellina* Gough, 1911
  - *Stilesia* Ralliet, 1893
  - *Thysaniezia* Skryabin, 1926
  - *Thysanosoma* Diesing, 1835
  - *Wyominia* Scott, 1941

FAMILY CATENOTAENIIDAE SPASSKII, 1950 [6 GENERA]

- Subfamily Catenotaeniinae Spassky, 1950
  - *Catenotaenioides* Haukisalmi, Hardman & Henttonen, 2010
  - *Catenotaenia* Janicki, 1904
  - *Hemicatenotaenia* Tenora, 1977
  - *Pseudocatenotaenia* Tenora, Mac-Coma, Murai & Feliu, 1980
- Subfamily Skrjabinotaeniinae Genov & Tenora, 1979
  - *Meggittina* Lynsdale, 1953
  - *Skrjabinotaenia* Akhumyan, 1946

FAMILY DAVAINEIDAE BRAUN, 1900 [37 GENERA]

- Subfamily Davaineinae Braun, 1900
  - *Abuladzugnia* Spasskii, 1973
  - *Baerfainia* Yamaguti, 1959
  - *Calostaurus* Sanders, 1957
  - *Cotugnia* Diamare, 1893
  - *Davainea* Blanchard, 1891
  - *Davaineoides* Fuhrmann, 1920
  - *Delamuretta* Spasskii, 1977
  - *Demidovella* Spasskii & Spasskaya, 1976
  - *Diorchiraillietina* Yamaguti, 1959
  - *Dollfusoquenta* Spasskii, 1973
  - *Fernandezia* López-Neyra, 1936
  - *Fuhrmannetta* Stiles & Orleman, 1926
  - *Gvosdevinia* Spasskii, 1973
  - *Houttuynia* Furhmann, 1920
  - *Idiogenoides* López-Neyra, 1929
  - *Manitaurus* Spasskaya & Spasskii, 1971
  - *Metadavainea* Baer & Fain, 1955
  - *Multicotugnia* Lópex-Neyra, 1943
  - *Numidella* Spasskaya & Spasskii, 1971
  - *Ophryocotyle* Friis, 1870
  - *Ophryocotyloides* Fuhrmann, 1920
  - *Ophryocotylus* Srivastava & Capoor, 1977
  - *Paroniella* Fuhrmann, 1920
  - *Paspalia* Spasskaya & Spasskii, 1971
  - *Pentocoronaria* Matevosyan & Movsesyan, 1966
  - *Pluviantaenia* Jones, Khalil & Bray, 1992
  - *Porogynia* Railliet & Henry, 1909
  - *Raillietina* Fuhrmann, 1920
  - *Skrjabinia* Fuhrmann, 1920
  - *Soninotaurus* Spasskii, 1973
  - *Vadifresia* Spasskii, 1973
- Subfamily Idiogeninae Fuhrmann, 1907
  - *Chapamania* Monticelli, 1893
  - *Idiogenes* Krabbe, 1868
  - *Otiditaenia* Beddard, 1912
  - *Pseudoidiogenes* Movsesyan, 1971

Satyanarayana Khan, 1984
Sphyroncotaenia Ransom, 1911

FAMILY DILEPIDIDAE FUHRMANN, 1907 [90 GENERA]

Acanthocirrus Fuhrmann, 1907
Aelurotaenia Cameron, 1928
Alcataenia Spasskaya, 1971
Alproma Spasskii, 1982
Amoebotaenia Cohn, 1899
Angularella Strand, 1928
Anomolepis Spasskii, Yurpalova & Kornyushin, 1968
Anomotaenia Cohn, 1900
Apokrimi Bona, 1994
Apoliga Bona, 1994
Arctotaenia Baer, 1956
Arlenelepis Georgiev & Vaucher, 2004
Arostellina Neiland, 1955
Bakererpes Rausch, 1947
Birovilepis Spasskii, 1975
Bonaia Mariaux & Vaucher, 1990
Bucerolepis Spasskii & Spasskii, 1967
Burhinotaenia Spasskii & Spasskaya, 1965
Capsulata Sandeman, 1959
Chimaerula Bona, 1994
Chitinorecta Meggitt, 1927
Choanotaenia Railliet, 1896
Cinclotaenia Macy, 1973
Cotylorhipis Blanchard, 1909
Cuculincola Bona, 1994
Dictymetra Clark, 1952
Dilepidoides Spasskii & Spasskaya, 1954
Dilepis Weinland, 1858
Eburneotaenia Bona, 1994
Echinotaenia Mokhehle, 1951
Emberizotaenia Spasskaya, 1970
Ethiopotaenia Mettrick, 1961
Eugonodaeum Beddard, 1913
Eurycestus Clark, 1954
Fuhrmannolepis Spasskii & Yurpalova, 1967
***Gibsonilepis* Dimitrova, Mariaux & Georgiev, 2013**
Glanduluncinata Bona, 1994
Gruitaenia Spasskii, Borgarenko & Spasskya, 1971
Hepatocestus Bona, 1994
Himantaurus Spasskaya & Spasskii, 1971
Hirundinicola Birova-Volosinovicova, 1969
Hunkeleria Spasskii, 1992
Imparmargo Davidson, Doster & Prestwood, 1974
Ivritaenia Singh, 1962
Kintneria Spasskii, 1968
Kotlanolepis Murai & Georgiev, 1987
Kowalewskiella Baczynska, 1914
Krimi Burt, 1944
Laritaenia Spasskaya & Spasskii, 1971
Lateriporus Fuhrmann, 1907
Liga Weinland, 1857
Malika Woodland, 1929
Megacirrus Beck, 1951
Megalacanthus Moghe, 1926
Mirandula Sanders, 1956

Molluscotaenia Spasskii & Andreiko, 1971
Monoliga Bona, 1994
Monopylidium Fuhrmann, 1899
Monosertum Bona, 1994
Multitesticulata Meggitt, 1927
Neoliga Singh, 1952
Neovalipora Baer, 1962
Neyralla Johri, 1955
Nototaenia Jones & Williams, 1967
Onderstepoortia Ortlepp, 1938
Ovosculpta Bona, 1994
Paraliga Belopolskaya & Kulachkova, 1973
Paricterotaenia Fuhrmann, 1932
Parorchites Fuhrmann, 1932
Platyscolex Spasskaya, 1962
Polycercus Villot, 1883
Prochoanotaenia Meggitt, 1924
Pseudangularia Burt, 1938
Pseudochoanotaenia Burt, 1938
Ptilotolepis Spasskii, 1969
Rallitaenia Spasskii & Spasskaya, 1975
Rauschitaenia Bondarenko & Tomilovskaja, 1979
Reticulotaenia Hoberg, 1985
Sacciuterina Matevosyan, 1963
Sobolevitaenia Spasskaya & Makarenko, 1965
Spasskytaenia Oshmarin, 1956
Spasspasskya Bona, 1994
Spiniglans Yamaguti, 1959
Spinilepis Oshmarin, 1972
Spreotaenia Spasskii, 1969
Stenovaria Spasskii & Borgarenko, 1973
Trichocephaloidis Sinitzin, 1896
Tubanguiella Yamaguti, 1959
Unciunia Skrjabin, 1914
Vitta Burt, 1938

FAMILY DIOICOCESTIDAE SOUTHWELL, 1930 [5 GENERA]
Subfamily Dioicocestinae Southwell, 1930
Dioicocestus Fuhrmann, 1900
Subfamily Gyrocoeliinae Yamaguti, 1959
Gyrocoelia Fuhrmann, 1899
Infula Burt, 1939
Shipleya Fuhrmann, 1908
Echinoshipleya Tolkacheva, 1979

FAMILY DIPYLIDIIDAE RAILLIET, 1896 [3 GENERA]
Dipylidium Leuckart, 1863
Diplopylidium Beddard, 1913
Joyeuxiella Fuhrmann, 1935

FAMILY GRYPORHYNCHIDAE SPASSKII & SPASSKAYA, 1973 [16 GENERA]
Amirthalingamia Bray, 1974
Ascodilepis Guildal, 1960
Baerbonaia Deblock, 1966
Bancroftiella Johnston, 1911
Clelandia Johnston, 1909
Cyclorchida Fuhrmann, 1907
Cyclustera Fuhrmann, 1901
Dendrouterina Fuhrmann, 1912
Glossocercus Chandler, 1935
Mashonalepis Beverley-Burton, 1960

Neogryporhynchus Baer & Bona, 1960
Paradilepis Hsü, 1935
Parvitaenia Burt, 1940
Proorchida Fuhrmann, 1908
Proparadilepis Kornyushin & Greben, 2014
Valipora Linton, 1927

FAMILY HYMENOLEPIDIDAE PERRIER, 1897 [130 GENERA]
Allohymenolepis Yamaguti, 1956
Amazilolepis Schmidt & Dailey, 1992
Amphipetrovia Spasskii & Spasskaya, 1954
Anatinella Spasskii & Spasskaya, 1954
Aploparaksis Clerc, 1903
Armadolepis Spasskii, 1954
Armadoskrjabinia Spasskii & Spasskaya, 1954
Arostrilepis Mas-Coma & Tenora, 1997
Arvicolepis Makarikov, Gulyaev & Chechulin, 2005
Avocettolepis Spasskii & Kornyushin, 1971
Biglandatrium Spasskaya, 1961
Blarinolepis Tkach & Kornyushin, 1997
Branchiopodataenia Bondarenko & Kontrimavichus, 2004
Calixolepis Macko & Hanzelova, 1997
Capiuterilepis Oschmarin, 1962
Chimaerolepis Spasskii & Spasskaya, 1972
Chitinolepis Baylis, 1926
Cladogynia Baer, 1938
Cloacotaenia Wolffhügel, 1938
***Colibrilepis* Widmer, Georgiev & Mariaux, 2013**
Confluaria Ablasov in Spasskaya, 1966
Coronacanthus Spasskii, 1954
Cryptocotylepis Skrjabin & Mathevossian, 1948
Debloria Spasskii, 1975
Dicranotaenia Railliet, 1892
Diorchilepis Lykova, Gulyaev, Melnikova & Karpenko, 2006
Diorchis Clerc, 1903
Diplogynia Baer, 1925
Diploposthe Jacobi, 1896
Ditestolepis Soltys, 1952
Dollfusilepis Vasileva, Georgiev & Genov, 1998
Drepanidotaenia Railliet, 1892
Dubininolepis Spasskii & Spasskaya, 1954
Echinatrium Spasskii & Yurpalova, 1965
Echinocotyle Blanchard, 1891
Echinolepis Spasskii & Spasskaya, 1954
Echinorhynchotaenia Fuhrmann, 1909
Ecrinolepis Spasskii & Karpenko, 1983
Fimbriaria Fröhlich, 1802
Fimbriariella Wolffhügel, 1936
Fimbriarioides Fuhrmann, 1932
Fimbriasacculus Alexander & McLaughlin, 1996
Flamingolepis Spasskii & Spasskaya, 1954
Fuhrmannacanthus Spasskii, 1966
Gastrotaenia Wolffhügel, 1938
Geraldolepis Czapliński & Vaucher, 1994
Globarilepis Bondarenko, 1966
Gulyaevilepis Kornienko & Binkienė, 2014
Gvosdevilepis Spasskii, 1953
Hamatolepis Spasskii, 1962
Helicoductus Deblock & Canaris, 2001

Hilmylepis Skrjabin & Mathevossian, 1942
Hispaniolepis López-Neyra, 1942
Hunkelepis Czapliński & Vaucher, 1994
Hymenandrya Smith, 1954
Hymenolepis Weinland, 1858
Jardugia Southwell & Hilmy, 1929
Lineolepis Spasskii, 1959
Lobatolepis Yamaguti, 1959
Lockerrauschia Yamaguti, 1959
Lophurolepis Spasskii, 1973
Mackoja Kornyushin, 1983
Mackolepis Spasskii, 1962
Mathevolepis Spasskii, 1948
Matiaraensis Dixit & Capoor, 1988
Microsomacanthus López-Neyra, 1942
Milina van Beneden, 1873
Monogynolepis Czapliński & Vaucher, 1994
Monorcholepis Oshmarin, 1961
Monotestilepis Gvosdev, Maksimova & Kornyushin, 1971
Nadejdlepis Spasskii & Spasskaya, 1954
Nematoparataenia Maplestone & Southwell, 1922
Neodiorchis Bilqees & Fatima, 1984
Neoligorchis Johri, 1960
Neomylepis Tkach, 1998
Neoskrjabinolepis Spassky, 1947
Nomadolepis Makarikov, Gulyaev & Krivopalov, 2010
Novobrachylepis Özdikmen, 2010
Octacanthus Spasskii & Spasskaya, 1954
Oligorchis Fuhrmann, 1906
Ortleppolepis Spasskii, 1965
Oschmarinolepis Spasskii & Spasskaya, 1954
Parabisaccanthes Maksimova, 1963
Paradicranotaenia López-Neyra, 1943
Parafimbriaria Voge & Read, 1954
Paramilina Makarikova, Gulyaev, Tiunov & Feng, 2010
Paraoligorchis Wason & Johnson, 1977
Pararetinometra Stock & Holmes, 1982
Pararodentolepis Makarikov & Gulyaev, 2009
Passerilepis Spasskii & Spasskaya, 1954
Pentorchis Meggitt, 1927
Podicipitilepis Yamaguti, 1959
Polytestilepis Oshmarin, 1960
Potorolepis Spasskii, 1994
Profimbriaria Wolffhügel, 1936
Protogynella Jones, 1943
Pseudandrya Fuhrmann, 1943
Pseudanoplocephala Baylis, 1927
Pseudhymenolepis Joyeux & Baer, 1935
Pseudobotrialepis Schaldybin, 1957
Pseudodiorchis Skrjabin & Mathevossian, 1948
Pseudoligorchis Johri, 1934
Relictolepis Gulyaev & Makarikov, 2007
Retinometra Spasskii, 1955
Rodentolepis Spasskii, 1954
***Sawadalepis* Makarikova & Makarikov, 2013**
Schmelzia Yamaguti, 1959
Skrjabinacanthus Spasskii & Morozov, 1959
Skrjabinoparaxis Krotov, 1949
Sobolevicanthus Spasskii & Spasskaya, 1954

Soricinia Spasskii & Spasskaya, 1954
Spasskylepis Schaldybin, 1964
Staphylepis Spasskii & Oschmarin, 1954
Staphylocystis Villot, 1877
Staphylocystoides Yamaguti, 1952
Sternolepis Dixit & Capoor, 1988
Sudarikovina Spasskii, 1951
Talpolepis Gulyaev & Melnikova, 2005
Thaumasiolepis Mariaux & Vaucher, 1989
Triodontolepis Yamaguti, 1959
Tschertkovilepis Spasskii & Spasskaya, 1954
Urocystis Villot, 1880
Vampirolepidoides Yamaguti, 1959
Vampirolepis Spasskii, 1954
Variolepis Spasskii & Spasskaya, 1954
Vaucherilepis Tkach, Vasileva & Genov, 2003
Vigisolepis Mathevossian, 1945
Vogelepis Czapliński & Vaucher, 1994
Wardium Mayhew, 1925
Wardoides Spasskii, 1963

FAMILY MESOCESTOIDIDAE PERRIER, 1897 [2 GENERA]
  Subfamily Mesocestoidinae Perrier, 1897
    Mesocestoides Vaillant, 1863
  Subfamily Mesogyninae Tschertkova & Kosupko, 1977
    Mesogyna Voge, 1952

FAMILY METADILEPIDIDAE SPASSKII, 1959 [10 GENERA]
Cracticotaenia Spasskii, 1966
Hamatofuhrmania Spasskii, 1969
Mariauxilepis Georgiev & Vaucher, 2003
Metadilepis Spasskii, 1949
Proparuterina Fuhrmann, 1911
Pseudadelphoscolex Mariaux, Bona & Vaucher, 1992
Schmidneila Spasskii & Spasskaya, 1973
Skrjabinoporus Spasskii & Borgarenko, 1960
Urutaulepis Georgiev & Vaucher, 2003
Yapolepis Mariaux, 1991

FAMILY NEMATOTAENIIDAE LÜHE, 1910 [5 GENERA]
Bitegmen Jones, 1987
Cylindrotaenia Jewell, 1916
Distoichometra Dickey, 1921
Lanfrediella Melo, Giese, Furtado, Soares, Gonçalves, Vallinoto & Santos, 2011
Nematotaenia Lühe, 1899

FAMILY PARUTERINIDAE FUHRMANN, 1907 [24 GENERA]
Anonchotaenia Cohn, 1900
Ascometra Cholodkowsky, 1912
Biuterina Fuhrmann, 1902
Cladotaenia Cohn, 1901
***Cucolepis* Phillips, Mariaux & Georgiev, 2012**
Culcitella Fuhrmann, 1906
Dictyterina Spasskii in Spasskaya & Spasskii, 1971
Francobona Georgiev & Kornyushin, 1994
Laterotaenia Fuhrmann, 1906
Lyruterina Spasskaya & Spasskii, 1971
Matabelea Mettrick, 1963
Metroliasthes Ransom, 1900
Mogheia López-Neyra, 1944
Neyraia Joyeux & Timon-David, 1934
Notopentorchis Burt, 1938

Octopetalum Baylis, 1914
Orthoskrjabinia Spasskii, 1947
Paruterina Fuhrmann, 1906
Parvirostrum Fuhrmann, 1908
Rhabdometra Cholodkowsky, 1906
Spasskyterina Kornyushin, 1989
Sphaeruterina Johnston, 1914
Triaenorhina Spasskii & Shumilo, 1965
Troguterina Spasskii, 1991

FAMILY PROGYNOTAENIIDAE FUHRMANN, 1936 [6 GENERA]
Subfamily Progynotaeniinae Fuhrmann, 1936
Leptotaenia Cohn, 1901
Paraprogynotaenia Rysavy, 1966
Progynotaenia Fuhrmann, 1909
Proterogynotaenia Fuhrmann, 1911
Subfamily Gynandrotaeniinae Fuhrmann, 1936
Gynandrotaenia Fuhrmann, 1936
Thomasitaenia Ukoli, 1965

FAMILY TAENIIDAE LUDWIG, 1886 [4 GENERA]
Subfamily Taeniinae Stiles, 1896
Hydatigera Lamarck, 1816
Taenia Linnaeus, 1758
***Versteria* Nakao, Lavikainen, Iwaki, Haukisalmi, Konyaev, Oku, Okamoto & Ito, 2013**
Subfamily Echinococcinae Abuladze, 1960
Echinococcus Rudolphi, 1801

FAMILY *INCERTAE SEDIS* [5 GENERA]
Quentinia Spasskii, 1969
Deltokeras Meggitt, 1927
Anoplotaenia Beddard, 1911
Dasyurotaenia Beddard, 1912
Insinuarotaenia Spasskii, 1948

7

Diphyllidea van Beneden in Carus, 1863

By

Janine N. Caira[1], Verónica A. Ivanov, Kirsten Jensen,
and Fernando P. L. Marques

DIPHYLLIDEA AS THEY WERE KNOWN PRIOR TO THE PBI PROJECT

Diversity and Classification. The Diphyllidea were established in 1863 by van Beneden in Carus (1863). Although their ordinal status has been questioned by some authors (e.g., Lühe, 1910; Southwell, 1925; Wardle and McLeod, 1952; Wardle et al., 1974), the order has been accepted by many others (e.g., Hyman, 1951; Rees, 1959; Yamaguti, 1959; Joyeux and Baer, 1961; Schmidt, 1986; Khalil, 1994; Ivanov and Hoberg, 1999; Tyler, 2006). The group initially housed only the family Echinobothriidae Perrier, 1897 with the single genus *Echinobothrium* van Beneden, 1849. In 1959, it was expanded by Rees to include the Ditrachybothridiidae Rees, 1959 for the enigmatic, unarmed, *Ditrachybothridium* Rees, 1959. It was further expanded by Khalil and Abdul-Salam (1989) to include the new family Macrobothridiidae Khalil & Abdul-Salam, 1989, erected to accommodate their new genus *Macrobothridium* Khalil & Abdul-Salam, 1989. However, *Macrobothridium* was later synonymized with *Echinobothrium* by Tyler (2006), and thus, so too were the Macrobothridiidae with the Echinobothriidae. Not unexpectedly, the examination of additional host taxa over time has increased the number of valid species. Whereas Schmidt (1986) recognized 21, Ivanov and Hoberg (1999) recognized 31, and Tyler (2006) recognized 34 valid diphyllidean species. It is beyond the scope of this chapter to revisit the complete taxonomic history of the order, however readers are referred to the comprehensive treatment of its history by Tyler (2006).

Morphology. In large part as a result of the works of Ivanov and Hoberg (1999) and Tyler (2006), diphyllidean morphology was relatively well understood prior to the PBI project. The scolex bears a single dorsal and single ventral bothrium (Figs. 1A, B, 2A). Among the key features used to distinguish most of its members from the other bothriate eucestode orders (i.e., the Bothriocephalidea, Diphyllobothriidea, Haplobothriidea, and Trypanorhyncha) is the presence of unique scolex armature. That armature may consist of four distinct elements: apical hooks (Fig. 1C, D), lateral hooklets (Fig. 1C, D), cephalic peduncle spines (Fig. 1A, B), and a corona of spines (Fig. 3H) between the apical organ and bothria. These components appear to have the potential to evolve independently from one another because taxa exhibiting different combinations of the presence or absence of each of these components are known.

Diphyllideans are generally small worms with relatively few proglottids (Fig. 1H). By far the largest valid species is *Echinobothrium rhynchobati* (Khalil & Abdul-Salam, 1989) Tyler, 2006, which attains a maximum length of 43 mm with 115 proglottids (see Khalil and Abdul-Salam, 1989). Diphyllideans are typically apolytic, shedding gravid proglottids from the strobila. Distinctive elements of the proglottid anatomy of diphyllideans include a gential

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[1] Corresponding author (janine.caira@uconn.edu)

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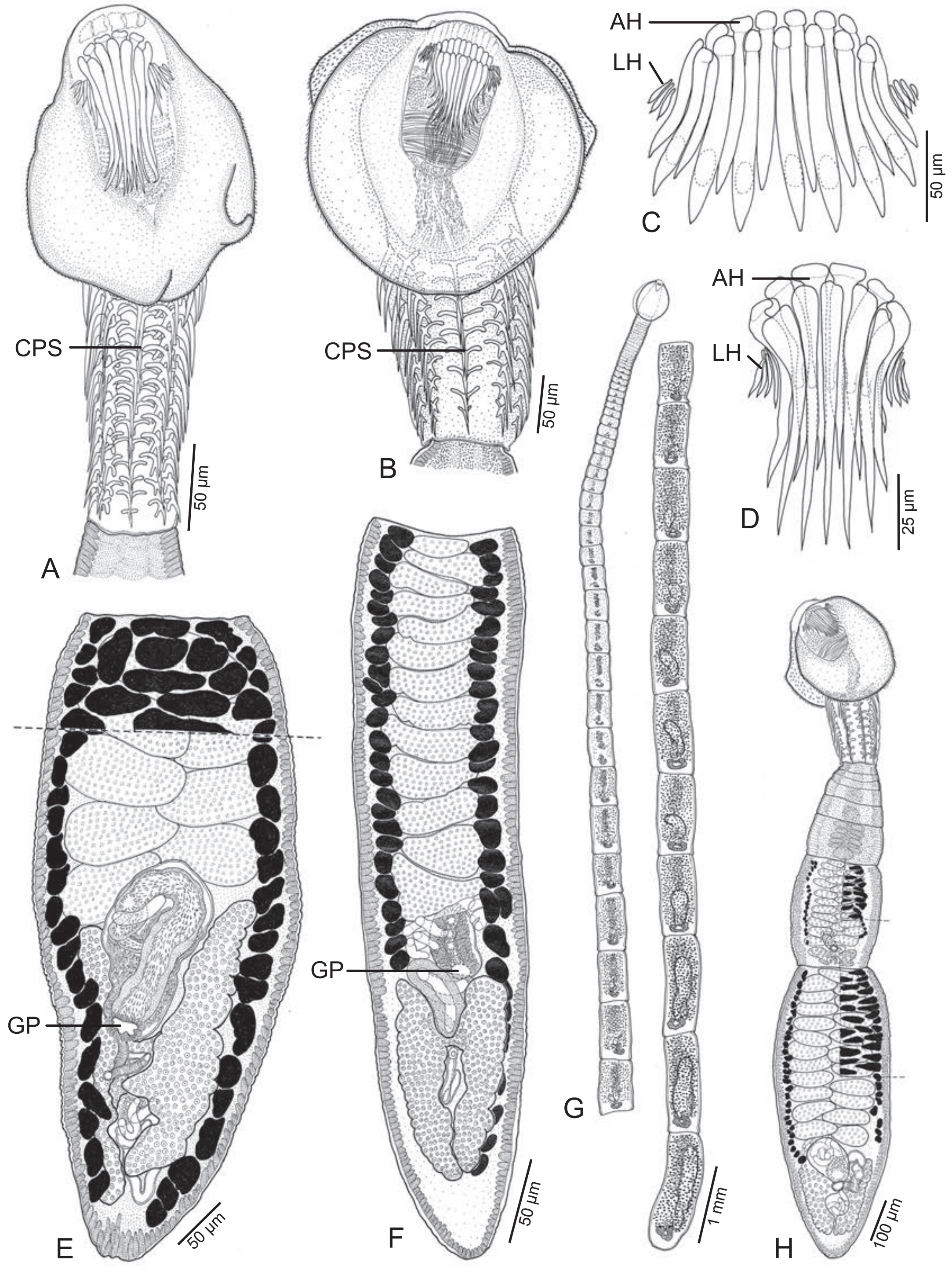
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LH
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GP
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F
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100 µm
H

pore that is medio-ventral in position (Fig. 1E, F), a vagina that opens posterior to the cirrus-sac (Fig. 1E), an ovary that is bilobed in cross-section, testes that are entirely anterior to the ovary (Fig. 1E, F), a cirrus covered with spinitriches, vitelline follicles that are either arranged in lateral bands (Fig. 1F) or are circumcortical (Fig. 1E), a saccate uterus that lacks a uterine pore, and eggs that may bear polar filaments. Scolex spinithrix diversity includes, palmate (Fig. 2E–G), pectinate (Fig. 2D), trifid (Fig. 2I), and trifurcate (Fig. 2C, H) forms (*sensu* Chervy [2009]). These are distributed on the different surfaces of the scolex in patterns that differ among species. The surface of the cephalic peduncle lacks spinitriches (Fig. 2B).

Diphyllideans are one of only two orders of elasmobranch-hosted cestodes in which key taxonomic features of the adult scolex develop in the metacestode in the final intermediate host. As a consequence, several species are known only from their crustacean (e.g., *E. benedeni* Ruszkowski, 1927 [see Ruszkowski, 1927]) or gastropod (e.g., *E. levicolle* Lespès, 1857 [see Lespés, 1857]; *E. nigracanthum* Reimer, 1975 [see Reimer, 1975]) intermediate hosts.

PHYLOGENETIC RELATIONSHIPS. Prior to 2008, diphyllidean phylogenetic relationships had been formally assessed based solely on phylogenetic analyses of morphological features (Ivanov and Hoberg, 1999; Tyler, 2006). Both studies included fairly broad representation of diphyllidean taxa (24 and 30 species, respectively). While the topologies resulting from the two studies were largely incongruent relative to one another, they provided important first insights into the evolutionary histories of the diphyllideans. For example, the trees resulting from both studies called into question the monophyly of *Echinobothrium* relative to *Macrobothridium*. Tyler's (2006) formal recognition of *Macrobothridium* as a junior synonym of *Echinobothrium* was based on this earlier work.

As a result of their efforts to identify metacestodes (specifically plerocerci) found parasitizing a deep-sea catshark (*Apristurus laurussonii* [Saemundsson]) and a skate (identified as resembling *Rajella bigelowi* [Stehmann]), Bray and Olson (2004) provided the first molecular phylogeny for the Diphyllidea. Although they treated only six members of the order, their results were intriguing and they were the first to suggest that *Echinobothrium* was not monophyletic with respect to *Ditrachybothridium*. They too found no support for the monophyly of *Macrobothridium* relative to *Echinobothrium*.

Although, historically a variety of different hypotheses have been postulated regarding the affinities of the Diphyllidea with respect to the eucestodes overall (see Hoberg et al., 1997; Ivanov and Hoberg, 1999), one of the most convincing scenarios was that of Hoberg et al. (1997), who found diphyllideans followed by trypanorhynchs to be early diverging groups relative to a clade consisting of the "higher tetrafossates" (Hoberg et al., 1997; p. 1129) (= acetabulate taxa). The early diverging position of the Diphyllidea relative to the acetabulate cestode orders was subsequently supported by the molecular analyses of Olson and Caira

◄—FIGURE 1. Line drawings of diphyllidean species. **(A)** Scolex of *Echinobothrium dougbermani* from *Rhinobatos annulatus* from South Africa (modified from Caira et al. [2013a]). **(B)** Scolex of *Andocadoncum meaganae* from *Leucoraja wallacei* from South Africa (modified from Abbott and Caira [2014]). **(C)** Apical hooks and lateral hooklets of *Echinobothrium joshuai* from *Cruriraja hulleyi* from South Africa (modified from Rodriguez et al. [2011]). **(D)** Apical hooks and lateral hooklets of *Echinobothrium yiae* from *Raja ocellifera* from Senegal (modified from Caira et al. [2013b]). **(E)** Terminal proglottid of *E. yiae* (modified from Caira et al. [2013b]); vitelline follicles indicated as circumcortical in anterior region of proglottid only. **(F)** Terminal proglottid of *E. dougbermani* (modified from Caira et al. [2013a]). **(G)** Whole worm of *Ahamulina catarina* from *Scyliorhinus haeckelii* from Brazil (modified from Marques et al. [2012]). **(H)** Whole worm of *Andocadoncum meganae* (modified from Abbott and Caira [2014]); vitelline follicles indicated as circumcortical in anterior quarter of proglottid only. *Abbreviations*: AH, apical hooks; CPS, cephalic peduncle spines; LH, lateral hooklets; GP, genital pore.

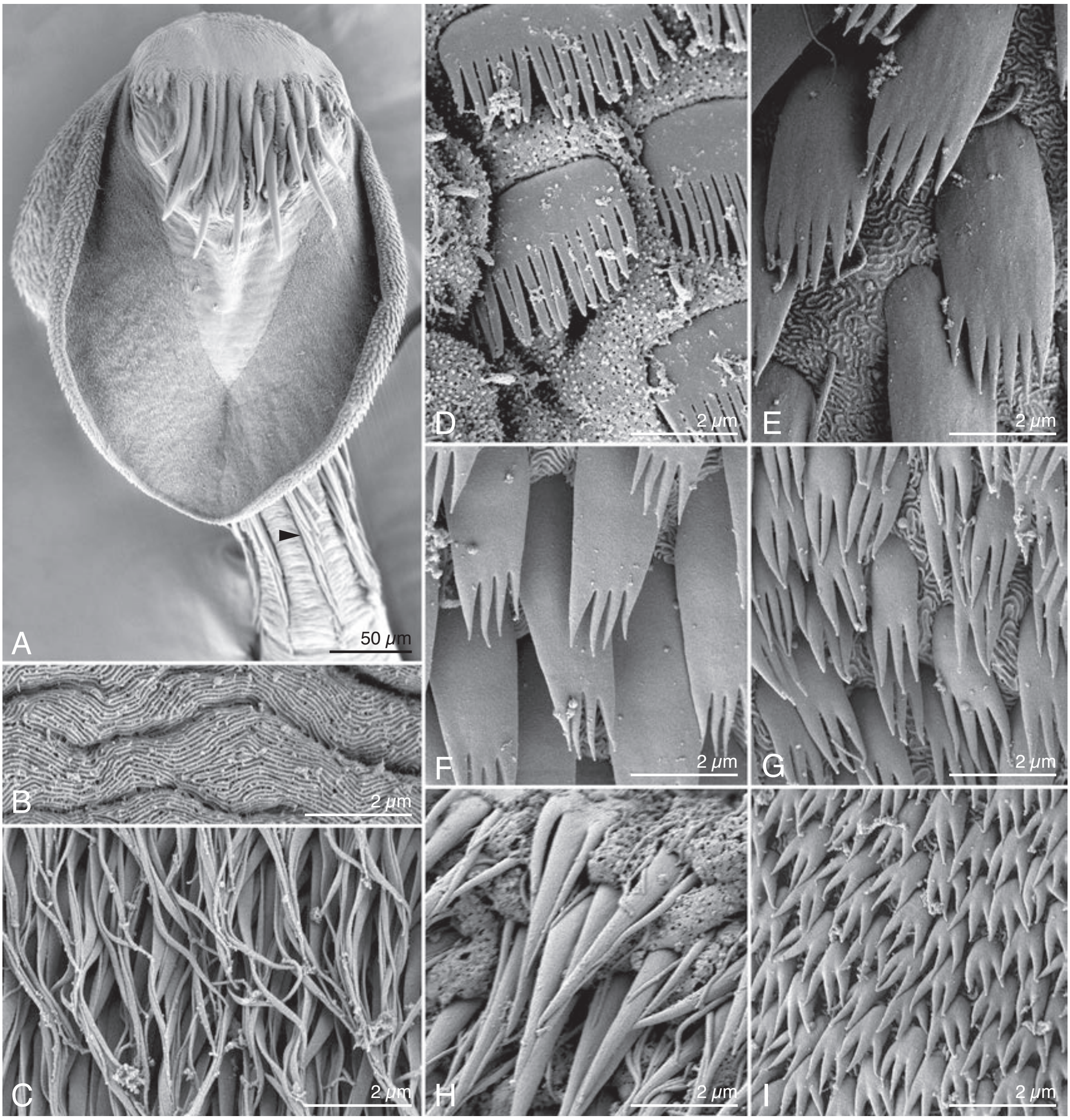

FIGURE 2. Scanning electron micrographs of scolex features of diphyllidean species. **(A)** Scolex of *Echinobothrium tetabuanense* from *Glaucostegus* cf. *typus* from Malaysian Borneo; arrowhead indicates cephalic peduncle spines. **(B)** Surface of cephalic peduncle between spines of *Echinobothrium dorothyae* from *Raja straeleni* from South Africa. **(C)** Distal surface of bothrium of *Echinobothrium dorothyae*. **(D)** Proximal surface of bothrium of *Echinobothrium hoffmanorum* from *Urobatis maculatus* from the Gulf of California. **(E)** Proximal surface of bothrium of *Echinobothrium yiae* from *Raja ocellifera* from Senegal (modified from Caira et al. [2013b]). **(F, G, I)** Proximal surface of different regions of bothrium of *Echinobothrium dorothyae* from *Raja straeleni* from South Africa (modified from Caira et al. [2013a]). **(H)** Distal bothrial surface of *Ditrachybothridium macrocephalum* (modified from Tyler [2006]).

(1999), Olson et al. (2001), and Waeschenbach et al. (2007). Even closer affinities between the diphyllideans and the trypanorhynchs were detected by Brabec et al. (2006) and Waeschenbach et al. (2007), both of whom found these orders to be sister taxa.

Host Associations. In 1986, Schmidt (1986; pg. 165) characterized diphyllideans as parasites of "rays," without mention of Rees's (1959) report of *Ditrachybothridium macrocephalum* Rees, 1959 from a catshark and two species of skates. Tyler (2006) provided a more detailed account of the host groups known to be parasitized by diphyllideans, which consisted of: the Triakidae Gray (houndsharks), the Pentanchidae Smith and "Scyliorhinidae" Gill (catsharks), the "Rhinobatidae" Müller & Henle (guitarfishes), rajiforms, *Rhinoptera* von Hasselt, *Aetobatus* Blainville, *Myliobatis* Cuvier, the Urotrygonidae Müller & Henle (American round stingrays), and the Dasyatidae Jordan (whiptail stingrays). In terms of the degree of host specificity, with only a few exceptions the diphyllideans are generally considered to exhibit oioxenous specificity (*sensu* Euzet and Combes [1980]) for their elasmobranch hosts (see Tyler, 2006). Nonetheless, the exceptions are worthy of further investigation, ideally using replicated specimens preserved for both morphological and molecular work. For example, Rees (1959) reported *Ditrachybothridium macrocephalum* from a catshark and two different species of skates. Ramadevi (1969) reported *Echinobothrium reesae* Ramadevi, 1969 from *Brevitrygon walga* (Müller & Henle) (as *Trygon walga* Müller & Henle) and *Himantura uarnak* (Gmelin) (as *Trygon uarnak* [Gmelin]). Tyler and Caira (1999) reported *Echinobothrium fautleyae* Tyler & Caira, 1999 from both *Rhinoptera steindachneri* Evermann & Jenkins and *Myliobatis californica* Gill, and Tyler (2001) reported *E. hoffmanorum* Tyler, 2001 from three sympatric species of *Urobatis* Garman.

Geographic Distribution. The cosmopolitan nature of the order has been recognized for some time. Indeed the map of diphyllidean distributions presented by Tyler (2006; fig. 145) serves to illustrate the truly global nature of the diphyllideans as they were known in 2006. The regions most conspicuously lacking records of the order were the waters of the northern Nearctic and Palearctic realms. While this may have reflected the lack of representation of this order from these regions, it may also be the result of a lack of sampling of elasmobranchs from these regions.

CURRENT STATUS OF THE DIPHYLLIDEA

Diversity and Classification. In total, 21 new species of diphyllideans have been described since 2008 (see Kuchta and Caira, 2010; Rodriguez et al., 2011; Haseli et al., 2012; Ivanov and Caira, 2012; Marques et al., 2012; Caira et al., 2013a, b; Ivanov and Caira, 2013; Abbott and Caira, 2014; Moghadam and Haseli, 2014; Haseli and Azad, 2015); 18 of these were the result of PBI efforts. The order now includes 59 valid species (see Table 3). The molecular analyses of Caira et al. (2013c) included 16 species that have not yet been described, but for which vouchers were deposited in the Lawrence R. Penner Parasitology (LRP) collection at the University of Connecticut to guide future descriptive work. Evidence of an additional 42 undescribed species exists among the specimens resulting from the collections from elasmobranchs we conducted over the course of the PBI project but that we have not yet had a chance to examine in detail. In combination, the described and undescribed material brings the total number of known diphyllidean species to almost 120 (see Tables 1, 2).

In an effort to develop a classification scheme that reflects monophyletic groups, and guided in part by the results of their molecular phylogenetic analyses, Caira et al. (2013c) substantially reconfigured the generic classification of the order. In addition to *Ditrachybothridium* (with 2 spp.) and *Echinobothrium* (with 33 spp.), the following four genera were erected: *Ahamulina* Marques, Jensen & Caira, 2012 (with 1 sp.), *Andocadoncum* Abbott & Caira, 2014 (with 1 sp.), *Coronocestus* Caira, Marques, Jensen, Kuchta & Ivanov, 2013 (with 6 spp.), and *Halysioncum* Caira, Marques, Jensen, Kuchta & Ivanov, 2013 (with 16 spp.). Differences in scolex armature

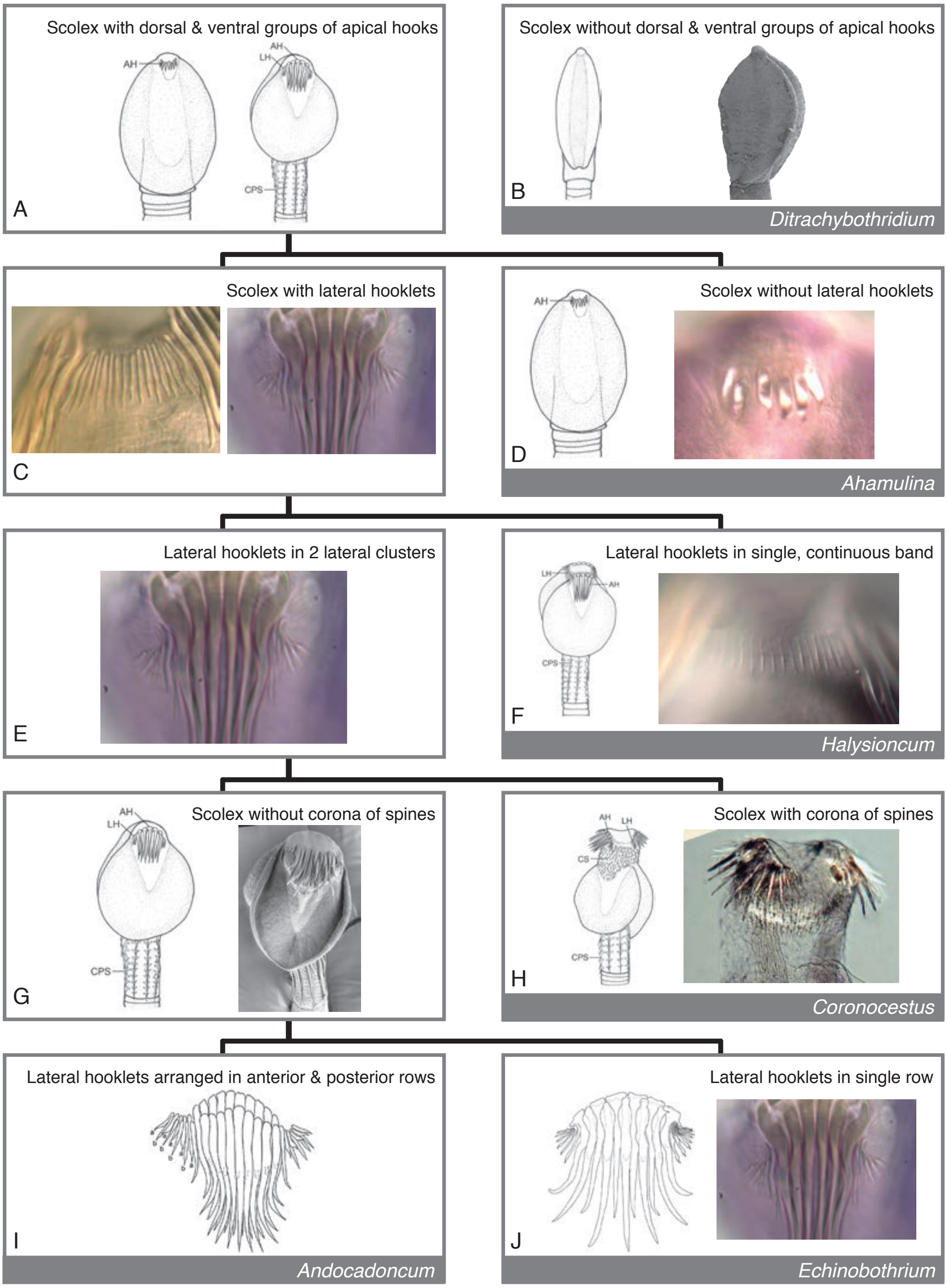

Figure 3. Pictoral key to scolex features of valid diphyllidean genera. *Abbreviations*: AH, apical hooks; CPS, cephalic peduncle spines; CS, corona of spines; LH, lateral hooklets.

serve as effective morphological features for distinguishing among the six genera. A key to these genera based on these features is provided in Figure 3. The features identified by Rees (1959) as unique to *Ditrachybothridium* remain viable in the context of the newly established generic novelty—the scolex of members of this genus lack all four elements of armature (Fig. 3B). *Ahamulina*, erected by Marques et al. (2012), lacks cephalic peduncle spines and lateral hooklets but possesses feeble dorsal and ventral groups of unarticulated hooks arranged in a single row (Fig. 3D). *Andocadoncum*, the most recently established genus (see Abbott and Caira, 2014), bears very elaborate scolex armature that consists of dorsal and ventral groups of articulating apical hooks that are arranged in alternating anterior (A) and posterior (B) rows, as well as two groups of lateral hooklets on each side of the dorsal and ventral groups of hooks arranged in one anterior (a) and one posterior (b) row (Fig. 3I), and eight columns of cephalic peduncle spines. Both the original (van Beneden, 1849) and subsequent (Tyler, 2006; Polyakova, 2015) concepts of *Echinobothrium* were refined by Caira et al. (2013c) to include only species that bear dorsal and ventral groups of articulating apical hooks that are arranged in alternating anterior and posterior rows as well as two groups of lateral hooklets that do not alternate in position (Fig. 3J). The scolex armature of species of *Halysioncum* most closely resembles that seen in species of *Echinobothrium*, differing only in that the lateral hooklets are arranged in a continuous row between the dorsal and ventral groups of hooks (Fig. 3F), rather than in two groups (Fig. 3E). Both Tyler (2006) and Kuchta and Caira (2010) noted that this feature might have greater taxonomic significance; the nature of that significance was not apparent until placed into a phylogenetic context by Caira et al. (2013c). *Coronocestus* was established by Caira et al. (2013c) for the species that bear the most complex scolex armature seen among the six diphyllidean genera—in addition to all of the elements exhibited by *Andocaduncum*, members of this genus bear a corona of spines surrounding the scolex immediately posterior to the apical hooks and lateral hooklets (Fig. 3H). However, a robust family-level classification for the order remains to be established. For lack of a better solution, all six genera were considered to belong to the single family Echinobothriidae by Caira et al. (2013c).

MORPHOLOGY. Among the most significant morphological discoveries over the course of the PBI project was the scolex armature seen in *Ahamulina*. In addition to being relativley large worms at 23–45 mm in length, the armature of the only member of this genus shows that the apical hooks can evolve independently from the lateral hooklets because *A. catarina* bears apical hooks but not lateral hooklets. Furthermore, whereas the apical hooks of all other hooked diphyllidean genera are arranged in anterior and posterior rows, those of *Ahamulina* are arranged in a single row, and unlike other diphyllidean hooked taxa, adjacent apical hooks do not articulate with one another. Recognition of the fact that the lateral hooklets in *Andocadoncum* are arranged in one anterior and one posterior row (Fig. 3I), rather than in a single row (Abbott and Caira, 2014) was also a novel discovery. However, careful study reveals a similar hooklet arrangement seen in species of *Coronocestus* (see Robinson, 1959; Ivanov, 1997; Ivanov and Lipshitz, 2006; Haseli et al., 2012). Essentially no novelty of note was discovered with respect to proglottid anatomy. Dallarés et al. (2015) provided substantial detail on the plerocerci and adults of specimens identified as *Ditrachybothridium macrocephalum* from the catshark *Galeus melastomus* Rafinesque and included the first description of the egg of a member of this genus.

The non-homology of diphyllidean hooks to those of other cestode groups seems apparent from their unique morphology and configuration relative to that of other armed cestode orders. The comparative amino acid profile information presented by Caira and Jensen (2014) provides compositional support for this lack of homology. In fact, their data provide particularly strong evidence that the hooks of diphyllideans are composed of different proteins from those of hooks of member of all other armed orders.

Phylogenetic Relationships. Caira et al. (2013c) generated the first comprehensive assessment of the phylogenetic relationships among the diphyllideans using molecular data. Their analyses were based on a combination of mitochondrial (COI) and nuclear (28S rDNA and 18S rDNA) sequence data generated for 31 diphyllidean (12 described and 19 then undescribed) species for which material fixed in ethanol for molecular work was available. Their results supported some of the affinities implied by previous work. For example, Ivanov and Hoberg (1999) found two of the three species included in their analysis that parasitize sharks and bear a corona of spines to group as sister taxa, noting that the corona may serve as a synapomorphy for a subclade of the diphyllideans that parasitize sharks. Caira et al. (2013c) invoked this feature as a synapomorphy for the clade of valid species that parasitize triakid-sharks that they assigned to their new genus *Coronocestus*. Similarly, Tyler's (2006) morphological analysis yielded a subclade consisting of the ten species bearing continuous bands of lateral hooklets. Caira et al. (2013c) identified this feature as a synapomorphy for their new genus *Halysioncum*. While the six subclades of diphyllideans assigned to genera by Caira et al. (2013c) were all reasonably well supported, their analyses included only a small proportion (12 of 59) of described diphyllidean species. The affinities postulated by their analyses would be interesting to explore in the context of much broader taxon sampling. The tree in Figure 4, which includes updated names of hosts and diphyllideans as appropriate, provides a summary of the groupings supported by the analyses of Caira et al. (2013c) and in so doing illustrates the high degree of uncertainty regarding diphyllidean interrelationships that remains.

We have resisted the temptation to assign the three main subclades of diphyllideans (i.e., species of *Halysionchum*, the shark-parasitizing groups + species of *Andocadoncum* and *Echinobothrium*) that emerged from the molecular phylogenetic analyses of Caira et al. (2013c) to families, not only because the support for them was weak, but more importantly because we have been unable to identify unambiguous morphological features that characterize each of these groups. Particularly problematic in this respect is the group that includes the shark-parastizing taxa, for this clade includes a full spectrum of morphologies from entirely naked (*Ditrachybothridium*) to fully armed (*Coronocestus*).

Although several of the molecular phylogenetic analyses focused on eucestode ordinal interrelationships have included representation of the Diphyllidea (e.g., Waeschenbach et al., 2012; Caira et al., 2014), the sister taxon to the Diphyllidea has yet to be identified with confidence. Waeschenbach et al. (2012) found weak support for the Trypanorhyncha as sister taxa to the Diphyllidea. Caira et al. (2014) found the Diphyllidea to group, but again with weak support, as the earliest diverging bothriate order subtending the large clade of acetabulate groups that were the focus of their study. In this context, it is interesting that Chervy (2009) called attention to the fact that one of the most distinctive forms of microtriches seen on the scolex of cestodes, referred to as palmate spinitriches, is found only in some diphyllideans and trypanorhynchs.

Host Associations. With respect to the degree of host specificity exhibited by diphyllideans, work conducted over the course of the PBI project (e.g., Kuchta and Caira, 2010; Caira et al., 2013c) lends further support to earlier assessments of the predominantly oioxenous nature of their associations. We concur with Tyler (2006) that many of the reports of diphyllidean species parasitizing greater then one species of host likely represent mixtures of species, but this requires confirmation. None of the 18 new species discovered as a result of

PBI project work were found parasitizing more than a single species of host, although Ivanov and Caira (2012) remarked that specimens potentially conspecific with *E. sematanensis* Ivanov & Caira, 2012 were found parasitizing a species of *Glaucostegus* (i.e., *G. typus* [Anonymous (Bennett), 1830]) other than the type host of that species, *Glaucostegus thouin* (Anonymous [Lacepède], 1798).

Intrigue remains surrounding the identity, and thus also the host specificity, of members of *Ditrachybothridium*. For example, while some authors have raised concerns about the conspecificity of specimens identified as *Ditrachybothridium macrocephalum* taken from a variety of catshark and skate species (e.g., Caira et al., 2013c), other authors (e.g., Dallarés et al., 2015) consider such specimens to be conspecific. As a result of the relatively simple morphology of members of this genus, molecular sequence data provide important insights for resolving this question. Indeed, Dallarés et al. (2015) provided partial 28S rDNA sequence

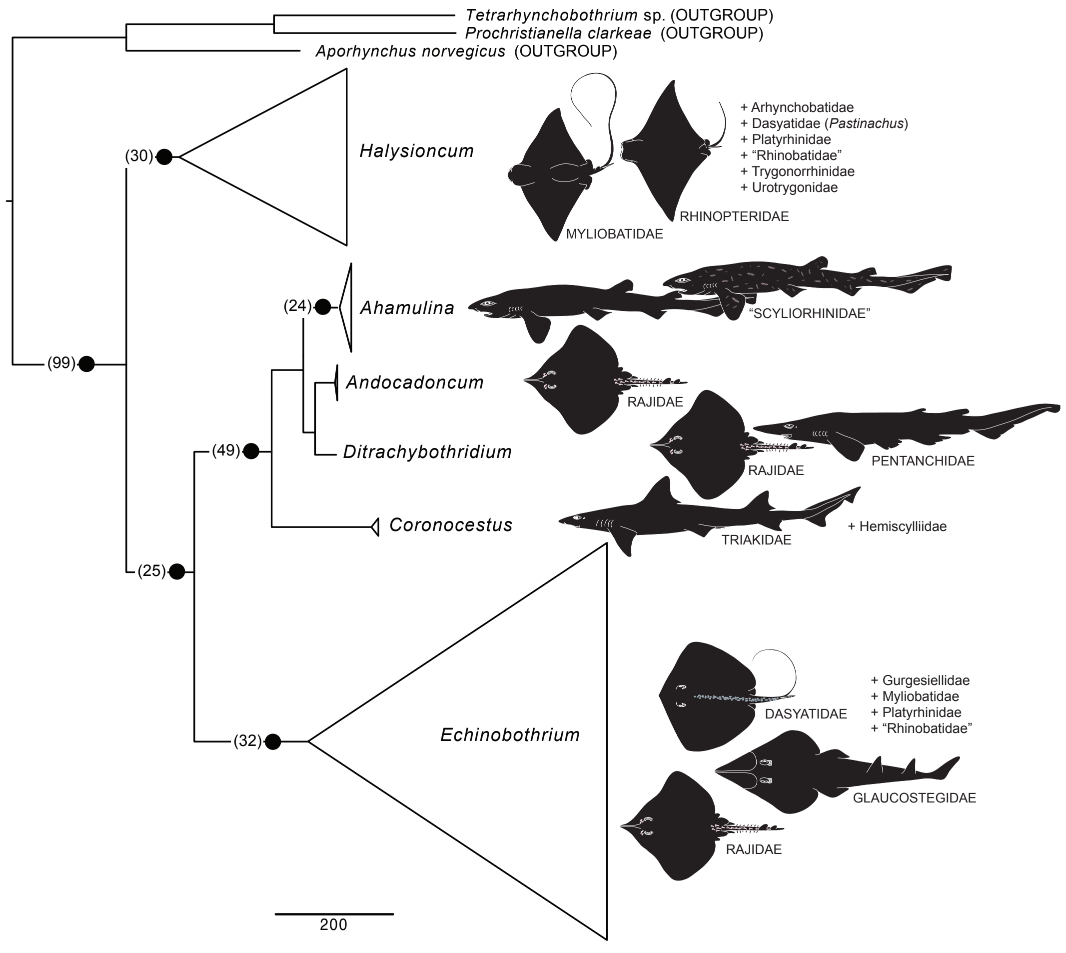

Figure 4. Schematic representation of relationships of diphyllidean genera modified from Caira et al. (2013c); nodal support given as Goodman-Bremer values (in parentheses) and bootstrap values of >95% (black dots). Elasmobranch icons represent major host families parasitized by the respective diphyllidean genus; minor host families are listed. Elasmobranch families in quotes were shown to be paraphyletic by Naylor et al. (2012a).

data for plerocercoids, immature worms, and an adult worm from *Galeus melastomus* to supplement existing data generated by Bray and Olson (2004) for specimens identified as *D. macrocephalum* from *Apristurus laurussoni*. While their sequence data for the seven specimens from *G. melastomus* were identical with one another, these sequences differed from the sequence reported by Bray and Olson (2004) by four bases. Thus, we believe that additional data and specimens are required to definitely resolve this issue.

As a result of PBI collections, two additional families of elasmobranchs are now known to host diphyllideans, specifically the pygmy skates (Gurgesiellidae De Buen) (see Rodriguez et al., 2011) and the finback catsharks (Proscylliidae Compagno) (unpubl. data). New collections also added 16 genera to the list of elasmobranchs known to host diphyllideans, specifically: the false catshark genus *Eridacnis* Smith (unpubl. data); the catshark genera *Atelomycterus* Garman (unpubl. data), and *Holohalaelurus* Fowler (see Caira at al., 2013); the stingray genera, *Hemitrygon* Müller & Henle, *Makulabatis* Last, Naylor & Manjaji-Matsumoto, *Pastinachus* Rüppel (see Kuchta and Caira, 2010), *Pateobatis* Last, Naylor & Manjaji-Matsumoto, and the paraphyletic "*Telatrygon*" Last, Naylor & Manjaji-Matsumoto (*sensu* Last et al. [2016a]); the butterfly ray genus *Gymnura* van Hasselt (unpubl. data); the stingaree genus *Urolophus* Müller (unpubl. data); the eagle ray genus *Aetomylaeus* Garman (see Ivanov and Caira, 2013); the shovelnose rays genus *Aptychotrema* Norman (unpubl. data); the electric ray genera *Diplobatis* Bigelow and *Narcine* Henle (unpubl. data); the sand skate genus *Psammobatis* Günther (unpubl. data); the skate genus *Okamejei* Ishyama (unpubl. data); the white skate genus *Rostroraja* Hulley (unpubl. data); and the legskate genus *Cruriraja* Bigelow & Schroeder (see Rodriguez et al., 2011).

These new host taxa highlight the fact that the most productive host groups to explore for additional diphyllidean diversity among sharks are the Triakidae (houndsharks), Pentanchidae, and the paraphyletic "Scyliorhinidae" (catsharks) (see below). Among batoids, the potentially most productive groups are the stingray families Dasyatidae (stingrays) and Myliobatidae Bonaparte (eagle rays), the guitarfish family "Rhinobatidae" Müller & Henle (guitarfishes; considered to be paraphyletic *sensu* Last et al. [2016b]), and three of the four families of skates: Arhynchobatidae Fowler (softnose skates), Gurgesiellidae (pygmy skates), and Rajidae Bonaparte (skates). Although potentially less productive, the Rhinopteridae Jordan & Evermann (cownose rays), Urolophidae (round rays), and Urotrygonidae McEachran, Dunn & Miyake (American round stingrays) will likely also yield additional diphyllidean species.

The host associations of the 119 known (described and undescribed) species of diphyllideans can be used to develop a relatively robust picture of the elasmobranch genera and families that host diphyllideans. Based on the number of known species in each elasmobranch genus, the average number of diphyllidean species reported parasitizing species examined in a genus, and assuming essentially oioxenous host specificity, we can predict the global total number of diphyllidean species (Tables 1, 2). We would note that work questioning the monophyly of the family Scyliorhinidae (i.e., catsharks) (e.g., Iglésias et al., 2005; Naylor et al., 2012a, b), which suggests its members may represent as many as three distinct families (e.g., Scyliorhinidae I, II, and III of Naylor et al. [2012a, b]), has implications for predictions in this case. As records stand, we believe species belonging to Scyliorhinidae I (of Naylor et al. [2012a]) (= Pentanchidae Smith & Radcliffe in Smith of Iglésias et al. [2005]) will be most likely to yield diphyllideans and our estimates reflect this assumption. As our data stand, our global estimate for diphyllidean diversity is 421 species; of these, more than 300 remain to be discovered, and 85% remain to be formally described.

Geographic Distribution. The already extensive geographic distribution of diphyllideans summarized by Tyler (2006) has been expanded by PBI work to include Brazil, Indonesia, Norway, Solomon Islands, South Africa, and Taiwan. With the exception of the far north, the order is essentially cosmopolitan in distribution. At this point the most northern record is that of Heller (1949) at 64°N for *E. raji* Heller, 1949 from Iceland and the most southern record is that of Wojciechowska (1991) at 54°S for *E. acanthocolle* Wojciechowska, 1991 from South Georgia. We predict the distribution of the order will ultimately be extended to include all regions in which their diverse host groups occur, most notably cooler, northern- or southern-most waters primarily occupied by skates. While the majority of existing diphyllidean records come from coastal localities, this appears to be an artifact of the sampling that has been conducted to date. In fact, a few records of species of *Ditrachybothridium* exist from the deep-sea; the deepest is that of Bray and Olson (2004) from 1,360 m. Representative of the candidate host families and genera (Tables 1, 2) occurring in oceanic regions will likely ultimately be found to also host diphyllideans.

CONCLUSIONS

New collections conducted over the course of the PBI project led to the description of 18 new species, bringing the total number of valid diphyllidean species to 59. These collections also yielded material of approximately 60 undescribed species. Reconfiguration of generic boundaries to bring them into line with results of a comprehensive molecular phylogenetic analysis led to the erection of four new genera, increasing the number of valid diphyllidean genera from two to six. Morphological novelty discovered over the course of the project provided insight into the evolution of elements of scolex armature; no particularly novel features of proglottid anatomy were discovered. The essentially cosmopolitan geographic distribution of the order was expanded to include Brazil, Indonesia, Norway, the Solomon Islands, South Africa, and Taiwan; however, it remains unknown from the far north. In contrast, the host associations of the order were substantially expanded and now include two additional families and 16 genera of elasmobranchs not previously known to host the order. Given the extent of our sampling, we do not anticipate finding diphyllideans in any additional families beyond the four shark and 13 batoid families already known to host them. We do anticipate finding diphyllideans in genera and species of these families that have not yet been examined. We predict that the total global fauna of diphyllideans will be found to exceed 420 species; more than half of these remain to be discovered and 85% remain to be described. The interrelationships among diphyllideans are fairly well understood, although the family-level classification would benefit from additional attention. The monophyletic Diphyllidea has affinities with the other bothriate eucestode orders, but its exact affinities among these groups remain to be definitively resolved.

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TABLE 1. Expected global shark associations of diphyllidean species (in yellow). Number of shark species per genus given in parentheses (includes known undescribed shark species). First column: number of diphyllidean species parasitizing each shark taxon as of 2017 (includes known undescribed cestode species); second column: predicted total number of diphyllidean species parasitizing each shark taxon globally. Quotes indicate non-monophyletic taxa (Naylor et al., 2012a). Question marks indicate genera not yet examined for cestodes. * Designation New genus D is for *Scyliorhinus torazame* (Tanaka).

	Diphyllidean spp.	
	2017	**ESTIM.**
SELACHOIDEA		
CARCHARHINIFORMES	**21**	**93**
Carcharhinidae	**0**	**0**
Carcharhinus (44 spp.)	0	0
Galeocerdo (2 spp.)	0	0
Glyphis (6 spp.)	0	0
Isogomophodon (1 sp.)	?	0
Lamiopsis (2 spp.)	0	0
Loxodon (2 spp.)	0	0
Nasolamia (1 sp.)	?	0
Negaprion (2 spp.)	0	0
Prionace (1 sp.)	0	0
Rhizoprionodon (10 spp.)	0	0
Scoliodon (3 spp.)	0	0
Triaenodon (1 sp.)	0	0
Hemigaleidae	**0**	**0**
Chaenogaleus (2 spp.)	?	0
Hemigaleus (2 spp.)	0	0
Hemipristis (1 sp.)	0	0
Paragaleus (4 spp.)	0	0
Leptochariidae	**0**	**0**
Leptocharias (1 sp.)	0	0
Pentanchidae	**7**	**34**
Apristurus (46 spp.)	4	18
Asymbolus (9 spp.)	0	3
Cephalurus (1 sp.)	?	0
Galeus (18 spp.)	2	5
Halaelurus (7 spp.)	0	2
Haploblepharus (4 spp.)	0	1
Holohalaelurus (5 spp.)	1	3
Parmaturus (11 spp.)	?	2
Pentanchus (1 sp.)	?	0
Proscylliidae	**1**	**6**
Ctenacis (1 sp.)	?	1
Eridacnis (3 spp.)	1	3
Proscyllium (3 spp.)	?	2
Pseudotriakidae	**0**	**0**
Gollum (2 spp.)	?	0
Planonasus (1 sp.)	?	0
Pseudotriakis (1 sp.)	0	0
"Scyliorhinidae"	**4**	**23**
Atelomycterus (6 spp.)	1	5
Aulohalaelurus (2 spp.)	?	1
Bythaelurus (11 spp.)	?	4
Cephaloscyllium (18 spp.)	0	0
Figaro (3 spp.)	?	1
New genus D* (1 sp.)	0	1
Poroderma (2 spp.)	0	0
Schroederichthys (5 spp.)	?	1
Scyliorhinus (15 spp.)	3	10
Sphyrnidae	**0**	**0**
Eusphyra (1 sp.)	0	0
Sphyrna (12 spp.)	0	0
Triakidae	**9**	**30**
Furgaleus (1 sp.)	0	1
Galeorhinus (1 sp.)	0	0
Gogolia (1 sp.)	?	1
Hemitriakis (8 spp.)	0	2
Hypoglaeus (1 sp.)	?	1
Iago (5 spp.)	3	6
Mustelus (30 spp.)	6	15
Scylliogaleus (1 sp.)	?	1
Triakis (5 spp.)	0	3
HETERODONTIFORMES	**0**	**0**
HEXANCHIFORMES	**0**	**0**
LAMNIFORMES	**0**	**0**
ORECTOLOBIFORMES	**2**	**3**
Brachaeluridae	**0**	**0**
Brachaelurus (2 spp.)	0	0
Ginglymostomatidae	**0**	**0**
Ginglymostoma (2 spp.)	0	0
Nebrius (1 sp.)	0	0
Pseudoginglymostoma (1 sp.)	0	0
Hemiscylliidae	**2**	**3**
Chiloscyllium (9 spp.)	2	3
Hemiscyllium (9 spp.)	0	0
Orectolobidae	**0**	**0**
Eucrossorhinus (1 sp.)	0	0
Orectolobus (10 spp.)	0	0
Sutorectus (1 sp.)	0	0
Parascylliidae	**0**	**0**
Cirrhoscyllium (3 spp.)	0	0
Parascyllium (5 spp.)	0	0
Rhincodontidae	**0**	**0**
Rhincodon (1 sp.)	0	0
Stegostomatidae	**0**	**0**
Stegostoma (1 sp.)	0	0
PRISTIOPHORIFORMES	**0**	**0**
SQUALIFORMES	**0**	**0**
SQUATINIFORMES	**0**	**0**
SHARK TOTAL	**23**	**96**

TABLE 2. Expected global batoid associations of diphyllidean species (in yellow). Number of batoid species per genus given in parentheses (includes known undescribed batoid species). First column: number of diphyllidean species parasitizing each batoid taxon as of 2017 (includes known undescribed cestode species); second column: predicted total number of diphyllidean species parasitizing each batoid taxon globally. Quotes indicate non-monophyletic taxa (Naylor et al., 2012a; Last et al., 2016a, b). Question marks indicate genera not yet examined for cestodes. Estimated total number of diphyllidean species parasitizing elasmobranchs globally given at bottom of Table.

	Diphyllidean spp.	
	2016	ESTIM.
BATOIDEA		
MYLIOBATIFORMES	**45**	**128**
Aetobatidae	**2**	**3**
Aetobatus (7 spp.)	2	3
Dasyatidae	**24**	**80**
“*Bathytoshia*” (3 spp.)	0	0
Brevitrygon (5 spp.)	1	5
Dasyatis (5 spp.)	0	0
Fluvitrygon (3 spp.)	2	3
Fontitrygon (4 spp.)	0	2
Hemitrygon (10 spp.)	1	5
Himantura (8 spp.)	1	8
Hypanus (12 spp.)	0	0
Maculabatis (13 spp.)	3	13
Makararaja (1 sp.)	?	1
Megatrygon (1 sp.)	0	0
Neotrygon (13 spp.)	4	13
Pastinachus (6 spp.)	4	10
Pateobatis (7 spp.)	3	7
Pteroplatytrygon (1 sp.)	0	0
Taeniura (5 spp.)	4	8
Taeniurops (2 spp.)	0	1
“*Telatrygon*” (4 spp.)	1	4
Urogymnus (7 spp.)	0	0
Gymnuridae	**1**	**2**
Gymnura (15 spp.)	1	2
Hexatrygonidae	**0**	**0**
Hexatrygon (1 sp.)	0	0
Mobulidae	**0**	**0**
Mobula (10—8 spp.)	0	0
Myliobatidae	**10**	**20**
Aetomylaeus (9 spp.)	5	9
Myliobatis (11 spp.)	5	11
Plesiobatidae	**0**	**1**
Plesiobatis (1 sp.)	0	1
Potamotrygonidae	**0**	**0**
Heliotrygon (2 spp.)	**?**	0
Styracura (2 spp.)	0	0
Paratrygon (1 sp.)	0	0
Plesiotrygon (2 spp.)	0	0
Potamotrygon (27 spp.)	0	0
Rhinopteridae	**5**	**8**
Rhinoptera (8 spp.)	5	8
Urolophidae	**2**	**8**
Spinilophus (1 sp.)	?	0
Trygonoptera (6 spp.)	0	0
Urolophus (21 spp.)	2	8
Urotrygonidae	**1**	**6**
Urobatis (6 spp.)	1	3
Urotrygon (12 spp.)	0	3
RHINOPRISTIFORMES	**21**	**40**
Glaucostegidae	**9**	**9**
Glaucostegus (9 spp.)	9	9
Platyrhinidae	**2**	**3**
Platyrhina (5 spp.)	1	2
Platyrhinoidis (1 sp.)	1	1
“Pristidae”	**0**	**0**
Anoxypristis (1 sp.)	0	0
Pristis (5 spp.)	0	0
Rhinidae	**0**	**0**
Rhina (1 sp.)	0	0
Rhynchobatus (8 spp.)	0	0
Rhynchorhina (1 sp.)	?	0
“Rhinobatidae”	**8**	**23**
Acroteriobatus (8 spp.)	1	8
Pseudobatos (8 spp.)	4	8
Rhinobatos (16 spp.)	3	7
Trygonorrhinidae	**2**	**5**
Aptychotrema (3 spp.)	1	2
Trygonorrhina (2 spp.)	0	1
Zapteryx (3 spp.)	1	2
Zanobatidae	**0**	**0**
Zanobatus (2 spp.)	0	0
TORPEDINIFORMES	**2**	**2**
Hypnidae	**0**	**0**
Hypnos (1 sp.)	0	0
Narcinidae	**2**	**2**
Benthobatis (4 spp.)	?	0
Diplobatis (4 spp.)	1	1
Discopyge (2 spp.)	0	0
Narcine (15 spp.)	1	1
Narcinops (5 spp.)	0	0
Narkidae	**0**	**0**
Crassinarke (1 sp.)	?	0
Electrolux (1 sp.)	?	0
Heteronarce (3 spp.)	?	0
Narke (3 spp.)	0	0
Temera (1 sp.)	?	0
Typhlonarke (1 sp.)	0	0
Torpedinidae	**0**	**0**
Tetronarce (9 spp.)	0	0
Torpedo (12 spp.)	0	0
RAJIFORMES	**28**	**155**
Anacanthobatidae	**0**	**0**
Anacanthobatis (1 spp.)	?	0
Indobatis (1 sp.)	?	0
Schroederobatis (1 sp.)	?	0
Sinobatis (8 spp.)	?	0
Springeria (2 spp.)	?	0
Arhynchobatidae	**4**	**42**
Arhynchobatis (1 sp.)	?	1
Atlantoraja (3 spp.)	0	2
Bathyraja (57 spp.)	2	20
Brochiraja (9 spp.)	0	2
Insentiraja (2 spp.)	?	1
Irolita (2 spp.)	?	1
Notoraja (12 spp.)	?	4
Pavoraja (6 spp.)	?	2
Psammobatis (8 spp.)	1	4
Pseudoraja (1 sp.)	?	1
Rhinoraja (3 spp.)	?	1
Rioraja (1 sp.)	0	1
Sympterygia (4 spp.)	1	2
Gurgesiellidae	**1**	**19**
Cruriraja (8 spp.)	1	8
Fenestraja (8 spp.)	?	8
Gurgesiella (3 spp.)	**?**	3
Rajidae	**23**	**94**
Amblyraja (9 spp.)	2	5
Beringraja (6 spp.)	2	6
Breviraja (5 spp.)	?	2
Dactylobatus (2 spp.)	?	1
Dentiraja (11 spp.)	?	5
Dipturus (52 spp.)	2	18
Hongeo (1 sp.)	?	1
Leucoraja (13 spp.)	5	10
Malacoraja (4 spp.)	0	2
Neoraja (5 spp.)	?	2
Okamejei (12 spp.)	1	4
Orbiraja (3 spp.)	0	0
Raja (17 spp.)	10	22
Rajella (20 spp.)	0	5
Rostroraja (10 spp.)	1	10
Spiniraja (1 sp.)	0	1
BATOID TOTAL	**96**	**325**
ELASMOBRANCH TOTAL	**119**	**421**

TABLE 3. List of valid diphyllidean taxa. New taxa and taxonomic actions resulting from PBI project activities indicated in bold. * Host identifications requiring confirmation.

VALID TAXA

FAMILY ECHINOBOTHRIIDAE PERRIER, 1897

Ahamulina Marques, Jensen & Caira, 2012

Ahamulina catarina Marques, Jensen & Caira, 2012 (type) ex *Scyliorhinus haeckelii* (as *Scyliorhinus besnardi*)

Andocadoncum Abbott & Caira, 2014

Andocadoncum meganae Abbott & Caira, 2014 (type) ex *Leucoraja wallacei*

Coronocestus Caira, Marques, Jensen, Kuchta & Ivanov, 2013

Coronocestus diamanti (Ivanov & Lipshitz, 2006) **Caira, Marques, Jensen, Kuchta & Ivanov, 2013** (type) ex *Iago omanensis*

Coronocestus coronatus (Robinson, 1959) **Caira, Marques, Jensen, Kuchta & Ivanov, 2013** ex *Mustelus lenticulatus*

Coronocestus ehsanentezarii Haseli & Azad, 2015 ex *Iago omanensis*

Coronocestus hormozganiense (Haseli, Malek, Palm & Ivanov, 2012) Caira, Marques, Jensen, Kuchta & Ivanov, 2013 ex *Mustelus mosis*

Coronocestus musteli (Pintner, 1889) **Caira, Marques, Jensen, Kuchta & Ivanov, 2013** ex *"Hundshai"*

Coronocestus notoguidoi (Ivanov, 1997) **Caira, Marques, Jensen, Kuchta & Ivanov, 2013** ex *Mustelus schmitti*

Ditrachybothridium Rees, 1959 **(revised diagnosis: Caira et al. [2013c])**

Ditrachybothridium macrocephalum Rees, 1959 (type) ex *Leucoraja fullonica*

Ditrachybothridium piliformis Faliex, Tyler & Euzet, 2000 ex *Galeus priapus*

Echinobothrium van Beneden, 1849 (syn. *Macrobothridium* Khalil & Abdul-Salam, 1989) **(revised diagnosis: Caira et al. [2013c])**

Echinobothrium typus van Beneden, 1849 (type) ex "raie bouclee"

Echinobothrium acanthinophyllum Rees, 1961 ex *Raja montagui*

Echinobothrium acanthocolle Wojciechowska, 1991 ex *Amblyraja georgiana*

Echinobothrium affine Diesing, 1863 ex *Raja clavata*

Echinobothrium benedeni Ruszkowski, 1927 ex *Hippolyte varians*

Echinobothrium brachysoma Pintner, 1889 ex "Rochenarten"

Echinobothrium chisholmae Jones & Beveridge, 2001 ex *Glaucostegus typus*

Echinobothrium clavatum Probert & Stobart, 1989 ex *Raja clavata*

Echinobothrium coenoformum Alexander, 1963 ex *Dipturus nasuta* (as *Raja nasuta*)

Echinobothrium dorothyae Caira, Pickering, Schulman & Hanessian, 2013 ex *Raja straelini*

Echinobothrium dougbermani Caira, Pickering, Schulman & Hanessian, 2013 ex *Rhinobatos annulatus*

Echinobothrium elegans Tyler, 2001 ex *Taeniura lymma**

Echinobothrium euterpes (Neifar, Tyler & Euzet, 2001) Tyler, 2006 ex *Rhinobatos rhinobatos*

Echinobothrium harfordi McVicar, 1976 ex *Leucoraja naevus*

Echinobothrium helmymohamedi Saoud, Ramadan & Hassan, 1982 ex *Taeniura lymma**

Echinobothrium heroniense Williams, 1964 ex *Taeniura lymma**

Echinobothrium joshuai Rodriguez, Pickering & Caira, 2011 ex *Cruriraja hulleyi*

Echinobothrium longicolle Southwell, 1925 ex *Neotrygon kuhlii**

Echinobothrium marquesi Abbott & Caira, 2014 ex *Leucoraja wallacei*

Echinobothrium mathiasi Euzet, 1951 ex *Myliobatis aquila*

Echinobothrium mercedesae Caira, Rodriguez & Pickering, 2013 ex *Raja parva* (as *R.* cf. *miraletus* 2 *sensu* Naylor et at. [2012b])

Echinobothrium minutamicum Twohig, Caira & Fyler, 2008 ex *Brevitrygon heterura* (as *Himantura walga*)

Echinobothrium parsadrayaiense Moghadam & Haseli, 2014 ex *Aetomylaeus nichofii*

Echinobothrium persiense Haseli, Malek, Palm & Ivanov, 2012 ex *Rhinobatos punctifer*

Echinobothrium raji Heller, 1949 ex *Amblyraja radiata*

Echinobothrium reesae Ramadevi, 1969 ex *Brevitrygon walga**

Echinobothrium rhynchobati (Khalil & Abdul-Salam, 1989) Tyler, 2006 ex *Glaucostegus granulatus**

Echinobothrium sematanense Ivanov & Caira, 2012 ex *Glaucostegus thouin*

Echinobothrium sinensis (Li & Wang, 2007) **Kuchta & Caira, 2010** ex *Platyrhina sinensis*

Echinobothrium syrtensis (Neifar, Tyler & Euzet) Tyler, 2006 ex *Glaucostegus cemiculus*

Echinobothrium tetabuanense Ivanov & Caira, 2012 ex *Glaucostegus* cf. *typus sensu* Naylor et al. (2012b)

Echinobothrium weipaense Ivanov & Caira, 2012 ex *Glaucostegus typus*

Echinobothrium yiae **Caira, Rodriguez & Pickering, 2013** ex *Raja ocellifera* (as *Raja* cf. *miraletus* 1 *sensu* Naylor et al. [2012b])

Halysioncum **Caira, Marques, Jensen, Kuchta & Ivanov, 2013**

Halysioncum mexicanum (Tyler & Caira, 1999) **Caira, Marques, Jensen, Kuchta & Ivanov, 2013 (**type**)** ex *Myliobatis longirostris*

Halysioncum arafurense **Ivanov & Caira, 2013** ex *Aetomylaeus caeruleofasciatus* (as *Aetomylaeus nichofii*)

Halysioncum bonasum (Williams & Campbell, 1980) **Caira, Marques, Jensen, Kuchta & Ivanov, 2013** ex *Rhinoptera bonasus**

Halysioncum californiense (Ivanov & Campbell, 1980) **Caira, Marques, Jensen, Kuchta & Ivanov, 2013** ex *Platyrhinoidis triseriata*

Halysioncum euzeti (Campbell & Carvajal, 1980) **Caira, Marques, Jensen, Kuchta & Ivanov, 2013** ex *Sympterygia lima*

Halysioncum fautleyae (Tyler & Caira, 1999) **Caira, Marques, Jensen, Kuchta & Ivanov, 2013** ex *Rhinoptera steindachneri*

Halysioncum gibsoni **Ivanov & Caira, 2013** ex *Aetomylaeus maculatus*

Halysioncum hoffmanorum (Tyler, 2001) **Caira, Marques, Jensen, Kuchta & Ivanov, 2013** ex *Urobatis maculatus*

Halysioncum kishiense Moghadam & Haseli, 2014 ex *Aetomylaeus nichofii*

Halysioncum megacanathum (Ivanov & Campbell, 1998) **Caira, Marques, Jensen, Kuchta & Ivanov, 2013** ex *Myliobatis goodei*

Halysioncum nataliae **(Kuchta & Caira, 2010) Caira, Marques, Jensen, Kuchta & Ivanov, 2013** ex *Pastinachus solocirostris*

Halysioncum pigmentatum (Ostrowski de Núñez, 1971) **Caira, Marques, Jensen, Kuchta & Ivanov, 2013** ex *Zapteryx brevirostris*

Halysioncum raschii (Campbell & Andrade, 1997) **Caira, Marques, Jensen, Kuchta & Ivanov, 2013** ex *Bathyraja taranetzi* (as *Rhinoraja longi*)

Halysioncum rayallemangi (Tyler, 2001) **Caira, Marques, Jensen, Kuchta & Ivanov, 2013** ex *Pseudobatos leucorhynchus* (as *Rhinobatos leucorhynchus*)

Halysioncum reginae **(Kuchta & Caira, 2010) Caira, Marques, Jensen, Kuchta & Ivanov, 2013** ex *Pastinachus ater* (as *Pastinachus atrus*)

Halysioncum vojtai **(Kuchta & Caira, 2010) Caira, Marques, Jensen, Kuchta & Ivanov, 2013** ex *Pastinachus gracilicaudus* (as *Pastinachus* sp.)

8

Diphyllobothriidea Kuchta, Scholz, Brabec & Bray, 2008

By

Roman Kuchta[1] and Tomáš Scholz

DIPHYLLOBOTHRIIDEA AS THEY WERE KNOWN PRIOR TO THE PBI PROJECT

Diversity and Classification. The order Diphyllobothriidea was established in 2008 by Kuchta and colleagues, who formally subdivided the order traditionally recognized as the Pseudophyllidea van Beneden in Carus, 1863 into two orders after its non-monophyly had been firmly established (see Kuchta et al., 2008). In fact, the division of the Pseudophyllidea had been proposed much earlier by Wardle et al. (1974), who recommended that the name Pseudophyllidea *sensu stricto* be retained for the taxa now corresponding more or less to the Bothriocephalidea as defined by Kuchta et al. (2008), and that the name Diphyllidea Wardle, McLeod & Radinovsky, 1974 (*nec* Diphyllidea van Beneden in Carus, 1863 applied earlier to a group of elasmobranch-hosted cestodes but considered by Wardle et al. [1974] to be a *nomen oblitum*) be applied to the tetrapod-hosted taxa now assigned to the Diphyllobothriidea by Kuchta et al. (2008).

The classification and taxonomic history of the taxa now recognized as the Diphyllobothriidea have been both controversial and complicated (Delyamure, 1955; Yurakhno, 1992; Bray et al., 1994; Kamo, 1999). The first species of the group was recognized in the 16th century when Thaddeus Dunus of Locarno in 1592 reported the human broad tapeworm. That species was subsequently formally described as *Taenia lata* L., 1758 by Linnaeus (1758). *Ligula* Bloch, 1782—the first genus in the group—was also erected in the 18th century, for *Ligula piscium* Bloch, 1782 (now *L. intestinalis*). Most of the remaining valid genera were established in the 19th century (e.g., *Bothridium* de Blainville in Bremser, 1824, *Schistocephalus* Creplin, 1829, *Diphyllobothrium* Cobbold, 1858, *Duthiersia* Perrier, 1873, *Pyramicocephalus* Monticelli, 1890, *Diplogonoporus* Lönnberg, 1892, *Scyphocephalus* Riggenbach, 1898, and *Dibothriocephalus* Lühe, 1899; the latter genus was synonymized with *Diphyllobothrium* by Lühe [1910]). Among these, *Diphyllobothrium* is by far the most taxonomically difficult group with respect to the delimitation of species (Lühe, 1910; Stunkard, 1949; Wardle and McLeod, 1952; Delyamure, 1955). The first family of the group was established by Claus (1868) for the monotypic Ligulidae Claus, 1868, which later included the three genera *Digramma* Cholodkovsky, 1914, *Ligula*, and *Schistocephalus* (see Dubinina, 1980a). One of the other earliest recognized family-group names in the group was the subfamily Solenophorinae Monticelli & Crety, 1891, established for two genera parasitizing "reptiles" (i.e., *Bothridium* [syn. *Solenophorus* Creplin, 1839] and *Duthiersia*).

The taxa assigned to the group, which had historically been given only family-level status in the Pseudophyllidea, have varied considerably over time. Wardle and McLeod (1952) recognized 16 genera in the Diphyllobothriidae Lühe, 1910. Yamaguti (1959) considered the

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[1] Corresponding author (krtek@paru.cas.cz)

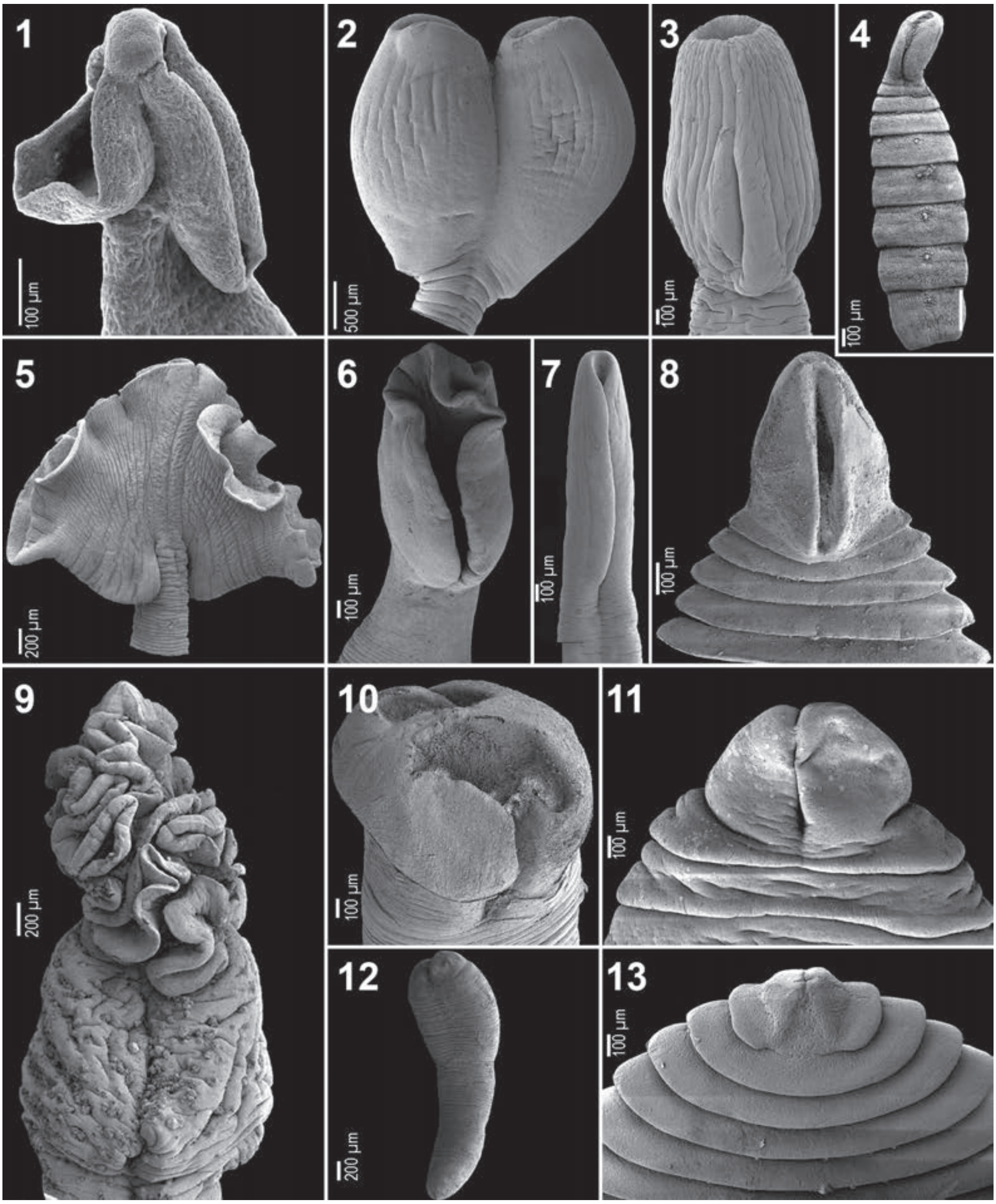
Kuchta, R. and T. Scholz. 2017. Diphyllobothriidea Kuchta, Scholz, Brabec & Bray, 2008. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 167–189.

family to house 16 genera with 76 valid species (and 12 *species inquirendae*) that parasitize mammals, and established the new family Cephalochlamydidae Yamaguti, 1959 and the new genus *Pseudocephalochlamys* Yamaguti, 1959 for *P. xenopi* (Portlepp, 1926) Yamaguti, 1959 (now a synonym of *Cephalochlamys namaquensis* [Cohn, 1906] Blanchard, 1908) for parasites from frogs. Delyamure et al. (1985) revised membership in the Diphyllobothriidae, recognizing nine genera with 50 valid species (and 5 *species inquirendae*), but excluded the genus *Spirometra* Faust, Campbell & Kellogg, 1929. Schmidt (1986) recognized 17 genera with 101 valid species (and 9 *species inquirendae*) within two families (Diphyllobothriidae and Cephalochlamydidae). Yurakhno (1992) had the most inclusive vision of the group, recognizing 19 genera in the two superfamilies Diphyllobothrioidea and Scyphocephaloidea Freze, 1974. Bray et al. (1994) considered the diphyllobothriideans to house 16 genera within two families (Diphyllobothriidae and Cephalochlamydidae). In the most recent revision of the family Diphyllobothriidae published prior to the PBI project, Kamo (1999) considered it to house seven genera and 49 valid species, but excluded the genera *Ligula* (syn. *Digramma*), *Schistocephalus*, and the polygonoporids (*Tetragonoporus* Skryabin, 1961 and related genera).

The taxonomic histories of many of the genera have been similarly confusing. For example, Faust et al. (1929) divided *Diphyllobothrium* into the subgenera *Diphyllobothrium* and *Spirometra*, for species that possess rosette-shaped uterine coils and rounded eggs, versus spiral uterus with few coils and pointed eggs, respectively. *Spirometra* was elevated to generic level by Mueller (1937) who, rather than Faust et al. (1929), was erroneously considered as its authority by several subsequent authors (e.g., Wardle and McLeod, 1952; Yamaguti, 1959; Wardle et al., 1974). Mueller (1937) also recognized, but did not name, a third genus for parasites from pinnipeds closely related to *D. lanceolatum* (Krabbe, 1865) Cooper, 1921. However, *Spirometra* is also problematic because Faust et al. (1929) did not specify a type species. It was Mueller (1937), as the first author to revise the group, who established *Spirometra erinaceieuropaei* (Rudolphi, 1819) Faust, Campbell & Kellogg, 1929 (misspelled as *S. erinacei*) as the type of the genus. Unfortunately, Rudolphi's (1819) description of this species, which he named *Dubium erinacei europaei* because it was based on plerocercoids from the hedgehog (*Erinaceus europaeus* L.), was very brief and provided little information about the morphology of the species (see Wardle and McLeod, 1952). Nevertheless, this taxon has been recognized as the type species of *Spirometra* by all subsequent authors, including Bray et al. (1994) and Kamo (1999).

Substantial taxonomic confusion has also surrounded the validity of the name *Spirometra*. Baer (1924) erected the genus *Lueheella* Baer, 1924 (incorrectly spelled as *Lüheella*) as the type of the family Lueheellidae Baer, 1924 (as Lüheellidae) for his new species, *Lueheella pretoriensis* Baer, 1924, from the bat-eared fox, *Otocyon megalotis* (Desmarest) (Canidae Fischer de Waldheim) from Africa. Baer's generic diagnosis of *Lueheella* is virtually identical to that provided five years later by Faust et al. (1929) for *Spirometra*. The older name, *Lueheella,* and its associated family were never accepted or even mentioned by subsequent workers (Schmidt, 1974). Instead, *Spirometra* has been the name in common use and, as the genus includes species that are causative agents of the potentially serious human disease called sparganosis, a substantial body of literature has developed that has used this name.

In 1908, Stiles erected *Gatesius* Stiles, 1908 to accommodate the species known as *Sparganum proliferum* Ijima, 1905 found in humans. However, this species has not been recognized as valid because of uncertainty surrounding its identity and has thus generally been considered a *species inquirenda*. In fact, Schmidt (1974) suggested that, for stability, the International Commission on Zoological Nomenclature be petitioned to give precedence to *Spirometra* and



FIGURES 1–13. Scanning electron micrographs of scoleces of selected diphyllobothriideans. **(1)** *Cephalochlamys namaquensis* ex *Xenopus laevis* (Pipidae), USA. **(2)** *Bothridium pithonis* ex *Xenopeltis unicolor* (Xenopeltidae), Vietnam. **(3)** *Scyphocephalus bisculcatus* ex *Varanus salvator* (Varanidae), Vietnam. **(4)** *Diphyllobothrium wilsoni* ex *Ommatophoca rossii* (Phocidae), Antarctica. **(5)** *Duthiersia fimbriata* ex *V. exanthematicus* (Varanidae), Ghana. **(6)** *Adenocephalus pacificus* ex *Callorhinus ursinus* (Otariidae), USA (Alaska). **(7)** *Diphyllobothrium latum* ex *Mesocricetus auratus* (Cricetidae), experimental infection. **(8)** *Diphyllobothrium lanceolatum* ex *Phoca vitulina* (Phocidae), Norway (Svalbard). **(9)** *Pyramicocephalus phocarum* ex *Pusa hispida* (Phocidae), Norway (Svalbard). **(10)** *Glandicephalus perfoliatus* ex *Leptonychotes weddellii* (Phocidae), Antarctica. **(11)** *Ligula intestinalis* ex *Podiceps cristatus* (Podicipedidae), Czech Republic. **(12)** Plerocercoid of *Diphyllobothrium latum* ex *Perca fluviatilis* (Percidae), Italy. **(13)** *Schistocephalus solidus* ex *in vitro* experimental culture.

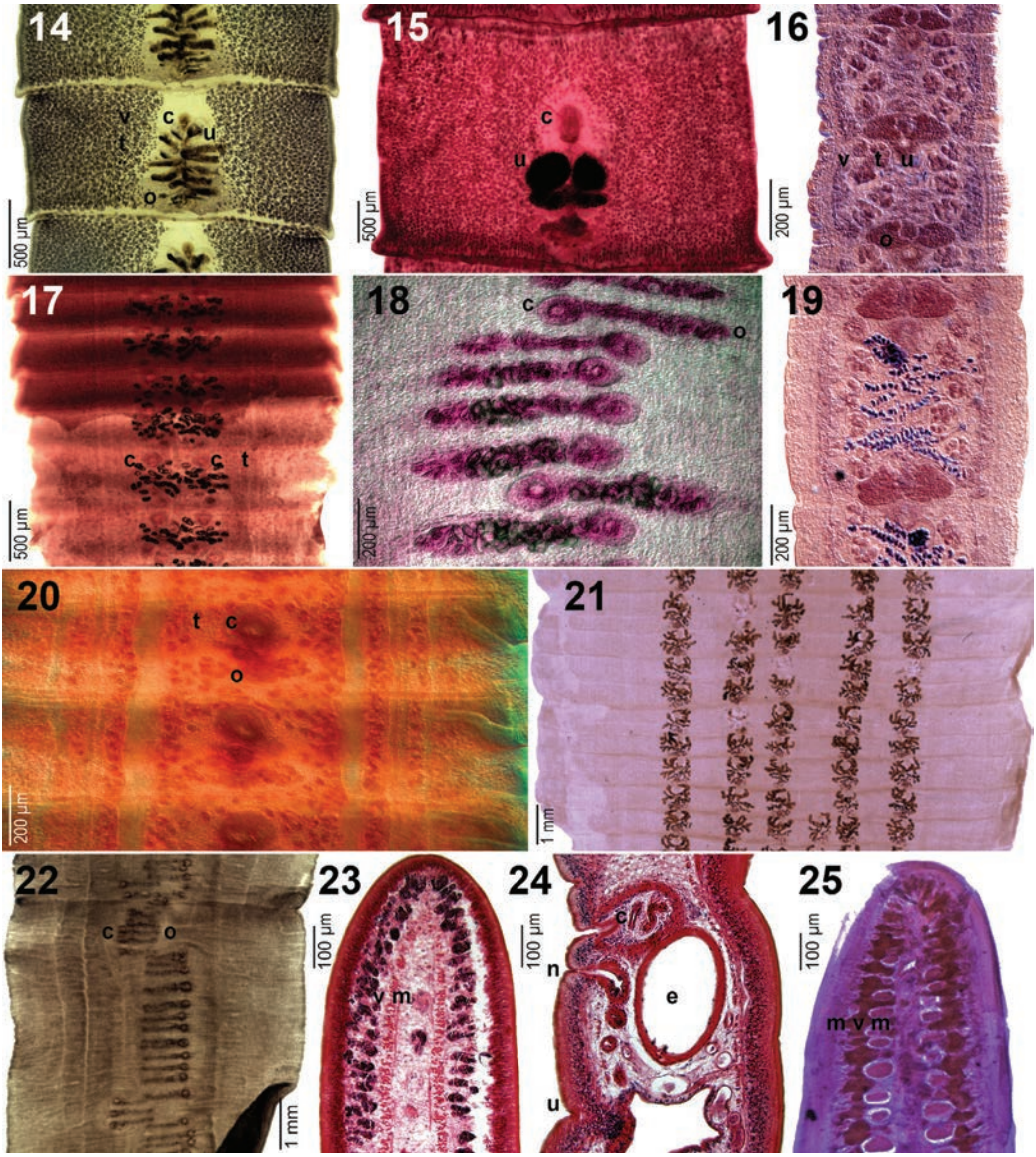
suppress both *Gatesius* and *Lueheella* because neither older name had been in use. Although that petition was never submitted to the ICZN (M. Grygier, International Commission on Zoological Nomenclature, pers. com.), neither *Gatesius* nor *Lueheella* were ever recognized as valid genera (e.g., Yamaguti, 1959; Delyamure et al., 1985; Schmidt, 1986; Bray et al., 1994; Kuchta et al., 2008).

Perhaps the most radical changes in the classification of diphyllobothriids were those suggested by Wardle et al. (1947) in their paper titled "Lühe's '*Diphyllobothrium*' (Cestoda)" which was later modified by Wardle et al. (1974) in "Advances in the Zoology of Tapeworms, 1950–1970." Wardle et al. (1947) proposed that Lühe's (1910) concept of *Diphyllobothrium* be revised to include only the two species known to parasitize toothed whales (i.e., *D. stemmacephalum* Cobbold, 1858 and *D. fuhrmanni* Hsü, 1935). They transferred all remaining valid species previously assigned to the genus to one of the six other genera, *Adenocephalus* Nybelin, 1931, *Diplogonoporus* Lönnberg, 1892, *Dibothriocephalus*, *Glandicephalus* Fuhrmann, 1921, *Spirometra*, and their newly erected genus *Cordicephalus* Wardle, McLeod & Stewart, 1947. Unfortunately, their new genus comprised four markedly dissimilar species from pinnipeds, all of which are now recognized in yet other genera: as *Baylisiella tecta* (von Linstow, 1892) Markowski, 1952, *Pyramicocephalus phocarum* (Fabricius, 1780) Monticelli, 1890, *Adenocephalus pacificus* Nybelin, 1931 (a senior synonym of *Cordicephalus arctocephalinus* [Johnston, 1937] Wardle, McLeod & Stewart, 1947 [see Hernández-Orts et al., 2015]), and *Diphyllobothrium quadratum* (von Linstow, 1892) Railliet & Henry, 1912. The other taxonomic changes suggested by Wardle et al. (1947) have also not been generally accepted and *Cordicephalus* was determined to be a junior synonym of *Pyramicocephalus* Monticelli, 1890 by Stunkard (1948) just one year later.

In an attempt to generate some order out of the chaos that existed in the speciose *Diphyllobothrium*, which by 1987 housed 80 species, Andersen (1987; pg. 422) recognized four subgroups of marine species (i.e., "Groups I–IV"), based largely on overall body and scolex size and shape. Moreover, she identified "model" (i.e., exemplar) species for each group as follows: *D. stemmacephalum* Cobbold, 1858 for Group I, *D. elegans* (Krabbe, 1865) Meggitt, 1924 for Group II, *D. cordatum* (Leuckart, 1863) Gedoelst, 1911 for Group III, and *D. wilsoni* (Shipley, 1907) Railliet & Henry, 1912 for Group IV.

However, despite the substantial amount of work on the morphology, ecology, and life-cycles conducted since Cobbold's (1858) erection of *Diphyllobothrium* (e.g., by Lühe, 1910; Stunkard, 1949; Wardle and McLeod, 1952; Delyamure et al., 1985; Andersen, 1987; Kamo, 1999), species boundaries in this taxonomically rich genus remain unclear. In fact, at the start of the PBI project in 2008, taxonomic resolution in this difficult group had not been achieved; it remained essentially as it had been characterized by noted American cestodologist Justus Mueller, who, in a letter to the eminent parasitologist Horace W. Stunkard wrote "I don't have the slightest idea as to the validity of species and genera in the diphyllobothriid cestodes. I know less about them now than I did 15 years ago. I do not think we will be in a position to give rigid specific or generic designations to these cestodes until their life histories and physiology have been worked out in much greater detail. The problem is one that might lead a respectable taxonomist to give up and go into molecular biology." (Stunkard, 1965; pg. 281)

Some progress was made in terms of the taxonomic status of the polygonoporal genera (i.e., genera bearing proglottids with more than a single set of genital organs). *Multiductus* Clarke, 1962 was synonymized with *Tetragonoporus* Skryabin, 1961 by Delyamure and Skryabin (1968). Bray et al. (1994; pg. 238) subsequently considered *Polygonoporus* Skryabin, 1967 and *Tetragonoporus* to be junior synonyms of *Diplogonoporus* (but, confused the issue by listing



FIGURES 14–25. Photomicrographs of diphyllobothriidean proglottids. **(14)** Whole mount of *Diphyllobothrium latum* ex *Homo sapiens* (Hominidae), Italy. **(15)** Whole mount of *Spirometra erinaceieuropaei* ex *Felis catus* (Felidae), experimental infection. **(16, 19)** Whole mounts of *Cephalochlamys namaquensis* ex *Xenopus laevis* (Pipidae), USA; mature (16) and gravid (19) proglottids. **(17)** Whole mount of *Diplogonoporus tetrapterus* ex *Callorhinus ursinus* (Otariidae), USA (Alaska); cortical layer of posterior proglottids removed. **(18)** Whole mount of *Ligula colymbi* ex *Podiceps cristatus* (Podicipedidae), Russia; detail of genitalia. **(20)** Whole mount of *Duthiersia expansa* ex *Varanus salvator* (Varanidae), Vietnam; cortical layer of proglottids removed. **(21, 25)** Gravid proglottids of *Tetragonoporus calyptocephalus* ex *Physander catadon* (Physeteridae), Russia (Bering Sea); whole mount (21) and cross-section (25). **(22)** Whole mount of *Baylisia baylisi* Markowski, 1952 ex *Lobodon carcinophagus* (Phocidae), Antarctica; anterior region of gravid proglottid. **(23, 24)** Sections of *Adenocephalus pacificus* ex *C. ursinus*, Alaska; sagittal (24) and cross-section (23) through gravid proglottid. *Abbreviations*: c, cirrus-sac; e, external seminal vesicle; m, longitudinal musculature; n, vagina; o, ovary; t, testes; u, uterine pore; v, vitelline follicles.

both of the former genera as synonyms of *Hexagonoporus* Gubanov in Delyamure, 1955 in the key to genera they presented on pg. 242). However, *Hexagonoporus* was considered a *genus inquirendum* by Kuchta et al. (2008) because its original description was incomplete. Based in part on results of analyses of molecular sequence data, Kuchta et al. (2008) also synonymized *Digramma* with *Ligula*—a taxonomic action that was in agreement with the ideas of Wardle and McLeod (1952) who considered *Digramma* to merely represent a rare diplogonadic type of *Ligula*. As a result, the only valid genus of polygonoporal diphyllobothriids recognized at the initiation of the PBI project was *Tetragonoporus* (see Kuchta et al., 2008).

The monogeneric family Cephalochlamydidae, comprising taxa using anurans as definitive hosts, was revised by Jackson and Tinsley (2001) who described two new species and erected a second genus, *Paracephalochlamys* Jackson & Tinsley, 2001, in the family. In contrast, diphyllobothriidean cestodes using "reptiles" as definitive hosts (recognized in the Scyphocephalidae Freze, 1974 by Kuchta et al. [2008]), have not been revised in recent times, with the most comprehensive accounts published more than 75 years ago by Baer (1927), Joyeux and Baer (1927), and Woodland (1940).

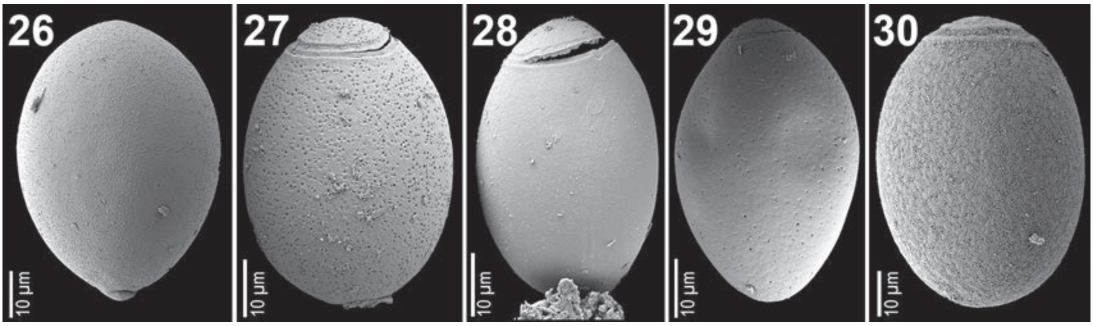
Morphology. Several morphological works focused on subsets of taxa in the group have been conducted. Delyamure et al. (1985) treated members of the family Diphyllobothriidae, but not species of *Spirometra* or ligulids. Dubinina (1980a) provided detailed morphological descriptions of all taxa in the genera *Ligula*, *Digramma*, and *Schistocephalus*, albeit as members of the family Ligulidae—genera considered by most authors to belong to the Diphyllobothriidae (see Bray et al., 1994). Kamo (1999) provided a revision of most diphyllobothriid taxa, but that study, written in Japanese, was largely a compilation of previously published data on well-known species and, although it included some new synonymies, did not provide justifications for these synonymies.

The pronounced morphological uniformity seen among most members of the group and high degree of intraspecific variation in most morphological and morphometric characteristics are largely responsible for the complicated taxonomy and systematics of the Diphyllobothriidea; this is especially the case for the genus *Diphyllobothrium*. Species identifications are generally based on the shape and size of the scolex (Figs. 1–13), presence or absence of a neck, relative position and shape of the cirrus-sac and external seminal vesicle as seen in sagittal section (Fig. 24), as well as the degree of development of the longitudinal musculature (Figs. 23, 25). However, these characters commonly overlap among species (Vik, 1964; Stunkard, 1965; Delyamure et al., 1985). In multiple cases, new species have been described based on limited material making it almost impossible to distinguish intraspecific morphological and morphometric variation from interspecific variation.

Diphyllobothriideans are usually robust, thick-bodied worms with well-developed longitudinal musculature and extensive fields of vitelline follicles that fill the cortex. As a consequence, genital organs situated in the medulla are difficult or almost impossible to observe in cleared specimens. A variety of methods have been used in the past with the goal of improving consistency for specimen identification. To overcome issues associated with contraction, experts such as K. I. Andersen and R. L. Rausch developed methods to relax worms in water or saline prior to fixation (Rausch and Hilliard, 1970; Andersen, 1975). However, this process can lead to artifacts such as detachment of the tegument including its microtriches. Furthermore, measurements of worms that have been relaxed in water or saline are often not comparable to those from specimens fixed in hot fixative, immediately after removal from freshly killed hosts. A technique that highly improves the visibility of genital organs within proglottids in whole mounts of robust tapeworms is their skinning (i.e., removal of the outer layers of the body consisting of the cortex and the inner longitudinal musculature) (see Figs. 17, 20). Taxonomic problems have also arisen because authors have failed to consider the possibility of host-induced intraspecific morphological variation that may be associated with host size, age, or geographic origin. The use of molecular sequence data to confirm or revise species boundaries in diphyllobothriideans is a particularly promising method for assisting with overcoming these issues.

The configuration of the reproductive organs of a typical diphyllobothriidean cestode includes genital openings that are situated medially on the ventral surface of the proglottid, either in a common genital pore or as separate male and female pores, positioned anterior to the uterine pore, although some specimens of *Ligula intestinalis* (L., 1758) Bloch, 1782 are unusual in that they possess pores that open on the dorsal surface of the proglottid (Dubinina, 1980a). In many species, the genital organs are vertically oriented, with the exception of those in species of *Ligula* and *Baylisiella* Markowski, 1952 in which genital organs are rotated horizontally 90° clockwise or anticlockwise, respectively (Figs. 18, 22). The testes are medullary, numerous, and oval to spherical in shape. The vas deferens expands to form a prominent external seminal vesicle at its proximal part (i.e., near the cirrus-sac; Fig. 24); the size and position of the external seminal vesicle, as observed in sagittal section, has been used to differentiate among some species of *Diphyllobothrium*. A cirrus-sac is present in all diphyllobothriideans with the exception of the cephalochlamydids (Figs. 16, 19). The cirrus is unarmed. A bilobed ovary is situated medially in the posterior third of the proglottid. The fields of vitelline follicles are extensive, cortical (Fig. 23), and extend medially to fill all but the central region of the proglottid housing the uterus (Figs. 14, 15); the cephalochlamydids are unusual in this respect in that their vitelline follicles are arranged in two distinct lateral fields (Figs. 16, 19). Species of *Tetragonoporus* are unique in their possession of vitelline follicles positioned between two concentric layers of the inner longitudinal musculature (Fig. 25). The uterus forms a few (usually 3–5) tightly coiled spiral loops in cephalochlamydids, solenophorids, *Ligula*, *Spirometra*, and *Schistocephalus* (Figs. 15, 16, 18–20) or a rosette of loops in most other genera (Figs. 14, 17, 21). The eggs of most diphyllobothriids are polylecithal, thick-shelled, operculate (Figs. 26–30), quite variable in size, and unembryonated when laid (i.e., without fully formed oncospheres). In contrast, the cephalochlamydids possess unoperculate eggs that are embryonated when laid (Thurston, 1967).

HOST ASSOCIATIONS. In general the Diphyllobothriidae were considered to parasitize mammals as definitive hosts. However, prior to the PBI project, the host associations of the Diphyllobothriidae had not been studied overall in any detail; historically, emphasis had been placed on species parasitizing marine mammals (Delyamure, 1955). Delyamure et al. (1985) analyzed selected general patterns of host-parasite relationships of members of the family Diphyllobothriidae overall, but omitted species of *Spirometra* and ligulids; the latter were considered by most Russian authors to belong to a separate family Ligulidae. In total, they reported 62 species of mammals (including 37 species of marine mammals) in 13 families, and 14 species of birds in seven families as definitive hosts of diphyllobothriid cestodes. Host specificity in diphyllobothriideans is generally considered to be fairly relaxed, but the literature is littered with numerous misidentifications and erroneous host records. For example, *D. latum* (L., 1758) Lühe, 1910 has been reported from as many as 47 species of marine and terrestrial mammals (including humans) across 11 families and four orders (Rosenberg, 1977; Delyamure et al., 1985; Kamo, 1999). As a consequence, information published before molecular sequence data were used in identification should be considered



FIGURES 26–30. Scanning electron micrographs of diphyllobothriidean eggs. **(26)** *Diphyllobothrium latum* ex *Homo sapiens* (Hominidae), Italy. **(27)** *Adenocephalus pacificus* ex *Callorhinus ursinus* (Otariidae), USA (Alaska). **(28)** *Ligula colymbi* ex *Podiceps cristatus* (Podicipedidae), Czech Republic. **(29)** *Spirometra decipiens* (syn. of *S. erinaceieuropaei*) ex *Puma concolor* L. (Felidae), Brazil. **(30)** *Tetragonoporus calyptocephalus* ex *Physeter macrocephalus* (Physeteridae), Russia (Bering Sea).

with caution. Nonetheless, these data indicate that diphyllobothriideans generally exhibit euryxenous host specificity (*sensu* Caira et al. [2003]). There do, however, appear to be a few diphyllobothriideans that seem to be oioxenous (*sensu* Euzet and Combes [1980]; i.e., infecting a single host species). *Scyphocephalus bisculcatus* Riggenbach, 1898, for example, has been reported exclusively from the monitor lizard, *Varanus salvator* (Laurenti), and *Tetragonoporus calyptocephalus* Skryabin, 1961 is known only from the sperm whale, *Physeter macrocephalus* L. As noted above, reliable assessment of host specificity in most diphyllobothriidean species has been impeded by the unsatisfactorily resolved nature of the taxonomy of the group (Markowski, 1952; Delyamure et al., 1985; Andersen, 1987).

It is perhaps the host associations of cephalochlamydids that have been examined in most detail. In their comprehensive work, Jackson and Tinsley (2001) considered cephalochlamydids to be parasites of clawed frogs of the genus *Xenopus* Wagler (Pipidae Gray; found in 11 species), which on occasion parasitize dicroglossid and pyxicephalid frogs in Africa.

GEOGRAPHIC DISTRIBUTION. Prior to the PBI project, the primary works examining the geographic distributions of diphyllobothriids were those of Delyamure (1955) and Delyamure et al. (1985). These authors reported marine diphyllobothriids in all six oceanic bioregions recognized by Russian authors with most species occurring in the Boreo-Pacific, Antarctic, and Boreo-Atlantic regions (15, 14, and 13 species, respectively). In contrast, the distributions of terrestrial and freshwater species had not been analyzed in detail, but they were known from all continents.

According to Jackson and Tinsley (2001), the geographic distributions of the cephalochlamydids were perhaps most well known; members of that family have been reported naturally across sub-Saharan Africa, but have been introduced into the USA (California) and the UK (Isle of Wight) by anthropogenic dispersion of the clawed frog *Xenopus laevis* (Daudin) through the pet trade.

PHYLOGENETIC RELATIONSHIPS. Prior to the PBI project, the evolutionary history of the diphyllobothriideans had been studied by very few authors. Lönnberg (1897; pg. 730) recognized a clade of "Pseudophyllida" that included the spathebothriideans (*Bothrimonus* Duvernoy, 1842), bothriocephalideans, and possibly also the caryophyllideans along with the diphyllobothriids, with "reptilian" cestodes of the genus *Bothridium* as the earliest diverging group. Among the diphyllobothriideans, he considered *Diplogonoporus* close to *Diphyllobothrium* (as *Bothriocephalus*) and *Ligula* close to *Schistocephalus*.

On the basis of embryonic development, Freeman (1973) divided the Pseudophyllidea into two unnamed suborders, one consisting of the families whose members have unoperculate eggs (i.e., Amphicotylidae Lühe, 1889, Cephalochlamydidae, and Ptychobothriidae [some species of which have operculate eggs; see Kuchta et al., 2008]), and the other consisting of the families whose members have operculate eggs (i.e., Bothriocephalidae, Diphyllobothriidae, and Echinophallidae). Freeman (1973) considered the families of the former suborder as evolutionarily early diverging groups.

Later, Dubinina (1980b) attempted to reconstruct the evolutionary history of pseudophyllideans on the basis of attachment organ morphology and type of definitive host. In her scenario, the first appearance of pseudophyllideans (specifically groups now considered in the Bothriocephalidea and Haplobothriidea) coincided with the first appearance of teleosts; later, a few taxa (groups now considered in the Bothriocephalidae and Cephalochlamydidae) adapted to amphibians; this was followed by others (groups now considered in the Solenophoridae) that colonized "reptiles;" finally some groups (now considered in the Diphyllobothriidae) colonized warm-blooded vertebrates.

In contrast, Delyamure et al. (1985) speculated that there are two principal lineages of diphyllobothriids. One of these included the predecessor of present day *Diphyllobothrium* (but with a different ecology and host spectrum), genera with multiple genital complexes per proglottid (i.e., *Diplogonoporus* and *Baylisia* Markowski, 1952), as well as genera with a highly modified scolex (i.e., *Pyramicocephalus*, *Plicobothrium* Rausch & Margolis, 1969, and *Baylisiella*). The other consisted entirely of species of *Polygonoporus* Skryabin, 1967, which they considered to be the most highly derived and specialized members of the order as it was then circumscribed.

A completely different scenario was proposed by Yurakhno and Maltsev (see Table 1; Yurakhno, 1992; Yurakhno and Maltsev, 1999). These authors divided the then Pseudophyllidea into three suborders: (1) an early diverging Bothriocephalata, (2) the more recently evolved suborder Polygonoporiata, which included *Tetragonoporus* Skryabin, 1961 and their relatives, and (3) the most recently diverging group, the Diphyllobothriata, comprising four superfamilies (Table 1). Unlike Dubinina (1980b), Yurakhno (1992) postulated simplification of the scoleces of pseudophyllidean cestodes over their evolutionary history.

Brooks and McLennan (1993) were the first to employ cladistic methods for assessing the phylogenetic relationships among the group, then as the Pseudophylliformes. Coding for 28 morphological characters, they concluded that the two diphyllobothriidean families (Cephalochlamydidae and Diphyllobothriidae) form a monophyletic group that is sister to the haplobothriideans. Later, Bray et al. (1999) conducted a cladistics analysis based on 36 morphological characters coded for 15 type genera of putative families and found the diphyllobothriideans represented by seven genera to be polyphyletic.

The first molecular sequence data of diphyllobothriideans generated for phylogenetic work, were those of the small subunit nuclear rDNA (18S rDNA) and the mitochondrial NADH dehydrogenase subunit 3 (nad3) of *Spirometra* by Kokaze et al. (1997) and Liu et al. (1997). Shortly thereafter, 18S rDNA data were generated for the broad fish tapeworm, *Diphyllobothrium latum*, in the pioneering molecular phylogenetic study of cestodes by Mariaux (1998). A year later, sequence data for the same locus and elongation factor-1α (Ef-1α) of *Diphyllobothrium stemmacephalum* and *Schistocephalus solidus* (Müller, 1776) Steenstrup, 1857 were included in the molecular phylogenetic study by Olson and Caira (1999), and 18S rDNA of *Duthiersia fimbriata* (Diesing, 1854) Monticelli & Crety, 1891 by Kodedová et al. (2000). Zhu et al. (2002) used single-strand conformation polymorphism (SSCP) to detect single-base variation in the COI gene in populations of *Spirometa* parasitizing different second intermediate hosts. Sequence data for the second internal transcribed spacer (ITS2) were used by Luo et al. (2003) in studies of plerocercoids of ligulid cestodes from different fish intermediate hosts. Logan et al. (2004) used data for the same marker to assess the interrelationships of the diphyllobothriid genera *Digramma*, *Diphyllobothrium*, *Ligula*, and *Schistocephalus*. That study revealed the existence of a species complex in *Ligula intestinalis* and questioned the validity of the genus *Digramma*. However, the synonymy of *Digramma* with *Ligula* was not formally proposed (see Logan et al., 2004).

Brabec et al. (2006) used analyses of 18S rDNA and 28S rDNA sequence data from previous studies (see above) and data they generated *de novo* for a species each of *Cephalochlamys*, *Diagramma*, *Ligula*, and two species of *Diphyllobothrium* to explore relationships within and among the Diphyllobothriidae and other taxa. In the results of their phylogenetic analyses the species of *Cephalochlamys* (Cephalochlamydidae; i.e., a parasite of frogs) grouped as the earliest diverging lineage among the species included in their study, followed by the species of *Duthiersia* (Solenophoridae; a parasite of "reptiles"), which grouped as sister to a diphyllobothriid clade comprising the single species of *Schistocephalus*, three species of *Diphyllobothrium*, and the single species each of *Digramma* and *Ligula*.

CURRENT STATUS OF THE DIPHYLLOBOTHRIIDEA

DIVERSITY AND CLASSIFICATION. Only one species, *Scyphocephalus jadhavi* Kalyankar & Nanware, 2010 (considered here as a new synonym of *Duthiersia expansa* Perrier, 1873), was described since 2008, albeit not as a result of PBI project efforts. Nearly 20 new generic and specific synonyms and new combinations, however, were proposed as part of the this project (Table 2). *Adenocephalus* was resurrected to accommodate its original type species *A. pacificus*; the validity of this genus was supported by morphological and molecular data (Hernández-Orts et al., 2015). Largely following the revisions of Delyamure et al. (1985) and Kamo (1999), and until the taxonomic actions described below are implemented, a total of 70 species in 18 genera are currently recognized as valid in the order (Table 2). These genera are arranged in three families: the Diphyllobothriidae, Cephalochlamydidae, and Solenophoridae. This classification scheme is supported by molecular phylogenetic analyses (Brabec et al., 2006; Waeschenbach et al., accepted).

Kornyushin (2009) proposed subdividing *Diphyllobothrium* into three subgenera, based on host associations, scolex morphology, and whether or not a neck was present. These subgenera are: *Diphyllobothrium sensu stricto* for species parasitizing cetaceans, *Dibothriocephalus* for freshwater and terrestrial species, and an unnamed subgenus for species parasitizing seals, which he subdivided into three additional groups: (a) species with a wider or elongated scolex similar to *D. roemeri* (Zschokke, 1903) Meggitt, 1924; (b) small species from Weddell seals; and (c) species with a cordate scolex similar to *D. cordatum*. We will refrain from recognizing these subgenera until their validity is confirmed in a phylogenetic framework.

We consider *Tetragonoporus calyptocephalus* to be the only valid polygonoporal species and hereby designate both *Tetragonocephalus physeteris* (Clarke, 1952) Delyamure & Skryabin, 1968 and *Polygonoporus giganticus* Skryabin, 1967 as its junior synonyms (Table 2). In contrast, the genera *Adenocephalus*, *Glandicephalus* Fuhrmann, 1921, and *Flexobothrium* Yurakhno, 1989 are considered to be valid because their species possess unique diagnostic traits (i.e., a unique scolex morphology in *Flexobothrium*, papilla-like protuberances on the proglottids in *Adenocephalus*, and a strongly craspedote strobila in *Glandicephalus*) (see Kuchta et al., 2008; Hernández-Orts et al., 2015).

Collaborative efforts made collection of new material of 15 species in 11 genera for molecular phylogenetic studies possible. This material also served as the basis for redescriptions of several species (see below) and helped resolve taxonomic issues in problematic taxa, such as the human-infecting species *Adenocephalus pacificus* (see Hernández-Orts et al., 2015). Preliminary results of molecular phylogenetic analyses (Waeschenbach et al., accepted) indicate that both *Diplogonoporus* and *Diphyllobothrium* are polyphyletic, the latter genus comprising at least three separate lineages. Further taxonomic revisions of the order, and especially of *Diphyllobothrium*, are pending. Preliminary molecular results regarding this genus (Waeschenbach et al., accepted) and at least a subset of its 30 species suggest the following: (1) species from cetaceans, including the type species *Diphyllobothrium stemmacephalum* and the species currently identified as *Diplogonoporus balaenopterae* Lönnberg, 1892, represent *Diphyllobothrium sensu stricto* as proposed by Kornyushin (2009); (2) the species from terrestrial mammals and birds form a more derived clade witin the genus and, following Kornyushin's proposal, should be considered members of the subgenus *Dibothriocephalus*; and (3) the remaining species (i.e., 19 valid species) parasitizing pinnipeds compose a polyphyletic *Diphyllobothrium*. Taxonomic issues in all 17 of the remaining diphyllobothriidean genera are much less complex given that none house more than seven species (Table 2).

Molecular data have also been widely used for the identification of human-infecting tapeworms in clinical samples, which generally consist of merely gravid proglottids expelled from infected humans and eggs in stool (Kuchta et al., 2015). This work has confirmed the utility of mitochondrial genes for systematic studies and diagnostics of clinical samples. The most widely used marker, COI, allows for differentiation among congeneric diphyllobothriidean species. In contrast, nuclear markers such as 18S rDNA and 28S rDNA are unable to unambiguously differentiate among congeneric species, such as for example *D. dendriticum* (Nitzsch, 1824) Lühe, 1910, *D. ditremum* (Creplin, 1825) Lühe, 1910, *D. latum*, and *D. nihonkaiense* Yamane, Kamo, Bylund & Wikgren, 1986 (see Kuchta et al., 2015).

Some attention has also been paid to molecular characterization of clinical samples of species of *Spirometra* and their plerocercoids from their amphibian, lizards, and snake intermediate hosts (Kuchta et al., 2015). According to a morphology-based revision carried out by Kamo (1999), the genus contains only four valid species, including the cosmopolitan *S. erinaceieuropaei*. However, preliminary analyses of molecular data provide evidence of substantial differences among specimens collected from different geographic regions. These include at least two clades in Eurasia (i.e., *S.* cf. *erinaceieuropaei*), three clades in North and South America (i.e., *S.* cf. *mansonoides*), and one clade in Africa (i.e., *S.* cf. *folium*) (R. Kuchta and J. Brabec, unpubl. data).

Morphology. Many diphyllobothriideans are large tapeworms, around 1 m long, with a subset of species reaching lengths of up to 30 m (e.g., *T. calyptocephalus* from sperm whales; Delyamure and Skryabin [1968]). The scolex is unarmed, consisting of one dorsal and one ventral bothrium. The bothria can, however, be modified to be, for example, highly folded (as in *Baylisia*, *Baylisiella*, *Duthiersia*, *Flexobothrium*, *Plicobothrium*, and *Pyramicocephalus*; see Figs. 5, 9), or fused into muscular tubes, or even reduced as in some solenophorids (Figs. 2, 3); the scolex of *Tetragonoporus* bears an apical disc. A neck may be present or not, but this character is often difficult to assess and depends on the state of contraction of the worm.

In contrast, strobilar morphology is rather uniform across taxa; the exceptions are the cephalochlamydids, which lack a cirrus-sac (Figs. 16, 19). Most diphyllobothriideans have a single genital complex per proglottid (Fig. 14–16, 19, and 20), although aberrant proglottids bearing two or multiple genital complexes may be present in some specimens of monogonoporal species. Species of genera such as *Ligula*, *Diplogonoporus*, and *Tetragonoporus* typically possess from two to 14 horizontal sets of genital complexes per proglottid (Figs. 17, 18, 21). The most peculiar situation occurs in both species of *Baylisia*, with as many as 307 genital complexes organized in tandem in a single proglottid (Fig. 22; see Yurakhno, 1992). However, the number of the genital complexes per proglottid may vary among specimens of the same species or even within one strobila, and thus is not a suitable diagnostic feature (e.g., *Ligula* vs. *Digramma*). Plerocercoids of species of *Ligula*, which develop in the body cavity of teleosts, have almost fully developed genitalia but do not become gravid until they reach the definitive host (Dubinina, 1980a).

The taxonomy of diphyllobothriideans is insufficiently resolved. Identification of individual species, especially those in the species-rich genus *Diphyllobothrium*, is complicated by the relatively uniform strobilar morphology seen across taxa and the high amount of intraspecific and intraindividual variation seen for most morphometric and morphological characters across the order (Hernández-Orts et al., 2015). Descriptions of many species lack sufficient detail; decriptions of other species do not provide sufficient differentiation from congeners (e.g., measurements with overlapping ranges were used to differentiate species). While in the cases of some features this variation may be the result of definitive host-induced variation (Andersen, 1972, 1975; Halvorsen and Andersen, 1974; Maltsev and Gavrilova, 1994; Hernández-Orts et al., 2015), other features of potential taxonomic value may also be influenced by methods of fixation (e.g., contraction or deformation of specimens fixed with cold fixatives, decomposition of worms relaxed in water, etc.).

The re-examination of extensive material of diphyllobothriidean cestodes over the course of the PBI project (Kuchta et al., 2013; Hernández-Orts et al., 2015) has confirmed the high intraspecific, and even intraindividual, variation seen in characteristics of diphyllobothriideans, such as body length, distribution of vitelline follicles, extension of the testicular field, and number of uterine loops containing fully developed eggs—a fact observed earlier by other authors (Wardle and McColl, 1937; Maltsev and Gavrilova, 1994). Also problematic are features such as the angle between the longitudinal axes of the external seminal vesicle and the cirrus-sac for it is now clear that this angle can vary considerably intraspecifically (Hernández-Orts et al., 2015). Of particular note is the variation in features such as scolex shape and length, and neck length, which have been used as discriminative characters in the delimitation of species now assigned to the Diphyllobothriidea (see Andersen, 1972, 1975; Delyamure et al., 1985; Hernández-Orts et al., 2015). As a consequence, these characteristics should be used as criteria for species identifications with caution, as recommended previously by several authors (Wardle and McColl, 1937; Stunkard, 1965; Meyer, 1966; Hernández-Orts et al., 2015).

Testis number, which is a feature that serves as a taxonomically important character for species differentiation in a diversity of other cestode orders, is of limited utility in the Diphyllobothriidea for the following reasons. First, most species possess well-developed outer longitudinal musculature and numerous vitelline follicles situated in the cortex. This combination of features hinders the precise determination of testis number. Second, the number of testes is usually extremely high (i.e., hundreds) and thus accurate counts are difficult to obtain. Finally, detailed comparative studies assessing intraspecific variation in testis number are scarce (Maltsev and Gavrilova, 1994; Hernández-Orts et al., 2015).

In contrast, size of the cirrus-sac and external seminal vesicle measured in sagittal section or in whole mount (i.e., in frontal view), appear to be relatively invariable within a species and thus, may serve as useful diagnostic features (Hernández-Orts et al., 2015). Egg morphology and size may also be suitable taxonomic characters in a subset of diphyllobothriidean taxa (Maltsev and Gavrilova, 1994), including, for example, human-infecting species of *Diphyllobothrium* (see Leštinová et al., 2016). Furthermore, whereas diphyllobothriideans parasitizing freshwater and anadromous vertebrates, such as a subset of species of *Diphyllobothrium* (Fig. 26), *Ligula* (Fig. 28), and solenophorids, possess eggs with a smooth surface, the surface of the eggs of diphyllobothriideans parasitizing marine hosts (e.g., species of *Adenocephalus* [Fig. 27], *Diphyllobothrium* from marine mammals, and *Tetragonoporus* [Fig. 30]) is densely covered with deep pits (Leštinová et al., 2016).

Ultrastructural features of diphyllobothriideans examined using scanning and transmission electron microscopy, have been described recently (Bruňanská et al., 2012; Hernández-Orts et al., 2015; Yoneva et al., 2015), but only very few features (e.g., presence or absence of transverse papilla-like protuberances along the median line of proglottids in *A. pacificus*) appear to be suitable for taxonomic purposes (Hernández-Orts et al., 2015). This is true even for features that have been shown to be of taxonomic importance in other cestode orders, such as microthrix shape, vitellogenesis, spermiogenesis, and the ultrastructure of sperm and vitellocytes (see Yoneva et al., 2015).

What is now clear is that for optimal results, live diphyllobothriideans should be fixed in hot 4% formalin (or, if not available, in hot water followed by transfer to alcohol or formalin) for morphological work. However, to maximize the use of specimens, prior to fixation, a part of the specimen should be preserved in ethanol for future molecular work; this approach is feasible because of the large size of most diphyllobothriideans. The traditional practice of relaxing diphyllobothriidean specimens in water or saline and then fixing them under strong pressure is discouraged because these methods cause artifacts such as deformation and/or contraction and ultimately even result in over-relaxation or maceration. Unfortunately, helminths of marine mammals are usually recovered from stranded, dead hosts or from frozen hosts originally captured as by-catch from fisheries. As a result, gastrointestinal helminths collected, and especially cestodes, are usually macerated, deformed, or incomplete because their hosts had been dead for a considerable time or had been frozen prior to parasitological examination. Furthermore, it is necessary to remove the thick cortical layer and longitudinal muscle bundles of mature and gravid proglottids to effectively study the anatomy of large-sized diphyllobothriideans (Hernández-Orts et al., 2015) (Fig. 17).

Host Associations. The three main lineages (i.e., families) of diphyllobothriideans reflect the evolutionary history of their respective tetrapod definitive hosts and the variation in the complexity of their life-cycles. The three species that belong to the earliest diverging lineage (i.e., Cephalochlamydidae) all parasitize frogs (Dicroglossidae Anderson, Pipidae, and Pyxicephalidae Bonaparte) as definitive hosts. Their life-cycles involve only a copepod intermediate host (Thurston, 1967).

In contrast, the Solenophoridae parasitize monitor lizards, snakes, and rarely iguanas. The life-cycles of solenophorids are unknown, but given the diets of their definitive hosts, in addition to a copepod first intermediate host (Solomon, 1932), involvement of a second intermediate and also possibly a paratenic host (a vertebrate) seems probable.

The life-cycles of the species-rich family Diphyllobothriidae are complex as they involve a copepod as the first intermediate host and a vertebrate as the second intermediate host, and also possibly a vertebrate paratenic host (Delyamure et al., 1985). Members of this family predominantly use mammals and, to a lesser extent, birds as definitive hosts. The mammals involved are principally carnivores (families Canidae, Felidae Fischer de Waldheim, Herpestidae Bonaparte, Hyaenidae Gray, Mephitidae Bonaparte, Mustelidae

Fischer de Waldheim, Otariidae Gray, Phocidae Gray, Procyonidae Gray, and Ursidae Fischer de Waldheim), rarely cetaceans (Balaenopteridae Gray, Delphinidae Gray, Eschrichtiidae Ellerman & Morrison-Scott, Monodontidae Gray, Phocoenidae Gray, and Physeteridae Gray), and primates (i.e., humans). Species of *Diphyllobothrium* have been found in naturally infected rodents only once (i.e., *D. dendriticum* from the common water rat *Hydromys chrysogaster* Geoffroy; Stephanson et al., 1987), but hamsters, rats, and mice have been used as suitable experimental definitive hosts for several diphyllobothriidean taxa (Andersen, 1972; Delyamure et al., 1985). We consider records of adult specimens of *Diphyllobothrium* from other hosts (e.g., *Diphyllobothrium salvelini* Yeh, 1955 in a teleost, the Arctic char [*Salvelinus alpinus* L.], from Greenland; see Table 2; Yeh, 1955) to be erroneous. The spectrum of birds that host diphyllobothriids is rather broad and consists primarily of core water birds (clade Aequornithes of Yuri et al. [2013]) but also members of the orders Anseriformes, Podicipediformes, and Charadriiformes, and rarely Accipitriformes, Gruiformes, and Passeriformes (see Dubinina, 1980a; Delyamure et al., 1985). Only one species, *D. scoticum* (Rennie & Reid, 1912) Meggitt, 1924, has been reported from penguins (as *Dibothriocephalus pygoscelis* Rennie & Reid, 1912), but seals seem to be typical definitive hosts of this species (Delyamure et al., 1985).

In species of *Spirometra*, the vertebrate second intermediate host (and paratenic host) may be a snake. *Diphyllobothrium serpentis* Yamaguti, 1935 was found only once in the Chinese cobra, *Naja atra* Cantor, from Taiwan. This snake may have represented a post-cyclic host accidentally infected with this cestode (Stunkard, 1949). This species, which is the only member of *Diphyllobothrium* reported from snakes was not listed by Delyamure et al. (1985), but was synonymized without any explanation with *S. erinaceieuropaei* by Kamo (1999). We considered *D. serpentis* to be a *species inquirenda* (Table 2).

It thus appears that, based on habitat, the diphyllobothriids can be divided into two primary ecological groups. The first is a marine group, which includes 37 species that employ marine mammals as their definitive hosts. The second is a terrestrial group, which comprises 21 species that parasitize terrestrial mammals including humans, but primarily carnivores such as canids and felids, and, on occasion, fish-eating birds. The majority of the members of the terrestrial group (i.e., species of the genera *Diphyllobothrium* [*Dibothriocephalus sensu* Kornyushin (2009)], *Ligula*, and *Schistocephalus*) use freshwater and anadromous teleosts as second intermediate hosts, whereas species of *Spirometra* use tetrapods, mainly amphibians and "reptiles," but never fish as second intermediate hosts (Kuchta et al., 2015). Adults of *Diphyllobothrium dendriticum* and *D. ditremum* have been reported from fish-eating birds (Delyamure et al., 1985; Kuchta et al., 2013).

Although a robust molecular phylogenetic analysis of diphyllobothriids has yet to be completed, preliminary work (e.g., Hernández-Orts et al., 2015; Waeschenbach et al., accepted) suggests that the earliest diverging diphyllobothriids were parasites of terrestrial carnivores and fish-eating birds (species of *Spirometra* and *Schistocephalus*), and that one lineage of more recently evolved taxa colonized marine mammals (species of *Diphyllobothrium*, *Adenocephalus*, and other genera in seals and cetaceans), whereas members of the other lineage of more recently evolved diphyllobothriids adapted to fish-eating birds, terrestrial carnivores, and humans (*Ligula*, *Diphyllobothrium*).

In terms of host specificity, species of *Ligula* and *Schistocephalus* exhibit a very low degree of host specificity for their definitive hosts, with adults of these genera having been reported from nearly 80 species of fish-eating birds (e.g., Dubinina, 1980a). For example, *S. solidus* has been reported from as many as 42 species in eight bird orders (Vik, 1954). That said, it is interesting that this and other species of *Ligula* and *Schistocephalus* spend only a very short time (a few days) in their definitive host because their plerocercoids are almost sexually mature by the time they leave the second intermediate host (i.e., the teleost) and thus the definitive host is needed only for the production and dispersal of eggs (Dubinina, 1980a). Plerocercoids of species of *Ligula* and *Schistocephalus* have also been reported from a diversity of mammals, including seals, dogs, otters, and even humans (Delyamure et al., 1964, 1980; Rausch et al., 1967; Dubinina, 1980a; Sinisalo et al., 2003), but these infections have been considered incidental, resulting from the passage of cestodes through the digestive tract of animals that had consumed infected fish intermediate hosts (Sinisalo et al., 2003; Scholz and Kuchta, 2016).

In terms of marine mammals, seals (Phocidae and Otariidae) are a dominant group and have been reported to serve as definitive hosts for nearly 30 species of diphyllobothriideans. Among these, phocids host a much richer fauna (Table 2; Hernández-Orts et al., 2015) than do eared seals (i.e., otariids), which have been reported to host only a handful of species. Only *Adenocephalus pacificus* is exclusively specific to otariids. Cetaceans (Balaenopteridae, Delphinidae, and Eschrichtiidae) host only nine species.

Seventeen species of four diphyllobothriid genera (i.e., *Adenocephalus*, *Diphyllobothrium* [and *Dibothriocephalus sensu* Kornyushin (2009)], *Diplogonoporus*, and *Spirometra*) have been reported from humans; however, most human cases involve *D. latum*, *D. nihonkaiense*, or *D. dendriticum* (Kuchta et al., 2015; Scholz and Kuchta, 2016). Diphyllobothriosis is usually not a life-threatening human disease, which is in contrast to some cases of sparganosis—a human disease caused by plerocercoids of species of *Spirometra* (Kuchta et al., 2015).

GEOGRAPHIC DISTRIBUTION. Many diphyllobothriideans occur predominately in colder climates, generally between 50–60° northern and 40–70° southern latitudes (Delyamure et al., 1985). However, some species (e.g., *Diphyllobothrium fuhrmanni* Hsü, 1935, *D. cameroni* Rausch, 1969, *D. minutus* Andersen, 1987, and *D. rauschi* Andersen, 1987) parasitize dolphins and the Hawaiian monk seal in the tropical Indo-Pacific region (Delyamure et al., 1985; Andersen, 1987). Similarly, some species, such as *D. stemmacephalum* and *Diplogonoporus balaenopterae*, have been reported from cetaceans (dolphins and whales, respectively) in the tropical Atlantic Ocean (Zam et al., 1971; Delyamure et al., 1985) and in the Red Sea (Kleinertz et al., 2014). Species of Cephalochlamydidae and Solenophoridae occur exclusively in tropical and subtropical latitudes and members of the genus *Spirometra* occur in temperate and tropical zones (Kuchta et al., 2015).

In total, 55 species of diphyllobothriideans (i.e., 79% of species in the order) are known from the Northern Hemisphere, whereas 31 species (i.e., 44% of species in the order) have been reported from the Southern Hemisphere. We note that three marine species (*A. pacificus*, *D. stemmacephalum*, and *Diplogonoporus balaenopterae*), a few terrestrial taxa (i.e., species of *Ligula*, *S. erinaceieuropaei*, *D. latum*, and *D. dendriticum*), and some solenophorids and cephalochlamydids are known to occur in both hemispheres (Delyamure et al., 1985; Hernández-Orts et al., 2015; R. Kuchta, unpubl. data). A total of 14 species in four genera (i.e., *Baylisia*, *Baylisiella*, *Flexobothrium*, and *Glandicephalus*) are endemic to Antarctic seals (Delyamure et al., 1985; Yurakhno, 1992; Kamo, 1999).

Regarding non-marine environments, terrestrial and freshwater species, which represent 44% of the total species richness (32 species) of the order, occur in the Palaearctic (16 species, i.e., 22%), Nearctic (10 species, i.e., 14%), and Afrotropic (8 species; i.e., 10%) realms. Human-infecting species dominate in temperate zones of the Holarctic realm (*D. latum*, *D. dendriticum*, and *D. nihonkaiense*), but the two former species are also known from Chile and Argentina; *D. dendriticum* has been reported from Tasmania (Stephanson et al., 1987). The origin of these taxa in South America and Australia is unclear, but their original distribution was likely limited to the Northern Hemisphere (Kuchta et al., 2013).

Some taxa have a cosmopolitan distribution, whereas others have more restricted, but still extensive distributions. *Diphyllobothrium nihonkaiense* may occur in both marine and freshwater environments because anadromous Pacific salmonids serve as their second intermediate host (Scholz et al., 2009). Species of *Schistocephalus* are distributed in colder reagions of the Holarctic realm, mainly in coastal areas, whereas *Ligula* is cosmopolitan, with species occurring on all continents except Antarctica. Cephalochlamydids are endemic to the Afrotropic realm (Jackson and Tinsley, 2001), whereas solenophorids have a much wider distribution, with records from the Afrotropic, Indomalayan, Australasian, and, most probably, Neotropical realms.

PHYLOGENETIC RELATIONSHIPS. The application of molecular phylogenetics for addressing questions of diphyllobothriidean interrelationships represents a milestone in unraveling interrelationships of diphyllobothriidean cestodes. Molecular data were also crucial in the establishment of the order Diphyllobothriidea (previously part of polyphyletic Pseudophyllidea—see Kuchta et al., 2008). However, molecular data generated to date, including complete mitochondrial genomes, emphasize human-infecting taxa (i.e., *A. pacificus*, *D. latum*, *D. nihonkaiense*, *D. dendriticum*, and species of *Spirometra*). Sequence data have yet to be generated for the majority of diphyllobothriidean species. In particular, molecular data are not currently available for species with unusual morphologies, especially with respect to scolex morphology; they are similarly lacking for species parasitizing evolutionarily interesting host groups such as *Tetragonoporus* from the sperm whale, *Plicobothrium* from whales, species of endemic Antarctic genera such as *Baylisia* from the crabeater seal, and *Baylisiella* and *Flexobothrium* from the southern elephant seal.

Available molecular data invariably provide evidence for the polyphyly of the genera *Diphyllobothrium* and *Diplogonoporus* (see Yamasaki et al., 2012) as they are currently configured (see Table 2). *Diphyllobothrium* does not appear to be monophyletic relative to *Diplogonoporus* (Waeschenbach et al., accepted). *Diphyllobothrium* is composed of at least three independent lineages for which a revised classification will be proposed when data on morphological, ecological, and life-cycle traits make it possible to circumscribe individual monophyletic assemblages (Hernández-Orts et al., 2015; Waeschenbach et al., accepted).

One of the most unexpected results from published phylogenetic analyses is the relatively divergent placement of species of *Ligula* and *Schistocephalus* relative to one another (see Brabec et al., 2006). This is in stark contrast to these genera having been placed in the same family, Ligulidae (synonymized with Diphyllobothriidae), in the past based on their similar gross morphology, including weakly developed attachment organs on the scolex and life-cycles involving copepods and planktivorous fishes as intermediate hosts and fish-eating birds as definitive hosts (Dubinina, 1980a).

CONCLUSIONS

Although no new diphyllobothriidean taxa were described as part of the PBI project, the project made possible the collection of a considerable amount of diphyllobothriidean material from around the world for morphological and molecular evaluation. It is now obvious that the taxonomic problems that remain in this order cannot be resolved without the use of molecular methods; these methods are especially useful for reliable species identifications of clinical samples. Assessment of intraspecific morphological variation should be based on properly-fixed specimens, preferably from freshly killed hosts. As is the case for other cestode orders, for morphological work, live cestodes should be fixed in hot 4% formalin (or, if not available, in hot water subsequently placed in alcohol or formalin). However, prior to fixation, it should be obligatory to preserve a piece of each specimen in ethanol for molecular work, ideally the posterior-most gravid proglottids. The order is confirmed to be monophyletic and not all that closely related to the Bothriocephalidea (members of both orders were previously placed in the order Pseudophyllidea). The Diphyllobothriidea now includes three families, 18 genera, and 70 species. Diphyllobothriideans parasitize members of all tetrapod groups, occur in all environments and all over the globe, although only a few species are cosmopolitan. Despite preliminary molecular work, phylogenetic relationships of diphyllobothriideans remain to be insufficiently known, especially because a number of taxa are not available for molecular analyses.

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TABLE 1. The classification system of the "Diphyllobothriata" proposed by Yurakhno (1992) and Yurakhno and Maltsev (1999).

- DIPHYLLOBOTHRIATA Mordivenci, 1966
  - Baylisioidea Yurakhno, 1992
    - Baylisiidae Yurakhno, 1989
      - *Baylisia* Markowski, 1952
  - Baylisielloidea Yurakho & Maltsev, 1999
    - Baylisiellidae Yurakhno & Maltsev, 1999
      - *Baylisiella* Markowski, 1952
    - Ligulidae Claus, 1868
      - Ligulinae Monticeli & Grety, 1959
        - *Ligula* Bloch, 1782
        - *Digramma* Cholodkovsky, 1914
  - Diphyllobothrioidea Lühe, 1910
    - Diphyllobothriidae Lühe, 1910
      - Diphyllobothriinae Lühe, 1910
        - *Diphyllobothrium* Cobbold, 1858
        - *Diplogonoporus* Lönnberg, 1892
        - *Plicobothrium* Rausch & Margolis, 1969
        - *Pyramicocephalus* Monticelli, 1890
    - Glandicephalidae Yurakhno & Maltsev, 1995
      - *Glandicephalus* Fuhrmann, 1921
    - Schistocephalidae Yurakhno, 1992
      - *Schistocephalus* Creplin, 1829
  - Scyphocephaloidea Freze, 1974
    - Cephalochlamidae Yamaguti, 1959
      - *Cephalochlamys* Blanchard, 1908
    - Scyphocephalidae Freze, 1974
      - *Bothridium* de Blainville, 1824
      - *Duthiersia* Perrier, 1873
      - *Scyphocephalus* Riggenbach, 1898
- POLYGONOPORIATA Yurakhno, 1992
  - Polygonoporidae Yurakhno, 1992
    - Polygonoporinae Delyamure & Skryabin, 1968
      - *Hexagonoporus* Gubanov in Delyamure, 1955
      - *Multiductus* Clarke, 1962
      - *Polygonoporus* Skryabin, 1967
      - *Tetragonoporus* Skryabin, 1961

TABLE 2. List of valid diphyllobothriidean taxa with type hosts, and *genera* and *species inquirendae*. New taxa and taxonomic actions resulting from PBI project activities indicated in bold. * Species of the subgenus *Dibothriocephalus* from terrestrial mammals and birds based on Kornyushin (2009). † Species of the polyphyletic *Diphyllobothrium* from pinnipeds.

VALID TAXA

- FAMILY CEPHALOCHLAMYDIDAE YAMAGUTI, 1959
  - *Cephalochlamys* Blanchard, 1908
    - *Cephalochlamys namaquensis* (Cohn, 1906) Blanchard, 1908 (type) ex *Xenopus laevis*
    - *Cephalochlamys compactus* Jackson & Tinsley, 2001 ex *Xenopus muelleri*
  - *Paracephalochlamys* Jackson & Tinsley, 2001
    - *Paracephalochlamys papilionis* Jackson & Tinsley, 2001 ex *Pseudhymenochirus merlini*

- FAMILY DIPHYLLOBOTHRIIDAE LÜHE, 1910
  - *Adenocephalus* Nybelin, 1931
    - *Adenocephalus pacificus* Nybelin, 1931 (type) ex *Arctocephalus philippii*

- *Baylisia* Markowski, 1952
  - *Baylisia baylisi* Markowski, 1952 (type) ex *Lobodon carcinophagus*
  - *Baylisia supergonoporis* Yurakhno, 1989 ex *Lobodon carcinophagus*
- *Baylisiella* Markowski, 1952
  - *Baylisiella tecta (*von Linstow, 1892) Markowski, 1952 (type) ex *Mirounga leonina*
- *Diphyllobothrium* Cobbold, 1858
  - *Diphyllobothrium stemmacephalum* Cobbold, 1858 (type) ex *Phocoena phocoena*
  - *Diphyllobothrium alascense* Rausch & Williamson, 1958* ex *Canis familiaris*
  - *Diphyllobothrium archeri* (Leiper & Atkinson, 1914) Meggitt, 1924† ex *Leptonychotes weddellii*
  - *Diphyllobothrium cameroni* Rausch, 1969† ex *Monachus schauinslandi*
  - *Diphyllobothrium cordatum* (Leuckart, 1863) Gedoelst, 1911† ex *Erignathus barbatus*
  - *Diphyllobothrium dalliae* Rausch, 1956* ex *Larus glaucescens*
  - *Diphyllobothrium dendriticum* (Nitzsch, 1824) Lühe, 1910* ex *Rissa tridactyla*
  - *Diphyllobothrium ditremum* (Creplin, 1825) Lühe, 1910* ex *Gavia immer* **(new syn.** *Diphyllobothrium vogeli* Kuhlow, 1953 **[present study])**
  - *Diphyllobothrium elegans* (Krabbe, 1865) Meggitt, 1924† ex *Cystophora cristata* **(new syn.** *Diphyllobothrium pterocephalum* Delyamure & Skryabin, 1967 **[present study])**
  - *Diphyllobothrium fayi* Rausch, 2005† ex *Odobenus rosmarus*
  - *Diphyllobothrium fuhrmanni* Hsü, 1935 ex *Neophocaena phocaenoides*
  - *Diphyllobothrium gondo* Yamaguti, 1942 ex *Globicephala macrorhynchus*
  - *Diphyllobothrium hians* (Diesing, 1850) Meggitt, 1924† ex *Monachus monachus*
  - *Diphyllobothrium lanceolatum* (Krabbe, 1865) Cooper, 1921† ex *Erignathus barbatus* **(new syn.** *Diphyllobothrium skriabini* Yurakhno & Maltsev, 1993 **[present study])**
  - *Diphyllobothrium lashleyi* (Leiper & Atkinson, 1914) Meggitt, 1924† ex *Leptonychotes weddellii*
  - *Diphyllobothrium latum* (Linnaeus, 1758) Lühe, 1910* ex *Homo sapiens*
  - *Diphyllobothrium lobodoni* Yurakhno & Maltsev, 1994† ex *Lobodon carcinophagus*
  - *Diphyllobothrium macroovatum* Yurakhno, 1973 ex *Eschrichtius robustus*
  - *Diphyllobothrium minutus* Andersen, 1987† ex *Monachus schauinslandi*
  - *Diphyllobothrium mobile* (Rennie & Reid, 1912) Meggitt, 1924† ex *Leptonychotes weddellii*
  - *Diphyllobothrium nihonkaiense* Yamane, Kamo, Bylund & Wikgren, 1986* ex *Homo sapiens*
  - *Diphyllobothrium orcini* Hatsushika & Shiruzu, 1990 ex *Orcinus orca*
  - *Diphyllobothrium phocarum* Delyamure, Kurochkin & Skryabin, 1964† ex *Pusa caspica*
  - *Diphyllobothrium polyrugosum* Delyamure & Skryabin, 1966 ex *Orcinus orca*
  - *Diphyllobothrium pseudowilsoni* Wojciechowska & Zdzitowiecki, 1995† ex *Hydrurga leptonyx*
  - *Diphyllobothrium quadratum* (von Linstow, 1892) Railliet & Henry, 1912† ex *Hydrurga leptonyx*
  - *Diphyllobothrium rauschi* Andersen, 1987† ex *Monachus schauinslandi*
  - *Diphyllobothrium roemeri* (Zschokke, 1903) Meggitt, 1924† ex *Odobenus rosmarus*
  - *Diphyllobothrium schistochilos* (Germanos, 1895) Cooper, 1921† ex *Erignathus barbatus*
  - *Diphyllobothrium scoticum* (Rennie & Reid, 1912) Meggitt, 1924† ex *Hydrurga leptonyx*
  - *Diphyllobothrium ursi* Rausch, 1954* ex *Ursus arctos*
  - *Diphyllobothrium wilsoni* (Shipley, 1907) Railliet & Henry, 1912† ex *Ommatophoca rossii*
- *Diplogonoporus* Lönnberg, 1892
  - *Diplogonoporus balaenopterae* Lönnberg, 1892 (type) ex *Balaenoptera borealis*
  - *Diplogonoporus tetrapterus* (von Siebold, 1848) Ariola, 1896 ex *Phoca vitulina*
- *Flexobothrium* Yurakhno, 1989
  - *Flexobothrium microovatum* Yurakhno, 1989 (type) ex *Mirounga leoninae*
- *Glandicephalus* Fuhrmann, 1921
  - *Glandicephalus antarcticus* (Baird, 1853) Fuhrmann, 1921 (type) ex *Ommatophoca rossii*
  - *Glandicephalus perfoliatus* (Railliet & Henry, 1912) Markowski, 1952 ex *Leptonychotes weddellii*
- *Ligula* Bloch, 1782 (syn. *Digramma* Cholodkovsky, 1914)
  - *Ligula intestinalis* (Linnaeus, 1758) Gmelin, 1790 (type) ex "fish" (fish intermediate host)
  - *Ligula colymbi* Zeder, 1803 ex *Colymbus cristatus*
  - *Ligula alternans* Rudolphi, 1810 ex *Rissa tridactyla*
  - *Ligula nemachili* (Dubinina, 1957) **Kuchta & Scholz n. comb.** ex *Mergellus albellus*
  - *Ligula pavlovskii* Dubinina, 1959 ex *Benthophilus stellatus* (fish intermediate host)
- *Plicobothrium* Rausch & Margolis, 1969
  - *Plicobothrium globicephalae* Rausch & Margolis, 1969 (type) ex *Globicephala melaena*
- *Pyramicocephalus* Monticelli, 1890
  - *Pyramicocephalus phocarum* (Fabricius, 1780) Monticelli, 1890 (type) ex *Erignathus barbatus*

Schistocephalus Creplin, 1829
  - *Schistocephalus solidus* (Müller, 1776) Steenstrup, 1857 (type) ex *Gasterosteus aculeatus* (fish intermediate host)
  - *Schistocephalus cotti* Chubb, Seppälä, Lüscher, Milinski & Valtonen, 2005 ex *Cottus gobio* (fish intermediate host)
  - *Schistocephalus nemachili* Dubinina, 1959 ex *Mergus merganser*
  - *Schistocephalus pungitii* Dubinina, 1959 ex *Pungitius pungitius* (fish intermediate host)
  - *Schistocephalus thomasi* Garoian, 1960 ex *Larus argentatus*

Spirometra Faust, Campbell & Kellogg, 1929
  - *Spirometra erinaceieuropaei* (Rudolphi, 1819) Faust, Campbell & Kellogg, 1929 (type) ex *Erinaceus europaeus* (mammalian intermediate host)
  - *Spirometra mansonoides* (Mueller, 1935) Mueller, 1936 ex *Felis catus*
  - *Spirometra pretoriensis* (Baer, 1924) Wardle, McLeod & Stewart, 1947 ex *Otocyon megalotis*
  - *Spirometra theileri* (Baer, 1924) Opuni & Muller, 1974 ex *Leptailurus serval*

Tetragonoporus Skryabin, 1961
  - *Tetragonoporus calyptocephalus* Skryabin, 1961 (type) ex *Physeter macrocephalus* **(new syns.** *Tetragonocephalus physeteris* [Clarke, 1952] Delyamure & Skryabin, 1968 and *Polygonoporus giganticus* Skryabin, 1967 **[present study])**

FAMILY SOLENOPHORIDAE MONTICELLI & CRANDY, 1891 **(NEW SYN. SCYPHOCEPHALIDAE FREZE, 1974 [PRESENT STUDY])**

Bothridium de Blainville in Bremser, 1824
  - *Bothridium pithonis* de Blainville in Bremser, 1824 (type) ex a "python"
  - *Bothridium kugii* Sawada & Kugi, 1973 ex *Eunectes murinus*
  - *Bothridium obovatum* (Molin, 1858) Sambon, 1907 ex *Boa constrictor*
  - *Bothridium ornatum* Maplestone & Southwell, 1923 ex *Morelia spilota*
  - *Bothridium ovatum* (Diesing, 1850) Yamaguti, 1959 ex *Python sebae* **(new syns.** *Bothridium longicephalum* Sawada & Kugi, 1973; *Bothridium longiorum* Sawada & Kugi, 1973; *Bothridium microdisciformis* Sawada & Kugi, 1973; *Bothridium orientalis* Sawada & Kugi, 1973 **[present study])**
  - *Bothridium sawadai* Sawada & Kugi, 1973 ex *Epicrates cenchria*

Duthiersia Perrier, 1873
  - *Duthiersia expansa* Perrier, 1873 (type) ex *Varanus bivittatus* **(new syns.** *Duthiersia sindensis* Bilqees & Masood, 1973; *Duthiersia gomatii* Gupta & Sinha, 1980; *Duthiersia chengi* Gupta & Parmar, 1989; *Scyphocephalus jadhavi* Kalyankar & Nanware, 2010 **[present study])**
  - *Duthiersia fimbriata* (Diesing, 1854) Monticelli & Crety, 1891 ex *Varanus niloticus*

Scyphocephalus Riggenbach, 1898
  - *Scyphocephalus bisulcatus* Riggenbach, 1898 (type) ex *Varanus salvator* **(new syn.** *Scyphocephalus longus* Sawada & Kugi, 1973 **[present study])**

GENERA & SPECIES INQUIRENDAE

Hexagonoporus Gubanov in Delyamure (1955)
Hexagonoporus physeteris Gubanov in Delyamure, 1955 ex *Physander catadon*
Diphyllobothrium arctomarinum Serdyukov, 1969 ex *Stercorarius parasiticus*
Diphyllobothrium salvelini Yeh, 1955 ex *Salvelinus alpinus*
Diphyllobothrium serpentis Yamaguti, 1935 ex *Naja atra*
Sparganum proliferum Ijima, 1905 ex *Homo sapiens*

9

Gyrocotylidea Poche, 1926

By
Roman Kuchta[1], Tomáš Scholz, and Haakon Hansen

GYROCOTYLIDEA AS THEY WERE KNOWN PRIOR TO THE PBI PROJECT

Diversity and Classification. Members of this group are exclusively parasites of the spiral intestine of holocephalans (Chimaeriformes), commonly known as ratfishes. Even though these parasites have been known for more than 150 years, gyrocotylideans remain among the most poorly known cestode orders in terms of their diversity, classification, and biology. In fact, a complete life-cycle is not yet known for any species. Their relationships to other parasitic flatworms (i.e., the Neodermata) have been the subject of discussion for decades (for a review see Williams et al. [1987]). Simmons (1974) referred to *Gyrocotyle* Diesing, 1850 as a "century-old enigma" in the title of a chapter focussed on the genus; the enigmatic status of the group persists today.

To date, 17 nominal species of gyrocotylideans belonging to four genera have been described, namely *Gyrocotyle*, *Amphiptyches* Grube & Wagener in Wagener, 1852, *Crobylophorus* Krøyer, 1852, and *Gyrocotyloides* Fuhrmann, 1931. However, authors (e.g., Bandoni and Brooks, 1987) have generally tended to recognize only ten species in a single genus, *Gyrocotyle*, all described prior to 1969. But even the validity of these ten species has been somewhat controversial, with some authors questioning the validity of more than half of these ten species (Colin et al., 1986; Williams et al., 1987). In fact, Wardle and McLeod (1952) recognized only two of the eight species described at that time as valid (i.e., *Gyrocotyle urna* [Grube & Wagener in Wagener, 1852] Wagener, 1858 and *Gyrocotyloides nybelini* Fuhrmann, 1931).

The first gyrocotylidean species described was *Gyrocotyle rugosa* Diesing, 1850. Unfortunately, Diesing (1850) indicated the host to be a South African antelope (as "*Antilope pyarga*" in 1850; pg. 408). Reports of gyrocotylideans since then indicate that the identity of this host is certainly an error. In fact, Diesing (1858) later reported that *G. rugosa* was not an intestinal parasite of antelopes from South Africa, rather it was an ectoparasite of the marine bivalve *Mulinia edulis* (King) (as *Mactra edulis* King) off Valparaiso, Chile (see Williams et al. [1987] for more detail). However, it was Monticelli (1889) who ultimately identified the true host of this gyrocotylidean to be the holocephalan *Callorhinchus antarcticus* Fleming (= *Callorhinchus callorynchus* [L.]) off Dunedin, New Zealand. This remains the accepted host of this gyrocotylidean species—which is now considered to occur throughout the Southern Hemisphere (Bandoni and Brooks, 1987).

The second genus, *Crobylophorus* Krøyer, 1852, was erected by Krøyer (1852) for *Crobylophorus chimaerae* Krøyer, 1852 from the rabbit fish, *Chimaera monstrosa* L., off Norway. Later that same year, Grube and Wagener in Wagener (1852) erected *Amphiptyches* Grube & Wagener in Wagener, 1852 to accommodate *Amphiptyches urna* Grube & Wagener in Wagener,

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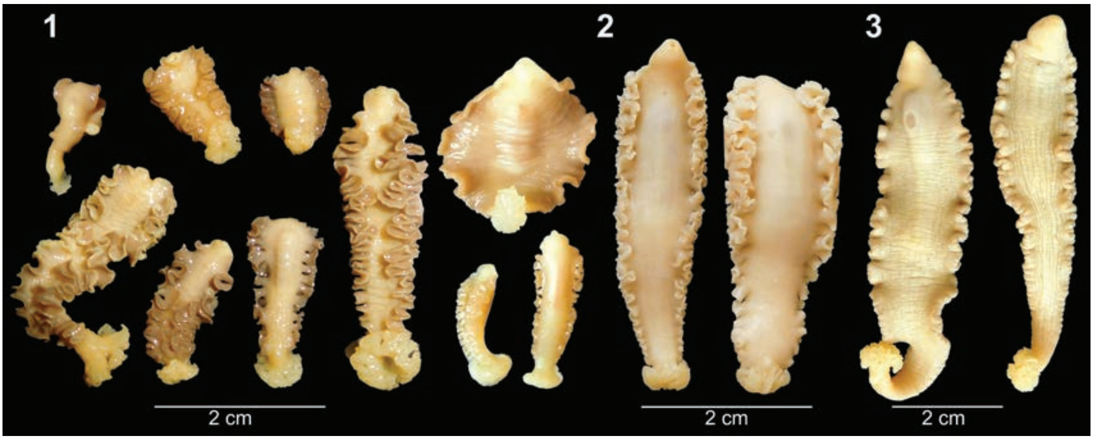
[1] Corresponding author (krtek@paru.cas.cz)

Kuchta, R., T. Scholz, and H. Hansen. 2017. Gyrocotylidea Poche, 1926. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 191–199.

1852 from the same host species off France. Shortly thereafter, both genera were synonymized with *Gyrocotyle* by both Diesing (1858) and Wagener (1858). The fourth genus, *Gyrocotyloides* Fuhrmann, 1931, was proposed by Fuhrmann (1931) for *Gyrocotyloides nybelini* also from *C. monstrosa* in the North Sea.

MORPHOLOGY. Gyrocotylideans are relatively large worms, reaching lengths of up to 3 cm, with a stout, fusiform to elongate monozoic body (Figs. 1–4). The anterior extremity bears a muscular, sucker-like organ differentially referred to as a sucker by Wardle and McLeod (1952), an acetabulum by Williams et al. (1987), and an apical invagination by Bandoni and Brooks (1987). The remainder of the body is attenuated and normally terminates in a rosette-like adhesive organ (also referred to as the rosette organ) in the form of a funnel—a feature which differentiates gyrocotylideans from members of all other orders of tapeworms (Gibson, 1994). The lateral margins of the body are usually, but not always (e.g., *G. nybelini*), plicate or crenulate. The surface of the body of most species is completely, or partly, covered with sclerites (or spines of different sizes and shapes) with the exception of one species, *G. nybelini* (see fig. 5 in Bandoni and Brooks [1987]; Xylander and Poddubnaya, 2009), and with fillitriches, as in all other tapeworms (Poddubnaya et al., 2006; Chervy, 2009). The rosette organ was reported to bear three different types of unicellular gland cells by Poddubnaya et al. (2006, 2008).

Gyrocotylidean anatomy is rather homogeneous across the order (Gibson, 1994). The osmoregulatory system is somewhat unusual among cestodes in that it consists of a subtegumental reticulate network of canals with two anterior pores. The testes are numerous and are arranged in two fields anterolateral to the uterus. A cirrus-sac is absent. Instead the male copulatory organ, referred to as a penis (as in some monogeneans), is armed with spinitriches, and a muscular ejaculatory duct is present. The male and female genital pores open separately. The male pore is medioventral, located between the anterior extremity of the body and the uterine pore. The vaginal pore is dorsal and lateral to the male pore. The ovary is follicular, V- or U-shaped and positioned posterior to the uterus. A long vagina expands to form a proximally located seminal receptacle. The vitellarium is follicular; the vitelline follicles occupy both lateral regions of the body. The uterus is medially coiled between the seminal receptacle and the uterine pore. Its terminal part forms an elongate to oval uterine sac and



FIGURES 1–3. Photomicrographs of gyrocotylideans obtained from off the Outer Hebrides, Atlantic Ocean. **(1)** *Gyrocotyle urna* from *Chimaera monstrosa*. **(2)** *Gyrocotyle* sp. 2 from *Hydrolagus pallidus*. **(3)** *Gyrocotyle* sp. 1 from *Harriotta raleighana*.

4

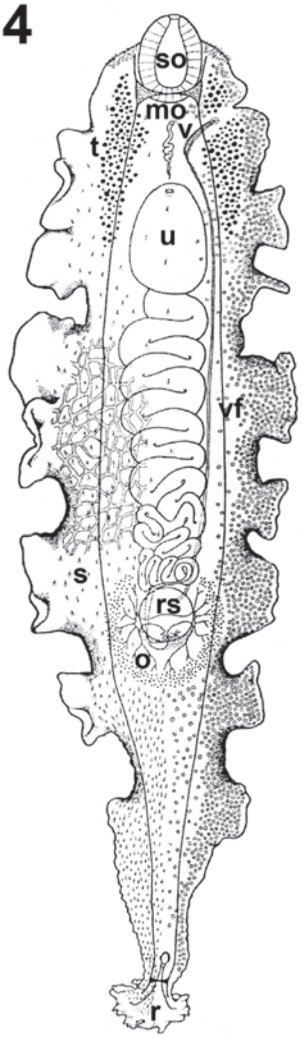


FIGURE 4. Morphology of *Gyrocotyle urna* from *Chimaera monstrosa* (modified from Williams et al. [1987]). *Abbreviations:* o, ovary; mo, ventral male opening; r, rosette with funnel; rs, seminal receptacle; s, body spines; so, sucker-like organ; t, testes; u, uterus; v, vagina and dorsal vaginal opening; vf, vitelline follicles.

the medioventral uterine pore is located in the anterior part of the body (Gibson, 1994). The intra-uterine eggs are operculate and unembryonated in all species, except *G. rugosa*. The latter has thin-walled, untanned eggs (coupled with the absence of phenolic substances in the vitelline follicles), which are mostly embryonated *in utero*. The uterus of *G. rugosa* also differs from that of other gyrocotylideans in being highly branched, rather than coiled, in shape (Williams et al., 1987).

Unfortunately, morphological studies of adult gyrocotylideans are complicated by the fact that species are large and muscular, and thus are highly contractile. This results in substantial morphological variation in body size and shape for most species depending on the method of fixation, making identifications difficult (Colin et al., 1986; Bristow, 1992; Gibson, 1994).

A ciliated larva, referred to as the lycophore or decacanth, because it possesses a total of ten (4 ventral and 6 dorsal) posteriorly-situated hooks which are identical in shape and size, hatches from the egg (see Xylander [1987, 1990] for comprehensive data on the ultrastructure of the lycophore of *G. urna*). Beyond this stage, little is known about the life-cycle of gyrocotylideans. An intermediate host has yet to be identified in nature. Attempts to experimentally infect the snail *Buccinulum linea* (Martyn) (as *Buccinulum multilineatum* Powell), the bivalve *Aulacomya maoriana* (Iredale), and hermit crabs of the superfamily Paguroidea Latreille with lycophores of *G. urna* and *G. rugosa* have failed (see Ruszkowski, 1932; Manter, 1951; Simmons, 1974). This has led some authors (e.g., Llewellyn, 1986) to conclude that the gyrocotylideans, like monogeneans, have a direct life-cycle. In contrast, other authors have proposed that, despite existing gaps in our understanding of the life-cycle, strong evidence exists to support an indirect life-cycle for gyrocotylideans. Xylander (1989) nicely summarized this evidence: (1) Even the smallest stages of gyrocotylideans found in the spiral intestine of chimaeras already possess a distinct anterior groove; this groove appears to be homologous to that seen in the Pseudophyllidea (now the Bothriocephalidea and Diphyllobothriidea), Tetraphyllidea, and Amphilinidea, all of which develop in crustacean intermediate hosts; (2) young chimaeras, which feed solely on yolk, are never infected suggesting that infective stages are ingested with some sort of food item; and (3) the lycophore larva is an actively swimming stage with a well-developed nervous system, which is consistent with active searching for a host.

HOST ASSOCIATIONS. Gyrocotylideans occur as adults exclusively in holocephalans (i.e., Chimaeriformes). Their association with this group of hosts is hypothesized to have existed for more than 350 million years, however, the origin of the group may extend back even further in geological time (Williams et al., 1987). Three families, six genera, and 49 valid species of holocephalans are generally recognized (Weigmann, 2016). Prior to the PBI project, gyrocotylideans had been reported from all three families of holocephalans, but from only four genera and ten species within these families (Williams et al., 1987). Reports of adult gyrocotylideans from other hosts are considered to be erroneous. These include a bivalve (Diesing, 1858; see above), the freshwater walking catfish *Clarias batrachus* (L.) from Bangladesh by Ali (1968), and the jellyfish *Athorybia rosacea* (Forsskål) (von Linstow, 1903; i.e., *Gyrocotyle medusarum* von Linstow, 1903, considered as a species *incertae sedis*). In addition, MacDonagh (1927) described *Gyrocotyle maxima* MacDonagh, 1927 from a shark identified as *Mustelus asterias* Cloquet from a fish market in La Plata, Argentina. This gyrocotylidean species was later synonymized with *Gyrocotyle meandrica* Mendivil-Herrera, 1946 from *Callorhinchus callorynchus* from Uruguay by Szidat (1968). The record from the shark most probably represents the accidental infection of a post-cyclic host (*sensu* Odening [1976]) (Bandoni and Brooks, 1987).

Gyrocotylideans are considered to be highly host specific (oioxenous *sensu* Euzet and Combes [1980]), with each species parasitizing only a single species of ratfish. However, it is common for a holocephalan species to harbor more than one species; instances of two (e.g., in *Callorhinchus callorynchus*, *Hydrolagus affinis*, *Hydrolagus colliei*, and *Rhinochimaera atlantica* Holt & Byrne) or even three (in *Chimaera monstrosa*) species of gyrocotylideans in the same host species have been reported (e.g., Hogan and Hurlbut, 1984; Bandoni and Brooks, 1987; Williams et al., 1987). In such instances, it is usually the case that one species is common and one is rare (Williams et al., 1987; Xylander, 2005). Some authors (e.g., Colin et al., 1986; Williams et al., 1987) have concluded that such cases of multiple species are in fact merely forms of a single, variable taxon. However, after examining numerous gyrocotylidean specimens, most other authors (e.g., Yamaguti, 1959; Schmidt, 1986; Bandoni and Brooks, 1987; Bristow and Berland, 1988; Bristow, 1992; Gibson, 1994), have recognized multiple valid species within a single holocephalan species based on morphological and biochemical (i.e., electrophoretic) evidence. In contrast, records such as that of *G. rugosa* in *Callorhinchus milii* Bory de Saint-Vincent by Manter (1951) and also in *Hydrolagus colliei* (Lay & Bennett) by Olson and Caira (1999) indicate that some gyrocotylidean species may occur in more than one holocephalan host species. Nevertheless, misidentification of specimens cannot be ruled out because of the difficult morphology and complicated taxonomy of the group, and thus such reports require confirmation.

Whereas young holocephalans may harbor heavy infections of juvenile gyrocotylideans, older holocephalans are generally parasitized by only two adult gyrocotylideans (Rohde, 2011). In these early infections, juvenile worms are usually present free in the host's spiral intestine, or even hyperparasitic in the parenchyma of other gyrocotylideans, rather than attached by their rosette to the mucosa of the spiral intestine (Fuhrmann, 1931; Halvorsen and Williams, 1968; Rohde, 2011). Halvorsen and Williams (1968) speculated that such infections begin when young hosts first start feeding. However, the fate of the majority of the juvenile worms remains unknown (Halvorsen and Williams, 1968). Pathological effects of gyrocotylidans on their holocephalan hosts are uncommon and, when observed, are restricted to heavily infected host individuals (Williams et al., 1987).

GEOGRAPHIC DISTRIBUTION. Like their holocephalan hosts, gyrocotylideans are widely distributed, with most occurring mainly in the deep-sea or cold shelf waters (Rohde, 2011). Gyrocotylideans have been studied most intensively in European (eastern North Atlantic Ocean and Mediterranean Sea), North American (eastern North Pacific and western North

Atlantic Oceans) and Australian waters, with a few records off South America (western South Atlantic Ocean) (see Williams et al. [1987] for details of distributions).

PHYLOGENETIC RELATIONSHIPS. The phylogenetic position of gyrocotylideans among parasitic flatworms (Platyhelminthes: Neodermata) has been a matter of intensive discussion. They have been considered to be the earliest diverging group of cestodes (*sensu lato*) in most phylogenetic studies based on morphological, ultrastructural, and life-cycle data (Ehlers, 1985; Brooks, 1989), although a few other workers (e.g., Llewellyn, 1986) included them among the Monogenea. Bandoni and Brooks (1987) presented the first detailed hypothesis of the interrelationships of gyrocotylideans based on morphological characters. They concluded that the origin of the group predates the breakup of Pangaea, and that there were two phases in the evolution of the gyrocotylideans: an initial phase of coevolution, and a later phase of colonization and dispersal.

Prior to the inception of the PBI project, sequence data were available for only three gyrocotylidean species. Baverstock et al. (1991) generated partial 18S rDNA sequence data for *Gyrocotyle rugosa* from *Callorhinchus milii* off South Australia; Olson and Caira (1999) generated additional 18S rDNA data and Olson et al. (2001) generated 28S rDNA data for specimens identified as this same species from *Hydrolagus colliei* off Alaska. However, as noted above, the identification of this specimen from *H. colliei* requires verification. Littlewood et al. (1999) generated 18S rDNA and 28S rDNA data for *G. urna* from *Chim. monstrosa* off Bergen, Norway; Olson et al. (2001) and Lockyer et al. (2003) expanded the 28S rDNA data for the latter species. Olson et al. (2008) generated 18S rDNA and 28S rDNA sequence data for an unidentified species of *Gyrocotyle* from *Callo. milii* collected off Tasmania. In their phylogenetic analyses of these data and those available for the other two species, the latter authors found *G. rugosa* and *G. urna* to be sister taxa with the unidentified species of *Gyrocotyle* as the sister to that group. However, even the earliest molecular work including representation of multiple cestode orders confirmed the cestode affinities of the Gyrocotylidea (see Olson and Caira, 1999; Olson et al., 2001; Olson and Tkach, 2005).

CURRENT STATUS OF THE GYROCOTYLIDEA

DIVERSITY AND CLASSIFICATION. The minor nature of this order meant that, beyond the collection of some new material, the order received little attention over the course of the PBI project. As a consequence, no changes in the taxonomy of the order have been proposed. The classification presented here follows that of Bandoni and Brooks (1987) and Gibson (1994) in recognizing only single family (Gyrocotylidae) and the single genus (*Gyrocotyle*), which houses ten valid species (Table 1). Nevertheless, it is important to note that preliminary molecular work by one of the authors (H. H.; see Hansen et al., 2015) suggests that *Gyrocotyloides,* with its single species *G. nybelini*, may also be valid.

MORPHOLOGY. No new information on the gross morphology of gyrocotylideans was generated over the course of the PBI project. However, new ultrastructural data on the uterus, ovary, anterior organ, and rosette organ of *G. urna* were presented by Poddubnaya et al. (2009, 2010, 2015). The results of these ultrastructural studies are intriguing in that they reveal similarities between gyrocotylideans and non-cestode neodermatans, such as the monogeneans.

HOST ASSOCIATIONS. Collections conducted over the course of the PBI project resulted in new material of *G. urna* from *Chim. monstrosa* (prevalence 92%; n = 22), as well as of *Gyrocotyle* sp. 1 from *Harriotta raleighana* Goode & Bean (new host record; prevalence 100%; n = 2), and of *Gyrocotyle* sp. 2 from *Hydrolagus pallidus* Hardy & Stehmann (new host record; prevalence

100%; n = 2) off the Outer Hebrides, Scotland (Figs. 1–3). Additional material of *G. urna* was also collected from *Chim. monstrosa* off Bergen, Norway (prevalence 75%; n = 28). Unidentified gyrocotylideans were also collected in the Southern Hemisphere from *Callorhinchus capensis* Duméril off South Africa (new host record; prevalence 50%; n = 4), from *Hydrolagus bemisi* Didier (new host record; prevalence 33%; n = 3) and *Hydrolagus novaezealandinae* (Fowler) (new host record; prevalence of 50%; n = 6) off New Zealand, as well as from two unidentified species of *Hydrolagus* and *Harriotta* off Indonesia. At this point, gyrocotylideans have been reported from all but one (*Neoharriotta* Bigelow & Schroeder) of the six currently recognized genera of holocephalans and 14 of the 49 recognized extant species. As mentioned above, all records from other types of hosts are considered doubtful.

GEOGRAPHIC DISTRIBUTION. The gyrocotylideans are known from all oceans mainly in temperate and subpolar areas. They generally occur in hosts that occupy deep-sea habitats, with the deepest record from 2,900 m (Klimpel et al., 2009), but they have also been reported from a holocephalan captured at shelf area depths of less than 70 m (Simmons and Laurie, 1972; Mauchline and Gordon, 1984; Klimpel et al., 2009). Gyrocotylideans have been reported from waters of the Arctic Ocean (Canada and Greenland), temperate Australia (Australia, New Zealand), the temperate North Atlantic Ocean (Canada, Ireland, France, the Netherlands, Norway, Russia, and United Kingdom), the temperate North Pacific Ocean (Canada, Japan, and the USA), temperate South America (Argentina), and temperate southern Africa (South Africa) (Bandoni and Brooks, 1987; Williams et al., 1987; Klimpel et al., 2009; J. N. Caira and K. Jensen, pers. com.). The report here of gyrocotylideans off Java, Indonesia (T. Walter, pers. com.) is the first record of the order from the Tropics.

PHYLOGENETIC RELATIONSHIPS. A large contiguous fragment of the mitochondrial genome of *G. urna* was sequenced by Waeschenbach et al. (2012) as part of the PBI project. Their work lends further support for the gyrocotylideans as the earliest diverging group of cestodes. As noted above, the preliminary molecular phylogenetic work by one of the authors (H. H.; see Hansen et al., 2015) has implications for recognition of *Gyrocotyloides*, but this work has yet to be formally published.

CONCLUSIONS

Gyrocotylideans are one of the most peculiar, but poorly known groups of tapeworms with only ten described species in one genus. Their early diverging phylogenetic position suggests they have played an important role in the evolution of cestodes. They are widely distributed in deep seas and exclusively parasitize holocephalans as adults, having been reported from 14 of 52 species recognized so far. Gyrocotylideans are a relictual and evolutionary ancient group of parasitic flatworms; like their hosts, they could be termed “living fossils.”

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TABLE 1. List of valid and *incertae sedis* gyrocotylidean taxa with their type hosts.

VALID TAXA

FAMILY GYROCOTYLIDAE BENHAM, 1901

- *Gyrocotyle* Diesing, 1850 (syns. *Amphiptyches* Grube & Wagener, 1852 in Wagener, 1852; *Crobylophorus* Krøyer, 1852; *Gyrocotyloides* Fuhrmann, 1931)
  - *Gyrocotyle rugosa* Diesing, 1850 (type) ex *Callorhinchus callorynchus* (but wrongly reported also *Callorhinchus milii*)
  - *Gyrocotyle abyssicola* van der Land & Templeman, 1968 ex *Hydrolagus affinis*
  - *Gyrocotyle confusa* van der Land & Dienske, 1968 ex *Chimaera monstrosa*
  - *Gyrocotyle fimbriata* Watson, 1911 ex *Hydrolagus colliei*
  - *Gyrocotyle major* van der Land & Templeman, 1968 ex *Hydrolagus affinis*
  - *Gyrocotyle maxima* MacDonagh, 1927 ex *Mustelus asterias* (likely correct host *Callorhinchus callorynchus*)
  - *Gyrocotyle nigrosetosa* Haswell, 1902 ex *Hydrolagus ogilbyi*
  - *Gyrocotyle nybelini* (Fuhrmann, 1931) Bandoni & Brooks, 1987 ex *Chimaera monstrosa*
  - *Gyrocotyle parvispinosa* van der Land & Dienske, 1968 ex *Hydrolagus colliei*
  - *Gyrocotyle urna* (Grube & Wagener, 1852 in Wagener, 1852) Wagener, 1858 ex *Chimaera monstrosa*

SPECIES *INCERTAE SEDIS*

- *Gyrocotyle medusarum* von Linstow, 1903 ex *Athorybia rosacea* (Hydrozoa)

10

Haplobothriidea Joyeux & Baer, 1961

By
Roman Kuchta and Tomáš Scholz[1]

HAPLOBOTHRIIDEA AS THEY WERE KNOWN PRIOR TO THE PBI PROJECT

Diversity and Classification. The order Haplobothriidea is a very small, but morphologically peculiar group consisting of one genus and only two described species, both of which parasitize the bowfin (*Amia calva* L.) in North America (Jones, 1994). The first species of haplobothriidean was described by Cooper (1914a) as *Haplobothrium globuliforme* Cooper, 1914 on the basis of its possession of a secondary scolex (pseudoscolex) and secondary strobila. The genus *Haplobothrium* Cooper, 1914 was originally placed in the pseudophyllidean family Dibothriocephalidae Lühe, 1899 (Cooper, 1914a, b). Three years later Cooper (1917) discovered a primary scolex with tentacles and proposed the subfamily Haplobothriinae Cooper, 1917 to accommodate the genus and its single species. At that time, Cooper (1917; pg. 51) noted the resemblance between the tentacles of the primary scolex of *H. globuliforme* and those of elasmobranch-hosted trypanorhynchs stating "It thus bears a remarkable resemblance to the scolex of the members of the order Trypanorhyncha, which is emphasized by the fact that each proboscis consists of an eversible portion, a muscular bulb for its activation, and a permanently protruded stump, quite comparable morphologically as well as physiologically with the three divisions of the trypanorhynchid proboscis." Nonetheless, he retained the species and subfamily in the Diphyllobothriidae Lühe, 1910 based on the configuration of the reproductive organs, which resemble those of the Diphyllobothriinae Lühe, 1910.

The taxonomic position of *Haplobothrium* has been a topic of lively discussion for decades. Meggitt (1924) raised Cooper's (1917) subfamily Haplobothriinae to the rank of family as Haplobothriidae Cooper, 1917 in the order Pseudophyllidea (now Diphyllobothriidea; Kuchta et al., 2008). This action was accepted by many authors (e.g., Wardle and McLeod, 1952; Yamaguti, 1959; Schmidt, 1986). In contrast, other authors, such as Southwell (1929) and Fuhrmann (1931), considered *Haplobothrium* to represent an aberrant, basal trypanorhynch because of its possession of four partly retractable tentacles, reported to be covered with minute spines. This opinion was, however, not shared by Dollfus (1942; pg. 12) who wrote "To me, *Haplobothrium* is an isolated form, derived from Pseudophyllidea; it has evolved independently and its tentacles do not imply any affinity with Trypanorhyncha." Similarly, Thomas (1983) compared the tentacles of the primary scolex of *Haplobothrium* with those of trypanorhynchs and concluded that they differed substantially from one another. An ultrastructural study of spermatogenesis and sperm morphology of *H. globuliforme* by MacKinnon and Burt (1985a) further supported the affinities of the Haplobothriidea with the Pseudophyllidea.

Joyeux and Baer (1961) proposed a new order, Haplobothriidea (misspelled as

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[1] Corresponding author (tscholz@paru.cas.cz)

Kuchta, R. and T. Scholz. 2017. Haplobothriidea Joyeux & Baer, 1961. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 201–206.

Haplobothrioidea), in recognition of the unique morphology of *Haplobothrium* resembling both the Trypanorhyncha and the Pseudophyllidea. The order has been recognized as valid since that time (e.g., Jones, 1994; Khalil et al., 1994; Olson et al., 2001; Kuchta et al., 2008).

The second species in the order, *Haplobothrium bistrobilae* Premvati, 1969, was described from specimens collected in Florida also from the bowfin, *Amia calva*, by Premvati (1969). This species differs from *H. globuliforme* in the number of testes, persistence of a uterine pore in gravid proglottids, fully retractable tentacles (only partly in *H. globuliforme*), disposition of vitelline ducts, and smaller eggs (see Premvati, 1969). However, *H. bistrobilae* has not been reported since its original description and its validity remains to be confirmed.

MORPHOLOGY. Haplobothriideans are unique among cestodes in their possession of two types of strobilae and scoleces in the same individual (paratomy or delayed proglottization). The primary strobila attaches to the intestine with a primary club-shaped scolex with four partly or completely retractable tentacles; it consists of multiple intervals of proglottized regions, each of which separates to become a secondary strobila. The anterior proglottid of the secondary strobila is modified as a secondary scolex (sometimes referred to as a pseudoscolex), which is flattened or dome-shaped anteriorly and bears four shallow indentations around a raised apical disc. Anterior proglottids of the secondary strobila are craspedote with four flat laciniations (resembling lappets of some elasmobranch-hosted cestodes such as *Anthobothrium* van Beneden, 1850 or teleost-hosted onchoproteocephalideans such as *Scholzia* de Chambrier, Rego & Gil de Pertierra, 2005), and longer than wide (Fig. 1). Each proglottid bears one set of male and one set of female reproductive organs. The numerous testes surround the medially situated female reproductive organs as two lateral fields. The external seminal vesicle is present, posterior to cirrus-sac; the cirrus is armed with spinitriches. The male genital pore opens ventrally, anterior to the female pore. The ovary is medullary, inverted horseshoe-shaped, and located near the posterior margin of the proglottid. The vitellarium is follicular; numerous vitelline follicles are medullary, forming two lateral fields. The uterus is sacciform with a coiled uterine duct; the uterine pore is ventral and either persistent or transient. The eggs are operculate and embryonated (i.e., containing coracidium larvae) in utero. Ultrastructural studies by MacKinnon and Burt (1985a–c) of plerocercoids and adults, including the primary and secondary scolex, revealed several types of microtriches, including a unique club-shaped spinitriches (i.e., clavate *sensu* Chervy [2009]) on the primary scolex.

HOST ASSOCIATIONS. Both species of *Haplobothrium* are known only from the bowfin, *A. calva*, in North America. The bowfin is widely considered to be morphologically unchanged from its ancestral type (Long, 2010) and is estimated to have originated in the Cretaceous (~100 Ma; Maisey, 1996). *Amia calva* is the only extant species of the previously diverse order Amiiformes (Holostei), which dates from the Jurassic to the Eocene (Long, 2010; Poyato-Ariza and Martín-Abad, 2013). Some authors have considered haplobothriid cestodes of bowfin to be as ancient as their host and possibly primitive in body organization.

The life-cycle of *H. globuliforme* involves three hosts (Essex, 1929; Thomas, 1930; Meinkoth, 1947). The eggs develop *in utero* and a free-swimming coracidium larva, which hatches as soon as the eggs reach fresh water, is eaten by the first intermediate host, a copepod (Wardle and McLeod, 1952). After ingestion, the hexacanth inside the ciliated envelope of the coracidium penetrates into the copepod's haemocoel where it develops into a procercoid. Freshwater teleosts such as *Poecilia reticulata* Peters, *Lepomis gibbosus* (L.), and *Ameiurus nebulosus* (Lesueur) serve as second intermediate hosts, in which plerocercoids encyst in the liver. The bowfin is infected when it feeds on infected second intermediate or paratenic hosts (Essex, 1929; Thomas, 1930; Meinkoth, 1947).

GEOGRAPHIC DISTRIBUTION. Both known species are limited in their distribution to Canada and the USA (i.e., the distribution of their definitive host, the bowfin). *Haplobothrium globuliforme* appears to be widely distributed throughout North America in the Mississippi drainage from Ontario (Canada) to Florida (USA), whereas *H. bistrobilae* is known only from its original report in Lake Munson in Florida, USA (Hoffman, 1999).

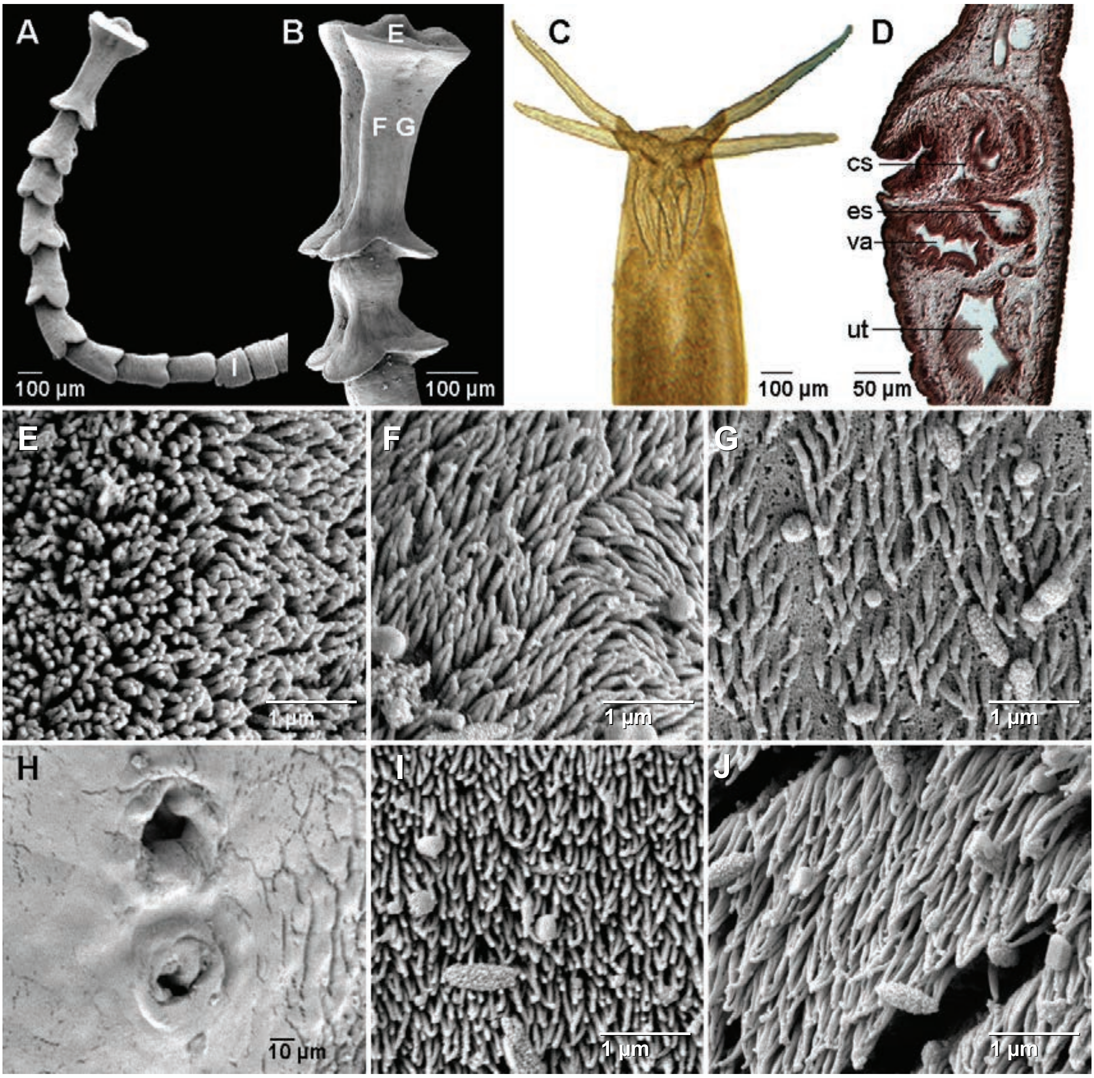

FIGURE 1. Photomicrographs of *Haplobothrium globuliforme* from *Amia calva*. **(A, B)**. Secondary scolex with anterior part of secondary strobila. Note: Small letters correspond to the figures showing higher magnification images of these surfaces. **(C)** Primary scolex (courtesy of J. E. Joy). **(D)** Sagittal section through gravid proglottid. **(E)** Surface of apical disc. **(F, G)** Surface of lateral surface of scolex. **(H)** Detail of uterine pore and genital atrium. **(I)** Surface of immature proglottid. **(J)** Surface of mature proglottid. *Abbreviations:* cs, cirrus-sac; es, external seminal vesicle; va, vagina; ut, uterus.

Phylogenetic Relationships. Despite the historical controversy surrounding the affinities and systematic position of *Haplobothrium*, sequence data for the 18S rDNA and Ef-1α loci of *H. globuliforme* from Lake Ontario, Canada obtained by Olson and Caira (1999) proved to be quite informative. In most of their analyses, *H. globuliforme* grouped as the sister lineage to the Diphyllobothriidea; this result was supported by the work of Kodedová et al. (2000), Brabec et al. (2006), and also by Waeschenbach et al. (2007) in their analyses of 18S rDNA and 28S rDNA sequence data of a specimen from Reelfoot Lake, Tennessee, USA. As a consequence it appears that tentacles on the primary scolex of species of *Haplobothrium* are non-homologous to tentacles found in trypanorhynchs, as suggested by Woodland (1927) and Dollfus (1942).

CURRENT STATUS OF THE HAPLOBOTHRIIDEA

Diversity and Classification. No additional collections of haplobothriideans were made over the course of the PBI project. The order remains the least speciose of the 19 cestode orders recognized with only one genus and two species. However, the validity of *H. bistrobilae* requires confirmation.

Morphology. No new morphological data were generated over the course of the PBI project, with the exception of those in a paper dealing with the pathological effect of *H. globuliforme* on its fish host (Joy et al., 2009).

Host Associations. Species of *Haplobothrium* appear to be restricted to the bowfin (*A. calva*) in North America. Records of adult worms from other host species such as the American eel, *Anguilla rostrata* (Lesueur), or the channel catfish, *Ictalurus punctatus* (Rafinesque) (see Hoffman, 1999), are considered doubtful, or may represent intermediate or paratenic host records.

Geographic Distribution. No new geographical records have been published over the course of the PBI project.

Phylogenetic Relationships. The molecular analyses of Waeschenbach et al. (2012), based on sequence data from a large mitochondrial fragment, conducted as part of the PBI project, confirms the sister taxon relationship between the Haplobothriidea and Diphyllobothriidea. Even though the former taxon could be recognized as a suborder of the Diphyllobothriidea, both groups are tentatively considered as two separate orders based on differences in their morphology, with the former taxon being distinguished from the Diphyllobothriidea by a number of unique traits (e.g., possession of primary and secondary strobila, a primary scolex with evertible tentacles and clavate microtriches, a secondary scolex with bothrium-like depressions, and an armed cirrus). Moreover, adult haplobothriideans parasitize a relictual fish host—an archaic holostean (vs. tetrapods only as hosts of diphyllobothriideans)—and exhibit a form of asexual reproduction truly unique among all cestodes (MacKinnon et al., 1985).

CONCLUSIONS

The Haplobothriidea are the least speciose cestode order but their morphology and parasitism of a relictual host (the only extant member of the holostean order Amiiformes) justify their validity. Molecular data show close affinities between haplobothriideans and diphyllobothriideans, indicating that they may be considered as a suborder of the latter taxon. However, the independent status of the order Haplobothriidea is tentatively retained because of the biology (paratomy) of its species (i.e., its possession of 2 types of strobila and scolex), a condition unique among cestodes.

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TABLE 1. List of valid haplobothriidean taxa with type hosts.

VALID TAXA

FAMILY HAPLOBOTHRIIDAE COOPER, 1917
  Haplobothrium Cooper, 1914
    Haplobothrium globuliforme Cooper, 1914 (type) ex *Amia calva*
    Haplobothrium bistrobilae Premvati, 1969 ex *Amia calva*

11

Lecanicephalidea Hyman, 1951

By
Kirsten Jensen[1], Joanna J. Cielocha, Kaylee S. Herzog, and Janine N. Caira

LECANICEPHALIDEA AS THEY WERE KNOWN PRIOR TO THE PBI PROJECT

Diversity and Classification. Historically, lecanicephalideans were first recognized at the family level, as the Lecanicephalidae Braun, 1900 (see Braun, 1900), most commonly within the order Tetraphyllidea. It was not until 1930 that Southwell (1930) recognized the group at the superfamilial level, as the Lecanicephaloidea Southwell, 1930. Hyman (1951) subsequently elevated the group to ordinal status, also under the name Lecanicephaloidea. Apparently unaware of Hyman's work, Wardle and McLeod (1952) erected the new order Lecanicephala for essentially the same group of taxa. But Euzet (1953) opposed recognition of tetraphyllideans and lecanicephalideans as separate orders, and consequently established what he considered to be the new superfamily Lecanicephalides Euzet, 1953 within the order Tetraphyllidea. However, only a few years later, he referred to the group as the "Super-famille Lecanicephaloidea T. Southwell, 1930" (Euzet, 1959; pg. 191), seemingly recognizing Southwell's (1930) earlier elevation of the group to superfamily level. Since 1959, the group's ordinal status has generally been accepted, either as the Lecanicephalidea (e.g., Yamaguti, 1959; Schmidt, 1970, 1986; Wardle et al., 1974; Euzet, 1994; Jensen, 2005) or the Lecanicephaliformes (e.g., Brooks and McLennan, 1993). The exception was Butler (1987a) who considered the lecanicephalideans as a family in the Tetraphyllidea.

Detailed accounts of the taxonomic history of the Lecanicephalidea, with emphasis on generic membership, were published by Butler (1987a), Euzet (1994), and Jensen (2005). Prior to 2008, as many as nine families had been recognized in the order, but no more than five of these were included in the order at any one time. Several of the families (e.g., the Disculicepitidae Joyeux & Baer, 1936 and Balanobothriidae Pintner, 1928) included in the order by some authors (e.g., Yamaguti, 1959; Schmidt, 1970, 1986; Brooks and McLennan, 1993) were considered to belong to different orders by other authors (e.g., Wardle and McLeod, 1952; Euzet, 1994; Jensen, 2005). In his 1994 classification, Euzet recognized five valid genera in four families: *Anteropora* Subhapradha, 1955 in the Anteroporidae Euzet, 1994; *Polypocephalus* Braun, 1878 in the Polypocephalidae Meggitt, 1924; *Lecanicephalum* Linton, 1890 in the Lecanicephalidae Braun, 1900; and *Tetragonocephalum* Shipley & Hornell, 1906 and *Tylocephalum* Linton, 1890 in the Tetragonocephalidae Yamaguti, 1959. By 2005, when Jensen's monograph of the order was published, five additional genera had been erected (i.e., *Aberrapex* Jensen, 2001, *Corrugatocephalum* Caira, Jensen & Yamane, 1997, *Healyum* Jensen, 2001, *Paraberrapex* Jensen, 2001, and *Quadcuspibothrium* Jensen, 2001) (Caira et al., 1997; Jensen, 2001); only *Corrugatocephalum* was assigned to a family (see Caira et al., 1997), in this case the Lecanicephalidae. Furthermore, two genera (*Eniochobothrium* Shipley & Hornell, 1906 and

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[1] Corresponding author (jensen@ku.edu)

Jensen, K., J. J. Cielocha, K. S. Herzog, and J. N. Caira. 2017. Lecanicephalidea Hyman, 1951. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 207–229.

Hornellobothrium Shipley & Hornell, 1906), considered to be "Lecanicephalidea *incertae sedis*" by Euzet (1994; pg. 200), had been shown to be valid by Jensen (2005).

Taxonomic treatments of the Lecanicephalidea that focused on species diversity included, for example, Southwell (1925), who recognized 17 species in seven genera, Yamaguti (1959), who recognized 24 species in eight genera, Schmidt (1986), who recognized 45 species in ten genera, and Jensen (2005), who recognized 65 species in 12 genera. By 2008 a total of 154 nominal species of lecanicephalideans had been described. Unfortunately, at the start of the PBI project, only 66 of these 154 species were considered valid. In the cases of more than 100 species, this was because descriptions were superficial, and types had either been lost (e.g., species described by Shipley and Hornell [1906], Shipley [1900], and Southwell [1930]) or were never designated. In the cases of species described after 1999, the unavailability of types violates Article 16.4 of the International Code of Zoological Nomenclature [ICZN, 1999]) and such names were thus considered to be unavailable. In the cases of many species described prior to 1999, the majority from India (e.g., Chincholikar and Shinde, 1978, 1980; Shinde and Deshmukh, 1979; Shinde and Jadhav, 1981, 1990; Deshmukh et al., 1982; Andhare and Shinde, 1994; Shinde et al., 1985; Murlidhar, 1986; Shinde and Solunke, 1986; Jadhav and Shinde, 1989; Shinde et al., 1991; Sanaka et al., 1992; Jadhav and Jadhav, 1993; Hiware and Jadhav, 1999; Wankhede, 2003; Lanka et al., 2006), there is no evidence that types were ever deposited in a museum. Unfortunately, only one of the 12 species described between 2006 and 2007, *Aberrapex manjajii* Jensen, 2006, is valid (see Jensen, 2006); the remaining 11 (see Lanka et al., 2006; Pramanik and Manna, 2006, 2007; Vankara et al., 2006, 2007; Jadhav, 2007) are either unavailable names or were so insufficiently described that they were treated as *species inquirendae*. As a consequence, the collection of new material of these previously described species is key to resolution of their identities.

PHYLOGENETIC RELATIONSHIPS. Prior to the PBI project, the phylogenetic relationships among lecanicephalideans had received only preliminary attention. Caira et al. (1999, 2001) included representative lecanicephalideans (8 species in 8 genera, and 21 species in 16 genera, respectively) in their broader phylogenetic analyses of selected elasmobranch-hosted tapeworm groups, and the analyses of Jensen (2005) included one or two species of each of the 12 lecanicephalidan genera she considered valid at that time; all three studies were based on morphological data. Across these studies, lecanicephalideans generally clustered as a clade based on their possession of an apical structure in the adult form. In instances in which they were included, the lecanicephalidean genera lacking an apical structure placed as the earliest diverging lineages within the order (e.g., Caira et al., 2001; Jensen, 2005). However, especially in the more comprehensive analyses of Caira et al. (1999, 2001), possible affinities with the cyclophyllideans and the adult apical structure-bearing rhinebothriidean genera *Pseudanthobothrium* Baer, 1956 and *Echeneibothrium* van Beneden, 1850 were seen.

The first molecular phylogenetic analyses to include lecanicephalideans were those of Olson and Caira (1999), who generated and analyzed sequence data for the complete 18S rDNA gene and partial EF-1α gene for one species each of *Cephalobothrium* Shipley & Hornell, 1906 and *Eniochobothrium*. Subsequently, Olson et al. (2001) included a member of a third genus, *Tylocephalum*, and were the first to generate sequence data for the D1–D3 region of the 28S rDNA gene for any member of the order. The analyses of Waeschenbach et al. (2007) included sequence data (i.e., complete 18S rDNA and nearly complete 28S rDNA) for a member of a fourth genus, *Adelobothrium* Shipley, 1900.

The affinities of the Lecanicephalidea relative to other eucestode orders have generally been consistent across molecular studies conducted prior to the PBI (see Olson and Caira, 1999; Olson et al., 2001; Caira et al., 2005; Waeschenbach et al., 2007). In all cases, the lecanicephalidean species composed the earliest diverging clade among the acetabulate eucestode orders.

MORPHOLOGY. Lecanicephalideans are generally relatively small (i.e., <5 mm in total length) worms; few attain a total length of more than 6 cm (see Butler, 1987b). Both Fuhrmann (1931) and Hyman (1951) identified the possession of the following combination of features to distinguish lecanicephalideans from members of the other orders of elasmobranch-hosted tapeworms: an apical structure on the adult scolex (historically referred to as a pars apicalis [e.g., Euzet, 1994; Ivanov and Campbell, 2000] or myzorhynchus [e.g., Butler, 1987a, b]), four undivided suckers or bothridia, and proglottids in which the vagina opens into the genital atrium posterior to the cirrus-sac. Many lecanicephalideans exhibit additional features of proglottid anatomy that are unusual for elasmobranch-hosted tapeworms, such as a vas deferens that is expanded to form a conspicuous external seminal vesicle and relatively few testes (i.e., ≤6) (see Jensen, 2005). The remarkable variation of apical structures (considered to consist of an apical organ and apical modification of the scolex proper by Caira et al. [1999]) seen across lecanicephalideans has been noted by many authors (e.g., Pintner, 1928; Euzet, 1994; Jensen, 2005). The diversity of apical organ forms (e.g., large [Fig. 1F] or small [Fig. 1C]; muscular or glandular [Fig. 1H]; dome- or sucker-shaped; divided into tentacles [Fig. 1E] or intact) is a hallmark of the order. In fact, apical structure form has been used as a key feature for differentiating among lecanicephalidean families by many authors (see, e.g., Yamaguti, 1959; Schmidt, 1986; Euzet, 1994). Only *Aberrapex* and *Paraberrapex*—collectively with a total of three species prior to the PBI project—were known to lack an apical structure from their adult stage (Fig. 1A). Acetabular morphology in taxa described prior to 2008 was generally in the form of four undivided suckers or bothridia; only *Quadcuspibothrium* exhibited a slight variation on this theme in possessing bothridia that are diamond-shaped rather than round or oval (Jensen, 2001).

HOST ASSOCIATIONS. Prior to the PBI project, lecanicephalideans were known primarily as parasites of batoid elasmobranchs, although some valid records from sharks existed. In 2005, based on extensive new collections, Jensen summarized the elasmobranch groups known to host lecanicephalideans. At that time, lecanicephalideans, including both valid species and *species inquirendae*, were known from genera representing 14 families of batoids and five families of sharks (Jensen, 2005; table 5). Greater than 90% of lecanicephalidean records at that time were from members of the Myliobatiformes—specifically the families Aetobatidae Agassiz, Dasyatidae Jordan, Gymnuridae Bloch & Schneider, Mobulidae Gill, Myliobatidae Bonaparte, Rhinopteridae Jordan & Evermann, and Urotrygonidae McEachran, Dunn & Miyake; a few were from rhinopristiform (Rhinidae Müller & Henle, Pristidae Bonaparte, and Glaucostegidae Last, Séret & Naylor) hosts. With the exception of several unverified records of lecanicephalidean species parasitizing more than one host species (see Jensen, 2005), lecanicephalideans are considered to exhibit oioxenous specificity (*sensu* Euzet and Combes [1980]) for their elasmobranch hosts (i.e., each cestode species is restricted to a single species of host).

GEOGRAPHIC DISTRIBUTION. Some of the earliest records of lecanicephalideans are from the "ostindischen Meeren" (i.e., East Indian Ocean; Braun, 1878), western Atlantic Ocean (Linton, 1890), Loyalty Islands in the western Pacific Ocean (Shipley, 1900), and the waters around Sri Lanka (Shipley and Hornell, 1906). In 2005, Jensen summarized the geographic distribution of the order (Jensen, 2005; fig. 68) noting that most lecanicephalideans recognized at that time had been reported from localities located between 45° northern and 35° southern latitudes,

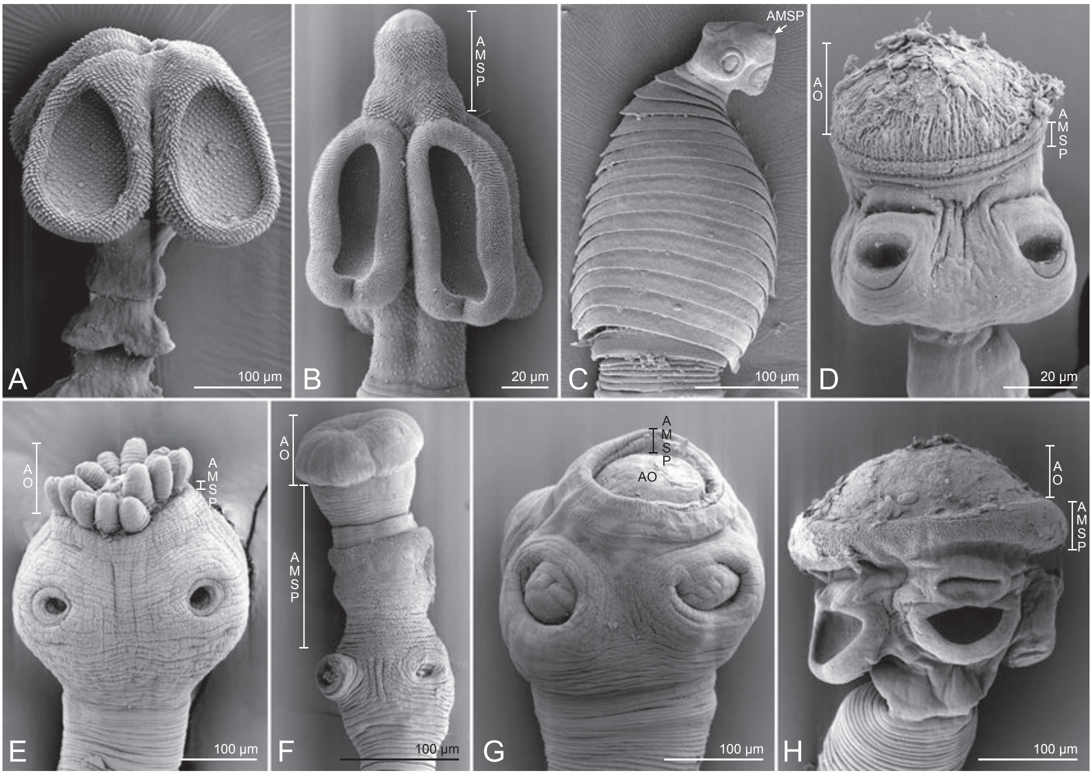

FIGURE 1. Scanning electon micrographs of lecanicephalidean scoleces. **(A)** *Aberrapex* sp. (Aberrapecidae) ex *Aetomylaeus bovinus* from Senegal. **(B)** *Anteropora joannae* (Polypocephalidae) ex *Taeniura lymma* 1 *sensu* Naylor et al. (2012a) from Malaysian Borneo. **(C)** *Eniochobothrium* sp. (Eniochobothriidae) ex *Rhinoptera* cf. *steindachneri sensu* Naylor et al. (2012a) from the Gulf of Mexico. **(D)** New genus 13 sp. *sensu* Jensen et al. (2016) (Cephalobothriidae) ex *Aetomylaeus verspertilio* from northern Australia. **(E)** *Polypocephalus* sp. (Polypocephalidae) ex *Urogymnus polylepis* from Malaysian Borneo. **(F)** *Seussapex* sp. (Polypocephalidae) ex *Maculabatis* cf. *pastinacoides* (as *Himantura* cf. *pastinacoides sensu* Naylor et al. [2012a]) from Malaysian Borneo. **(G)** *Stoibocephalum arafurense* (Lecanicephalidae) ex *Rhina ancylostoma* from northern Australia. **(H)** *Zanobatocestus major* (Zanobatocestidae) ex *Zanobatus schoeleinii* from Senegal. *Abbreviations*: AMSP, apical modification of scolex proper; AO, apical organ.

from all major oceans in tropical and subtropical regions in the Southern Hemisphere and tropical, subtropical, and the southern half of temperate regions in the Northern Hemisphere. Records of undescribed species for which specimens were examined at that time came from Madagascar, Singapore, Tahiti, Tanzania, and Thailand (see Jensen, 2005).

CURRENT STATUS OF THE LECANICEPHALIDEA

DIVERSITY AND CLASSIFICATION. Intensive new collections of tapeworms globally over the past 15 years, and especially more recently as part of the PBI project, have resulted not only in the discovery of an exceptional number of new taxa, but also in the recollection of many taxa not seen for over a century. Because of the unprecedented amount of generic novelty encountered early in the project, work on the Lecanicephalidea was focused mainly on the erection of new genera and evaluation of taxa considered *genera inquirendae* by Jensen (2005). As a result of these efforts, the following nine new genera were erected as part of the PBI project: *Collicocephalus* Koch, Jensen & Caira, 2012, *Corollapex* Herzog & Jensen, 2017, *Elicilacunosus* Koch, Jensen & Caira, 2012, *Floriparicapitus* Cielocha, Jensen & Caira, 2014, *Rexapex* Koch, Jensen & Caira, 2012, *Stoibocephalum* Cielocha & Jensen, 2013 (Fig. 1G), *Sesquipedalapex* Jensen, Nikolov & Caira, 2011, *Seussapex* Jensen & Russell, 2014 (Fig. 1F), and *Zanobatocestus* Jensen, Mojica & Caira, 2013 (Fig. 1H) (Jensen et al., 2011, 2014; Koch et al., 2012; Cielocha and Jensen, 2013; Mojica et al., 2013, 2014; Cielocha et al., 2014; Jensen and Russell, 2014; Herzog and Jensen, 2017). In addition, over the course of the PBI project, *Hexacanalis* Perrenoud, 1931 was formally resurrected (Cielocha and Jensen, 2011), *Adelobothrium*, *Cephalobothrium*, *Anthemobothrium* Shipley & Hornell, 1906, and *Flapocephalus* Deshmukh, 1979 were confirmed to be valid (see Cielocha et al., 2013; Caira and Jensen, 2014; Jensen et al., 2016), and *Sesquipedalapex* was placed in synonymy with *Anteropora* by Jensen et al. (2016). The number of valid genera in the Lecanicephalidea has risen from the five recognized by Euzet (1994) to 25 at present; an additional two genera were recognized but not formally erected by Jensen et al. (2016) (Table 3). Because their type species are unrecognizable based on their original descriptions, six *genera inquirendae* remain; the names of another two genera are unavailable because they were not validly published (see Table 3).

At present, only 90 of the approximately 207 nominal lecanicephalidean species are considered valid (Table 3). Among the 117 problematic species, 69 (54 of which were described from India) are *species inquirendae* (see Table 3) because they are unrecognizable based on their original descriptions. Another 41 (36 from India) are unavailable names, either because they were not validly published (i.e., *nomina nuda*) or, if published after 1999, because type specimens were not designated (see Table 3). These include all 14 new lecanicephalidean species described from India since 2008 (e.g., Dandwate and Jadhav, 2009; Mote, 2011). An additional seven lecanicephalidean species are likely valid, but their current generic placements should be reassessed; these species are considered *incertae sedis* herein (Table 3).

Species-level taxonomic efforts as part of the PBI project resulted in the description of 31 new species in 14 genera and four new combinations (see Table 3). Material of numerous additional novel species was also collected. Preliminary examination of this undescribed material suggests it includes over 280 species. As a consequence, we estimate of the total number of known, although not necessarily described, species of lecanicephalideans is 378 (Table 2).

The increase in number of valid genera called for a reassessment of Euzet's (1994) family-level classification scheme for the order. The comprehensive phylogenetic study of Jensen et al. (2016), based on molecular data with a detailed treatment of morphological features, provided a framework of generic interrelationships upon which a revised familial classification of the order was based. Jensen et al. (2016) doubled the number of families of Lecanicephalidea from four to eight. Five of these are the monogeneric Aberrapecidae Jensen, Caira, Cielocha, Littlewood & Waeschenbach, 2016, Eniochobothriidae Jensen, Caira, Cielocha, Littlewood & Waeschenbach, 2016, Paraberrapecidae Jensen, Caira, Cielocha, Littlewood & Waeschenbach, 2016, Tetragonocephalidae, and Zanobatocestidae Jensen, Caira, Cielocha, Littlewood & Waeschenbach, 2016. The remaining three, the Cephalobothriidae Pintner, 1928, Lecanicephalidae, and Polypocephalidae, comprise four, seven, and eight genera, respectively (see Table 1). *Corrugatocephalum*, *Healyum*, and *Quadcuspibothrium*, none of which were represented in the analyses of Jensen et al. (2016), remain *incertae sedis* at the family level pending formal assessment of their phylogenetic affinities. Preliminary analysis of partial 28S rDNA recently generated for a specimen each of *Healyum* and *Quadcuspibothrium* from the giant devilray, *Mobula mobular* (Bonnaterre), from Taiwan in the context of the lecanicephalidean taxa of Jensen et al. (2016) revealed that these two genera grouped together in a clade independent of the eight families of lecanicephaldieans recognized to date (unpubl. data; see Fig. 3).

PHYLOGENETIC RELATIONSHIPS. The phylogenetic position of the Lecanicephalidea as the earliest diverging lineage among the acetabluate eucestode orders has been confirmed by both of the analyses of molecular sequence data generated over the course of the PBI project in which they were represented. In the analyses of Waeschenbach et al. (2012), lecanicephalidean data came from a ~4,000 bp contiguous fragment of mitochondrial genome (mtDNA) of a species of *Tylocephalum* and 18S and 28S rDNA sequence data for a species of *Adelobothrium*. However, it was not until the extensive study by Caira et al. (2014) that more than three lecanicephalidean species were included in phylogenetic analyses based on molecular sequence data, allowing for the interrelationships among a sizable subset of lecanicephalideans to be assessed for the first time. Their analyses, which were based on complete 18S rDNA and partial 28S rDNA sequence data, targeted elasmobranch-hosted tapeworms and included 18 species representing 11 lecanicephalidean genera, as well as two undescribed genera (New genus 5 and 6 *sensu* Caira et al. [2014]). The latter genera were recently formally erected as *Floriparicapitus* (see Cielocha et al., 2014) and *Seussapex* (see Jensen and Russell, 2014), respectively.

However, by far the most comprehensive analyses of lecanicephalidean interrelationships were those of Jensen et al. (2016). Using complete 18S rDNA, partial 28S rDNA, partial COI, and 16S rDNA sequence data, Jensen et al. (2016) more than tripled the lecanicephalidean taxon sampling of previous studies to include 61 species in 25 genera, again including three undescribed genera (as New genus 11, 13, and 12; the latter recently erected as *Corollapex* by Herzog and Jensen [2017]). The results of Jensen et al. (2016) confirmed that (1) the order is monophyletic, (2) lecanicephalideans lacking an apical structure in the adult form are sister to the remaining, apical structure-bearing lecanicephalideans, (3) *Adelobothrium* and *Cephalobothrium* show close phylogenetic affinities with one another, and (4) *Flapocephalus*, *Polypocephalus*, *Hornellobothrium*, *Seussapex*, and *Anteropora* form a well-supported clade that is sister to *Tetragonocephalum*. Furthermore, the eight major groups that emerged from their analyses were formally recognized at the familial level (Fig. 3). The existing families Lecanicephalidae, Polypocephalidae, Tetragonocephalidae, and Cephalobothriidae were maintained and four new families were established (Aberrapecidae, Eniochobothriidae, Paraberrapecidae, and Zanobatocestidae). Jensen et al. (2016) presented a diagnosis for each family based on morphological features, which represents the first attempt to identify potential morphological synapomorphies supporting generic phylogenetic affinities in lecanicephalideans based on molecular sequence data, and towards facilitating familial placement of new taxa in the future.

The analyses of Jensen et al. (2016) did not however allow for robust assessments of generic interrelationships within each family or of the monophyly of most genera. Their analyses did cast doubt on the monophyly of *Polypocephalus*, *Adelobothrium*, and *Cephalobothrium*. Sequence data generated for additional loci, beyond the four used by Jensen et al. (2016), in combination with more dense taxon sampling, particularly of the more speciose genera, and especially of *Polypocephalus*, are needed to resolve these outstanding phylogenetic issues.

MORPHOLOGY. Not surprisingly, the discovery of nine new genera as part of the PBI project substantially increased the diversity of apical structure morphologies observed across the order even further. Despite the seemingly disparate apical structure morphology seen across lecanicephalideans, consistent application of the distinction between the apical modification of the scolex proper and the apical organ (*sensu* Caira et al. [1999]) (see Fig. 1) in taxa erected since 2005, has done much to assist with the identification of homologous parts of these complex structures across taxa. Similarly imperative was the consistent characterization of these apical parts as muscular and/or glandular, retractable and/or invaginable, internal and/or external (see, e.g., family diagnoses in Jensen et al. [2016]). Some of the more spectacular apical structure forms described over the course of the PBI project include: an oblong, tubular apical organ that is retractable (*Elicilacunosus*; Koch et al., 2012); an apical organ in the form of an inverted cone with 18 papilliform projections around its perimeter (*Rexapex*; Koch et al., 2012); an apical modification of scolex proper with an extensive aperture housing an apical organ in the form of a large, retractacle, muscular and glandular transverse oval pad (*Collicocephalus*; Koch et al., 2012); an apical organ in the form of a retractable, thick muscular pad (*Stoibocephalum*; Cielocha and Jensen, 2013; Fig. 1G); an apical modification with an extensive aperture bearing a retractable apical organ in the form of a wide, highly folded or appearing rugose muscular and glandular sheet (*Floriparicapitus*; Cielocha et al., 2014); an apical modification that can reach a length of several millimeters and is deeply embedded in the intestinal mucosa (*Anteropora comica* [Jensen, Nikolov & Caira, 2011] Jensen, Caira, Cielocha, Littlewood & Waeschenbach, 2016; Jensen et al., 2011); an apical organ in the form of a central disk surrounded by eight concave muscular membrane-bound pads and an internal glandular component (*Corollapex*; Herzog and Jensen, 2017); a bipartite apical modification of the scolex proper and bipartite apical organ, independently retractable, internally housing a glandular compartment (*Seussapex*; Jensen and Russell, 2014; Fig. 1F).

New acetabular morphologies and strobilar features were also discovered over the course of the project. With the erection of *Zanobatocestus* by Jensen et al. (2014), the Lecanicephalidea now include species with biloculated bothridia (Fig. 1H); all other lecanicephalideans possess uniloculated bothridia or suckers (e.g., Fig. 1A–G). Similarly unique is the musculo-glandular tissue seen along the midline of dorsal and ventral surfaces of the proglottids, manifested externally as a tandem series of depressions, in all three species of *Elicilacunosus* (see Koch et al., 2012). With the resurrection of *Hexacanalis* (see Cielocha and Jensen, 2011)—as the name suggests—the presence of three, rather than the more common condition of two, pairs of excretory vessels was confirmed. Cielocha and Jensen (2011) reviewed the disposition of the excretory vessels across lecanicephalidean genera (also see Cielocha and Jensen, 2013; Cielocha et al., 2014). Jensen et al. (2016) identified the unusual condition of a single, or three or more, pairs of excretory vessels as a diagnostic feature of the family Lecanicephalidae.

Egg and cocoon morphologies, when gravid proglottids were available, have also served as rich sources of characters. Recent studies have demonstrated that congeners may exhibit drastically different egg morphologies. For example, Jensen et al. (2011) described spherical eggs covered with protuberances in *Anteropora comica*, but described eggs with a corrugated surface and bipolar filaments in *Anteropora klosmamorphis* Jensen, Nikolov & Caira, 2011. Similarly, Jensen et al. (2014) found the eggs of *Zanobatocestus major* Jensen, Mojica & Caira, 2014 to be grouped in bipolar-filamented cocoons, predominantly in doublets (i.e., containing 2 eggs), while those of *Zanobatocestus minor* Jensen, Mojica & Caira, 2014 were arranged in cocoons in tandem strands of hundreds of eggs. More comprehensive knowledge about egg morphologies across the order is needed to determine the utility of egg features, for example, as genus- or family-level characters.

Specimens collected or studied as part of the PBI project also served as material for the first study of lecanicephalidean spermatozoan ultastructure (Cielocha et al., 2013), as well as for the first detailed descriptions of pathological changes caused by a lecanicephalidean

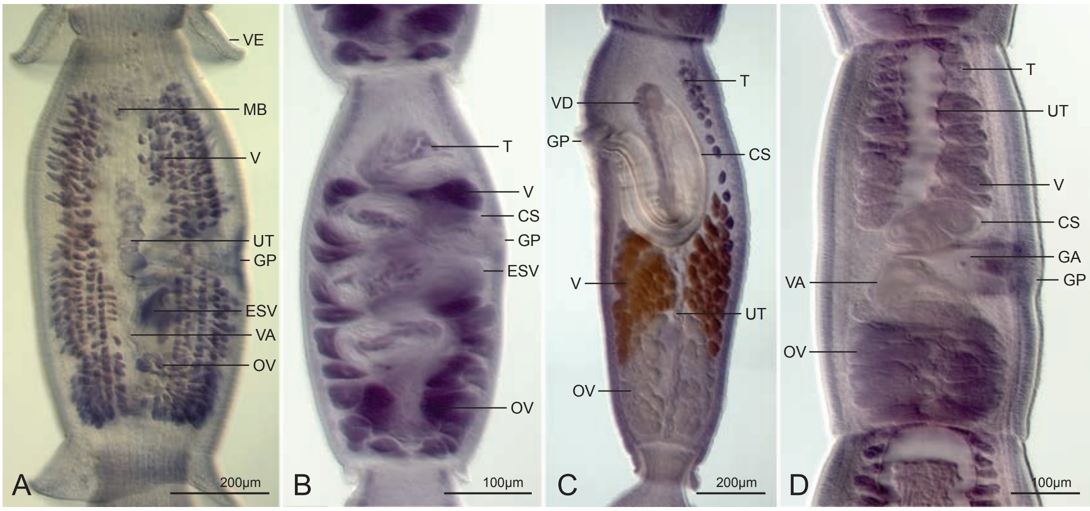

FIGURE 2. Light micrographs of representative lecanicephalidean proglottids. **(A)** *Adelobothrium* sp. (Cephalobothriidae) ex *Aetobatus ocellatus* from the Solomon Islands. **(B)** *Corollapex cairae* (Polypocephalidae) ex *Urogymnus granulatus* from the Solomon Islands. **(C)** *Eniochobothrium* sp. (Eniochobothriidae) ex *Rhinoptera jayakari* from Taiwan. **(D)** *Tetragonocephalum* sp. (Tetragonocephalidae) ex *Maculabatis gerrardi* from Indonesian Borneo. *Abbreviations*: CS, cirrus-sac; ESV, external seminal vesicle; GA, genital atrium; GP, genital pore; MB, corticle muscle bundle; OV, ovary; T, testis; UT, uterus; V, vitelline follicle; VA, vagina; VE, velum; VD, vas deferens.

tapeworm in its elasmobranch host at the site of attachment of the apical structure (see Jensen et al., 2011; Borucinska et al., 2013).

One of the most intriguing results to come from the phylogenetic analyses of Jensen et al. (2016) was the realization that proglottid anatomy in the Lecanicephalidea is generally much more conserved, and thus indicative of phylogenetic affinities, than scolex morphology. For example, members of the Cephalobothriidae are typically characterized by the presence of conspicuous circumcortical muscle bundles and extensive lateral bands of vitelline follicles (Fig. 2A); members of the Polypocephalidae possess four or six testes arranged in a single column (Fig. 2B); members of the Eniochobothriidae lack a vagina, and possess a thick-walled cirrus-sac and vitelline follicles arranged in lateral fields restricted to the region posterior to the genital pore (Fig. 2C); members of the Tetragonocephalidae possess a conspicuous genital atrium, a compact ovary, and a bisaccate uterus that is constricted at the level of the genital atrium (Fig. 2D). In contrast, many elements of scolex morphology appear to be homoplasious (see Jensen et al., 2016; fig. 2) or singularly unique across genera (e.g., Polypocephalidae; see Fig. 1B, E, and F) and are thus of limited utility for assessing phylogenetic relationships.

HOST ASSOCIATIONS. Despite the substantial number of taxa described as a result of PBI project efforts, our understanding of the higher-level host associations of the order have not significantly changed. Nonetheless, the number of elasmobranch species known to host lecanicephalideans has substantially increased. Batoids remain the primary hosts of lecanicephalideans. The spectrum of batoid families hosting the order has been expanded to include the Zanobatidae Fowler (see Jensen et al., 2014) and the Urolophidae Müller & Henle—the latter based on undescribed specimens preliminarily identified as members of *Aberrapex* found parasitizing *Trygonoptera imitata* Yearsley, Last & Gomon collected off New South Wales, Australia. The spectrum of batoid species known to host lecanicephalideans has been expanded to include species collected from freshwater environments (i.e., sawfishes

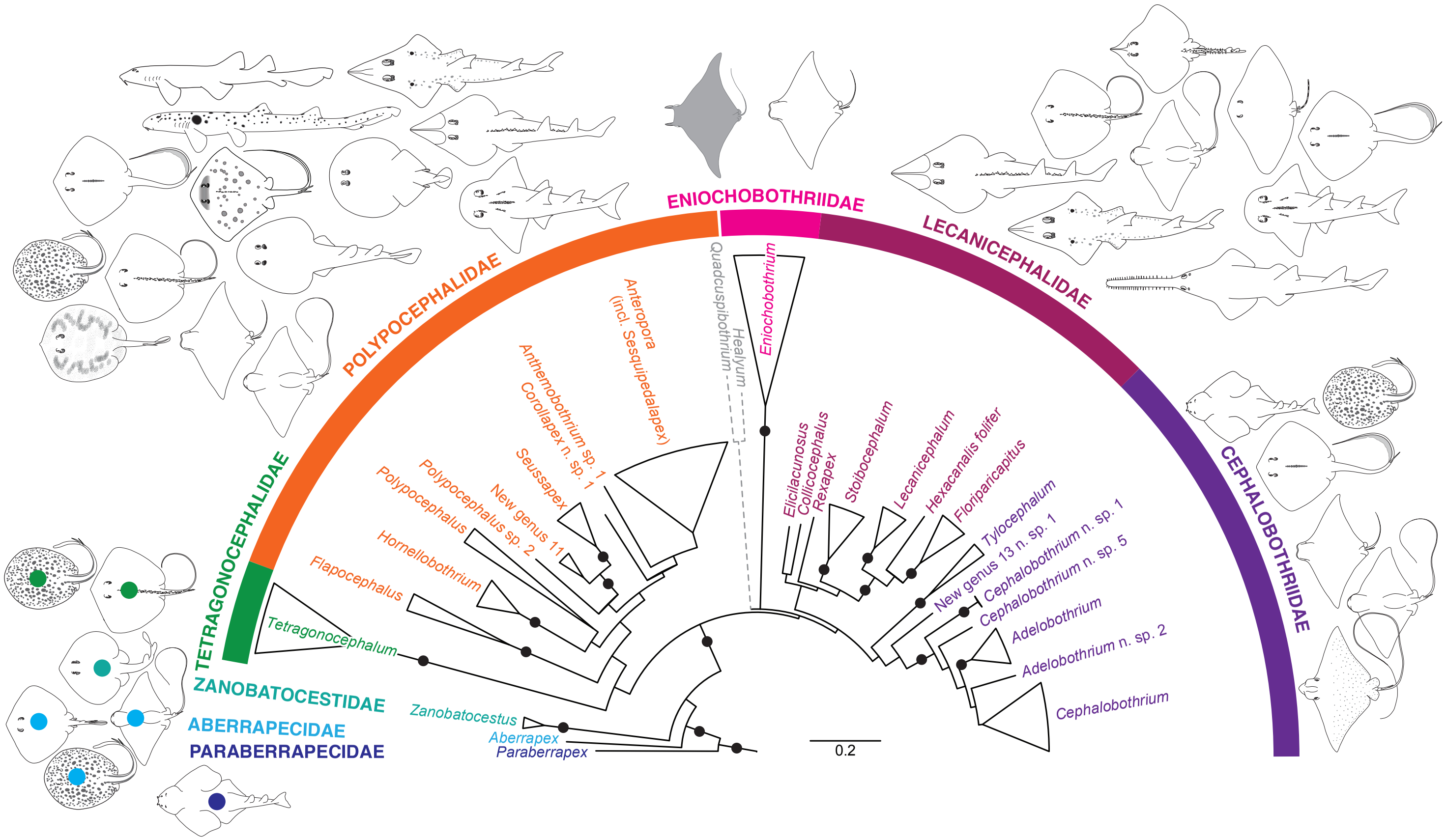

FIGURE 3. Diagrammatic representation of lecanicephalidean intergeneric relationships (modified from Jensen et al. [2016; fig. 5]) including representation of 23 of 25 valid lecanicephalidean genera and two undescribed genera (New genus 11 and 13 *sensu* Jensen et al. [2016]). Host icons indicate major host associations for each family as understood at the end of the PBI project based on both published and unpublished records. The tentative placements of *Healyum* and *Quadcuspibothrium* based on unpublished data are indicated in gray. Black dots indicate nodes with bootstrap values of 100% and posterior probabilites of 1. Scale bar indicates number of substitutions per site.

and the giant freshwater stingray *Urogymnus polylepis* [Bleeker]; Cielocha et al., 2014; Guyer, 2016). A summary of the host associations of lecanicephalidean families, based on data from published records, was presented by Jensen et al. (2016; fig. 5). These associations have been expanded in Figure 3 to include unpublished records.

The known numbers of lecanicephalidean species hosted by sharks and batoids are presented in Tables 1 and 2, respectively. When both valid and known undecribed novel species are included, the total number of known species is estimated to be 378. Collectively, these species parasitize all four orders of batoids (i.e., Myliobatiformes, Rhinopristiformes, Rajiformes, and Torpediniformes). Of these 378 species, 83% parasitize myliobatiforms, 14% parasitize rhinopristiforms, 1% (4 spp.; all in the genus *Anteropora*) parasitize torpediniforms, and only a single species is known from a rajiform. The remaining 2% (6 spp.) parasitize sharks.

Based on these data, we predict that hundreds of lecanicephalidean species remain to be discovered globally; much of this diversity will be hosted by batoid elasmobranchs (see Table 3), myliobatiforms in particular. Not only have a number of myliobatiform genera not yet been examined for lecanicephalideans (i.e., *Makararaja* Roberts and *Spinilophus* Yearsley & Last), but this is also the case for numerous species in myliobatiform genera known to host lecanicephalideans (e.g., *Aetobatus* Blainville, *Aetomylaeus* Garman, *Bathytoshia* Whitley, *Brevitrygon* Last, Naylor & Manjaji-Matsumoto, *Dasyatis* Rafinesque, *Gymnura* van Hasselt, *Hemitrygon* Müller & Henle, *Himantura* Müller & Henle, *Hypanus* Rafinesque, *Maculabatis* Last, Naylor & Manjaji-Matsumoto, *Neotrygon* Castenau, *Pastinachus* Rüppell, *Rhinoptera* van Hasselt, *Taeniura* Müller & Henle, *Taeniurops* Garman, *Trygonoptera* Müller & Henle, and *Urogymnus* Müller & Henle). In the recently erected *Maculabatis* alone, the nine (of 13) species examined to date, collectively host 38 species of lecanicephalideans (unpubl. data), all of which appear to exhibit oioxenous specificity (*sensu* Euzet and Combes [1980]) for their hosts; the range is 1–12 lecanicephalidean species per species of *Maculabatis*. This suggests that the four species of *Maculabatis* that have not yet been examined for lecanicephalideans collectively host an additional 24 species of lecanicephalideans. Exceptions are myliobatiform genera such as *Urotrygon* Gill and *Urobatis* Garman from the Pacific Ocean, as well as numerous species of the Potamogtrygonidae Garman. Existing records (Table 1; F. P. L. Marques, pers. com.) indicate that these taxa generally do not host lecanicephalideans. Among rhinopristiforms, certain genera (e.g., *Rhina* Gill, *Glaucostegus* Bonaparte, and *Rhynchobatis* Philippi) are particularly suitable hosts for lecanicephlideans and routinely host representatives of several genera and multiple congeners. We anticipate additional new lecanicephalidean taxa will be described in other rhinopristiform genera but not in large numbers.

Additional lecanicephalidean novelty in the Torpediniformes is likely, but potentially limited to the species of *Narcine* Henle and *Narke* Kaup that have not yet been examined. The single record of a lecanicephalidean from a skate (i.e., the *incertae sedis Lecanicephalum xiamenensis* Yang, Lui & Lin, 1995 with *Okamejei hollandi* [Jordan & Richardson] as its type host) by Yang et al. (1995) is curious and certainly requires confirmation. It is, however, conceivable that records from skates will be restricted to those few species, like *O. hollandi*, that inhabit shallower, more tropical waters.

Confirmed, published records of lecanicephalideans from sharks are now considered to be limited to the megamouth shark, *Megachasma pelagios* Taylor, Compagno & Struhsaker (family Megachasmidae Taylor, Compagno & Struhsaker) (Caira et al., 1997), the epaulet shark, *Hemiscyllium ocellatum* (Bonnaterre) (family Hemiscylliidae Gill) (Jensen, 2001), and angel sharks (*Squatina* Risso, family Squatinidae Bonaparte) (Yamaguti, 1934; Jensen, 2001; Mutti and

Ivanov, 2016). Although not yet published, PBI project collections yielded lecanicephalideans from *Chiloscyllium* Müller & Henle (family Hemiscylliidae). Additional novelty in sharks is only expected in as-of-yet unexamined species of hemiscylliids and angel sharks (*Squatina*). Reports of adult lecanicephalidean *species inquirendae* from carcharhinid sharks (e.g., Deshmukh et al., 1982; Pramanik and Manna, 2007) and the zebra shark (*Stegostoma* Müller & Henle) (Sanaka et al., 1993) are likely in error, as are records of adult lecanicephalideans from teleosts (Ramadan, 1986; Gairola et al., 1987); larval lecanicephalidean *species inquirendae* described from molluscs (Seurat, 1906; Jameson, 1912) will remain unrecognizable.

The host associations of the 378 (i.e., described and in-hand undescribed) known species of lecanicephalideans, 372 of which parasitize batoids and six parasitize sharks, lead us to estimate the global diversity of lecanicephalideans to be likely somewhere on the order of 667 species (647 in batoids and 20 in sharks) (Tables 1, 2).

GEOGRAPHIC DISTRIBUTION. New collections over the course of the PBI project and taxonomic work on previously collected material from around the world confirmed the circumglobal distribution of the order as suggested by Jensen (2005). The distribution of lecanicephalideans has been expanded to include the Gulf of Oman (Roohi Aminjan & Malek, 2016), Senegal (Jensen et al., 2014), and the Solomon Islands (Cielocha et al., 2013; Herzog and Jensen, 2017), as well as Belize, Taiwan, and Vietnam (Jensen et al., 2016). In addition, undescribed material comes from elasmobranchs off Ecuador, Mozambique, and Puerto Rico.

At present lecanicephalideans are known from eight of the 12 marine biogeographic realms recognized by Spalding et al. (2007). The greatest diversity (69%) is found in the Central Indo-Pacific (e.g., South China Sea, Coral Triangle, and the Arafura Sea), followed by the Western Indo-Pacific (14%) (e.g., Red Sea, Arabian [Persian] Gulf, western Indian Ocean, and the South Indian Shelf), the Temperate Northern Pacific (5%) (e.g., Gulf of California and the Sea of Japan), the Tropical Atlantic and Temperate Northern Atlantic (5% each), and Eastern Indo-Pacific, Temperate Australasia, Temperate South America, and Tropical Eastern Pacific (<1% each).

The order is, however, absent from the Arctic, Southern Ocean, and Temperate Southern Africa marine realms. Collections from poorly sampled tropical regions such as the western Indian Ocean (incl. the Gulf of Oman) and from the Central Indo-Pacific and Tropical Atlantic, will likely expand the known geographic distribution of the order. Despite extensive collecting efforts, lecanicephalideans have not been reported from parts of the Temperate Northern Atlantic (e.g., Europe, including the Mediterranean Sea) and South Africa.

In summary, the order is known from three ocean basins (i.e., Atlantic, Pacific, and Indian), and appears to be limited to tropical, subtropical, and more moderate temperate ocean regions, with average sea surface temperatures of >16°C (National Center for Atmospheric Research Staff, 2014).

CONCLUSIONS

Systematic and phylogenetic efforts as part of the PBI project significantly enhanced our understanding of the taxonomic and morphological diversity of the order as a whole and also the interrelationships among its members. Of the 25 genera now considered valid, over half were established as part of the project. With that, the diversity in apical structure morphology exhibited by members of this order was expanded even further and we now know the Lecanicephalidea to possess biloculate acetabula in addition to the more common condition of uniloculate acetabula. The revised family-level classification is based on a solid phylogenetic framework with dense taxon sampling at the generic level, and represents a useful starting point for investigation of the evolution of morphological features and host associations of the order. Emerging patterns of lecanicephalidean diversity derived from intensive collecting efforts, particularly of batoids, lead us to believe that global species diversity is grossly underestimated. We estimate total global lecanicephalidean diversity to be 670 species. In contrast, generic diversity is unlikely to increase at the rate seen over the last decade. The current geographic distribution of the order is between 40° northern and southern latitudes, in eight of the 12 recognized marine realms. It is expected that the Central Indo-Pacific realm will remain the center of lecanicephalidean diversity and that the existing paucity of records from the western Indian Ocean in particular will be shown to be an artifact of insufficient sampling.

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TABLE 1. Expected global shark associations of lecanicephalidean species (in yellow). Number of shark species per genus given in parentheses (includes known undescribed shark species). First column: number of lecanicephalidean species parasitizing each shark taxon as of 2017 (includes known undescribed cestode species); second column: predicted total number of lecanicephalidean species parasitizing each shark taxon globally.

	Lecanicephalidean spp.	
	2017	ESTIM.
SELACHOIDEA		
CARCHARHINIFORMES	**0**	**0**
HETERODONTIFORMES	**0**	**0**
HEXANCHIFORMES	**0**	**0**
LAMNIFORMES	**1**	**1**
Alopiidae	**0**	**0**
Alopias (3 spp.)	0	0
Cetorhinidae	**0**	**0**
Cetorhinus (1 sp.)	0	0
Lamnidae	**0**	**0**
Carcharodon (1 sp.)	0	0
Isurus (2 spp.)	0	0
Lamna (2 spp.)	0	0
Megachasmidae	**1**	**1**
Megachasma (1 sp.)	1	1
Mitsukurinidae	**0**	**0**
Mitsukurina (1 sp.)	0	0
Odontaspididae	**0**	**0**
Carcharias (1 sp.)	0	0
Odontaspis (2 spp.)	0	0
Pseudocarcharhiidae	**0**	**0**
Pseudocarcharias (1 sp.)	0	0
ORECTOLOBIFORMES	**2**	**6**
Brachaeluridae	**0**	**0**
Brachaelurus (2 spp.)	0	0
Ginglymostomatidae	**0**	**0**
Ginglymostoma (2 spp.)	0	0
Nebrius (1 sp.)	0	0
Pseudoginglymostoma (1 sp.)	0	0
Hemiscylliidae	**2**	**6**
Chiloscyllium (9 spp.)	1	2
Hemiscyllium (9 spp.)	1	4
Orectolobidae	**0**	**0**
Eucrossorhinus (1 sp.)	0	0
Orectolobus (10 spp.)	0	0
Sutorectus (1 sp.)	0	0
Parascylliidae	**0**	**0**
Cirrhoscyllium (3 spp.)	0	0
Parascyllium (5 spp.)	0	0
Rhincodontidae	**0**	**0**
Rhincodon (1 sp.)	0	0
Stegostomatidae	**0**	**0**
Stegostoma (1 sp.)	0	0
PRISTIOPHORIFORMES	**0**	**0**
SQUALIFORMES	**0**	**0**
SQUATINIFORMES	**3**	**13**
Squatinidae	**3**	**13**
Squatina (23 spp.)	3	13
SHARK TOTAL	**6**	**20**

Table 2. Expected global batoid associations of lecanicephalidean species (in yellow). Number of batoid species per genus given in parentheses (includes known undescribed batoid species). First column: number of lecanicephalidean species parasitizing each batoid taxon as of 2017 (includes known undescribed cestode species); second column: predicted total number of lecanicephalidean species parasitizing each batoid taxon globally. Quotes indicate non-monophyletic taxa (Naylor et al., 2012a; Last et al., 2016a, b). Question marks indicate genera not yet examined for cestodes. Estimated total number of lecanicephalidean species parasitizing elasmobranchs globally given at bottom of Table.

	Lecanicephalidean spp.	
	2017	ESTIM.
BATOIDEA		
Myliobatiformes	**315**	**526**
Aetobatidae	**30**	**40**
Aetobatus (7 spp.)	30	40
Dasyatidae	**223**	**387**
“*Bathytoshia*” (3 spp.)	4	10
Brevitrygon (5 spp.)	6	15
Dasyatis (5 spp.)	3	13
Fluvitrygon (3 spp.)	0	0
Fontitrygon (4 spp.)	2	6
Hemitrygon (10 spp.)	7	28
Himantura (8 spp.)	38	44
Hypanus (12 spp.)	8	24
Maculabatis (13 spp.)	38	62
Makararaja (1 sp.)	?	3
Megatrygon (1 sp.)	2	2
Neotrygon (13 spp.)	9	27
Pastinachus (6 spp.)	32	39
Pateobatis (7 spp.)	20	32
Pteroplatytrygon (1 sp.)	0	2
Taeniura (5 spp.)	26	31
Taeniurops (2 spp.)	1	4
“*Telatrygon*” (4 spp.)	5	11
Urogymnus (7 spp.)	22	34
Gymnuridae	**5**	**13**
Gymnura (15 spp.)	5	13
Hexatrygonidae	**0**	**1**
Hexatrygon (1 sp.)	0	1
Mobulidae	**3**	**6**
Mobula (8 spp.)	3	6
Myliobatidae	**33**	**45**
Aetomylaeus (9 spp.)	27	35
Myliobatis (11 spp.)	6	10
Plesiobatidae	**0**	**1**
Plesiobatis (1 sp.)	0	1
Potamotrygonidae	**0**	**0**
Heliotrygon (2 spp.)	0	0
Styracura (2 spp.)	0	0
Paratrygon (1 sp.)	0	0
Plesiotrygon (2 spp.)	0	0
Potamotrygon (27 spp.)	0	0
Rhinopteridae	**20**	**24**
Rhinoptera (8 spp.)	20	24
Urolophidae	**1**	**7**
Spinilophus (1 sp.)	?	1
Trygonoptera (6 spp.)	1	5
Urolophus (21 spp.)	0	2
Urotrygonidae	**1**	**2**
Urobatis (6 spp.)	1	2
Urotrygon (12 spp.)	0	0
Rhinopristiformes	**51**	**101**
Glaucostegidae	**24**	**36**
Glaucostegus (9 spp.)	24	36
Platyrhinidae	**0**	**2**
Platyrhina (5 spp.)	0	2
Platyrhinoidis (1 sp.)	0	0
“Pristidae”	**5**	**6**
Anoxypristis (1 sp.)	1	1
Pristis (5 spp.)	4	5
Rhinidae	**17**	**33**
Rhina (1 sp.)	5	6
Rhynchobatus (8 spp.)	12	24
Rhynchorhina (1 sp.)	?	3
“Rhinobatidae”	**2**	**14**
Acroteriobatus (8 spp.)	0	2
Pseudobatos (8 spp.)	0	0
Rhinobatos (16 spp.)	2	14
Trygonorrhinidae	**0**	**5**
Aptychotrema (3 spp.)	0	3
Trygonorrhina (2 spp.)	0	2
Zapteryx (3 spp.)	0	0
Zanobatidae	**3**	**5**
Zanobatus (2 spp.)	3	5
Torpediniformes	**4**	**16**
Hypnidae	**0**	**0**
Hypnos (1 sp.)	0	0
Narcinidae	**3**	**14**
Benthobatis (4 spp.)	?	0
Diplobatis (4 spp.)	0	0
Discopyge (2 spp.)	0	0
Narcine (15 spp.)	3	12
Narcinops (5 spp.)	0	2
Narkidae	**1**	**2**
Crassinarke (1 sp.)	?	0
Electrolux (1 sp.)	?	0
Heteronarce (3 spp.)	?	0
Narke (3 spp.)	1	2
Temera (1 sp.)	?	0
Typhlonarke (1 sp.)	0	0
Torpedinidae	**0**	**0**
Tetronarce (9 spp.)	0	0
Torpedo (12 spp.)	0	0
Rajiformes	**1**	**4**
Anacanthobatidae	**0**	**0**
Anacanthobatis (6 spp.)	?	0
Indobatis (1 sp.)	?	0
Schroederobatis (1 sp.)	?	0
Sinobatis (9 spp.)	?	0
Springeria (2 spp.)	?	0
Arhynchobatidae	**0**	**0**
Arhynchobatis (1 sp.)	?	0
Atlantoraja (3 spp.)	0	0
Bathyraja (56 spp.)	0	0
Brochiraja (9 spp.)	0	0
Insentiraja (2 spp.)	?	0
Irolita (2 spp.)	?	0
Notoraja (12 spp.)	?	0
Pavoraja (6 spp.)	?	0
Psammobatis (8 spp.)	0	0
Pseudoraja (1 sp.)	?	0
Rhinoraja (3 spp.)	0	0
Rioraja (1 sp.)	0	0
Sympterygia (4 spp.)	0	0
Gurgesiellidae	**0**	**0**
Cruriraja (8 spp.)	0	0
Fenestraja (8 spp.)	?	0
Gurgesiella (3 spp.)	?	0
Rajidae	**1**	**4**
Amblyraja (19 spp.)	0	0
Beringraja (2 spp.)	0	0
Breviraja (5 spp.)	?	0
Dactylobatus (2 spp.)	?	0
Dentiraja (11 spp.)	?	0
Dipturus (52 spp.)	0	0
Hongeo (1 sp.)	?	0
Leucoraja (13 spp.)	0	0
Malacoraja (4 spp.)	0	0
Neoraja (5 spp.)	?	0
Okamejei (13 spp.)	1	4
Orbiraja (3 spp.)	0	0
Raja (17 spp.)	0	0
Rajella (20 spp.)	0	0
Rostroraja (10 spp.)	0	0
Spiniraja (1 sp.)	0	0
BATOID TOTAL	**372**	**647**
ELASMOBRANCH TOTAL	**378**	**667**

Table 3. List of lecanicephalidean taxa and, for valid taxa and taxa *incertae sedis*, their type hosts. New taxa and taxonomic actions resulting from PBI project activities indicated in bold. * Host identifications requiring confirmation.

VALID TAXA

- Family Aberrapecidae Jensen, Caira, Cielocha, Littlewood & Waeschenbach, 2016
  - *Aberrapex* Jensen, 2001
    - *Aberrapex senticosus* Jensen, 2001 (type) ex *Myliobatis californica*
    - *Aberrapex arrhynchum* (Brooks, Mayes & Thorson, 1981) Jensen, 2001 ex *Myliobatis goodei*
    - *Aberrapex ludmilae* Menoret, Mutti & Ivanov, 2017 ex *Myliobatis goodei*
    - *Aberrapex manjajiae* Jensen, 2006 ex *Taeniura lymma* 1 *sensu* Naylor et al. (2012a) (as *Taeniura lymma*)
    - *Aberrapex sanmartini* Menoret, Mutti & Ivanov, 2017 ex *Myliobatis goodei*
    - *Aberrapex vitalemuttiorum* Menoret, Mutti & Ivanov, 2017 ex *Myliobatis ridens*
    - ***Aberrapex weipanesis* Koch, Jensen & Caira, 2012** ex *Aetomylaeus vespertilio*
- Family Cephalobothriidae Pintner, 1928
  - *Adelobothrium* Shipley, 1900
    - *Adelobothrium aetiobatidis* Shipley, 1900 (type) ex *Aetobatus ocellatus** (as *Aetobatus narinari*)
  - *Cephalobothrium* Shipley & Hornell, 1906
    - *Cephalobothrium aetobatidis* Shipley & Hornell, 1906 (type) *Aetobatus ocellatus** (as *Aetobatus narinari*)
  - **New genus 13 *sensu* Jensen et al. (2016)**
    - **New genus 13 n. sp. 1 *sensu* Jensen et al. (2016)** ex *Aetomylaeus nichofii*
  - *Tylocephalum* Linton, 1890 (syn. *Spinocephalum* Deshmukh, 1890)
    - *Tylocephalum pingue* Linton, 1890 (type) ex *Rhinoptera bonasus* (as *Rhinoptera quadriloba*)
    - *Tylocephalum bonasum* Campbell & Williams, 1984 ex *Rhinoptera bonasus*
    - *Tylocephalum brooksi* Ivanov & Campbell, 2000 ex *Rhinoptera bonasus*
    - *Tylocephalum marsupium* Linton, 1916 ex *Aetobatus narinari*
    - *Tylocephalum squatinae* Yamaguti, 1934 ex *Squatina japonica*
    - *Tylocephalum yorkei* Southwell, 1925 ex *Aetobatus ocellatus** (as *Aetobatus narinari*)
- Family Eniochobothriidae Jensen, Caira, Cielocha, Littlewood & Waeschenbach, 2016
  - *Eniochobothrium* Shipley & Hornell, 1906
    - *Eniochobothrium gracile* Shipley & Hornell, 1906 (type) ex *Rhinoptera javanica*
    - *Eniochobothrium euaxos* Jensen, 2005 ex *Rhinoptera neglecta* (as *Rhinoptera* sp.)
    - *Eniochobothrium qatarense* Al Kawari, Saoud & Wanas, 1994 ex *Rhinoptera javanica* (as *Rhinoptera adspersa*)
- Family Lecanicephalidae Braun, 1900
  - ***Collicocephalus* Koch, Jensen & Caira, 2012**
    - ***Collicocephalus baggioi* Koch, Jensen & Caira, 2012** (type) ex *Aetomylaeus vespertilio*
  - ***Elicilacunosus* Koch, Jensen & Caira, 2012**
    - ***Elicilacunosus sarawakensis* Koch, Jensen & Caira, 2012** (type) ex *Aetomylaeus maculatus*
    - ***Elicilacunosus dharmadii* Koch, Jensen & Caira, 2012** ex *Aetomylaeus nichofii*
    - ***Elicilacunosus fahmii* Koch, Jensen & Caira, 2012** ex *Aetomylaeus nichofii*
  - *Flapocephalus* Deshmukh, 1979
    - *Flapocephalus trygonis* Deshmukh, 1979 (type) ex *Pastinachus sephen**
    - *Flapocephalus saurashtri* Shinde & Deshmukh, 1979 ex *Pastinachus sephen**
  - ***Floriparicapitus* Cielocha, Jensen & Caira, 2014**
    - ***Floriparicapitus euzeti* Cielocha, Jensen & Caira, 2014** (type) ex *Pristis clavata*
    - ***Floriparicapitus juliani* Cielocha, Jensen & Caira, 2014** ex *Pristis pristis*
    - ***Floriparicapitus plicatilis* Cielocha, Jensen & Caira, 2014** ex *Glaucostegus typus*
    - *Floriparicapitus rhinobatidis* (Subhapradha, 1955) **Cielocha, Jensen & Caira, 2014** ex *Glaucostegus granulatus* (as *Rhinobatus granulatus*)
    - *Floriparicapitus variabilis* (Southwell, 1911) **Cielocha, Jensen & Caira, 2014** ex *Anoxypristis cuspidata* (as *Pristis cuspidatus*)
  - *Hexacanalis* Perrenoud, 1931
    - *Hexacanalis abruptus* (Southwell, 1911) Perrenoud, 1931 (type) ex *Gymnura micrura** (as *Pteroplatea micrura*)
    - ***Hexacanalis folifer* Cielocha & Jensen, 2011** ex *Gymnura zonura*
    - *Hexacanalis pteroplateae* (Zaidi & Khan, 1976) **Cielocha & Jensen, 2011** *Gymnura micrura** (as *Pteroplatea micrura*)
  - *Lecanicephalum* Linton, 1890
    - *Lecanicephalum peltatum* Linton, 1890 (type) ex *Hypanus centroura* (as *Trygon centrura* [sic])
    - *Lecanicephalum coangustatum* Jensen, 2005 ex *Hypanus centroura* (as *Dasyatis centroura*)

- ***Rexapex*** **Koch, Jensen & Caira, 2012**
  - ***Rexapex nanus*** **Koch, Jensen & Caira, 2012** (type) ex *Aetomylaeus vespertilio*
- ***Stoibocephalum*** **Cielocha & Jensen, 2013**
  - ***Stoibocephalum arafurense*** **Cielocha & Jensen, 2013** (type) ex *Rhina ancylostoma*
  - *Stoibocephalum campanulatum* (Butler, 1987) **Jensen, Caira, Cielocha, Littlewood & Waeschenbach, 2016** ex *Rhina ancylostoma*
  - *Stoibocephalum koenneckeorum* (Jensen, 2005) **Jensen, Caira, Cielocha, Littlewood & Waeschenbach, 2016** ex *Rhynchobatus palpebratus* (as *Rhynchobatus australiae*)

Family Paraberrapecidae Jensen, Caira, Cielocha, Littlewood & Waeschenbach, 2016

- *Paraberrapex* Jensen, 2001
  - *Paraberrapex manifestus* Jensen, 2001 (type) ex *Squatina californica*
  - *Paraberrapex atlanticus* Mutti & Ivanov, 2016 ex *Squatina guggenheim*

Family Polypocephalidae Meggitt, 1924

- *Anteropora* Subhapradha, 1955 (syn. ***Sesquipedalapex*** **Jensen, Nikolov & Caira, 2011**)
  - *Anteropora indica* Subhapradha, 1955 (type) ex *Narcine timlei*
  - ***Anteropora comica*** **(Jensen, Nikolov & Caira, 2011) Jensen, Caira, Cielocha, Littlewood & Waeschenbach, 2016** ex *Narcine maculata*
  - ***Anteropora cuba*** **Mojica, Jensen & Caira, 2013** ex *Maculabatis macrura* (as *Himantura gerrardi* 1 *sensu* Naylor et al. [2012a])
  - ***Anteropora glandapiculis*** **Mojica, Jensen & Caira, 2013** ex *Maculabatis pastinacoides* (as *Himantura pastinacoides* 1 *sensu* Naylor et al. [2012a])
  - *Anteropora japonica* (Yamaguti, 1934) Euzet, 1994 ex *Narke japonica*
  - ***Anteropora joannae*** **Mojica, Jensen & Caira, 2013** ex *Taeniura lymma* 1 *sensu* Naylor et al. (2012a)
  - ***Anteropora klosmamorphis*** **Jensen, Nikolov & Caira, 2011** ex *Narcine maculata*
  - *Anteropora leelongi* Jensen, 2005 ex *Hemiscyllium ocellatum*
  - ***Anteropora patulobothridium*** **Mojica, Jensen & Caira, 2013** ex *Taeniura lymma* 1 *sensu* Naylor et al. (2012a)
  - ***Anteropora pumilionis*** **Mojica, Jensen & Caira, 2013** ex *Maculabatis pastinacoides* (as *Himantura pastinacoides* 1 *sensu* Naylor et al. [2012a])
- *Anthemobothrium* Shipley & Hornell, 1906
  - *Anthemobothrium pulchrum* Shipley & Hornell, 1906 (type) ex *Pastinachus sephen**
- ***Corollapex*** **Herzog & Jensen, 2017**
  - ***Corollapex cairae*** **Herzog & Jensen, 2017** (type) ex *Urogymnus granulatus*
  - ***Corollapex tingoi*** **Herzog & Jensen, 2017** ex *Urogymnus granulatus*
- *Hornellobothrium* Shipley & Hornell, 1906
  - *Hornellobothrium cobraformis* Shipley & Hornell, 1906 (type) ex *Aetobatus ocellatus** (as *Aetobatus narinari*)
  - *Hornellobothrium extensivum* Jensen, 2005 ex *Aetobatus ocellatus*
  - ***Hornellobothrium gerdaae*** **Mojica, Jensen & Caira, 2014** ex *Aetobatus ocellatus*
  - ***Hornellobothrium iotakotta*** **Mojica, Jensen & Caira, 2014** ex *Aetobatus ocellatus*
  - ***Hornellobothrium kolossakotta*** **Mojica, Jensen & Caira, 2014** ex *Aetobatus ocellatus*
  - ***Hornellobothrium najaforme*** **Mojica, Jensen & Caira, 2014** ex *Aetobatus ocellatus*
- **New genus 11 *sensu* Jensen et al. (2016)**
  - **New genus 11 n. sp. 1 *sensu* Jensen et al. (2016)** ex *Rhynchobatus palpebratus* (as *Rhynchobatus cf. laevis*)
  - **New genus 11 n. sp. 2 *sensu* Jensen et al. (2016)** ex *Glaucostegus typus*
- **New genus 12 *sensu* Jensen et al. (2016)**
  - **New genus 12 n. sp. 1 *sensu* Jensen et al. (2016)** ex *Maculabatis gerrardi* (as *Himantura* cf. *gerrardi* 2 *sensu* Naylor et al. [2012b])
- *Polypocephalus* Braun, 1878 (syn. *Parataenia* Linton, 1890)
  - *Polypocephalus radiatus* Braun, 1878 (type) ex *Glaucostegus granulatus* (as *Rhinobatus granulatus*)
  - *Polypocephalus affinis* Subhapradha, 1951 ex *Glaucostegus granulatus* (as *Rhinobatus granulatus*)
  - *Polypocephalus caribbensis* (Gardner & Schmidt, 1984) Jensen, 2005 ex *Urobatis jamaicensis* (as *Urolophus jamaicensis*)
  - *Polypocephalus coronatus* Subhapradha, 1951 ex *Rhynchobatus djiddensis**
  - *Polypocephalus elongatus* (Southwell, 1912) Southwell, 1925 ex *Neotrygon kuhlii* (as *Trygon kuhlii*)
  - *Polypocephalus helmuti* Jensen, 2005 ex *Rhinoptera neglecta* (as *Rhinoptera* sp.)
  - *Polypocephalus lintoni* Subhapradha, 1951 ex *Rhynchobatus djiddensis**
  - *Polypocephalus medusia* (Linton, 1890) Southwell, 1925 ex *Hypanus centroura* (as *Trygon centrura* [sic])
  - *Polypocephalus moretonensis* Butler, 1987 ex *Hemitrygon fluviorum* (as *Dasyatis fluviorum*)
  - *Polypocephalus rhinobatidis* Subhapradha, 1951 ex *Glaucostegus granulatus* (as *Rhinobatus granulatus*)
  - *Polypocephalus rhynchobatidis* Subhapradha, 1951 ex *Rhynchobatus djiddensis**

Polypocephalus saoudi Hassan, 1982 ex *Taeniura lymma**
Polypocephalus vesicularis Yamaguti, 1960 ex *Rhinobatos schlegelii**
Polypocephalus vitellaris Subhapradha, 1951 ex *Rhynchobatus djiddensis**
***Seussapex* Jensen & Russell, 2014**
***Seussapex karybares* Jensen & Russell, 2014** (type) ex *Himantura australis* (as *Himantura uarnak* 2 *sensu* Naylor et al. [2012a])
Seussapex narinari (MacCallum, 1917) **Jensen & Russell, 2014** ex *Aetobatus ocellatus** (as *Aetobatus narinari*)

Family Tetragonocephalidae Yamaguti, 1959
Tetragonocephalum Shipley & Hornell, 1905
Tetragonocephalum trygonis Shipley & Hornell, 1905 (type) ex *Brevitrygon walga** (as *Trygon walga*)
***Tetragonocephalum kazemii* Roohi Aminjan & Malek, 2017** ex *Pastinachus sephen*
***Tetragonocephalum mackenziei* Roohi Aminjan & Malek, 2017** ex *Pastinachus sephen*
Tetragonocephalum passeyi Jensen, 2005 ex *Himantura leopard* (as *Himantura undulata*)
***Tetragonocephalum sabae* Roohi Aminjan & Malek, 2016** ex *Maculabatis randalli* (as *Himantura randalli*)
***Tetragonocephalum salarii* Roohi Aminjan & Malek, 2016** ex *Maculabatis randalli* (as *Himantura randalli*)
Tetragonocephalum simile (Pintner, 1928) Ivanov & Campbell, 2000 ex *Brevitrygon walga** (as *Trygon walga*)
Tetragonocephalum uarnak (Shipley & Hornell, 1906) Pintner, 1928 ex *Himantura uarnak** (as *Trygon uarnak*)
Tetragonocephalum yamagutii Muralidhar, 1988 ex *Brevitrygon walga** (as *Trygon walga*)

Family Zanobatocestidae Jensen, Caira, Cielocha, Littlewood & Waeschenbach, 2016
***Zanobatocestus* Jensen, Mojica & Caira, 2014**
***Zanobatocestus minor* Jensen, Mojica & Caira, 2014** (type) ex *Zanobatus schoeleinii*
***Zanobatocestus major* Jensen, Mojica & Caira, 2014** ex *Zanobatus schoeleinii*

Family *incertae sedis*
Corrugatocephalum Caira, Jensen & Yamane, 1997
Corrugatocephalum ouei Caira, Jensen & Yamane, 1997 (type) ex *Megachasma pelagios*
Healyum Jensen, 2001
Healyum harenamica Jensen, 2001 (type) ex *Mobula mobular* (as *Mobula japanica*)
Healyum pulvis Jensen, 2001 ex *Mobula mobular* (as *Mobula japanica*)
Quadcuspibothrium Jensen, 2001
Quadcuspibothrium francisi Jensen, 2001 (type) ex *Mobula mobular* (as *Mobula japanica*)

SPECIES *INCERTAE SEDIS*

Discobothrium myliobatidis Dailey & Mudry, 1968 ex *Myliobatis californica*
Eniochobothrium trygonis Chincholikar & Shinde, 1978 ex *Pastinachus sephen**
Lecanicephalum xiamenensis Yang, Lui & Lin, 1995 ex *Okamejei hollandi* (as *Raja holandi* [sic])
Tetragonocephalum aetiobatidis Shipley & Hornell, 1905 ex *Aetobatus ocellatus** (as *Aetobatus narinari*)
Tetragonocephalum akajeinensis Yang, Liu & Lin, 1995 ex *Hemitrygon akajei* (as *Dasyatis akajei*)
Tylocephalum elongatum Subhapradha, 1955 ex *Rhynchobatus djiddensis**
Tylocephalum rhinobatii (Deshmukh, 1980) Jensen, 2005 ex *Glaucosteus granulatus* (as *Rhinobatus granulatus*)

GENERA & SPECIES INQUIRENDAE

Anoplocephala globocephala MacCallum, 1921 ex "a small ray"
Calycobothrium Stiles & Hassell, 1912
Calycobothrium typicum (Southwell, 1911) Stiles & Hassell, 1912 ex *Aetobatus ocellatus** (as *Aetobatis narinari*)
Cephalobothrium alii Jadhav & Jadhav, 1993 ex *Pastinachus sephen** (as *Trygon sephen*)
Cephalobothrium gangeticus Gairola, Malhotra & Sukul, 1987 ex *Mystus vittatus* (Siluriformes)
Cephalobothrium ghardagense Ramadan, 1986 ex *Cetoscarus*? *bicolor*? (as *Scarus bicolar*) (Perciformes)
Cephalobothrium gogadevensis Pramanik & Manna, 2005 ex *Glaucostegus granulatus* (as *Rhinobatus granulatus*)
Cephalobothrium gymnurai Zaidi & Khan, 1976 ex *Gymnura* sp.
Cephalobothrium longisegmentum Wang, 1984 ex *Neotrygon kuhlii** (as *Dasyatis kuhlii*)
Cephalobothrium neoaetobatidis Sanaka, Vijaya Lakshmi & Hanumantha Rao, 1992 ex *Rhina ancylostoma*
Cephalobothrium singhi Jadhav & Jadhav, 1993 ex *Pastinachus sephen** (as *Trygon sephen*)
Cephalobothrium stegostomi Sanaka, Vijaya Lakshmi & Hanumantha Rao, 1993 ex *Stegostoma fasciatum*
Cephalobothrium taeniurai Ramadan, 1986 ex *Taeniura lymma*
Cephalobothrium trygoni Shinde & Solunke, 1986 ex *Pastinachus sephen** (as *Trygon sephen*)
Guptaia Malhotra, 1985
Guptaia garhwalensis Malhotra, 1985 ex *Schizothorax richardsonii* (Cypriniformes)

Hexacanalis indirajii Murlidhar, 1986 ex *Pastinachus sephen** (as *Trygon sephen*)
Hexacanalis sasoonensis Srivastava & Capoor, 1980 ex *Himantura marginata* (as *Trygon marginatus*)
Hexacanalis thapari Shinde, Jadhav & Jadhav, 1991 ex *Telatrygon zugei* (as *Trygon zugei*)
Hexacanalis yamagutii Shinde & Deshmukh, 1979 ex *Mobula kuhlii* (as *Dicerobatis eregoodoo*)
Hexacanalis zugeis Shinde & Deshmukh, 1979 ex *Telatrygon zugei* (as *Trygon zugei*)
Kystocephalus Shipley & Hornell, 1906
Kystocephalus translucens Shipley & Hornell, 1906 ex *Aetobatus ocellatus** (as *Aetobatis narinari*)
Lecanicephalum maharashtrae Chincholikar & Shinde, 1978 ex *Pastinachus sephen** (as *Trygon sephen*)
Lecanicephalum ratnagiriensis Hiware & Jadhav, 1999 ex *Pastinachus sephen** (as *Trygon sephen*)
Polypocephalus alii Shinde & Jadhav, 1981 ex *Rhynchobatus djiddensis** (as *Rhynchobatus djeddensis*)
Polypocephalus bombayensis Shinde, Dhule & Jadhav, 1991 ex *Aetobatus flagellum*
Polypocephalus digholensis Deshmukh, Jadhav & Shinde, 1982 ex *Mobula kuhlii* (as *Dicerobatis eregoodoo*)
Polypocephalus djeddensis Jadhav & Shinde, 1989 ex *Rhynchobatus djiddensis** (as *Rhynchobatus djeddensis*)
Polypocephalus himanshui Pramanik & Manna, 2006 ex *Rhynchobatus djiddensis** (as *Rhynchobatus djeddensis*)
Polypocephalus indicus Deshmukh, Jadhav & Shinde, 1982 ex *Scoliodon laticaudus* (as *Cercharias laticaudus*)
Polypocephalus karbharii Deshmukh, Jadhav & Shinde, 1982 ex *Mobula kuhlii* (as *Dicerobatis eregoodoo*)
Polypocephalus katpurensis Shinde & Jadhav, 1981 ex *Rhynchobatus djiddensis** (as *Rhynchobatus djeddensis*)
Polypocephalus maharashtra Deshmukh, Jadhav & Shinde, 1982 ex *Pastinachus sephen** (as *Trygon sephen*)
Polypocephalus pratibhai Deshmukh, Jadhav & Shinde, 1982 ex *Pastinachus sephen** (as *Trygon sephen*)
Polypocephalus ratnagiriensis Jadhav, Shinde & Sarwade, 1986 ex *Telatrygon zugei* (as *Trygon zugei*)
Polypocephalus singhii Shinde & Jadhav, 1981 ex *Rhynchobatus djiddensis** (as *Rhynchobatus djeddensis*)
Polypocephalus thapari Shinde & Jadhav, 1981 ex *Pastinachus sephen** (as *Trygon sephen*)
Polypocephalus visakhapatnamensis Vankara, Vijaya Lakshmi & Vijaya Lakshmi, 2007 ex *Himantura uarnak**
Staurobothrium Shipley & Hornell, 1905
Staurobothrium aetiobatidis Shipley & Hornell, 1905 ex *Aetobatus ocellatus** (as *Aetiobatis narinari*)
Tetragonocephalum alii Deshmukh & Shinde, 1979 ex *Pastinachus sephen** (as *Trygon sephen*)
Tetragonocephalum aurangabadensis Shinde & Jadhav, 1990 ex *Telatrygon zugei* (as *Trygon zugei*)
Tetragonocephalum bhagawatii Shinde, Mohekar & Jadhav, 1985 ex *Pastinachus sephen** (as *Trygon sephen*)
Tetragonocephalum madhulatae (Andhare & Shinde, 1994) Jensen, 2005 ex *Telatrygon zugei* (as *Trygon zugei*)
Tetragonocephalum madrasensis (Andhare & Shinde, 1994) Jensen, 2005 ex *Telatrygon zugei* (as *Trygon zugei*)
Tetragonocephalum raoi Deshmukh & Shinde, 1979 ex *Telatrygon zugei* (as *Trygon zugei*)
Tetragonocephalum ratnagiriensis Shinde & Jadhav, 1990 ex *Telatrygon zugei* (as *Trygon zugei*)
Tetragonocephalum sephensis Deshmukh & Shinde, 1979 ex *Pastinachus sephen** (as *Trygon sephen*)
Tetragonocephalum shipleyi Shinde, Mohekar & Jadhav, 1985 ex *Pastinachus sephen** (as *Trygon sephen*)
Thysanobothrium Shipley & Hornell, 1906
Thysanobothrium uarnakense Shipley & Hornell, 1906 ex *Himantura uarnak** (as *Trygon uarnak*)
Trygonicephalum Shinde & Jadhav, 1984
Trygonicephalum ratnagiriensis Shinde & Jadhav, 1984 ex *Pastinachus sephen** (as *Trygon sephen*)
Tylocephalum alii Andhare & Shinde, 1994 ex *Telatrygon zugei* (as *Trygon zugei*)
Tylocephalum aurangabadensis Jadhav & Shinde, 1987 ex *Aetobatus ocellatus** (as *Aetobatis narinari*)
Tylocephalum bombayensis Jadhav, 1983 ex *Pastinachus sephen** (as *Trygon sephen*)
Tylocephalum chiralensis Vijaya Lakshmi & Sanaka, 1995 ex *Himantura uarnak** (as *Dasyatis uarnak*)
Tylocephalum choudhurai Pramanik & Manna, 2007 ex *Pateobatis bleekeri** (as *Dasyatis bleekeri*)
Tylocephalum dasguptai Pramanik & Manna, 2007 ex *Carcharhinus limbatus*
Tylocephalum dierama Shipley & Hornell, 1906 ex *Aetomylaeus maculatus* (as *Myliobatis maculata*)
Tylocephalum girindrai Pramanik & Manna, 2007 ex *Aetobatus ocellatus** (as *Aetobatus narinari*)
Tylocephalum haldari Pramanik & Manna, 2007 ex *Pateobatis bleekeri** (as *Dasyatis bleekeri*)
Tylocephalum hanmantraoi Shinde & Jadhav, 1990 ex *Rhynchobatus djiddensis** (as *Rhynchobatus djeddensis*)
Tylocephalum krisnai Pramanik & Manna, 2007 ex *Pateobatis bleekeri** (as *Dasyatis bleekeri*)
Tylocephalum kuhli Shipley & Hornell, 1906 ex *Neotrygon kuhlii** (as *Trygon kuhli*)
Tylocephalum ludificans Jameson, 1912 ex *Pinctada imbricata* (as *Margaritifera vulgaris*) (Bivalvia)
Tylocephalum madhukarii Chincholikar & Shinde, 1980 ex *Pastinachus sephen** (as *Trygon sephen*)
Tylocephalum margaritiferae Seurat, 1906 ex *Margaritifera margaritifera* (Bivalvia)
Tylocephalum minimum Subhapradha, 1955 ex *Rhynchobatus djiddensis** (as *Rhynchobatus djeddensis*)
Tylocephalum minus Jameson, 1912 ex *Pinctada imbricata* (as *Margaritifera vulgaris*) (Bivalvia)
Tylocephalum minutum Southwell, 1925 ex "*Urogymnus* sp. (*asperrimus*?)"
Tylocephalum mukundai Pramanik & Manna, 2007 ex *Carcharhinus limbatus*
Tylocephalum pandurangi Shinde & Mahajan, 1994 ex *Pastinachus sephen** (as *Trygon sephen*)
Tylocephalum singhii Jadhav & Shinde, 1981 ex *Telatrygon zugei* (as *Trygon zugei*)

UNAVAILABLE NAMES (* *NOMINA NUDA*)

Adelobothrium carcharisase Mote, 2011
Adelobothrium kakinadinsis of Mote (2011)*
Aphanobothrium Seurat, 1906 in Herdmann and Hornell (1906)
Cephalobothrium subhapradhi Chincholikar & Shinde, 1977*
Discobothrium quadrisurculi Khambata & Bal, 1953*
Discobothrium redacta Khambata & Bal, 1953*
Hexacanalis ashae Khamkar, 2011
Hexacanalis govindi Wankhede, 2003
Hexacanalis sephanensis of Mohekar et al. (2002)*
Hexacanalis smythii Murlidhar, Shinde & Jadhav, 1986*
Lecanicephalum schmidti of Al Kawari (1992)*
Lecanicephalum trygoni of Mohekar et al. (2002)*
Polypocephalus braunii Shinde, 1981 of Jadhav et al. (1986)*
Polypocephalus budhadebae Jadhav, 2007
Polypocephalus harnesis Lanka, 2006
Polypocephalus kuhlii Vankara, Vijaya Lakshmi & Vijaya Lakshmi, 2006
Polypocephalus mirkarwarensis Dandwate & Jadhav, 2009
Polypocephalus pandei Pawar et al., 2005 of Jadhav (2007)*
Polypocephalus rakhamalii Dandwate & Jadhav, 2009*
Polypocephalus rhynchobatis of Mote (2012)*
Polypocephalus sakriensis Pawar et al., 2001 or 2005 of Jadhav (2007)*
Polypocephalus testicularis of Jadhav and Shinde (1989)*
Polypocephalus trygoni Jadhav & Threlfall, 1986*
Polypocephalus waltairensis Mote, 2012
Sephenicephallum or *Sephenicephalum* Shinde, Sarwade & Jadhav, 1980 or 1982
Sephenicephallum bombayensis Hiware, Jadhav & Bhosale, 1993*
Sephenicephallum or *Sephenicephalum maharashtrii* Shinde, Sarwade & Jadhav, 1980 or 1982*
Sephenicephalum dnyandevi Bhagwan & Shinde, 2002
Sephenicephalum marathwadensis "Pawar (1983)" of Bhagwan and Shinde (2002)*
Tetragonocephalum govindi Khamkar & Shinde, 2012
Tetragonocephalum janardane Wankhede, 1990*
Tetragonocephalum karachiensis Bilqees & Fatima, 1980 or 1982*
Tetragonocephalum marnrle Shipley & Hornell, 1906 of Lanka et al. (2013)*
Tetragonocephalum meenae of Mohekar et al. (2002)*
Tetragonocephalum panjiensis Khamkar, 2011
Tetragonocephalum pulensis Kankale, 2014
Tetragonocephalum sepheni Lanka, Hippargi & Patil, 2013
Tetragonocephalum shindei Shipley & Hornell, 1906 of Mohekar et al. (2002)*
Tetragonocephalum stegostomai Bilqees & Fatima, 1980 or 1982*
Tetragonocephalum varium Bilqees & Fatima, 1980 or 1982*
Tylocephalum damodarae Pathan & Bhure, 2013
Tylocephalum govindii Anarse, Borde, Gaware & Solunke, 2012
Tylocephalum mehdii of Mohekar et al. (2002)*

Cyclobothrium Southwell, 1911—homonym
Monoporophyllaeus Shinde & Chincholikar, 1977—invalid replacement name
Tenia in MacCallum (1917)—misspelled name

12

Litobothriidea Dailey, 1969

By
Janine N. Caira[1], Kaitlin Gallagher, and Kirsten Jensen

LITOBOTHRIIDEA AS THEY WERE KNOWN PRIOR TO THE PBI PROJECT

Diversity and Classification. The Litobothriidea are the second least speciose of the nine orders of cestodes parasitizing elasmobranchs. The order and its single family Litobothriidae Dailey, 1969 were erected in 1969 by Dailey to house *Litobothrium alopias* Dailey, 1969 and *Litobothrium coniformis* Dailey, 1969, both found parasitizing the spiral intestine of thresher sharks (*Alopias* Bonaparte) in the waters off California. Two years later, Dailey (1971) described a third member of the genus, *Litobothrium gracile* Dailey, 1971, from a smalltooth sand tiger shark (*Odontaspis ferox* [Risso]) also in the waters off California. Shortly thereafter, Kurochkin and Slankis (1973) described a fourth member of the genus, *Litobothrium daileyi* Kurochkin & Slankis, 1973, as well as the new genus *Renyxa* Kurochkin & Slankis, 1973 and species *Renyxa amplifica* Kurochkin & Slankis, 1973 from thresher sharks collected off western México. It was not until a decade later that *Litobothrium amsichensis* Caira & Runkle, 1993 was described from the goblin shark (*Mitsukurina owstoni* Jordan) off Australia by Caira and Runkle (1993). Recognizing that the medially recurved (rather than straight) nature of the margins of the fifth pseudosegment of the scolex was merely an autapomorphic feature in *R. amplifica*, Euzet (1994) synonymized *Renyxa* with *Litobothrium*, resulting in the transfer of this species to the latter genus as *L. amplifica* (Kurochkin & Slankis, 1973) Euzet, 1994. The final two species assigned to the genus prior to the PBI project (i.e., *L. janovyi* Olson & Caira, 2001 and *L. nickoli* Olson & Caira, 2001) also were described from thresher sharks collected in the Gulf of California, México by Olson and Caira (2001). Thus, at the inception of the PBI project, the order included a single family and genus, and eight species, all but two of which were known only from their original descriptions (see Olson and Caira, 2001).

Morphology. Dailey (1969) cited the distinctive configuration of the scolex (Figs. 1C, 2A–E) as justification for establishing a new order. However, controversy remains as to which of the anterior portions of the litobothriidean body (Fig. 1A) actually constitute the scolex. Dailey (1969; pg. 223) considered it to consist solely of the apical sucker, interpreting the region immediately posterior to the sucker as an “auxillary holdfast modification of the anterior segments.” In contrast, Caira et al. (1999, 2001) and Olson and Caira (2001) considered the scolex to comprise not only the apical sucker but also the region immediately posterior to that, bearing up to five pseudosegments, a subset of which are cruciform in cross-section (i.e., with muscular lateral and dorso-ventral extensions). Regardless of interpretations of homology, all eight members of the order described prior to 2008 bear such pseudosegments, although the total number ranges from three to five across species (Fig. 2A–E). All eight species known prior to the PBI project are relatively small worms (~1–16 mm in total length) with a strobilar

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[1] Corresponding author (janine.caira@uconn.edu)

Caira, J. N., K. Gallagher, and K. Jensen. 2017. Litobothriidea Dailey, 1969. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 231–241.

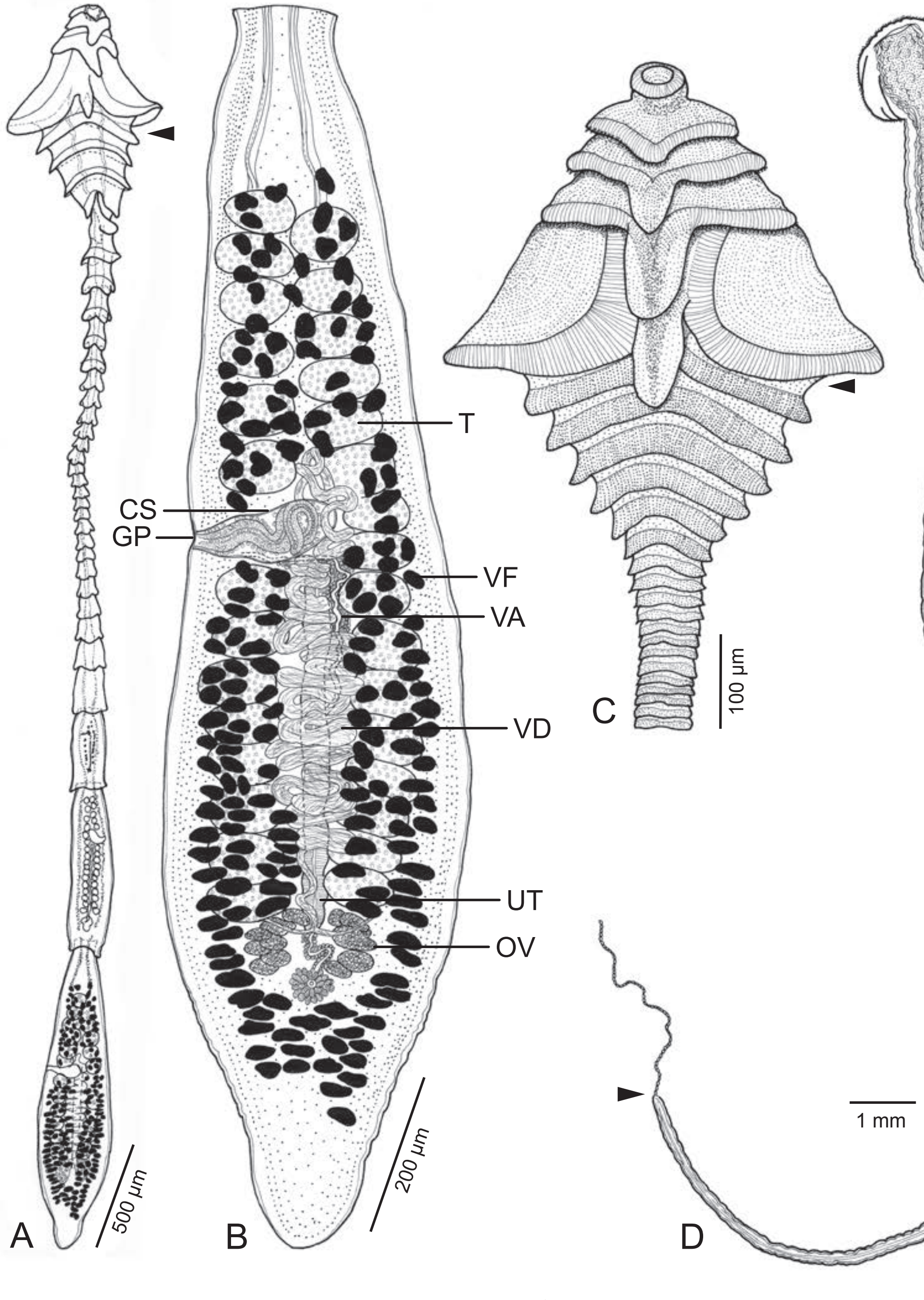

FIGURE 1. Line drawings of species of *Litobothrium*. **(A)** Complete worm of *Litobothrium nickoli* from *Alopias pelagicus* from the Gulf of California (modified from Olson and Caira [2001]). **(B)** Terminal proglottid of *L. nickoli* (modified from Olson and Caira [2001]). **(C)** Scolex of *L. nickoli* from *A. pelagicus* from Taiwan. **(D)** Complete worm of *Litobothrium aenigmaticum* from *A. pelagicus* from the Gulf of California. Arrowheads indicate boundary between scolex and strobila. *Abbreviations*: CS, cirrus-sac; GP, genital pore; OV, ovary; T, testis; UT, uterus; VA, vagina; VD, vas deferens; VF, vitelline follicle.

region posterior to the pseudosegments that bears 15–65 laciniate proglottids. Litobothriidean proglottid anatomy (Fig. 1B) is very much like that of some of the other elasmobranch-hosted cestode groups in that the genital pores are lateral and irregularly alternate along the length of the strobila, the testes are numerous and include a post-vaginal field, and the ovary is posterior in position. However, in addition to the somewhat unusual configuration of the scolex, the vagina enters the genital atrium at the same level as, rather than anterior to, the cirrus-sac, and the vitelline follicles are circum-medullary (Fig. 1B), rather than arranged in lateral fields.

PHYLOGENETIC RELATIONSHIPS. The status of members of the group as an order independent from the traditional concept of the Tetraphyllidea has been somewhat controversial. Based largely on similarities in proglottid anatomy, a number of authors (e.g., Brooks et al., 1991;

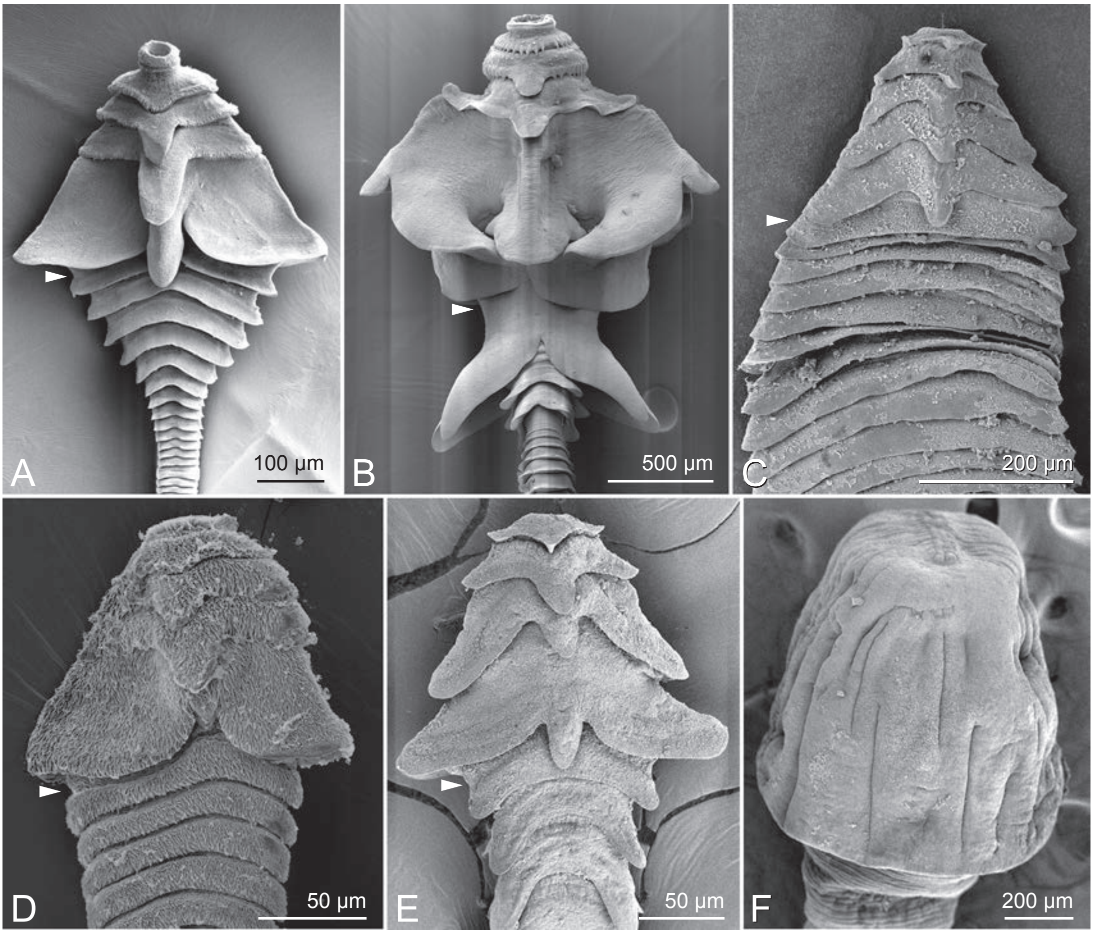

FIGURE 2. Scanning electron micrographs of scoleces of species of *Litobothrium*. Arrowheads indicate boundary between scolex and strobila. **(A)** *Litobothrium nickoli* from *Alopias pelagicus* from Taiwan. **(B)** *Litobothrium amplifica* from *A. pelagicus* from the Gulf of California. **(C)** *Litobothrium amsichensis* from *Mitsukurina owstoni* from Australia. **(D)** *Litobothrium daileyi* from *A. pelagicus* from the Gulf of California. **(E)** *Litobothrium janovyi* from *A. superciliosus* from the Gulf of California (modified from Caira et al. [2014]). **(F)** Scolex proper of *Litobothrium aenigmaticum* from *A. pelagicus* from the Gulf of California (modified from Caira et al. [2014]).

Euzet, 1994; Hoberg et al., 1997) considered the group as a family within the Tetraphyllidea. Influenced at least in part by the presence of unique pseudosegments in litobothriideans, most other authors (e.g., Wardle et al., 1974; Schmidt, 1986; Caira and Runkle, 1993; Olson and Caira, 2001) followed Dailey (1969) in recognizing the Litobothriidea as an independent order. In the trees resulting from the morphological phylogenetic analyses of Caira et al. (1999, 2001), the ordinal status of the group was supported. The single species of *Litobothrium* included in Caira et al. (1999) grouped in a polytomy with a clade containing a species each of *Cathetocephalus* Dailey & Overstreet, 1973 and *Disculiceps* Joyeux & Baer, 1936 (both now considered to be cathetocephalideans), and acetabulate elasmobranch-hosted taxa including a species each of *Monticellia* LaRue, 1911 and *Protocephalus* Weinland, 1858 (now considered to be members of the non-elasmobranch hosted Onchoproteocephalidea). In Caira et al. (2001), the three litobothriidean taxa clustered, in a clade that was the sister group of either a clade comprising the bothriate trypanorhynchs + diphyllideans, and cathetocephalideans (fig. 14.96), or a clade comprising trypanorhynchs + diphyllideans, *Zyxibothrium* Hayden & Campbell, 1981, and a taxon referred to by Caira et al. (2001) as New genus 1 (fig. 14.98).

Results from molecular phylogenetic analyses have been somewhat more mixed. Based on analyses of partial (i.e., D1–D3) 28S rDNA sequence data, Caira et al. (2005) found the two litobothriidean species they included in their analyses to group together as sister to the acetabulate cestode groups; the work of Waeschenbach et al. (2007) based on complete 28S rDNA and 18S rDNA sequence data yielded a similar result. In contrast, several studies found the phylogenetic position of the litobothriideans to be somewhat labile across loci and/or analyses (i.e., Olson and Caira [1999] based on complete 18S rDNA and partial Ef1-α data; Olson et al. [1999] based on partial 18S rDNA datal; and Olson et al. [2001] based on complete 18S rDNA and partial [D1–D3] 28S rDNA data). While in some trees the two litobothriidean species included grouped as sister to the acetabulate taxa, in other trees the litobothriideans were sister to lecanicephalidean or a subset of tetraphyllidean taxa.

Prior to 2008, all but one of these phylogenetic studies included only the single species *L. janovyi* (i.e., Waeschenbach et al., 2007) or *L. daileyi* (i.e., Caira et al., 1999), or only the pair of species *L. amplifica* and *L. janovyi* (i.e., Olson and Caira, 1999; Olson et al., 1999, 2001; Caira et al., 2005), and thus little was known of the interrelationships among litobothriidean species. The exception was the morphological study of Caira et al. (2001), which included *L. amplifica*, *L. amsichensis*, and *L. daileyi*. In trees resulting from that study the latter two taxa grouped as sister taxa to one another, with *L. amplifica* as their sister. It should be noted that *L. janovyi* was erroneously referred to as *L. alopias* by both Olson and Caira (1999) and Olson et al. (1999). That error was corrected by Olson and Caira (2001) when they described *L. janovyi*.

HOST ASSOCIATIONS. The host associations of the litobothriideans are among the most restricted of those seen across any of the 19 cestode orders. The eight species known prior to 2008 all parasitize the spiral intestine of sharks of the order Lamniformes. Within that order, one species parasitizes the goblin shark, *Mitsukurina owstoni* (monotypic family Mitsukurinidae Jordan), and one parasitizes the smalltooth sand tiger shark, *Odontaspis ferox* (family Odontaspidae Müller & Henle). The remaining six species collectively parasitize thresher sharks (family Alopiidae Bonaparte). Although five of these six species had originally been reported from the bigeye thresher shark, *Alopias superciliosus* Lowe, Olson and Caira (2001) presented evidence suggesting that the original host identifications of the two species described by Kurochkin and Slankis (1973) were in error. Based on new collections and revised host identifications, Olson and Caira (2001) concluded that three of the six species (i.e., *L. alopias*, *L. coniformis*, and *L. janovyi*) parasitize *A. superciliosus* and the remaining three (i.e., *L. amplifica*, *L. daileyi*, and *L. nickoli*) parasitize *A. pelagicus* Nakamura. To date, no litobothriideans have been reported from the third member of the genus, *Alopias vulpinus* (Bonnaterre).

GEOGRAPHIC DISTRIBUTION. The geographic distributions of the litobothriideans, as known prior to the PBI project, were also among the most restricted of those seen across cestode orders. Of the eight species, seven had been reported only from the eastern Pacific Ocean. Three of these were collected off California (Dailey, 1969, 1971), two from Tehuantepec Bay off western México (Kurochkin and Slankis, 1973), and two from the Gulf of California (Olson and Caira, 2001). The remaining species was collected from Ulladulla the water off the southeastern coast of New South Wales, Australia (Caira and Runkle, 1993).

CURRENT STATUS OF THE LITOBOTHRIIDEA

DIVERSITY, MORPHOLOGY, AND CLASSIFICATION. Only a single species of litobothriidean, *Litobothrium aenigmaticum* Caira, Jensen, Waeschenbach & Littlewood, 2014, found parasitizing pelagic thresher sharks in the Gulf of California, México and Taiwan, was described over the duration of the PBI project (Caira et al., 2014a). However, substantial intrigue surrounds the unusual nature of the morphology of this species relative to that of its eight congeners because the morphology of *L. aenigmaticum* is unlike that of any known cestode order! Nonetheless, based on partial (D1–D3) 28S rDNA sequence data, Caira et al. (2014a) found *Litobothrium aenigmaticum* to nest robustly among species of *Litobothrium* in their molecular phylogenetic analyses—despite its lack of essentially all of the diagnostic features of the order, family, and genus (compare Fig. 1A and F). Its scolex bears no apical sucker or cruciform pseudosegments and instead consists of a dome-shaped, grooved scolex proper (Fig. 2F) borne on a sizeable cephalic peduncle (Fig. 1D). The only evidence of a strobila was found on a small subset of specimens and consisted of a tiny, fragile chain of minute (~60 μm in length) immature proglottids at the posterior end of the cephalic peduncle (Fig. 1D). Caira et al. (2014a) did note that *L. aenigmaticum* shared the possession of the somewhat unusual microthrix type, referred to as coniform spinitriches by Chervy (2009) with its congeners—albeit in different locations on its body. Whereas these spinitriches are located on the posterior margins of the cruciform pseudosegments composing the scolex of typical litobothriideans (see Caira et al., 2014a; e.g., fig. 2D), they are located on the apex of the scolex proper and in a series of five bands on the tiny immature proglottids of *L. aenigmaticum* (see Caira et al., 2014a; fig. 5E and I, respectively). Given its unusual morphology, the taxonomic assignment of *L. aenigmaticum* necessitated major revisions to the generic, familial, and ordinal diagnoses. So as to avoid compromising the existing diagnoses, Caira et al. (2014a; pg. 240) addressed this by simply adding a phrase to the end of each diagnosis that reads "Or not as above and as follows: scolex proper dome-shaped, with extensive cephalic peduncle, containing four distinctive tissue types; proglottids extremely hyperapolytic; mature proglottids unknown."

Perhaps most puzzling, however, was the extensive collection of cell types of unknown function distributed throughout the length of the scolex of *L. aenigmaticum*. Based on histological sections of paraffin-embedded specimens, Caira et al. (2014a) originally identified four distinct concentrations of cells they referred to as tissues. Gallagher et al. (in press) subsequently used transmission electron microscopy to explore these cells in more detail and expanded the number of different types of cells to 11. All 11 types of cells were found to house electron dense vesicles and to stain positively with periodic acid-Schiff (PAS), suggesting the presence of a glycoprotein. A subset was found to also house electron lucent vesicles. Gallagher et al. (in press) also determined that the paired ducts seen on the lateral margins of the worms were associated with high concentrations of protonephridia and thus are likely excretory in function.

Beyond this enigmatic form, PBI work helped resolve the controversy surrounding which elements of the anterior region of a typical litobothriidean constitute the scolex. These insights came from data on the morphology of the early juvenile stages of *L. daileyi* and *L. janovyi*. In the case of all of the elasmobranch-hosted cestode orders, the basic elements of the scolex develop in the metacestode in its final intermediate host (see Jensen and Bullard, 2010 and references therein) and thus the early juvenile stages enter the definitive host with the rudiments of their scolex already in place. Caira et al. (2014a) showed that the earliest stage juveniles of *L. daileyi* (fig. 2A; see Fig. 3A) and *L. janovyi* (fig. 2E; see Fig. 3C,) bear an apical sucker and a number of simple pseudosegments consistent with the total number of cruciform and non-cruciform pseudosegments seen in the late stage juvenile (Fig. 3B and D, respectively) and the adult worm (i.e., 5 [Fig. 2D] and 4 [Fig. 2E], respectively) of these species. These data support the interpretation of Caira et al. (1999) and Olson and Caira (2001) that the scolex of litobothriideans should be considered to be composed of the apical sucker and the pseudosegments

For comparative purposes, we present here for the first time, scanning electron micrographs of an early juvenile stage of *L. aenigmaticum* (Fig. 3E–J) found parasitizing the spiral intestine of a pelagic thresher shark from Taiwan. The distribution of various microthrix types seen throughout the surfaces of the juvenile helps with interpretation of homology between its morphology and that of the adult as described by Caira et al. (2014a). The anterior, widest portion of the body of the juvenile, like that of the adult worm, bears coniform spinitriches (compare Fig. 3G with fig. 5E of Caira et al. [2014a]), suggesting this region will grow to become the cap-like scolex proper of the adult. The region immediately posterior to this, which appears to extend throughout the anterior half of the body of the juvenile, like the cephalic peduncle of the adult worm, bears only papilliform filitriches (compare Fig. 3H with fig. 5G of Caira et al. [2014a]), suggesting this region represents the precursor to the anterior region of the cephalic peduncle of the adult. Finally, the posterior half of the body of the juvenile bears capilliform filitriches (Fig. 3I); we believe this region represents the larval body. The spinitriches seen at the extreme posterior of the body of the juvenile of *L. aenigmaticum* (Fig. 3J) do not appear to have an equivalent in the adult body. However, spinitriches are seen at the posterior end of the body of the juveniles of both of the other species of *Litobothrium* for which juvenile stages are known (i.e., arrowheads in Fig. 3B, D) and these do not persist into the adult stage.

At present there are nine described species in the order (Table 2). However, we have preliminary morphological evidence to suggest that the bigeye thresher shark may host an as-of-yet undescribed species possessing the unusual morphology seen in *L. aenigmaticum*.

PHYLOGENETIC RELATIONSHIPS. The molecular phylogenetic analyses that included broad sampling of cestode orders that were conducted over the course of the PBI (i.e., Waeschenbach et al., 2012; Caira et al., 2014b) supported both the monophyly of the order, and its status as the sister group of the clade comprising the acetabulate cestode orders. In their analyses, which included four of the nine members of the order, Caira et al. (2014a) found *L. aenigmaticum* to group robustly as the sister taxon of *L. nickoli*, in a clade comprising the three species included in the study that parasitize pelagic thresher sharks; *L. janovyi*, from the bigeye thresher shark was the sister to that group. These interspecific relationships were consistent with those recovered from the analyses Caira et al. (2014b), both of which included only subsets of these species.

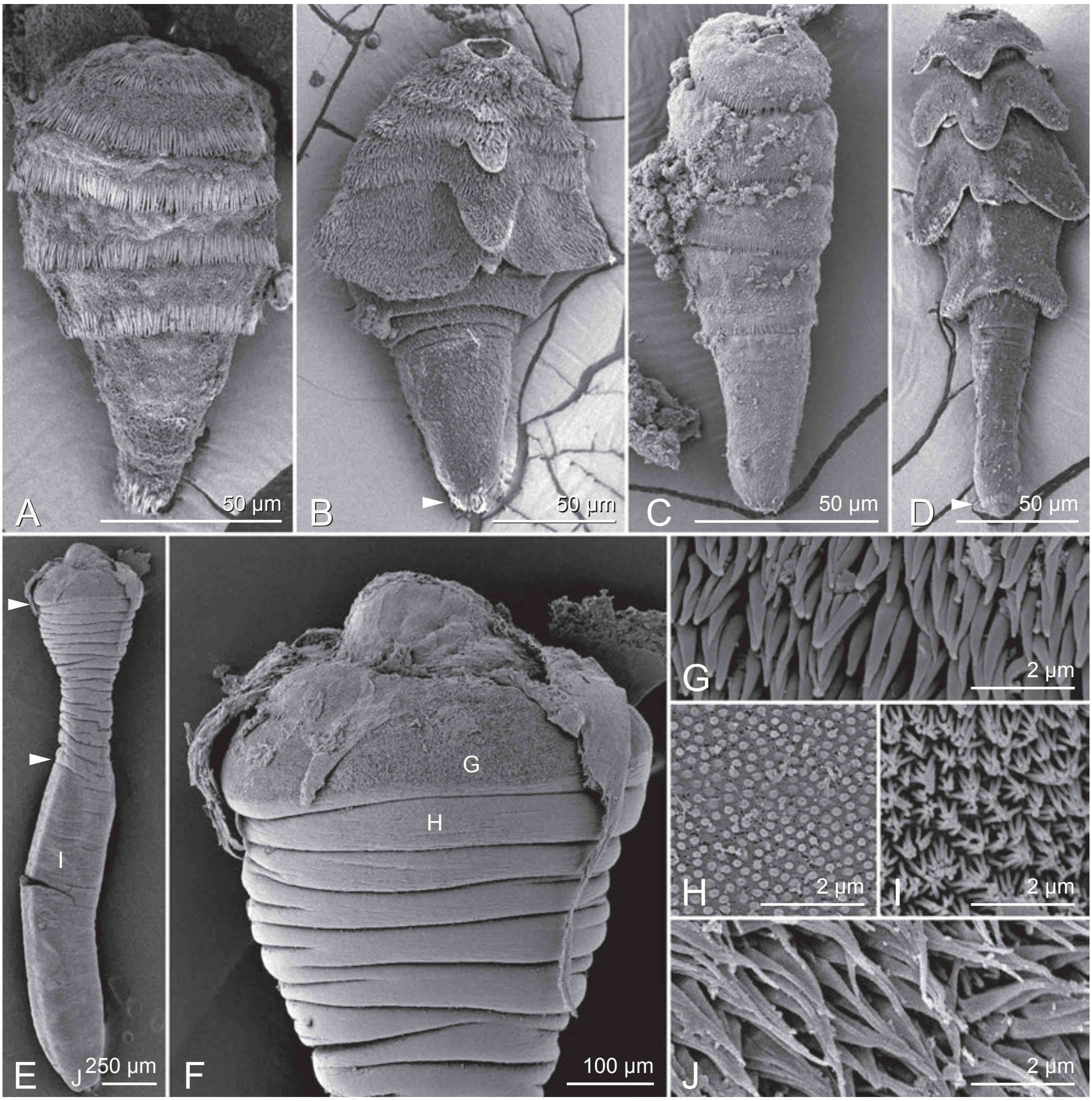

FIGURE 3. Scanning electron micrographs of juveniles of species of *Litobothrium* found in the spiral intestine of thresher sharks. **(A)** Early stage juvenile of *Litobothrium daileyi*. **(B)** Later stage juvenile of *Litobothrium daileyi*; arrowhead indicates location of ring of spinitriches at posterior of larval body. **(C)** Early stage juvenile of *Litobothrium janovyi* (modified from Caira et al. [2014a]). **(D)** Later stage juvenile of *Litobothrium janovyi*; arrowhead indicates location of ring of spinitriches at posterior of larval body (modified from Caira et al. [2014a]). **(E–J)** Juvenile stage of *Litobothrium aenigmaticum*. **(E)** Entire juvenile; anterior arrowhead indicates boundary between scolex proper and cephalic peduncle; posterior arrowhead indicates boundary between cephalic peduncle and larval body; small letters indicate location of details in Fig. 3I and J. **(F)** Detail of scolex proper and anterior cephalic peduncle; small letters indicate locations of details in Fig. 3G and H. **(G)** Detail of posterior region of scolex proper. **(H)** Detail of anterior of cephalic peduncle. **(I)** Detail of larval body at mid-level. **(J)** Detail of spinitriches at posterior of what is likely remnant of larval body.

We have recently identified material of *Litobothrium daileyi* preserved for molecular work and have generated partial (D1–D3) 28S rDNA data for two specimens of this species in order to present a more comprehensive assessment of the phylogenetic relationships of the group here. The tree resulting from a maximum likelihood analysis of those data in combination with those of Caira et al. (2014a) is presented in Figure 4. One of the most startling results of this work was that for this locus, *L. aenigmaticum* was found to be identical in sequence to *L. daileyi*. Thus, the use of additional loci for this group is clearly warranted.

Host Associations. Except for increasing the number of litobothriidean species known to parasitize *Alopias pelagicus* and possibly also *A. superciliosus* from three to four each, the host associations of the litobothriideans have not changed substantially over the course of the PBI project. The members of this order remain restricted to lamniform sharks, with a particular affinity for two of the three known species of thresher sharks. Examination of over 50 common thresher sharks (*A. vulpinus*) from the northwestern Atlantic Ocean over several decades confirms the absence of litobothriideans from this shark species (J.N. Caira, unpubl. data)—a phenomenon that remains to be satisfactorily explained. Our collections of cestodes from lamnids (incl. *Isurus paucus* Guitart-Manday off Taiwan, *Isurus oxyrinchus* [Rafinesque] from the northwestern Atlantic Ocean, and *Carcharodon carcharias* [Linnaeus] from both coasts of the USA), *Pseudocarcharias kamoharai* (Matsubara) in the monotypic Pseudocarchariidae Compagno off Ecuador, *Megachasma pelagios* Taylor, Compagno & Struhsaker in the monotypic Megachasmidae Taylor, Compagno & Struhsaker off Japan (e.g., Caira et al., 1997), and *Cetorhinus maximus* (Gunnerus) (e.g., Linton, 1922; Yamaguti, 1952; and our work off New England and California) in the monotypic Cetorhinidae Gill, suggest that these families are also unlikely hosts of litobothriideans.

To date, known litobothriideans have been reported from a total of only four species of lamniform sharks. Given that the smalltooth sandtiger, *Odontaspis ferox*, hosts a litobothriidean, we believe the additional diversity in the order is likely to be found in the three other species of sandtigers, *Odontaspis noronhai* (Maul), *Carcharias taurus* Rafinesque, and *Carcharias tricupidatus* Day. Even if each is found to host two species, total diversity in the order globally is predicted to remain below 15 species.

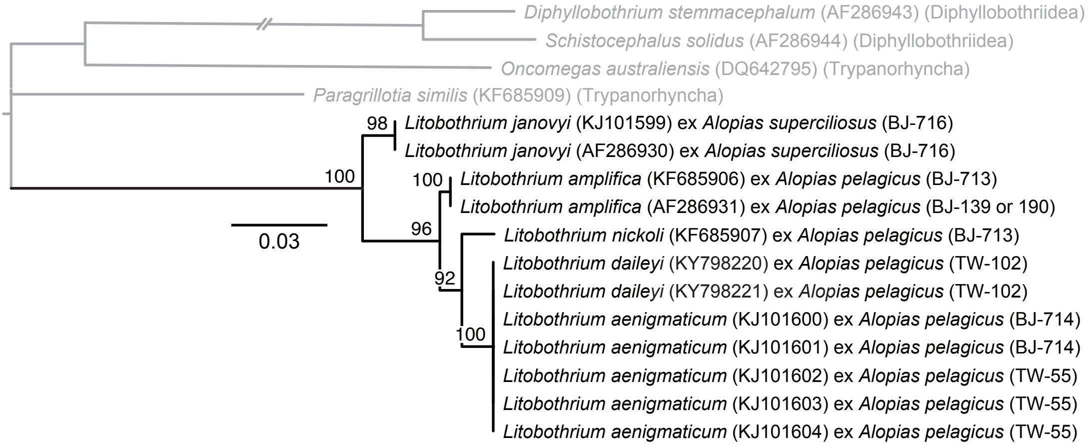

Figure 4. Tree resulting from maximum likelihood analysis of aligned matrix of 1,336 base pairs (of which 915 were invariable) of partial 28S rDNA (D1–D3) sequence data for species of *Litobothrium* using GARLI with GTR+Γ as the substitution model. Data for the two specimens of *Litobothrium daileyi* from *Alopias pelagicus* in Taiwan are new to this study. Nodal support is given as bootstrap values generated from 100 bootstrap replicates. Branch length scale bar indicates number of substitutions per site. GenBank numbers are provided in parentheses. Outgroup taxa are indicated in gray; the cestode order to which each belongs is indicated in parentheses following the GenBank number.

GEOGRAPHIC DISTRIBUTION. New collections from thresher sharks from Taiwan conducted over the course of the PBI project expanded the known distribution of *L. amplifica*, *L. daileyi*, *L. nickoli*, and *L. aenigmaticum* from the eastern Pacific Ocean to include the western Pacific Ocean. This leads us to believe that collections from elsewhere across the broad distributions of the lamniform species (see Ebert et al., 2013) known to host litobothriideans are likely to expand the distribution of the order even further to include coastal tropical waters globally, and in the case of *Mitsukurina owstoni* this could extend throughout most of the western Pacific seaboard.

CONCLUSIONS

The Litobothriidea are a small order of tapeworms that parasitize a subset of lamniform shark taxa, with a particular affinity for two of the three species of thresher sharks. PBI efforts expanded the group to include one additional, morphologically extremely unique, species, and expanded the order's known geographic distribution to include the western Pacific Ocean. It seems likely that additional collections will reveal the distribution of the order to be as extensive as that of its hosts and thus will ultimately be expanded to be at least circumtropical. Existing host data (Table 1) lead us to predict that litobothriidean diversity will not be found to substantially exceed that currently known. The remaining species of sandtigers are the most likely potential sources of additional new litobothriidean taxa. The bizarre morphology of one of the nine members of the order remains an enigma. It would ultimately be extremely interesting to explore gene expression data underlying this morphology and to investigate the possible existence of a second morphologically divergent form in the bigeye thresher shark.

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Table 1. Expected global elasmobranch associations of litobothriidean species (in yellow). Number of shark species per genus given in parentheses (includes known undescribed shark species). First column: number of litobothriidean species parasitizing each shark taxon as of 2017 (includes known undescribed cestode species); second column: predicted total number of litobothriidean species parasitizing each shark taxon globally. Estimated total number of litobothriidean species parasitizing elasmobranchs globally given at bottom of Table.

	Litobothriidean spp.	
	2017	**ESTIM.**
SELACHOIDEA		
Carcharhiniformes	**0**	**0**
Heterodontiformes	**0**	**0**
Hexanchiformes	**0**	**0**
Lamniformes	**9**	**12**
Alopiidae	**7**	**8**
Alopias (3 spp.)	7	8
Cetorhinidae	**0**	**0**
Cetorhinus (1 sp.)	0	0
Lamnidae	**0**	**0**
Carcharodon (1 sp.)	0	0
Isurus (2 spp.)	0	0
Lamna (2 spp.)	0	0
Megachasmidae	**0**	**0**
Megachasma (1 sp.)	0	0
Mitsukurinidae	**1**	**1**
Mitsukurina (1 sp.)	1	1
Odontaspididae	**1**	**3**
Carcharias (1 sp.)	0	1
Odontaspis (2 spp.)	1	2
Pseudocarcharhiidae	**0**	**0**
Pseudocarcharias (1 sp.)	0	0
Orectolobiformes	**0**	**0**
Pristiophoriformes	**0**	**0**
Squaliformes	**0**	**0**
Squatiniformes	**0**	**0**
SHARK TOTAL	**9**	**12**
BATOID TOTAL	**0**	**0**
ELASMOBRANCH TOTAL	**9**	**12**

Table 2. List of valid litobothriidean taxa with their type hosts. New taxa and taxonomic actions resulting from PBI project activities indicated in bold.

VALID TAXA

Family Litobothriidae Dailey, 1969

Litobothrium Dailey, 1969

Litobothrium alopias Dailey, 1969 (type) ex *Alopias superciliosus*

***Litobothrium aenigmaticum* Caira, Jensen, Waeschenbach & Littlewood, 2014** ex *Alopias pelagicus*

Litobothrium amplifica (Kurochkin & Slankis, 1973) Euzet, 1994 ex *Alopias pelagicus*

Litobothrium amsichensis Caira & Runkle, 1993 ex *Mitsukurina owstoni*

Litobothrium coniformis Dailey, 1971 ex *Alopias superciliosus*

Litobothrium daileyi Kurochkin & Slankis, 1973 ex *Alopias pelagicus*

Litobothrium gracile Dailey, 1971 ex *Odontaspis ferox*

Litobothrium janovyi Olson & Caira, 2001 ex *Alopias superciliosus*

Litobothrium nickoli Olson & Caira, 2001 ex *Alopias pelagicus*

13

Nippotaeniidea Yamaguti, 1939

By
Tomáš Scholz[1], Jan Brabec, and Roman Kuchta

NIPPOTAENIIDEA AS THEY WERE KNOWN PRIOR TO THE PBI PROJECT

Diversity and Classification. This small order of cestodes was erected by Yamaguti (1939) to accommodate a new family, Nippotaeniidae Yamaguti, 1939, a new genus, *Nippotaenia* Yamaguti, 1939, and a new species, *Nippotaenia chaenogobii* Yamaguti, 1939 collected from the freshwater gobioid fishes *Chaenogobius annularis urotaenia* Gill (now *Gymnogobius urotaenia* [Hilgendorf, 1879]), *Gobius similis* (Gill) (most likely *Rhinogobius kurodai* [Tanaka]; T. Shimazu, pers. com.), and *Mogurnda obscura* (Temminck & Schlegel) (most likely *Gymnogobius castaneus* [O'Shaughnessy]; Shimazu, 1997) in Japan. At that time, in addressing the systematic position of the new order among other cestode groups, Yamaguti (1939; pg. 287) wrote "In general internal anatomy, especially in the character of the vitellaria, this order resembles Cyclophyllidea more closely than any of the other four groups, in which the vitellaria are divided into numerous follicles, but differs distinctly in the main excretory system. In this respect it bears a certain resemblance to Pseudophyllidea, especially Caryophyllaeidae." The unique morphology of the scolex of members of the order, which consists of only a single apical sucker, has led to the general acceptance of the ordinal status of the group (Khalil et al., 1994).

Five additional species were subsequently described (Yamaguti and Miyata, 1940; Akhmerov, 1941; Hine, 1977) and one additional genus was erected (i.e., *Amurotaenia* Akhmerov, 1941 by Akhmerov [1941]). However, Akhmerov (1960) synonymized his new genus with *Nippotaenia*, and transferred its type and only species, *A. perccotti* Akhmerov, 1941, to *Nippotaenia*. Although numerous authors (e.g., Dubinina, 1962, 1971, 1987; Wardle and McLeod, 1952; Yamaguti, 1959; Demshin, 1985) have concurred with that action, others have not. For example, Hine (1977) retained *Amurotaenia* as valid and not only transferred *N. mogurndae* Yamaguti & Miyata, 1940 to that genus, but also described a third species, *A. decidua* Hine, 1977 in addition to two new species of *Nippotaenia*, *N. contorta* Hine, 1977 and *N. fragilis* Hine, 1977, both from New Zealand. Schmidt (1986) and Bray (1994) also recognized both genera as valid, differentiating them based on the possession of hyperapolytic proglottids (i.e., proglottids that mature away from the strobila) in species of *Amurotaenia* versus anapolytic proglottids (i.e., proglottids that do not detach from the strobila until gravid) in species of *Nippotaenia*. These authors also noted that the presence, rather than lack, of testes in gravid proglottids also distinguishes the two genera.

In terms of the total number of valid species, Dubinina (1962) synonymized *A. perccotti* with *N. mogurndae* without providing any justification for this synonymy, thus reducing the total number of species in the order to five. However, this opinion was not shared by

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[1] Corresponding author (tscholz@paru.cas.cz)

Scholz, T., J. Brabec, and R. Kuchta. 2017. Nippotaeniidea Yamaguti, 1939. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 243–250.

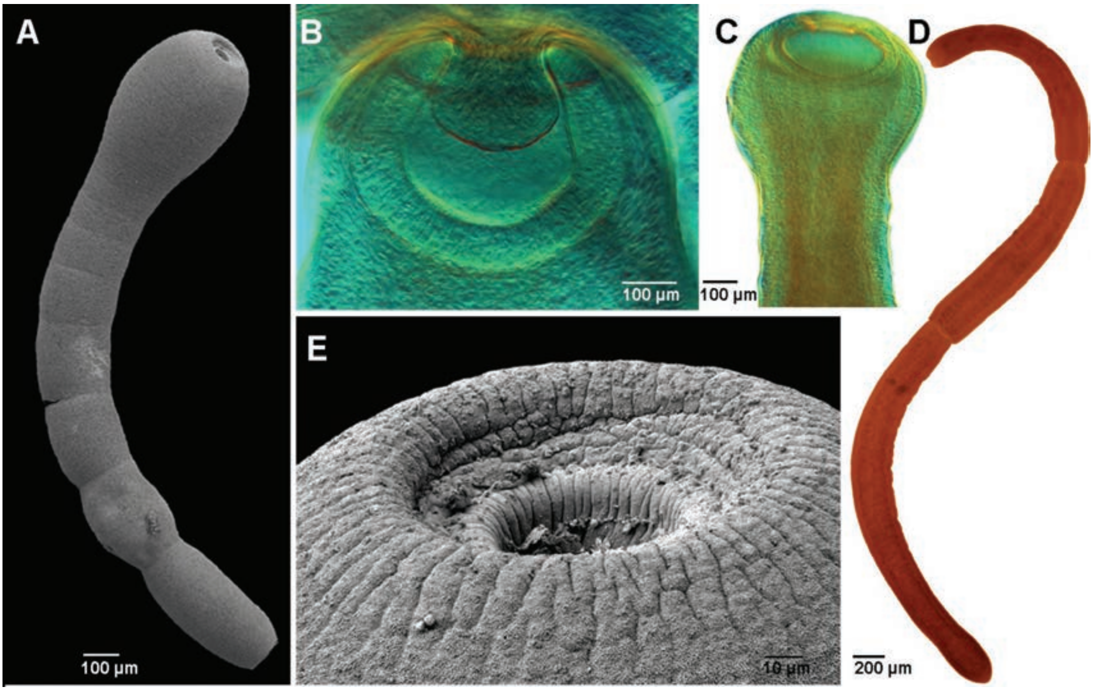

FIGURE 1. Photomicrographs of selected nippotaeniideans. **(A)** Entire worms of *Nippotaenia perccotti* ex *Perccottus glenii*, Slovakia. Scanning electron micrograph. **(B)** Apical sucker of *Nippotaenia chaenogobii* ex *Gymnogobius urotaenia*, Japan. **(C)** Scolex of *Nippotaenia mogurndae* ex *Odontobutis obscura*, Japan. **(D)** Strobila of *N. chaenogobii* ex *G. urotaenia*, Japan. **(E)** Opening of the apical sucker of *N. perccotti* ex *P. glenii*, Slovakia. Scanning electron micrograph.

Hine (1977), Schmidt (1986), or Bray (1994). Unfortunately, this synonymy has been widely accepted—although in our opinion incorrectly— in many accounts of this invasive parasite of the Chinese sleeper (*Perccottus glenii* Dybowski) (e.g., Davydov and Korneva, 2000; Korneva, 2002; Košuthová et al., 2004, 2008; Bombarová et al., 2005).

MORPHOLOGY. Nippotaeniideans are small- to medium-sized tapeworms, with a strobila that does not exceed 5.5 mm in length with 2–19 proglottids (except for *A. mogurndae* with 25–45 proglottids) in species assigned to *Amurotaenia* pre-PBI, and with a strobila 35 mm, exceptionally 72 mm, in length, with up to 7–30 proglottids in species assigned to *Nippotaenia* (see table 1 in Hine [1977]). The body of nippotaeniideans is essentially cylindrical (Fig. 1); each proglottid contains one set of genitalia (Fig. 2). Free proglottids of hyperapolytic species can grow up to nine mm in length (Hine, 1977).

The most peculiar morphological feature of nippotaeniideans is their possession of a scolex that bears only a single apical sucker and that lacks all other attachment organs (Yamaguti, 1939; Hine, 1977; Bray, 1994) (Fig. 1). The neck may contain genital primordia at its posterior margin. Fibers of the longitudinal musculature are not arranged in bundles, rather individual fibers are attached to the anterior margin of the apical sucker. Numerous, anastomosing longitudinal osmoregulatory vessels are found in the cortex, whereas a few occur in the medulla.

The numerous testes are medullary and limited to the region of the proglottid anterior to the vitellarium; they may be present or degenerated in gravid proglottids. The cirrus-sac is thin-walled and may contain an internal seminal vesicle. The genital pore is pre-equatorial and sublateral. The ovary consists of two symmetrical lobes connected by a central, ventral isthmus. The vitellarium is compact, composed of two symmetrical lobes, and is located anterior to the ovary (Fig. 2). The vagina opens into the genital atrium posterior to the cirrus-sac. The uterus forms transverse coils that may fill much of the medulla; a uterine pore is lacking. Intrauterine eggs are spherical, have three layers, and contain fully formed hexacanths.

The ultrastructure of the uterus of *N. perccotti* (Akhmerov, 1941) Akhmerov, 1960 (as *N. mogurndae*) was studied by Davydov and Korneva (2000). Chromosomes of the same species were studied by Bombarová et al. (2005).

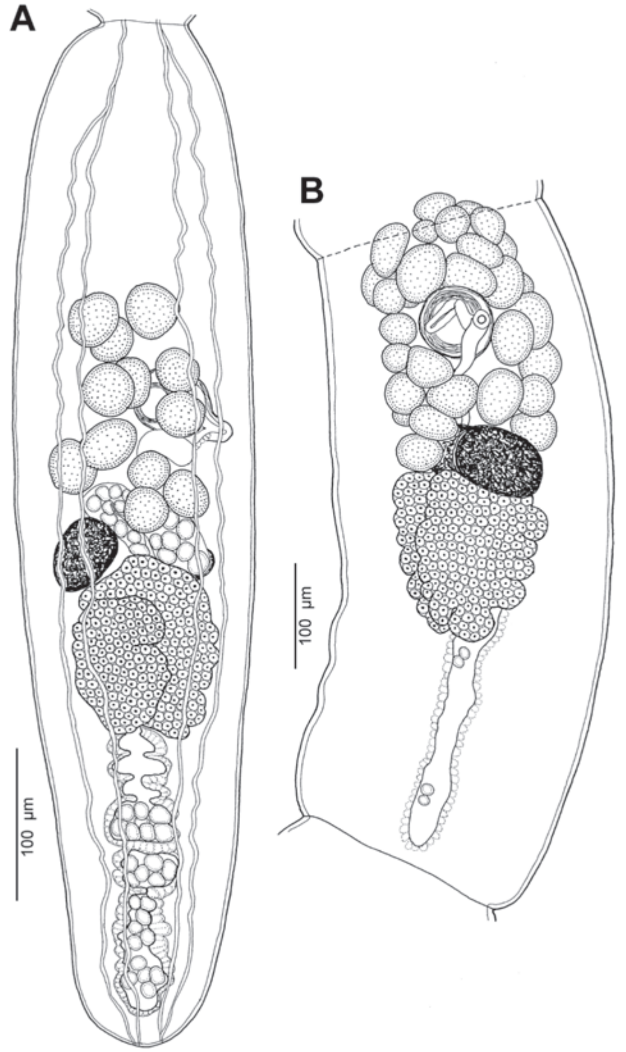

FIGURE 2. Pregravid proglottids of nippotaeniideans. **(A)** *Nippotaenia perccotti* ex *Perccottus glenii*, Russia. **(B)** *Nippotaenia chaenogobii* ex *Gymnogobius urotaenia*, Japan.

HOST ASSOCIATIONS. All species of nippotaeniideans occur exclusively in freshwater fishes of the suborders Gobioidei (order Perciformes: families Eleotridae Bonaparte, Odontobutidae Hoese & Gill, and Gobiidae Cuvier) and Osmeroidei (order Osmeriformes: families Galaxiidae Müller and Retropinnidae Gill). Records of *Nippotaenia* species from the galaxiid *Aplochiton taeniatus* Jenyns, the percichthyid *Percichthys trucha* (Valenciennes), and the salmonids *Oncorhynchus mykiss* (Walbaum) and *Salvelinus fontinalis* (Mitchill) in Argentina by Ortubay et al. (1994) and Rauque et al. (2003) are erroneous. In fact, two triaenophorid cestodes (Bothriocephalidea), namely *Galaxitaenia toloi* Gil de Pertierra & Semenas, 2005 from *Galaxius platei* Steindachner, and *Ailinella mirabilis* Gil de Pertierra & Semenas, 2006 from *Galaxius maculatus* Jenyns, were misidentified as nippotaeniideans, as recognized by Gil de Pertierra and Semenas (2005, 2006).

The life-cycle of nippotaeniideans involves only a single, copepod intermediate host in which metacestodes without a primary lacuna (i.e., plerocercoids according to Chervy, [2002]) develop (Yamaguti, 1951; Demshin, 1985; Shimazu, 1997). The apical sucker of the scolex is present in the earliest known life-cycle stage—the metacestode—in the copepod intermediate host (Demshin, 1985).

GEOGRAPHIC DISTRIBUTION. The geographic distribution of the order is somewhat disjunct. While three species occur in the eastern-most part of the Palaearctic realm (i.e., Japan, Russian Far East, and China), the remaining three species are endemic to New Zealand (Hine, 1977). The distribution of *A. perccotti* has expanded considerably as a result of the expansion of the distribution of its host *P. glenii* (e.g., Košuthová et al., 2004, 2008). Although native to the Russian Far East, over the twentieth century, this teleost has spread to large parts of the Danube, the Vistula, and other river basins (Lukina, 2011).

PHYLOGENETIC RELATIONSHIPS. The phylogenetic affinities of the order have been controversial for several decades. Freeman (1973) considered the order, like most other cestode orders, to have originated directly from the ancestral protocestode. In contrast, Brooks et al. (1991; pg. 661) considered the nippotaeniideans to occupy a "relatively plesiomorphic position" as the sister group of all "non-pseudophyllidean cestodes" (i.e., all proteocephalidean, lecanicephalidean, tetraphyllidean, tetrabothriidean, and cyclophyllidean taxa). Early phylogenetic inferences based on molecular sequence data from different loci (Olson and Caira, 1999; Kodedová et al., 2000; Olson et al., 2001; Waeschenbach et al., 2007) have unequivocally supported a close relationship between the nippotaeniideans and the so-called "higher tetrafossates" of Olson and Tkach (2005) (i.e., the Mesocestoididae [or Mesocestoidata], Tetrabothriidea, and Cyclophyllidea). It is interesting that all of these groups are characterized by their possession of a compact vitellarium. However, the interrelationships among these more derived cestode orders have differed across analyses (e.g., see fig. 2 in Olson and Tkach, 2005; Waeschenbach et al., 2007).

Prior to the PBI project, sequence data for one or more genes were available for specimens identified as the following three species: *Amurotenia decidua* from *Gobiomorus cotidianus* McDowall in Lake Taupo, New Zealand (28S rDNA, 18S rDNA, and Ef-1α), *A. mogurndae* from *O. obscura* in the Nukui River, Japan (28S rDNA and 18S rDNA), and *N. chaenogobii* from *G. urotaenia* in Lake Suwa, Japan (28S rDNA, 18S rDNA, and mtDNA) (Mariaux, 1998; Olson and Caira, 1999; Olson et al., 2001).

CURRENT STATUS OF THE NIPPOTAENIIDEA

DIVERSITY AND CLASSIFICATION. No new nippotaeniidean taxa were described over the course of the PBI project. However, specimens of a second species that had originally been assigned to *Amurotaenia* (i.e., *A. perccotti*) were collected and preserved in ethanol for the generation of molecular sequence data. Phylogenetic analyses of these data, in combination with comparable data for the three species included in earlier analyses (see above), helped resolve the disagreement surrounding the validity of *Amurotaenia*. The resulting tree (Fig. 3) supports Akhmerov's (1960) original synonymy of the latter genus with *Nippotaenia.* Our results also support recognition of *N. mogurndae* and *N. perccotti* as distinct species. In fact, we believe that almost all reports of *N. mogurndae* in Europe are misidentifications of *N. perccotti.* Thus, the order currently includes a total of six valid species and the single genus *Nippotaenia.*

MORPHOLOGY. Since 2008, although not formally part of PBI efforts, Korneva et al. (2014) and Korneva and Pronin (2015) studied the ultrastructure of the eggs and copulatory apparatus of *N. perccotti* (misidentified as *N. mogurndae*). Bruňanská et al. (2015) examined the ultrastructure of sperm and spermiogenesis in specimens of *N. perccotti*, albeit also erroneously identified as *N. mogurndae*. Specimens studied by Bruňanská et al. (2015) and Bombarová et al. (2009) and used to describe the composition of telomeres in chromosomes of *N. perccotti* by fluorescence *in situ* hybridization (FISH) with different telomeric repeat probes were collected in Slovakia by team member M. Oros as part of the PBI project.

HOST ASSOCIATIONS. No new host records for nippotaeniideans were discovered over the course of the PBI project. The order remains known only from freshwater fishes of the suborder Gobioidei (Perciformes), namely families Eleotridae, Gobiidae, and Odontobutidae, and Osmeroidei (Osmeriformes), namely families Retropinnidae and Galaxiidae. Reshetnikov et al. (2011) provided experimental evidence that larger individuals of Chinese sleepers can become infected with *N. mogurndae* (in fact, *N. perccotti*) through cannibalism.

GEOGRAPHIC DISTRIBUTION. The invasive *N. perccotti* (usually reported as *N. mogurndae*), a parasite of the Chinese sleeper, has been found recently in Slovakia, Poland, and the Ukraine (Oros and Hanzelová, 2009; Mierzejewska et al., 2010, 2012; Reshetnikov et al., 2011; Kvach et al., 2013) thereby expanding its range. The distribution of non-invasive nippotaeniideans has not been expanded since 2008.

PHYLOGENETIC RELATIONSHIPS. The close affinities between the Nippotaeniidea, the Tetrabothriidea, the Mesocestoididae, and the Cyclophyllidea are undisputable. The most recent molecular phylogenetic inferences of Waeschenbach et al. (2012) support the hypothesis that nippotaeniideans are the sister group to the Cyclophyllidea + Tetrabothriidea + Mesocestoididae. These affinities were also supported by the results of Bruňanská et al. (2015), who showed that spermiogenesis and spermatozoon ultrastructure of a nippotaeniidean closely resembles those of the mesocestoidids. The results of Caira et al. (2014) also support close affinities among the mesocestoidids, tetrabothriideans, and cyclophyllideans. However, they found support for a sister group relationship between the three species of nippotaeniideans and the Cyclophyllidea. Nevertheless, it should be noted that their study included only two species of the latter, highly speciose order.

New sequence data for two previously sequenced species, *N. chaenogobii* and *N. mogurndae* from Japan, as well as for *N. perccotti* (syn. *A. perccotti*) from Ukraine, for the fist time, were generated during the PBI project (present study). Sequence data are thus now available for four of the six known species of the order (Fig. 3). Phylogenetic analyses of sequence data for the 28S rDNA and 18S rDNA genes for these four species revealed the paraphyly of *Amurotaenia*. This confirms that the latter name should be suppressed as a junior synonym of *Nippotaenia* as proposed more than 50 years ago by Akhmerov (1960). *Nippotaenia perccotti* (Akhmerov, 1941) Akhmerov, 1960 is thus restored as a valid name. *Amurotaenia decidua* is hereby transferred to *Nippotaenia* establishing the new combination *Nippotaenia decidua* (Hine, 1977) n. comb. As a result, the order now comprises one monotypic family with only one genus composed of six valid species. Results from our preliminary phylogenetic analyses suggest that *N. decidua* is the sister taxon of the other three members of the order for which sequence data are available (Fig. 3).

CONCLUSIONS

With only six valid species, the Nippotaeniidea tie the Spathebothriidea in ranking as the second least speciose of the cestode orders; they are surpassed only by the Haplobothriidea, with two valid species. Molecular data generated over the course of the PBI project confirm that it is appropriate to consider the order to include the single genus *Nippotaenia*. To date, four of the six species have been included in molecular analyses; *N. contorta* and *N. fragilis* remain to be included in such analyses. The invasive *N. perccotti* (syn. *A. perccotti*) has been misidentified as *N. mogurndae* by almost all authors who published records from the Chinese sleeper recently introduced to Europe; validity of both species of *Nippotaenia* is confirmed by molecular data. Nippotaeniideans have been found only in freshwater fishes of three families of the suborder Gobioidei (Perciformes) and two families of the Osmeroidei (Osmeriformes).

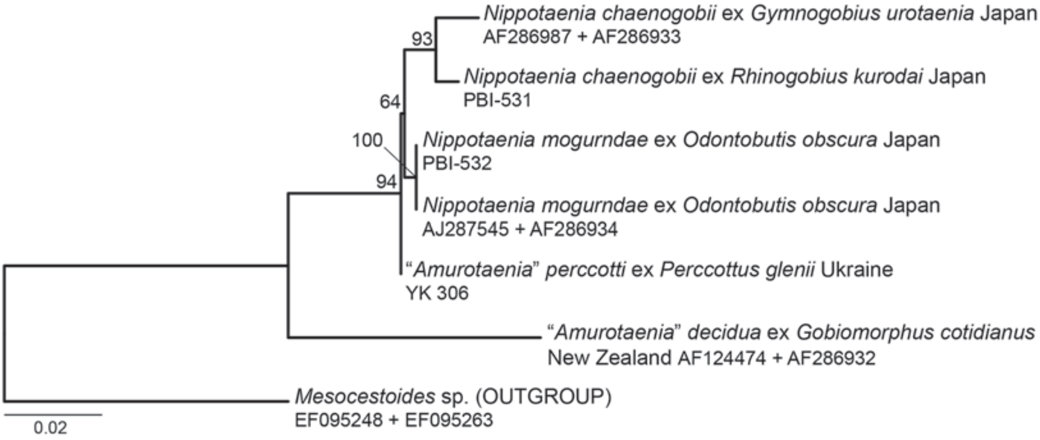

FIGURE 3. Phylogenetic tree resulting from a maximum likelihood analysis of concatenated 18S + 28S rDNA nucleotide sequence dataset. Genes were analyzed as separate partitions under the TIM+I and TrN+G models of nucleotide evolution, respectively. Nodal support is indicated by bootstrap proportions based on 100 resamples. Branch length scale bar indicates the number of substitutions per site.

The geographic distribution of the order is conspicuously disjunct, with one half of the species occurring in the eastern-most part of the Palaearctic region and the remaining three species being endemic to New Zealand. It is thus difficult to predict where, and in which fish hosts, new nippotaeniidean species might be found in the future.

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TABLE 1. List of valid nippotaeniidean taxa with type hosts. New taxonomic actions resulting from PBI project activities indicated in bold.

VALID TAXA

FAMILY NIPPOTAENIIDAE YAMAGUTI, 1939
- *Nippotaenia* Yamaguti, 1939 (syn. *Amurotaenia* Akhmerov, 1941)
  - *Nippotaenia chaenogobii* Yamaguti, 1939 (type) ex *Gymnogobius urotaenia*
  - *Nippotaenia contorta* Hine, 1977 ex *Retropinna retropinna*
  - *Nippotaenia decidua* (Hine, 1977) **Scholz, Brabec & Kuchta n. comb.** ex *Gobiomorphus cotidianus*
  - *Nippotaenia fragilis* Hine, 1977 ex *Retropinna retropinna*
  - *Nippotaenia mogurndae* Yamaguti & Miyata, 1940 ex *Odontobutis obscura*
  - *Nippotaenia perccotti* (Akhmerov, 1941) Akhmerov, 1960 ex *Perccottus glenii*

14

Onchoproteocephalidea I

Caira, Jensen, Waeschenbach, Olson & Littlewood, 2014

By

Alain de Chambrier, Tomáš Scholz[1], Jean Mariaux, and Roman Kuchta

The treatment of the Onchoproteocephalidea presented here differs from those of the 18 other cestode orders addressed in this Special Publication in that the members of this order are covered in two separate chapters. This, the first of these two chapters, focuses on groups that primarily parasitize freshwater fishes, snakes, and lizards. Although historically considered to compose the order Proteocephalidea, the integrated nature of the affinities of these tapeworms with a suite of hooked cestodes parasitizing stingrays and some sharks, all previously assigned to the tetraphyllidean family Onchobothriidae, is highly supported by molecular data (Olson and Caira, 1999; Kodedová et al., 2000; Olson et al., 2001; Caira et al., 2005; Waeschenbach et al., 2007, 2012; Healy et al., 2009). In 2014, Caira and co-authors formally established the new order Onchoproteocephalidea to house these taxa in a single monophyletic group. Although the taxa formally assigned to the Proteocephalidea (treated in the present chapter) constitute a monophyletic group, those parasitizing elasmobranchs (see Chapter 15 this volume as Onchoproteocephalidea II, Caira et al., 2017) do not. Instead, as discussed further in Chapter 15, the hook-bearing taxa appear to represent a series of independent early diverging lineages relative to a crown group composed of the Onchoproteocephalidea I.

Nonetheless, treating the two "groups" separately greatly facilitates discussion of their biology, geographic distribution, host associations, and predictions of diversity. As a consequence, the taxa formerly assigned to the Proteocephalidea are treated here under that name, while recognizing that in order to maintain the monophyly of higher cestode taxa, at the ordinal level, they should be considered members of the Onchoproteocephalidea.

PROTEOCEPHALIDEA AS THEY WERE KNOWN PRIOR TO THE PBI PROJECT

Diversity and Classification. The Proteocephalidea were established by Mola (1928). Until fairly recently, the order was accepted by most researchers. In terms of its diversity, Freze (1965) provided an extensive overview of proteocephalideans; he listed 180 species (and another 28 *species inquirendae*) in 38 genera (plus 2 *genera inquirendae*). More recently, Schmidt (1986) provided a list of all taxa in the group (259 species in 29 genera) and their hosts. However, his comprehensive account was expanded by intensive work in the Neotropical realm beginning in the mid-1980s by A. A. Rego, G. C. Pavanelli, A. de Chambrier, D. R. Brooks, R. M. Takemoto, A. A. Gil de Pertierra, N. J. Arredondo, and others, as well as by the

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[1] Corresponding author (tscholz@paru.cas.cz)

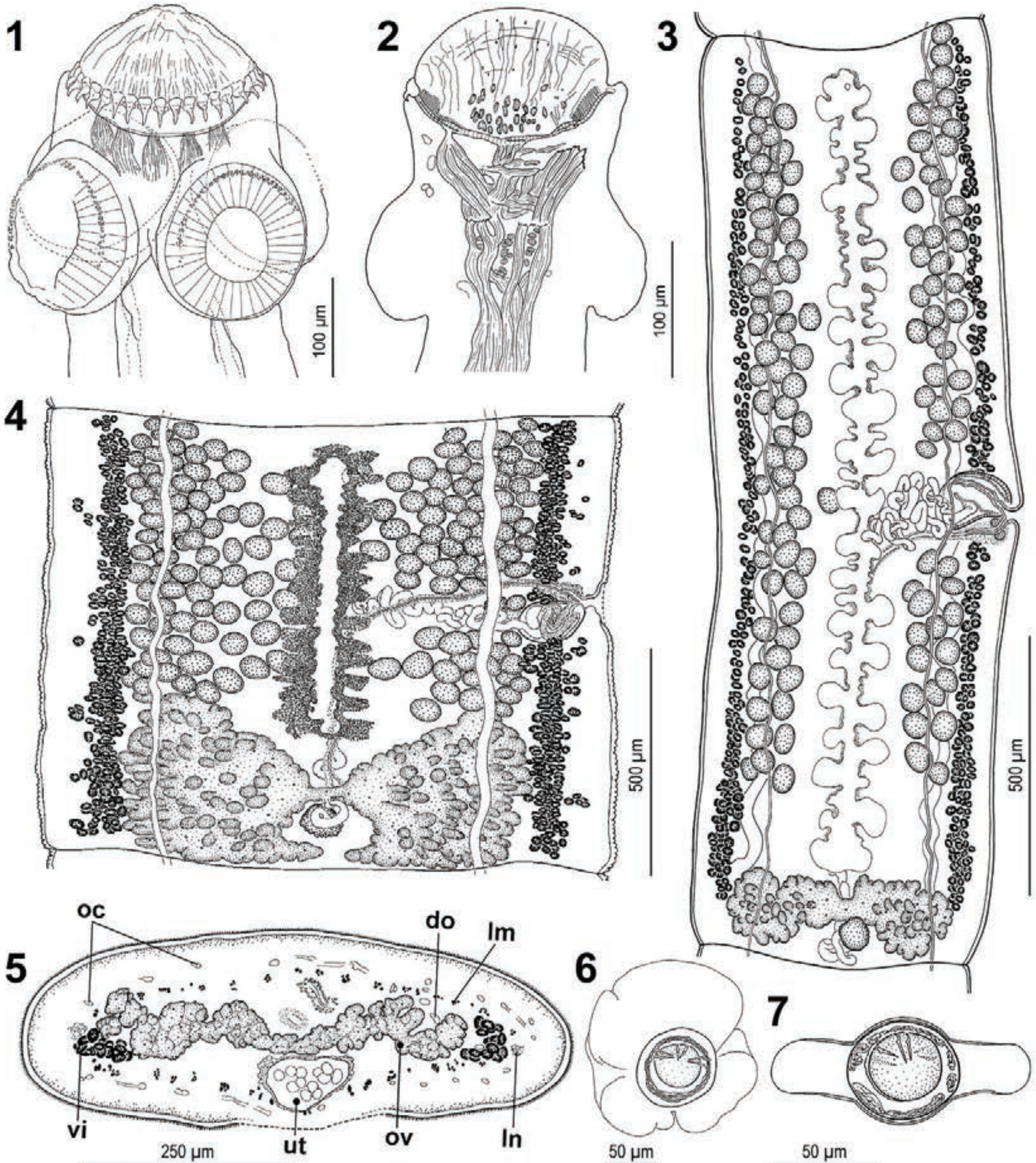
de Chambrier, A., T. Scholz, J. Mariaux, and R. Kuchta. 2017. Onchoproteocephalidea I Caira, Jensen, Waeschenbach, Olson & Littlewood, 2014. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 251–277.

work of Scholz and Hanzelová (1998) in the Palaearctic realm, which focused on *Proteocephalus* Weinland, 1858, the most diverse genus in the group.

The subfamily- and family-level classifications of the Proteocephalidea were initially established in a series of papers by Woodland (e.g., 1925, 1933, 1934a, b, 1935), based largely on the position of the testes, uterus, and vitelline follicles in relation to the inner longitudinal musculature (similar to the criteria used for the familial classification of the Caryophyllidea—see Mackiewicz, 1994 and Chapter 4 this volume, Scholz and Oros, 2017). Woodland's classification scheme was accepted by many subsequent authors (Yamaguti, 1959; Freze, 1965; Schmidt, 1986; Rego, 1994). In general, the group was divided into two families, the Proteocephalidae La Rue, 1911 and the Monticelliidae La Rue, 1911, each with several subfamilies (see Rego, 1994). Rego (1995), however, subsequently questioned the validity of this classification and did not recognize the Monticelliidae (and several subfamilies). Rego's (1995) revised classification was generally accepted as a well justified system and thus, prior to the PBI, the group consisted of the single family, Proteocephalidae, with the subfamilies Acanthotaeniinae Freze, 1963, Corallobothriinae Freze, 1965, Ephedrocephalinae Mola, 1929, Gangesiinae Mola, 1929, Marsypocephalinae Woodland, 1933, Monticelliinae Mola, 1929, Nupeliinae Pavanelli & Rego, 1991, Peltidocotylinae Woodland, 1934, Proteocephalinae Mola, 1929, Rudolphiellinae Woodland, 1935, Sandonellinae Khalil, 1960, and Zygobothriinae Woodland, 1933 (see Rego et al., 1999).

MORPHOLOGY. Proteocephalideans generally possess a scolex bearing four spherical or elongate, uniloculate suckers (or acetabula; Figs. 1, 8–13, 15, 16); although some taxa have bi- or triloculate suckers (Fig. 14; see also Rego, 1999). The apical region of the scolex may bear a rostellum-like muscular organ with hooks (Figs. 1, 9, 10), a functional or vestigial apical sucker (Fig. 8), or merely a concentration of gland cells. The strobila bears numerous, usually anapolytic, acraspedote proglottids, each with two pairs of excretory canals (narrower dorsal and wider ventral canals), a single set of reproductive organs including numerous testes, and a bilobed ovary situated near the posterior margin of the proglottid. The vitellarium usually forms two bands of follicles positioned lateral to the testicular fields. The cirrus and vagina open into a common genital atrium at the lateral margins of the proglottid (Figs. 3, 4). The uterus forms lateral diverticula; uterine pores may be present on the ventral side of proglottids. The inner longitudinal musculature is well developed in most species (Freze, 1965; Rego, 1994). Eggs are usually spherical, with a hyaline envelope that swells when released into water, thus serving as a flotation membrane; the embryophore is largely spherical and bi- or trilayered (Figs. 6, 7).

The morphology of proteocephalidean cestodes was relatively well understood prior to the PBI project. The first monograph dealing with the order as a whole was published by La Rue (1914), followed by a series of papers by Woodland (e.g., 1925, 1933, 1934a, b, 1935), in which he provided extensive data on the morphology of proteocephalideans from the Neotropical and Afrotropic realms. Freze (1965) expanded existing knowledge of proteocephalidean morphology. More recently, A. de Chambrier and co-authors (de Chambrier and Vaucher, 1999; de Chambrier et al., 2004a; de Chambrier and Scholz, 2008) identified new morphological characters suitable for distinguishing among taxa, primarily found in the Neotropics. Most importantly, de Chambrier et al. (2004a) discovered that uterine development in all proteocephalideans was of two basic types, each of which corresponds to one of the two main lineages of proteocephalideans revealed by their molecular phylogenetic analyses (see de Chambrier et al., 2004a; figs. 1, 2).

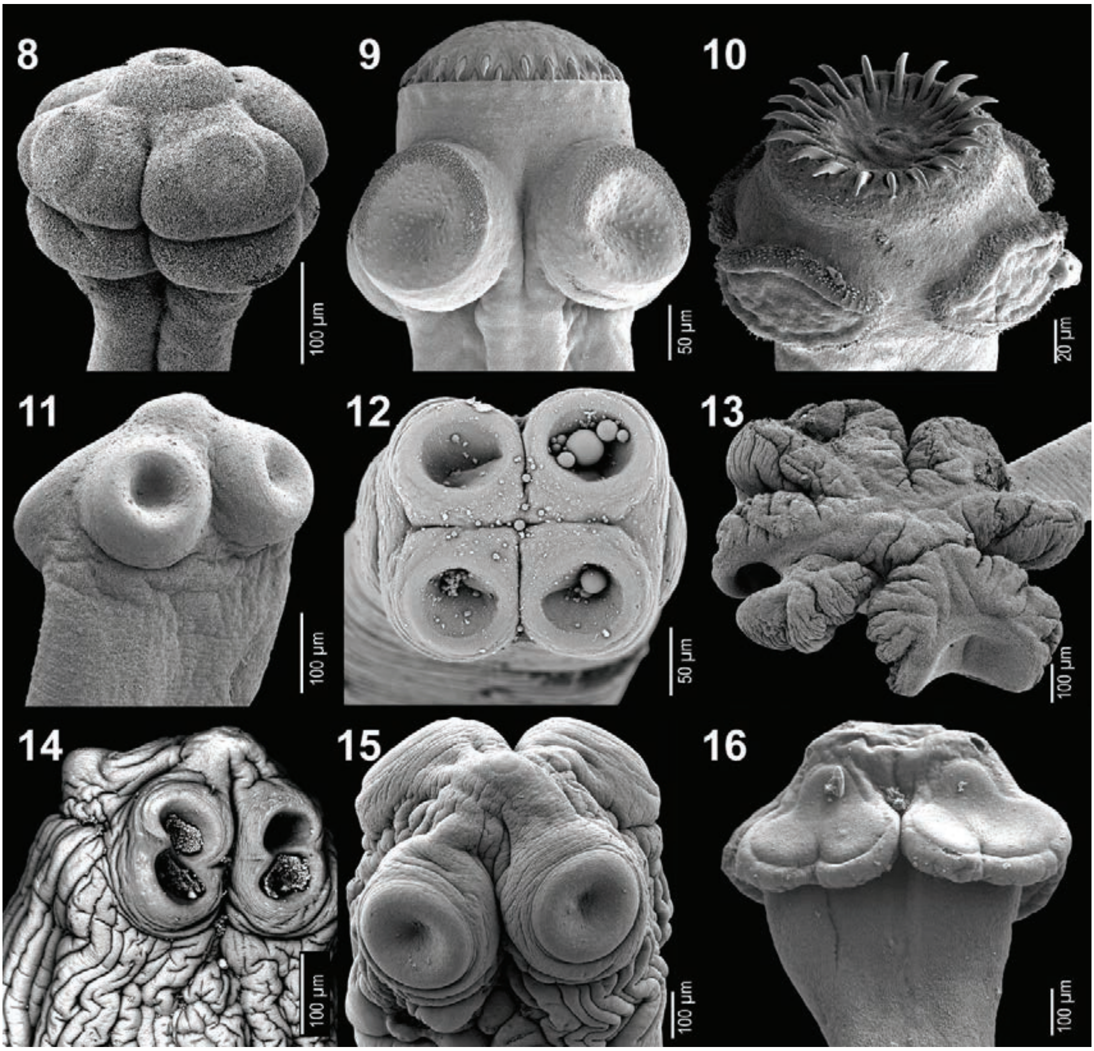


FIGURES 1–7. Line drawings of proteocephalidean cestodes. **(1, 2)** *Gangesia agraensis*, scolex in frontal view (1) and in frontal section (2) (modified from Ash et al. [2012]). **(3)** *Ophiotaenia georgievi*, gravid proglottid (modified from de Chambrier et al. [2010]). **(4)** *Ritacestus ritaii*, mature proglottid (modified from de Chambrier et al. [2011a]). **(5)** *Cairaella henrii*, cross-section at level of ovary; note numerous osmoregulatory canals in cortex (modified from Coquille and de Chambrier [2008]). **(6)** *Ritacestus ritaii*, egg (modified from de Chambrier et al. [2011a]). **(7)** *Proteocephalus synodontis*, egg (modified from de Chambrier et al. [2011b]). *Abbreviations*: do, dorsal osmoregulatory canal; lm, longitudinal musculature; ln, longitudinal nerve; oc, additional osmoregulatory canal; ov, ovary; ut, uterus; vi, vitelline follicles.

HOST ASSOCIATIONS. Proteocephalideans are intestinal parasites primarily infecting freshwater teleosts, with catfishes (Siluriformes) representing the most important host group. However, among freshwater teleosts, they also occur in a broad spectrum of other orders (e.g., members of the Anguilliformes, Characiformes, Cypriniformes, Gasterosteiformes, Gymnotiformes, Lepisosteiformes, Osteoglossiformes, Perciformes, Polypteriformes, Salmoniformes, and Synbranchiformes) (Freze, 1965; Schmidt, 1986; Scholz and Hanzelová, 1998; de Chambrier and Vaucher, 1999; Rego et al., 1999). In addition, a number of species have been reported from amphibians, and lizards and snakes. These include the Anura (e.g., Bufonidae Gray, Ceratophryidae Tschudi, Hylidae Rafinesque, and Ranidae Rafinesque), Caudata (e.g., Amphiumidae Gray and Salamandridae Goldfuss), and Lepidosaura (e.g., Agamidae Fitzinger, Iguanidae Oppel, Pygopodidae Boulenger, Scincidae Gray, Teiidae Gray, and Varanidae Merrem) and Serpentes (e.g., Boidae Gray, Colubridae Oppel, Elapidae Boie, and Viperidae Oppel) (Freze, 1965; Schmidt, 1986; de Chambrier and Vaucher, 1997, 1999; Marsella and de Chambrier, 2008; de Chambrier et al., 2012). One species, *Thaumasioscolex didelphidis* Cañeda-Guzmán, de Chambrier & Scholz, 2001, parasitizes marsupials (Cañeda-Guzmán et al., 2001).

GEOGRAPHIC DISTRIBUTION. Proteocephalideans have a worldwide distribution in freshwater and terrestrial habitats with the exception of Antarctica (Freze, 1965; Rego, 1994). However, a subset of hosts of three proteocephalidean species are known to enter brackish water (e.g., *Proteocephalus gobiorum* Dogiel & Bychowsky, 1939 in gobies [Gobiidae Cuvier] in the Palaearctic realm; *P. chamelensis* Pérez-Ponce de León, Brooks & Berman, 1995 in Pacific sleepers, *Gobiomorus maculatus* [Günther] [Eleotridae Bonaparte] in Mexico; and *Nomimoscolex arandasregoi* Fortes, 1981 [*species inquirenda*] in the ariid catfishes *Cathorops agassizii* [Eigenmann & Eigenmann], *Genidens barbus* [Lacepède], and *Genidens genidens* [Cuvier] in Brazil) (Dogiel and Bychowsky, 1939; Fortes, 1981; Pérez-Ponce de León et al., 1995), but no species are known exclusively from marine environments. The highest species diversity has been documented in the Neotropical realm, whereas proteocephalidean fauna in Southeast Asia is much less diverse, particularly in teleost hosts. Although no proteocephalideans have been reported from freshwater fishes of Australia, they are known from snakes, lizards, and frogs on that continent (e.g., Johnston, 1909, 1911, 1912, 1913, 1914, 1916).

PHYLOGENETIC RELATIONSHIPS. The relationships of proteocephalideans with other cestode orders were first informally assessed by Lönnberg (1897). However, the first phylogenetic analyses of their interrelationships were carried out by Brooks (1978, 1995), and Brooks and McLennan (1993). Rego et al. (1998) used cladistic analysis based on comparative morphology to examine the subfamily-level relationships within the group. Their analyses yielded a single most parsimonious tree with two subclades corresponding to the two families. Two subfamilies, the Acanthotaeniinae (historically in the Proteocephalidae) and Nupeliinae (historically in the Monticelliidae), grouped, however, as early diverging linages away from the other members of their families, indicating that neither family as currently conceived is monophyletic (Rego et al., 1998). Thus, contrary to Rego's (1995) recognition of only a single family in the order, Brooks and McLennan (1993) retained the concept of two families. They found unambiguous support for the Proteocephalidae, including the Corallobothriinae, Proteocephalinae, Gangesiinae, and Sandonellinae. They also found strong support for the Monticelliidae, and subclades corresponding to the subfamilies Marsypocephalinae, Zygobothriinae, Monticelliinae, Rudolphiellinae, Ephedrocephalinae, and Othinoscolecinae Woodland, 1933. Zoogeographic analysis demonstrated a strong Gondwanan association, indicating that proteocephalideans originated in Africa, and subsequently moved to South



FIGURES 8–16. Scanning electron micrographs of scoleces of proteocephalidean cestodes. **(8)** *Ritacestus ritaii*, frontal view (modified from de Chambrier et al. [2011a]). **(9)** *Gangesia bengalensis*, frontal view (modified from Ash et al. [2012]). **(10)** *Vermaia pseudotropii*, subapical view (modified from Ash et al. [2010]). **(11)** *Glanitaenia osculata*, frontal view. **(12)** *Ophiotaenia georgievi*, apical view (modified from de Chambrier et al. [2010]). **(13)** *Macrobothriotaenia ficta*, subapical view (modified from Scholz et al. [2013]). **(14)** *Peltidocotyle rugosa*, frontal view. **(15)** *Frezella vaucheri*, subapical view (modified from Alves et al. [2015]). **(16)** *Brayela karuatai*, frontal view (modified from de Chambrier et al. [2014]).

America (Rego et al., 1998). Colonization of the Northern Hemisphere by the proteocephalid subfamilies Proteocephalinae, Corallobothriinae, and Gangesiinae was apparently secondary (Rego et al., 1998). Analysis of parasite-host relationships failed to unambiguously resolve the earliest group of vertebrates likely to have hosted proteocephalideans overall. Independent colonization events of lizards and snakes by species of the Proteocephalinae and Acanthotaeniinae, and of amphibians by yet other Proteocephalinae taxa were also postulated (Rego et al., 1998).

The first study to use molecular sequence data to explore the phylogenetic interrelationships of proteocephalidean cestodes was that of Zehnder and Mariaux (1999), who generated partial mitochondrial 16S rDNA and partial nuclear 28S rDNA sequence data for 53 species of proteocephalideans. Their results failed to support the monophyly of the two families, most subfamilies, and most genera then recognized. The work of de Chambrier et al. (2004a) was based on partial 28S rDNA sequence data for 67 species in 30 genera. Their results were similar to those of Zehnder and Mariaux (1999) in terms of the lack of support they found for the monophyly of the families Proteocephalidae and Monticelliidae, and also for all but three subfamilies (Acantotaeniinae, Gangesiinae, and Peltidocotylinae) and most genera. Hypša et al. (2005) expanded the repertoire of genes for which sequence data were available for proteocephalideans to include partial 18S rDNA and ITS2 data, and also included data on the secondary structure of ITS2. Their results were generally consistent with those of earlier molecular work. However, better resolution was achieved in some clades such as the Neotropical clade specific to the pimelodid catfish *Phractocephalus hemioliopterus* (Bloch & Schneider). Other phylogenetic work conducted up to 2008 concentrated on relationships within specific genera or species groups (Zehnder and de Chambrier, 2000; Zehnder et al., 2000; Scholz et al., 2007).

The most serious impediment to additional phylogenetic studies on proteocephalideans pre-2008 was the lack of material of representative taxa preserved for molecular work. This was especially the case for species of monotypic genera and essentially all taxa from Africa and the Indomalayan realm.

CURRENT STATUS OF THE ONCHOPROTEOCEPHALIDEA I

DIVERSITY AND CLASSIFICATION. Taxonomic efforts over the course of the PBI project resulted in the description of 27 new species in 17 genera of proteocephalideans, 20 of which were described as part of the PBI project. In addition, 13 new genera (9 as part of the PBI project) from five biogeographic realms, as well as one new subfamily (the Testudotaeniinae de Chambrier, Coquille, Mariaux & Tkach, 2009) were erected (see Table 1). Moreover, expeditions funded by the PBI project yielded material of approximately 30 additional new species and three to five new genera that have yet to be fully characterized using morphological and molecular methods and formally described.

In addition to the aforementioned results, since 2008, 18 new combinations and as many as 48 nominal species were synonymized with other taxa, largely from the Indomalayan realm (i.e., 44 invalid species of *Gangesia* and *Silurotaenia*) (Table 1). Also since 2008, a replacement name, *Proteocephalus chandrae* de Chambrier & Gil de Pertierra, 2012, was proposed for *Proteocephalus bufonis* Chandra & Gupta, 2007 (preoccupied by *P. bufonis* Vigueras, 1942) by de Chambrier and Gil de Pertierra (2012) who also transferred the species to *Ophiotaenia* as *Ophiotaenia chandrae* (de Chambrier & Gil de Pertierra, 2012) de Chambrier & Gil de Pertierra, 2012 in that same publication. Taxonomic studies also resulted in emendation of the diagnoses of seven proteocephalidean genera, most from the Indomalayan and Neotropical realms. As many as 25 species in 11 genera, from all over the world, were redescribed based on the examination of type material (if available) and newly collected specimens, often also informed by molecular sequence data. A key to the subfamilies of the Proteocephalidae, the only family now recognized in the group, was provided by de Chambrier et al. (2009a). Ash et al. (2012) provided a key to the genera of the Gangesiinae.

Despite the substantial progress achieved since 2008 (see Table 1), our current knowledge of proteocephalidean diversity is far from complete, even beyond the high number of taxa awaiting description. We believe it is reasonable to assume that the number of undescribed species, especially of *Ophiotaenia* La Rue, 1911 from lizards and snakes throughout the world, as well as from siluriform catfishes in the Neotropical realm, remains high. However, it is interesting to note that a number of the new species discovered over the course of the PBI project were found in relatively well-known regions, such as the Palaearctic (new species of *Proteocephalus* in loaches in Far East Russia and gobies along the Black Sea coast) and the USA (4 new species of 2 new genera in gars, bowfin, and the flathead catfish *Pylodictis olivaris* [Rafinesque]) (Scholz et al., 2017; unpubl. data).

Synonymization of tens of species of *Gangesia* and *Silurotaenia*, especially from silurid catfishes (e.g., *Wallago attu* [Bloch & Schneider]) in the Indomalayan realm, was necessary because most of the previous taxonomic studies from that region were scientifically unsound and many violated the rules of the International Code of Zoological Nomenclature (see Ash et al., 2012). Substantial effort was also made to revise and emend generic membership and diagnoses. As a result of these efforts and previous work, updated generic diagnosis are now available for 54 of the 67 genera that parasitize teleosts and herptiles, as well as the one genus that parasitizes mammals. The proteocephalideans (i.e., the Onchoproteocephalidea I) are currently considered to include a total of 316 valid species in 68 genera (Table 1).

Beyond the establishment of the Testudotaeniinae by de Chambrier et al. (2009a), the higher-level classification of the group has not been substantially reconfigured since 2008, even though it is evident from previous (Zehnder and Mariaux, 1999; de Chambrier et al., 2004a; Hypša et al., 2005) and recent (de Chambrier et al., 2015a; see below and Fig. 17) molecular phylogenetic studies that most of the 14 subfamilies (Table 1) and species-rich genera such *Proteocephalus*, *Ophiotaenia*, and *Nomimoscolex* Woodland, 1934 are not monophyletic assemblages. The reconfiguration of these taxa, however, must await more detailed molecular phylogenetic and morphological analyses. At present, the most serious obstacle to the establishment of revised generic and subfamilial classifications is the identification of morphological features to characterize molecularly distinct lineages. For the purpose of facilitating such future work, the valid taxon list in Table 1 indicates the current subfamily assignments of the 67 valid genera.

MORPHOLOGY. Little novelty in proteocephalidean morphology was discovered over the course of the project. Some erroneous information presented in the literature was corrected, such as the report by Rego (1984) of as many as eight suckers on the scolex of *Brayela karuatayi* (Woodland, 1934) Rego, 1984 (see de Chambrier et al., 2014). More attention was paid to details of scolex morphology observed using scanning electron microscopy of hot formalin-fixed (i.e., non-deformed, relaxed) specimens (e.g., Ash et al., 2012) as well as to the morphology of strobilar features such as excretory canals (Fig. 5), extent and distribution of the inner longitudinal musculature, extent of the lateral bands of vitelline follicles, type of the uterus (e.g., de Chambrier et al., 2014, 2015a; Alves et al., 2015), and details of features of the eggs, such as the presence of a three-layered embryophore in some species (e.g., Scholz et al., 2013).

In taxonomic studies, additional attention was paid also to anatomical features of the scolex. These include features visible in longitudinal section (e.g., presence of gland cells, networks of excretory canals, retractor muscles, structure of apical organs [Fig. 2], etc.; see Scholz et al., 2009; Ash et al., 2010, 2012, 2015; de Chambrier et al., 2011a, b), as well as size and distribution of individual microthrix forms, especially in Neotropical taxa (e.g., de Chambrier et al., 2011a, b; Arredondo et al., 2013).

A new morphometric feature of potential phylogenetic utility (i.e., the ratio of ovarian size in relation to that of the entire proglottid) was identified (see Ammann and de Chambrier,

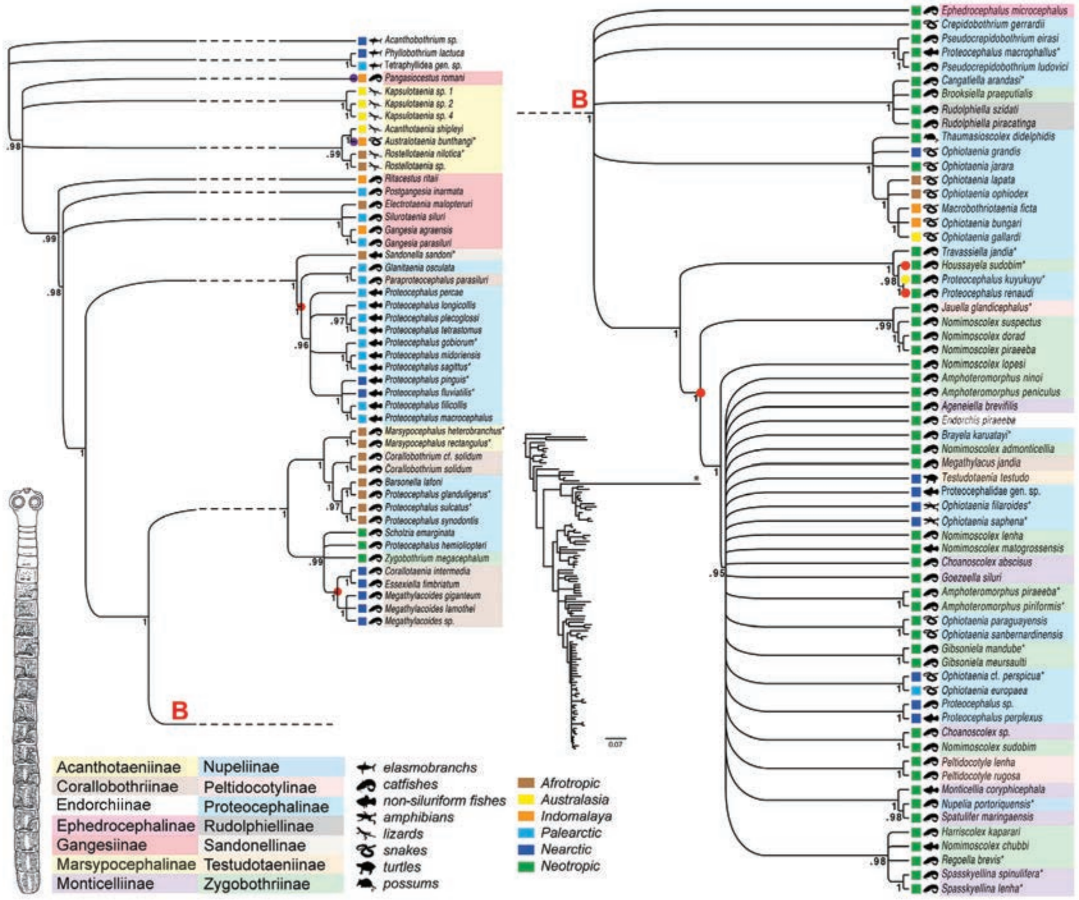


FIGURE 17. Phylogenetic tree of proteocephalidean interrelationships resulting from Bayesian analysis of partial 28S rDNA (in 2 parts); modified from de Chambrier et al. (2015a). Red circles refer to presence of "Type 2" uterine development; purple circles refer to presence of "intermediate type" uterine development; yellow circle indicates taxon for which uterine development unknown. A reduced-size phylogram of the same tree is presented between the two main trees illustrating the long branch leading to *Sandonella sandoni* marked with an asterisk.

2008; de Chambrier et al., 2012). Comparison of measurements of all of the species of *Ophiotaenia* and *Proteocephalus* (161 species) has shown that the ovary of species parasitic in snakes in the Americas, Africa, Asia, and Australia is not only considerably smaller than that of congeneric species from European hosts, but it is also smaller than that in all species of *Proteocephalus* parasitic in teleost fishes throughout the world (de Chambrier et al., 2012).

HOST ASSOCIATIONS. The period of the PBI project was characterized by increased sampling efforts focused on most major groups of potential definitive hosts, with 196 species (i.e., 61% of proteocephalideas) reported from teleosts. Collecting trips were conducted with a focus on: (i) recollection of known but insufficiently described species for which material appropriately fixed for generation of molecular sequence data was lacking (e.g., from the Nile River basin in the Sudan, Egypt, and Ethiopia; from Bangladesh, India, and Far East Russia; and from the southern USA); (ii) new collections from regions with known, but incompletely characterized, proteocephalidean faunas (e.g., Brazil and Peru); (iii) new collections from regions with only sporadic proteocephalidean records (e.g., Cambodia, Thailand, Vietnam, the Democratic Republic of the Congo, Gabon, and Madagascar) (see Table 2 in Chapter 3 on the Bothriocephalidea this volume, Kuchta and Scholz, 2017).

Numerous new host records were found, especially from South America (Brazil and Peru (e.g., Alves et al., 2015, 2017a; de Chambrier et al., 2015b). Particularly intensive sampling in Peruvian Amazonia (897 fish of 130 species) and Brazil (5 localities in the Amazon and Paraná River basins sampled in 2013 and 2014; 242 fish of 57 species; see Table 2 in Chapter 3 on the Bothriocephalidea this volume, Kuchta and Scholz, 2017), resulted in the collection of taxonomically comprehensive material from many previously unexamined host species, such as *Cichla kelberi* Kullander & Ferreira, *C. melaniae* Kullander & Ferreira, *C. temensis* Humboldt (Perciformes: Cichlidae Bonaparte), *Megalodoras uranoscopus* (Eigenmann & Eigenmann) (Siluriformes: Doradidae Bleeker), and *Tocantinsia piresii* (Miranda Ribeiro) (Siluriformes: Auchenipteridae Bleeker). This new material paves the way for the critical assessment of parasite-host associations and the degree of host specificity of individual cestode species that occur in closely related teleost hosts in different river basins throughout South America. Of particular interest are species such as *Proteocephalus macrophallus* (Diesing, 1850) La Rue, 1914 and *P. microscopicus* Woodland, 1935 from species of *Cichla* Bloch & Schneider, as well as cestodes parasitizing teleost species that were originally thought to occur in both of the principal river basins in South America (i.e., the Amazon and Paraná rivers), but which have recently been recognized to represent pairs of species, one of which is endemic to each basin, such as *Zungaro zungaro* (Humboldt) (Amazon) and *Z. jahu* (Ihering) (Paraná) and *Pseudoplatystoma fasciatum* (Linnaeus) (Amazon) and *P. reticulatum* Eigenmann & Eigenmann (Paraná) (Froese and Pauly, 2016).

One of the most remarkable new host associations discovered over the course of the PBI project led to the erection of *Australotaenia* de Chambrier & de Chambrier, 2010 to accommodate two new species from frogs endemic to Australia by de Chambrier and de Chambrier (2010). However, a third species was subsequently found in a snake from Cambodia by de Chambrier et al. (2012). Another remarkable record was the discovery of a new genus, *Pangasiocestus* Scholz & de Chambrier, 2012, in Southeast Asia, established by Scholz and de Chambrier (2012) to house a new species discovered in the catfish *Pangasius larnaudii* Bocourt in Cambodia. This is the first species of proteocephalidean described from pangasiid catfishes. Also of note is the discovery of a new species parasitizing the cichlid *Cichlasoma amazonarum* Kullander in Peru (de Chambrier et al., 2017). This is only the second record of a cestode from the widely distributed and species-rich genus *Cichlasoma* Swainson. Although most of the teleost species examined that were found to harbor proteocephalideans were previously known as hosts, it was crucial to collect new material for redescriptions of these taxa and, in particular, for molecular phylogenetic studies given that available museum material was largely fixed in formalin and is thus unsuitable for molecular work.

The occurrence of proteocephalideans in lizards is extremely rare. However, two families of lizards, namely the Gekkonidae Gray and the Dactyloidae Fitzinger, were found to harbor proteocephalidean cestodes for the first time. These animals hosted two new proteocephalideans, namely the new genus *Cairaella* Coquille & de Chambrier, 2008 and its new species *Cairaella henrii* Coquille & de Chambrier, 2008 from *Norops trachyderma* (Cope) (Dactyloidae) and *Ophiotaenia nicoleae* Coquille & de Chambrier, 2008 from *Thecadactylus rapicauda* (Houttuyn) (Gekkonidae) (Coquille & de Chambrier, 2008). Previously, only three species, *Ophiotaenia striata* Johnston, 1914 from *Lialis burtonis* Gray, *O. amphiboluri* Nybelin, 1917 from *Pogona barbata* Cuvier, and *O. greeri* (Bursey, Goldberg & Kraus, 2006) de Chambrier, Coquille, Mariaux & Tkach, 2009 from *Sphenomorphus aignanus* (Boulenger), were known to occur in lizards.

By far the majority of new host species examined over the course of the PBI project were snakes. Particular emphasis was placed on snakes endemic to Madagascar after a high degree of endemicity of proteocephalideans provisionally assigned to the paraphyletic *Ophiotaenia* was detected following evaluation of museum material (de Chambrier et al., 2010; Rambeloson et al., 2012).

With respect to the degree of host specificity exhibited by proteocephalideans, results obtained during the PBI project confirm that no general pattern appears to exist across all proteocephalideans (Freze, 1965; Scholz and Hanzelová, 1998; de Chambrier et al., 2015b). In some host groups, especially amphibians, snakes, and lizards, and most Neotropical catfishes, host specificity is predominantly oioxenous or stenoxenous (*sensu* Euzet and Combes [1980]; Caira et al., 2003). In contrast, some of the proteocephalidean species parasitizing teleosts in the Holarctic and Afrotropic realms exhibit more relaxed (i.e., euryxenous *sensu* Caira et al. [2003]) host specificity (see, e.g., de Chambrier et al., 2011b). Caution should, however, be exercised in such cases because future taxonomic work using combined morphological and molecular methods may reveal that the reports of proteocephalidean species parasitizing several different species of hosts represent mixtures of species.

Work conducted over the course of the PBI project confirmed that proteocephalidean cestodes infrequently parasitize amphibians, snakes, and lizards (with prevalences usually lower than 5%; see Ammann and de Chambrier, 2008). In contrast, the prevalence of proteocephalidean infections in African and South American siluriform fishes is usually much higher (de Chambrier and Vaucher, 1999; de Chambrier et al., 2006, 2015b). For example, *Scholzia emarginata* (Diesing, 1850) de Chambrier, Rego & Gil de Pertierra, 2005 was found in all ten specimens of *Phractocephalus hemioliopterus* (Bloch & Schneider) examined from the Peruvian Amazon; similarly *Spasskyellina lenha* (Woodland, 1933) Freze, 1965 and *Lenhataenia megacephala* (Woodland, 1934) de Chambrier & Scholz, 2008 were found in the 22 specimens of *Sorubimichthys planiceps* (Spix & Agassiz) examined in Peru with prevalences of 59% and 50%, respectively (de Chambrier and Scholz, 2008). Most other proteocephalidean species were found in ten to 25% of fish specimens examined (de Chambrier et al., 2015b).

Across all potential host specimens examined over the course of the PBI project, the intensity of infection varied considerably, but it was generally low in all host groups, only rarely exceeding ten worms per host, regardless of proteocephalidean species. The glaring exception was a specimen of *Phractocephalus hemioliopterus* (total length [TL] of 108 cm) from the Amazon River in Brazil. This individual catfish harbored a total of 12,228 proteocephalidean cestodes representing seven species; 10,641 of these specimens were of *Pseudocrepidobothrium eirasi*—one of the smallest species of proteocephalideans at only 2–8.5 mm TL (Ruedi and de Chambrier, 2012).

GEOGRAPHIC DISTRIBUTION. Over the course of the PBI project, proteocephalideans were collected from a number of new localities, especially in Africa (probably the first data on fish cestodes from the Central African Republic, the lower Congo River in the Democratic Republic of the Congo, and Gabon) and Asia (Cambodia) (see table 2 in Chapter 3 on the Bothriocephalidea this volume, Kuchta and Scholz, 2017). Expeditions to Brazil in 2013 and 2014 (Xingú River in Altamira, a tributary of the Amazon River; Miranda River in Pantanal, i.e., Paraná River basin; Araguarí River near Macapá; Araguaia River near Santa Isabel, a tributary of the Tocantins River) yielded samples from these additional, previously unstudied, localities.

Despite intensive sampling during three field trips to the region, no proteocephalideans were found in several dozens of catfishes examined in Thailand (Chao Phraya River basin) by the senior author (de Chambrier, unpubl. data). Similarly, the proteocephalidean fauna of siluriforms from the Mekong River basin in Cambodia and Vietnam was also found to be very poor. The only exceptions were the discovery of *Pangasiocestus romani* Scholz & de Chambrier, 2012 in *Pangasius larnaudii* Bocourt and the record of *Gangesia agraensis* Verma, 1928 in *Wallago attu* (Bloch & Schneider), both from Cambodia (Ash et al., 2012; Scholz and de Chambrier, 2012). Interestingly, the former species represents the earliest diverging taxon of all proteocephalideans (de Chambrier et al., 2015a). The absence or extremely rare occurrence of proteocephalideans in freshwater teleosts in Southeast Asia markedly contrasts with the extraordinarily rich fauna of proteocephalideans seen in freshwater teleosts, which include numerous species of siluriforms, in other regions, including the neighbouring India and Bangladesh, as well as the Russian Far East (Ash et al., 2012, 2015).

PHYLOGENETIC RELATIONSHIPS. Over the course of the PBI project, the phylogenetic relationships of several species groups and genera were assessed based on molecular sequence data, largely from a portion of the 28S rDNA gene (e.g., de Chambrier et al., 2008, 2009a; Scholz et al., 2011, 2013; Ash et al., 2012). The non-monophyly of the existing proteocephalidean classification, at multiple higher levels, was revealed by essentially all of these smaller studies and calls for the investigation of the phylogenetic relationships among proteocephalideans overall.

Two comprehensive investigations of proteocepalidean interrelationships based on molecular sequence data were conducted over the course of the PBI project. The first of these, which was based on 28S rDNA sequence data for 100 species representing 54 genera was completed (de Chambrier et al., 2015a). The second study, which takes a multigene approach and thus includes sequence data for both the nuclear genes 28S rDNA and 18S rDNA, and the mitochondrial genes 16S rDNA and COI, will be completed in due course. The 28S rDNA data used in both studies came from a representative set of proteocephalidean cestodes from all major geographic regions and host groups, and were generated at the Natural History Museum in Geneva, Switzerland. Sequencing for the multigene study, which, beyond the 28S rDNA data, also included data for the other three genes generated from 137 specimens representing most proteocephalidean genera, with representatives of multiple species in species-rich genera, was done by A. Waeschenbach at the Natural History Museum, London (laboratory of D. T. J. Littlewood). Most of the specimens from which the sequence data for both studies came were collected during expeditions completely or partly supported by the PBI project. Morphological vouchers are deposited in the Natural History Museum in Geneva, Switzerland (acronym MHNG INVE-PLAT).

The results of the analyses of de Chambrier et al. (2015a; see Fig. 17 herein) and unpublished data by A. Waeschenbach lead to the following observations:

(1) All seven subfamilies for which more than a single genus was included in the analyses by de Chambrier et al. (2015a) (i.e., Acanthotaeniinae, Corallobothriinae, Gangesiinae, Monticelliinae, Peltidocotylinae, Proteocephalinae, and Zygobothriinae) were recovered as non-monophyletic. This confirms that a full revision of the subfamilial classification of the group is needed.

(2) With the exception of one species of Gangesiinae, the Acanthotaeniinae, which include parasites of snakes and lizards throughout the world, are the earliest diverging lineage of proteocephalideans. They are followed by the Gangesiinae, comprising species parasitizing catfishes in Asia (southeastern Palaearctic and central Indomalayan regions). However, neither subfamily is monophyletic as currently configured.

(3) Most species-rich genera are not monophyletic and include assemblages of distantly related taxa with similar morphology, apparently as a result of convergent evolution. This calls into question the taxonomic value of some morphological features previously considered to be diagnostic for one or more groups (e.g., scolex morphology, distribution of the testes, etc.). For example, *Nomimoscolex* appears to represent seven separate lineages, *Ophiotaenia* represents ten distinct lineages, and *Proteocephalus* seven lineages.

(4) The *Proteocephalus* "aggregate," originally proposed to accommodate only European species of the genus by de Chambrier et al. (2004a; pg. 163), also includes *Proteocephalus fluviatilis* Bangham, 1925 and *Proteocephalus pinguis* La Rue, 1911 from North America. Both of these Nearctic species closely resemble their sister European taxa in scolex and strobilar morphology.

(5) The Nearctic species *Proteocephalus ambloplitis* (Leidy, 1887) Benedict, 1900, which is unique among North American fish proteocephalideans in having a three-host life-cycle, and *Proteocephalus perplexus* La Rue, 1911 from the bowfin, *Amia calva* are closely related to Neotropical proteocephalideans. This result is supported by the fact that both of these species differ substantially in scolex and strobilar morphology from their Nearctic congeners.

(6) All but one (i.e., *Sandonella sandoni* [Lynsdale, 1960] Khalil, 1960) of the proteocephalidean species that parasitize African freshwater fishes form a monophyletic group, even though they are currently assigned to four genera and three subfamilies (i.e., *Corallobothrium* Fritsch, 1886 in the Corallobothriinae; *Marsypocephalus* Wedl, 1861 in the Marsypocephalinae; and *Barsonella* de Chambrier, Scholz, Beletew & Mariaux, 2009 and "*Proteocephalus*" in the Proteocephalinae) (de Chambrier et al., 2009b). It is of note that *Sandonella sandoni* exhibits a unique morphology of the scolex and vitellarium relative to these other species (see de Chambrier et al., 2008).

(7) Species of *Ophiotaenia* from colubrid snakes represent two distinct clades. *Ophiotaenia europaea* Odening, 1963 from the Palaearctic clusters with *O. perspicua* La Rue, 1911 from the Nearctic; *O. paraguayensis* Rudin, 1917 clusters with *O. sanbernardensis* (Rudin, 1917) Harwood, 1933, both of which occur in the Neotropics.

(8) Neotropical taxa parasitizing siluriforms and cichlids do not form a monophyletic group. Instead they belong to several distantly related lineages, but their phylogenetic relationships remain largely unresolved. Nevertheless, the early diverging position of *Sciadocephalus megalodiscus* Diesing, 1850, along with a species of the recently erected *Cichlidocestus* de Chambrier, Pinacho-Pinacho, Hernández-Orts, & Scholz, 2017 (see de Chambrier et al., 2017) from cichlid fishes, and three species parasitizing the catfish *Phractocephalus hemioliopterus*, which group with Nearctic proteocephalideans from channel catfishes, placed in the Corallobothriinae (see Fig. 17), is unquestionable.

(9) There is support for the individual monophyly of a subset of the Neotropical genera (e.g., *Amphoteromorphus* Diesing, 1850, *Gibsoniela* Rego, 1984, *Peltidocotyle* Diesing, 1850, *Spatulifer* Woodland, 1934); many others are not monophyletic (e.g., *Choanoscolex* La Rue, 1911, *Mariauxiella* de Chambrier & Rego, 1995, *Monticellia* La Rue, 1911, *Nomimoscolex*, *Rudolphiella* Fuhrmann, 1916).

(10) Large species of *Ophiotaenia* from venomous snakes throughout the world (Africa, Australia, and South America) form a monophyletic group. That group also includes *Thaumasioscolex didelphidis*, the only proteocephalidean known to use a mammal (i.e., opossum in Mexico) as a definitive host.

Arguably the most revolutionary result of the molecular phylogenetic analyses conducted over the course of the PBI project (e.g., Waeschenbach et al., 2012; Caira et al., 2014) was confirmation of the close relationships between a subset of the hook-bearing onchobothriids from elasmobranchs and the taxa previously assigned to the Proteocephalidea. As noted at the beginning of this chapter, based on these affinities, Caira et al. (2014) proposed the new order Onchoproteocephalidea to include both members of the former order Proteocephalidea and members of the several genera of elasmobranch-hosted hooked genera of cestodes that clustered with the proteocephalidean lineage. Although Caira et al. (2014) identified a possible synapomorphy for this combined group as the presence of spinitriches throughout the length of the body of onchoproteocephalideans, this feature remains to be confirmed by detailed ultrastructural (SEM) study of microthrix patterns in more representatives of the order. Thus, even though the close affinities among these cestode taxa are unquestionable, the identification of additional morphological features to unite the group would be highly advantageous (e.g., see Arredondo et al., 2014).

CONCLUSIONS

The PBI project has led to considerable progress in our understanding of the diversity, host associations, and interrelationships of proteocephalidean cestodes. Since 2008, the total number of species has increased by 27 to a total of 316; the total number of genera was increased by 11 to a total of 67. Numerous taxonomic problems have been resolved because new, properly fixed material could be evaluated using both morphological and molecular methods. The worldwide distribution of the group was expanded even further to include additional regions of Africa and South America. The host associations of the group, which were already known to consist primarily of freshwater teleosts (especially siluriforms), amphibians, lizards, and snakes, were expanded to include a few additional species of snakes, especially from Madagascar, as well as additional species of teleosts from South America and frogs from Australia. One of most poorly known proteocephalidean faunas globally is that of freshwater teleosts of North America, especially in the southern USA (Scholz and Choudhury, 2014). Among the most important achievements of the project was the collection of specimens preserved for molecular work for a substantial and representative subset of proteocephalidean taxa. Phylogenetic analyses of newly generated sequence data have shown the current circumscription of subfamilies and many genera to be non-monopyletic and in need of substantial revision (Fig. 17). However, the high degree of homoplasy in the morphological features traditionally used for circumscription of proteocephalidean genera and subfamilies, suggests that new features must be identified if a natural classification scheme is to be developed. Future studies will focus on morphological circumscription of monophyletic lineages recovered from the phylogenetic analyses. Investigation of additional morphological features that members of the recently established Onchoproteocephalidea share would be a particularly fruitful line of research. As it stands the monophyly of the order, which consists of all taxa previously assigned to the Proteocephalidea as well as a series of hooked genera previously assigned to the Onchobothriidae is highly supported by molecular data.

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Table 1. List of valid proteocephalidean taxa and taxa considered *species inquirendae* with type host and country of type locality. New taxa and taxonomic actions resulting from PBI project activities indicated in bold. * Non-monophyletic subfamilies according to de Chambrier et al. (2015a). † Replacement name.

VALID TAXA

- Family Proteocephalidae
  - Subfamily Acanthotaeniinae Freze, 1963*
    - *Acanthotaenia* von Linstow, 1903
      - *Acanthotaenia shipleyi* von Linstow, 1903 (type) ex *Varanus salvator*; Sri Lanka
      - *Acanthotaenia beddardi* (Woodland, 1925) Schmidt, 1986 ex *Varanus bengalensis*; India
      - *Acanthotaenia biroi* (Ratz, 1900) Johnson, 1909 ex *Varanus* sp.; Papua New Guinea
      - *Acanthotaenia daileyi* Schmidt & Kuntz, 1974 ex *Varanus salvator*; Philippines
      - *Acanthotaenia gracilis* (Beddard, 1913) Rudin, 1917 ex *Varanus varius*; Australia
      - *Acanthotaenia overstreeti* Brooks & Schmidt, 1978 ex *Cyclura cornuta*; Puerto Rico
      - *Acanthotaenia pythonis* Wahid, 1968 ex *Morelia viridis*; London Zoo
      - *Acanthotaenia woodlandi* (Moghe, 1926) Schmidt, 1986 ex *Varanus bengalensis*; India
    - ***Australotaenia*** **de Chambrier & de Chambrier, 2010**
      - *Australotaenia hylae* (Johnston, 1911) **de Chambrier & de Chambrier, 2010** (type) **(redescription: de Chambrier & de Chambrier [2010])** ex *Ranoidea aurea*; Australia
      - ***Australotaenia bunthangi*** **de Chambrier & Scholz, 2012** ex *Enhydris enhydris*; Cambodia
      - ***Australotaenia grobeli*** **de Chambrier & de Chambrier, 2010** ex *Ranoidea moorei*; Australia
    - *Kapsulotaenia* Freze, 1965 (revised diagnosis: de Chambrier [2006])
      - *Kapsulotaenia sandgroundi* (Carter, 1943) Freze, 1965 (type) ex *Varanus komodoensis*; Komodo Islands
      - ***Kapsulotaenia chisholmae*** **Jones & de Chambrier, 2016** ex *Varanus spenceri*; Australia
      - *Kapsulotaenia frezei* Schmidt & Kuntz, 1974 ex *Varanus salvator*; Philippines
      - *Kapsulotaenia saccifera* (Ratz, 1900) Freze, 1965 ex *Varanus* sp.; Papua New Guinea
      - *Kapsulotaenia tidswelli* (Johnston, 1909) Freze, 1965 ex *Varanus varius*; Australia
      - *Kapsulotaenia varia* (Beddard, 1913) Freze, 1965 ex *Varanus varius*; Australia
    - *Rostellotaenia* Freze, 1963
      - *Rostellotaenia nilotica* (Beddard, 1913) Freze, 1965 (type) ex *Varanus niloticus*; North Africa
      - *Rostellotaenia beddardi* (Woodland, 1925) Freze, 1965 ex *Varanus bengalensis*; India
      - *Rostellotaenia woodlandi* (Moghe, 1926) Freze, 1965 ex *Varanus bengalensis*; India
    - ***Vandiermenia*** **de Chambrier & de Chambrier, 2010**
      - ***Vandiermenia beveridgei*** **de Chambrier & de Chambrier, 2010** (type) ex *Pseudechis porphyriacus*; Australia
  - Subfamily Corallobothriinae Freze, 1965*
    - *Corallobothrium* Fritsch, 1886 **(revised diagnosis: Scholz et al. [2011])**
      - *Corallobothrium solidum* Fritsch, 1886 (type) **(redescription: Scholz et al. [2011])**; ex *Malapterurus electricus*; North Africa
    - *Corallotaenia* Freze, 1965
      - *Corallotaenia parva* (Larsh, 1941) Freze, 1965 (type) ex *Ameiurus nebulosus*; Michigan, USA
      - *Corallotaenia intermedia* (Fritts, 1959) Freze, 1965 ex *Ameiurus nebulosus*; USA
      - *Corallotaenia parafimbriata* (Befus & Freeman, 1973) **Scholz, de Chambrier, Mariaux & Kuchta, 2011** ex *Ameiurus nebulosus*; Canada
    - ***Essexiella*** **Scholz, de Chambrier, Mariaux & Kuchta, 2011**
      - *Essexiella fimbriata* (Essex, 1928) **Scholz, de Chambrier, Mariaux & Kuchta, 2011** (type) ex *Ictalurus punctatus*; USA
    - *Megathylacoides* Jones, Kerley & Sneed, 1956
      - *Megathylacoides giganteum* (Essex, 1928) Jones, Kerley & Sneed, 1956 (type) ex *Ameiurus melas*; USA
      - *Megathylacoides intermedium* Fritts, 1959 ex *Ameiurus nebulosus*; USA
      - *Megathylacoides lamothei* (García-Prieto, 1990) Scholz, Rosas, Pérez-Ponce de Léon, Choudhury & de Chambrier, 2003 ex *Ictalurus furcatus*; Mexico
      - *Megathylacoides procerum* (Sneed, 1950) Freze, 1965 ex *Ictalurus furcatus*; USA
      - *Megathylacoides thompsoni* (Sneed, 1950) Freze, 1965 ex *Ictalurus lacustris*; USA
      - *Megathylacoides tva* Jones, Kerley & Sneed, 1956 ex *Pilodictis olivarius*; USA
    - *Megathylacus* Woodland, 1934 **(revised diagnosis: de Chambrier et al. [2014])**
      - *Megathylacus jandia* Woodland, 1934 (type) ex *Zungaro zungaro*; Brazil **(redescription: de Chambrier et al. [2014]; new synonymy: de Chambrier et al. [2014])**

Megathylacus travassosi Pavanelli & Rego, 1992 ex *Pseudoplatystoma corruscans*; Brazil **(redescription: de Chambrier et al. [2014])**
Paraproteocephalus Chen, 1962 (revised diagnosis: Shimazu [1993])
Paraproteocephalus parasiluri (Zmeev, 1936) Chen, 1962 (type) ex *Parasilurus asotus*; Russia
Sciadocephalus Diesing, 1850 (revised diagnosis: Rego et al. [1999])
Sciadocephalus megalodiscus Diesing, 1850 (type) ex *Cichla monoculus*; Brazil

Subfamily Endorchiinae Woodland, 1934
Endorchis Woodland, 1934 (revised diagnosis: de Chambrier & Vaucher [1999])
Endorchis piraeeba Woodland, 1934 (type) ex *Brachyplatystoma filamentosum*; Brazil
Endorchis auchenipteri de Chambrier & Vaucher, 1999 ex *Auchenipterus osteomystax*; Paraguay

Subfamily Ephedrocephalinae Mola, 1929
Ephedrocephalus Diesing, 1850
Ephedrocephalus microcephalus Diesing, 1850 (type) ex *Phractocephalus hemioliopterus*; Brazil

Subfamily Gangesiinae Mola, 1929*
Electrotaenia Nybelin, 1942 (revised diagnosis: de Chambrier et al. [2004b])
Electrotaenia malapteruri (Fritsch, 1886) Nybelin, 1942 (type) ex *Malapterurus electricus*; Egypt
Gangesia Woodland, 1924 **(revised diagnosis: Ash et al. [2012, 2015]; list of invalid species & unavailable names: Ash et al. [2012, 2015])**
Gangesia bengalensis (Southwell, 1913) Meggitt, 1927 (type) ex *Channa striata* or *Labeo rohita*; India **(redescription: Ash et al. [2012])**
Gangesia agraensis Verma, 1928 ex *Wallago attu*; India **(redescription: Ash et al. (2012); new synonymy: Ash et al. [2015])**
Gangesia macrones Woodland, 1924 ex *Sperata seenghala*; India **(redescription: Ash et al. [2012])**
Gangesia margolisi Shimazu, 1994 ex *Silurus biwaensis*; Japan
Gangesia oligonchis Roitman & Freze, 1964 ex *Tachysurus fulvidraco*; Russia **(redescription: Ash et al. [2015])**
Gangesia parasiluri Yamaguti, 1934 ex *Silurus asotus*; Japan
Gangesia polyonchis Roitman & Freze, 1964 ex *Silurus asotus*; Russia **(new synonymy: Ash et al. [2015])**
Gangesia vachai (Gupta & Parmar, 1988) **Ash, Scholz, de Chambrier, Brabec, Oros, Kar, Chavan & Mariaux, 2012 (redescription: Ash et al. [2012])** ex *Wallago attu*; India
***Pangasiocestus* Scholz & de Chambrier, 2012**
***Pangasiocestus romani* Scholz & de Chambrier, 2012** (type) ex *Pangasius larnaudii*; Cambodia
***Ritacestus* de Chambrier, Scholz, Ash & Kar, 2011**
Ritacestus ritaii (Verma, 1926) **de Chambrier, Scholz, Ash & Kar, 2011** (type) ex *Rita rita*; India **(redescription: de Chambrier et al. [2011a])**
Silurotaenia Nybelin, 1942 **(new synonymies from Indomalayan realm: Ash et al. [2012])**
Silurotaenia siluri (Batsch, 1786) Nybelin, 1942 (type) ex *Silurus glanis*; Europe
Vermaia Nybelin, 1942 **(revised diagnosis: Ash et al. [2010])**
Vermaia pseudotropii (Verma, 1928) Nybelin, 1942 (type) ex *Clupisoma garua*; India **(new synonymy: Ash et al. [2010])**

Subfamily Marsypocephalinae Woodland, 1933
Marsypocephalus Wedl, 1861
Marsypocephalus rectangulus Wedl, 1861 (type) ex "*Heterobranchus anguillaris*" (= *Clarias gariepinus*); Egypt
Marsypocephalus aegypticus El Naffar, Saoud & Hassan, 1984 ex *Clarias gariepinus*; Egypt
Marsypocephalus daveyi Woodland, 1937 ex *Heterobranchus bidorsalis*; Sierra Leone
Marsypocephalus heterobranchus Woodland, 1925 ex *Heterobranchus bidorsalis*; Sudan
Marsypocephalus tanganyikae (Furhmann & Baer, 1925) Janicki, 1928 ex *Clarias gariepinus*; Lake Tanganyika

Subfamily Monticelliinae Mola, 1929*
Ageneiella de Chambrier & Vaucher, 1999
Ageneiella brevifilis de Chambrier & Vaucher, 1999 (type) ex *Ageneiosus brevifilis* (= *Ageneiosus inermis*); Paraguay
Chambriella Rego, Chubb & Pavanelli, 1999 **(revised diagnosis & new synonymy: Alves et al. [2017b])**
Chambriella megacephala (Woodland, 1934) **Alves, de Chambrier, Luque & Scholz, 2017** (syn. *Chambriella agostinhoi* [Pavanelli & Dos Santos, 1992] Rego, Chubb & Pavanelli, 1999 [type]) ex *Sorubimichthys planiceps*; Brazil
Choanoscolex La Rue, 1911
Choanoscolex abscisus (Riggenbach, 1895) La Rue, 1911 (type) ex *Pseudoplatystoma corruscans*; Paraguay
Goezeella Fuhrmann, 1916 (revised diagnosis: de Chambrier et al. [2004c])
Goezeella siluri Fuhrmann, 1916 (type) ex *Cetopsis coecutiens*; Brazil
Goezeella danbrooksi de Chambrier, Rego & Mariaux, 2004 ex *Ageneiosus caucanus* (= *Ageneiosus pardalis*); Colombia

- *Manaosia* Woodland, 1935 (revised diagnosis: de Chambrier [2003])
  - *Manaosia bracodemoca* Woodland, 1935 (type) ex *Sorubim lima*; Brazil
- *Monticellia* La Rue, 1911 (revised diagnosis: Rego [1995])
  - *Monticellia coryphicephala* (Monticelli, 1891) La Rue, 1911 (type) ex *Salminus maxillosus* (= *Salminus brasiliensis*); Brazil
  - *Monticellia amazonica* de Chambrier & Vaucher, 1997 ex *Luciopimelodus pati*; Brazil
  - *Monticellia belavistensis* Pavanelli, Machado, Takemoto & dos Santos, 1994 ex *Pterodoras granulosus*; Brazil
  - *Monticellia dlouhyi* de Chambrier & Vaucher, 1999 ex *Acestrorhynchus altus*; Paraguay
  - *Monticellia magna* (Rego, Santos & Silva, 1974) de Chambrier & Vaucher, 1997 ex *Pimelodus blochii*; Brazil (revised diagnosis: Gil de Pertierra, 2004)
  - *Monticellia ophisterni* Scholz, de Chambrier & Salgado-Maldonado, 2001 ex *Ophisternon aenigmaticum*; Mexico
  - *Monticellia santafesina* Arredondo & Gil de Pertierra, 2010 ex *Megalonema platanum*; Argentina
  - *Monticellia ventrei* de Chambrier & Vaucher, 1999 ex *Pinirampus* sp.; Paraguay
- ***Regoella* Arredondo, de Chambrier & Gil de Pertierra, 2013**
  - ***Regoella brevis* Arredondo, de Chambrier & Gil de Pertierra, 2013** (type) ex *Pseudoplatystoma fasciatum*; Argentina
- ***Riggenbachiella* Alves, de Chambrier, Luque & Scholz, 2017**
  - ***Riggenbachiella amazonense* Alves, de Chambrier, Luque & Scholz, 2017** (type) ex *Sorubimichthys planiceps*; Peru
  - *Riggenbachiella paranaensis* (Pavanelli & Rego, 1989) **Alves, de Chambrier, Luque & Scholz, 2017** ex *Hemisorubim platyrhynchos*; Brazil
- *Spasskyellina* Freze, 1965 (revised diagnosis: de Chambrier & Scholz [2008])
  - *Spasskyellina lenha* (Woodland, 1933) Freze, 1965 (type) ex *Sorubimichthys planiceps*; Brazil
  - *Spasskyellina mandi* Pavanelli & Takemoto, 1996 ex *Pimelodus ornatus*; Brazil
  - *Spasskyellina spinulifera* (Woodland, 1935) Freze, 1965 ex *Pseudoplatystoma fasciatum*; Brazil
- *Spatulifer* Woodland, 1934
  - *Spatulifer surubim* Woodland, 1934 (type) ex *Pseudoplatystoma tigrinum*; Brazil
  - *Spatulifer maringaensis* Pavanelli & Rego, 1989 ex *Hemisorubim platyrhynchos*; Brazil
  - *Spatulifer rugosa* (Woodland, 1935) Brooks & Deardorff, 1980; ex *Pseudoplatystoma fasciatum*; Brazil

SUBFAMILY NUPELIINAE PAVANELLI & REGO, 1991

- *Nupelia* Pavanelli & Rego, 1991 (revised diagnosis: de Chambrier & Vaucher [1999])
  - *Nupelia portoriquensis* Pavanelli & Rego, 1991 (type) ex *Sorubim lima*; Brazil
  - *Nupelia tomasi* de Chambrier & Vaucher, 1999 ex *Trachelyopterus galeatus*; Paraguay

SUBFAMILY PELTIDOCOTYLINAE WOODLAND, 1934*

- *Amazotaenia* de Chambrier, 2001
  - *Amazotaenia yvettae* de Chambrier, 2001 (type) ex *Brachyplatystoma capapretum*; Brazil
- *Jauella* Rego & Pavanelli, 1985 (revised diagnosis: de Chambrier & Vaucher [1999])
  - *Jauella glandicephalus* Rego & Pavanelli, 1985 (type) ex *Zungaro jahu*; Brazil
- *Luciaella* Gil de Pertierra, 2009
  - *Luciaella ivanovae* Gil de Pertierra, 2009 (type) ex *Ageneiosus inermis*; Argentina
- *Mariauxiella* de Chambrier & Rego, 1995
  - *Mariauxiella pimelodi* de Chambrier & Rego, 1995 (type) ex *Pimelodus ornatus*; Brazil
  - *Mariauxiella piscatorum* de Chambrier & Vaucher, 1999 ex *Hemisorubim platyrhynchos*; Paraguay
- *Peltidocotyle* Diesing, 1850 (revised diagnosis: Zehnder & de Chambrier [2000])
  - *Peltidocotyle rugosa* Diesing, 1850 (type) ex *Pseudoplatystoma corruscans*; Brazil
  - *Peltidocotyle lenha* Woodland, 1933 ex *Sorubimichthys planiceps*; Brazil

SUBFAMILY PROTEOCEPHALINAE MOLA, 1929*

- *Barsonella* de Chambrier, Scholz, Beletew & Mariaux, 2009
  - *Barsonella lafoni* de Chambrier, Scholz, Beletew & Mariaux, 2009 (type) ex *Clarias gariepinus*; Ethiopia
- *Brayela* Rego, 1984 **(revised diagnosis: de Chambrier et al. [2014])**
  - *Brayela karuatayi* (Woodland, 1934) Rego, 1984 (type) **(redescription: de Chambrier et al. [2014])** ex *Platynematichthys notatus*; Brazil
- ***Cairaella* Coquille & de Chambrier, 2008**
  - ***Cairaella henrii* Coquille & de Chambrier, 2008** (type) ex *Norops trachyderma*; Ecuador
- *Cangatiella* Pavanelli & dos Santos, 1991 (revised diagnosis: Gil de Pertierra & Viozzi [1999])
  - *Cangatiella arandasi* Pavanelli & Dos Santos, 1991 (type) ex *Trachelyopterus galeatus*; Brazil
  - *Cangatiella macdonaghi* (Szidat & Nani, 1951) Gil de Pertierra & Viozzi, 1999 ex *Odontesthes bonariensis*; Argentina

- *Cichlidocestus* de Chambrier, Pinacho-Pinacho, Hernández-Orts, & Scholz, 2017
  - *Cichlidocestus gillesi* de Chambrier, Pinacho-Pinacho, Hernández-Orts, & Scholz, 2017 (type) ex *Cichlasoma amazonarum*; Peru
  - *Cichlidocestus janikae* de Chambrier, Pinacho-Pinacho, Hernández-Orts, & Scholz, 2017 ex *Hypsophrys nicaraguensis*; Costa Rica
- *Crepidobothrium* Monticelli, 1900 (revised diagnosis: de Chambrier [1989a, b])
  - *Crepidobothrium gerrardii* (Baird, 1860) Monticelli, 1900 (type) ex *Boa constrictor*; South America
  - *Crepidobothrium dollfusi* Freze, 1965 ex boid snake; South America
  - *Crepidobothrium garzonii* de Chambrier, 1988 ex *Bothrops alternatus*; Paraguay
  - *Crepidobothrium lachesidis* MacCallum, 1921 ex *Bothrops lanceolatus* (?); Trinidad
  - *Crepidobothrium viperis* (Beddard, 1913) Meggitt, 1927 ex *Bothrops alternatus*; South America
- *Deblocktaenia* Odening, 1963
  - *Deblocktaenia ventosaloculata* (Deblock, Rosé & Broussart, 1962) Odening, 1963 (type) ex *Ithycyphus miniatus*; Madagascar
- *Euzetiella* de Chambrier, Rego & Vaucher, 1999
  - *Euzetiella tetraphylliformis* de Chambrier, Rego & Vaucher, 1999 (type) ex *Zungaro jahu*; Brazil
- ***Frezella* Alves, de Chambrier, Scholz & Luque, 2015**
  - ***Frezella vaucheri* Alves, de Chambrier, Scholz & Luque, 2015** (type) ex *Tocantinsia piresi*; Brazil
- *Glanitaenia* de Chambrier, Zehnder, Vaucher & Mariaux, 2004 **(revised diagnosis: de Chambrier & Scholz [2016])**
  - *Glanitaenia osculata* (Goeze, 1782) de Chambrier, Zehnder, Vaucher, & Mariaux, 2004 (type) **(redescription: de Chambrier & Scholz [2016])** ex *Silurus glanis*; Europe
- *Macrobothriotaenia* Freze, 1965 **(revised diagnosis: Scholz et al. [2013])**
  - *Macrobothriotaenia ficta* (Meggitt, 1931) Freze, 1965 (type) **(redescription: Scholz et al. [2013])** ex *Xenopeltis unicolor*; Myanmar
- *Margaritaella* Arredondo & Gil de Pertierra, 2012
  - *Margaritaella gracilis* Arredondo & Gil de Pertierra, 2012 (type) ex *Callichthys callichthys*; Argentina
- *Ophiotaenia* La Rue, 1911 (revised diagnosis: Brooks [1978])
  - *Ophiotaenia perspicua* La Rue, 1911 (type) ex *Nerodia rhombifer*; USA
  - *Ophiotaenia adiposa* Rudin, 1917 ex *Bitis arietans*; Cameroon
  - *Ophiotaenia agkistrodontis* Harwood, 1933 ex *Agkistrodon piscivorus*; USA
  - ***Ophiotaenia alessandrae* Marsella & de Chambrier, 2008** ex *Hysiboas boans*; Ecuador
  - *Ophiotaenia alternans* Riser, 1942 ex *Amphiuma tridactylum*; North America
  - *Ophiotaenia amphiumae* (Zeliff, 1932) Riser, 1942 ex *Amphiuma tridactylum*; North America
  - *Ophiotaenia andersoni* Jensen, Schmidt & Kuntz, 1983 ex *Trimeresurus stejnegeri*; Taiwan
  - *Ophiotaenia arandasi* (Santos & Rolas, 1973) **Ammann & de Chambrier, 2008** ex *Erythrolamprus miliaris*; Brazil
  - *Ophiotaenia atretiumi* (Devi, 1973) **n. comb.** ex *Atretium schistosum*; India
  - *Ophiotaenia azevedoi* (de Chambrier & Vaucher, 1992) **Ammann & de Chambrier, 2008** ex *Bothrops jararaca*; Brazil
  - *Ophiotaenia barbouri* Vigueras, 1934 ex *Tretanorhinus variabilis*; Cuba
  - *Ophiotaenia bonariensis* Szidat & Soria, 1954 ex *Leptodactylus latrans*; Argentina
  - *Ophiotaenia bufonis* (Vigueras, 1942) Yamaguti, 1959 ex *Peltophryne fustiger*; Cuba
  - ***Ophiotaenia bungari* de Chambrier, Binh & Scholz, 2012** ex *Bungarus fasciatus*; Vietnam
  - *Ophiotaenia calmettei* Barrois, 1898 ex *Bothrops lanceolatus*; Martinique
  - *Ophiotaenia carpathica* Sharpilo, Kornyushin & Lisitsina, 1979 ex *Triturus cristatus*; Ukraine
  - *Ophiotaenia catzeflisi* (de Chambrier & Vaucher, 1992) **Ammann & de Chambrier, 2008** ex *Bothrops jararaca*; Brazil
  - *Ophiotaenia ceratophryos* (Parodi & Widakowich, 1916) Cordero, 1946 ex *Ceratophrys cornuta*; Argentina
  - ***Ophiotaenia chandrae* (de Chambrier & Gil de Pertierra, 2012)† de Chambrier & Gil de Pertierra, 2012** ex *Duttaphrynus melanostictus*; India
  - *Ophiotaenia chattoraji* Srivastava, 1980 ex *Naja kaouthia*; India
  - *Ophiotaenia cohopses* Cordero, 1946 ex *Hydromedusa tectifera*; Uruguay
  - *Ophiotaenia congolensis* Southwell & Lake, 1939 ex *Boaedon olivaceus*; Democratic Republic of the Congo
  - *Ophiotaenia crotali* Lopez-Neyra & Diaz-Ungria, 1958 ex *Crotalus durissus terrificus*; Venezuela
  - *Ophiotaenia crotaphopeltis* Sandground, 1928 ex *Crotaphopeltis tornieri*; Africa
  - *Ophiotaenia cryptobranchi* La Rue, 1914 ex *Cryptobranchus alleganiensis*; USA
  - *Ophiotaenia dubinini* Freze & Sharpilo, 1965 ex *Coronella austriaca*; Ukraine
  - *Ophiotaenia ecuadorensis* Dyer, 1986 ex *Hypsiboas geographicus*; Ecuador
  - *Ophiotaenia elapsoidae* Sandground, 1928 ex *Elapsoidea guntherii*; Africa
  - *Ophiotaenia elongata* Fuhrmann, 1927 ex Colubridae gen. sp.; Brazil
  - *Ophiotaenia europaea* Odening, 1963 ex *Natrix natrix*; Germany
  - *Ophiotaenia euzeti* (de Chambrier & Vaucher, 1992) **Ammann & de Chambrier, 2008** ex *Bothrops jararaca*; Brazil

Ophiotaenia faranciae MacCallum, 1921 ex *Farancia abacura*; North America
Ophiotaenia filaroides (La Rue, 1909) La Rue, 1911 ex *Ambystoma tigrinum*; North America
Ophiotaenia fima (Meggitt, 1927) Hilmy, 1936 ex *Amphiesma stolatum*; India
Ophiotaenia flava Rudin, 1917 ex *Coluber* sp.; Brazil
Ophiotaenia gabonica Beddard, 1913 ex *Bitis gabonica*; Africa
Ophiotaenia gallardi (Johnston, 1911) Freze, 1965 **(redescription: de Chambrier & de Chambrier [2010])** ex *Pseudechis porphyriacus*; Australia
***Ophiotaenia georgievi* de Chambrier, Ammann & Scholz, 2010** ex *Leioheterodon geayi*; Madagascar
***Ophiotaenia gilberti* Ammann & de Chambrier, 2008** ex *Thamnodynastes pallidus*; Paraguay
Ophiotaenia gracilis Jones, Cheng & Gillespie, 1958 ex *Lithobates catesbyanus*; North America
Ophiotaenia grandis La Rue, 1911 ex *Agkistrodon piscivorus*; USA
Ophiotaenia greeri (Bursey, Goldberg & Kraus, 2006) **de Chambrier, Coquille, Mariaux & Tkach, 2009** ex *Sphenomorphus aignanus*; Papua New Guinea
Ophiotaenia habanensis Freze & Rysavy, 1976 ex *Tropidophis pardalis*; Cuba
Ophiotaenia hanumanthai Ramadevi, 1974 ex *Rana cyanophylyctus*; India
Ophiotaenia hernandezi (Flores-Barroeta, 1955) de Chambrier, Coquille & Brooks, 2006 ex *Rana* sp.; Mexico
Ophiotaenia hyalina Rudin, 1917 ex *Coluber* sp.; Brazil
Ophiotaenia indica Johri, 1955 ex *Naja naja*; India
Ophiotaenia japonensis Yamaguti, 1935 ex *Rhabdophis tigrinus*; Japan
Ophiotaenia jarara Fuhrmann, 1927 ex *Bothrops jararaca*; Brazil
Ophiotaenia joanae (de Chambrier & Paulino, 1997) **Ammann & de Chambrier, 2008** ex *Xenodon neuwiedi*; Brazil
Ophiotaenia kuantanensis Yeh, 1956 ex *Ophiophagus hannah*; India
***Ophiotaenia lapata* Rambeloson, Rainavoson & de Chambrier, 2012** ex *Madagascarophis colubrinus*; Madagascar
Ophiotaenia loennbergii (Fuhrmann, 1895) La Rue, 1911 ex *Necturus maculosus*; North America
Ophiotaenia lopesi Rego, 1967 ex *Chelonoidis denticulatus*; Brazil
Ophiotaenia macrobothria Rudin, 1917 ex *Micrurus corallinus*; Brazil
Ophiotaenia magna Hannum, 1925 ex *Lithobates catesbeianus*; North America
Ophiotaenia marenzelleri (Barrois, 1898) La Rue, 1911 ex *Agkistrodon piscivorus*; USA
Ophiotaenia micruricola (Shoop & Corkum, 1982) Schmidt, 1986 ex *Micrurus diastema*; Mexico
Ophiotaenia mjobergi Nybelin, 1917 **(redescription: de Chambrier & de Chambrier [2010])** ex *Demansia psammophis*; Australia
Ophiotaenia najae Beddard, 1913 ex *Naja kaouthia*; India
Ophiotaenia nankingensis Hsü, 1935 ex *Ptyas dhumnades*; China
Ophiotaenia nattereri (Parona, 1901) La Rue, 1911 ex *Coluber* sp.; Brazil
***Ophiotaenia nicoleae* Coquille & de Chambrier, 2008** ex *Thecadactylus rapidicauda*; Ecuador
Ophiotaenia nigricollis Mettrick, 1963 ex *Naja nigricollis*; Zimbabwe
Ophiotaenia niuginii (Schmidt, 1975) **n. comb.** ex *Rana afarki*; Papua New Guinea
Ophiotaenia noei Wolffhugel, 1948 ex *Calyptocephalus caudiverbera*; Chile
Ophiotaenia nybelini Hilmy, 1936 ex *Meizodon coronatus*; Africa
Ophiotaenia olor (Ingles, 1936) Yamaguti, 1938 ex *Rana aurora*; USA
Ophiotaenia olseni Dyer & Altig, 1977 ex *Hypsiboas geographicus*; Ecuador
Ophiotaenia ophiodex Mettrick, 1960 ex *Causus rhombeatus*; North America
***Ophiotaenia oumanskyi* de Chambrier & Gil de Pertierra, 2012** ex *Lepidobatrachus laevis*; Paraguay
Ophiotaenia paraguayensis Rudin, 1917 ex *Hydrodynastes gigas*; Paraguay
Ophiotaenia phillipsi (Burt, 1937) Wardle & McLeod, 1952 ex *Trimeresurus trigonocephalus*; Sri Lanka
Ophiotaenia racemosa (Rudolphi, 1819) La Rue, 1911 ex *Coluber* sp.; Brazil
Ophiotaenia ranae Yamaguti, 1938 ex *Pelophylax nigromaculata*; Japan
Ophiotaenia rhabdophidis (Burt, 1937) Wardle & McLeod, 1952 ex *Amphiesma stolatum*; Sri Lanka
Ophiotaenia sanbernardinensis Rudin, 1917 ex *Helicops leopardinus*; Paraguay
Ophiotaenia saphena Osler, 1931 ex *Lithobates clamitans*; North America
Ophiotaenia schultzei (Hungerbühler, 1910) Dickley, 1921 ex *Pyxicephalus adspersus*; South Africa
Ophiotaenia sinensis Cheng & Lin, 2002 ex *Rhabdophis tigrinus*; China
Ophiotaenia southwelli Freze, 1965 ex *Causus rhombeatus*; Africa
Ophiotaenia spasskii Freze & Sharpilo, 1965 ex *Vipera berus*; Ukraine
Ophiotaenia theileri Rudin, 1917 ex *Naja haje*; Africa
Ophiotaenia tigrina (Woodland, 1925) de Chambrier, Coquille & Brooks, 2006 ex *Hoplobatrachus tigrinus*; India
Ophiotaenia trimeresuri (Parona, 1898) La Rue, 1911 ex *Trimeresurus sumatranus*; "India" (in fact Thailand)
Ophiotaenia variabilis (Brooks, 1978) **Ammann & de Chambrier, 2008** ex *Nerodia cyclopion*; North America

Ophiotaenia wuyiensis Cheng, Yuguang & Zao He, 2007 ex *Trimeresurus gramineus*; China
Ophiotaenia zschokkei Rudin, 1917 ex *Naja haje*; South Africa
Proteocephalus Weinland, 1858 (revised diagnosis: Scholz & Hanzelová [1998]; synonymies from the Palaearctic and Nearctic regions: Scholz & Hanzelová [1998], Hanzelová & Scholz [1999])
Proteocephalus ambiguus (Dujardin, 1845) Willemsee, 1968 (type) ex *Pungitius pungitius*; Europe
Proteocephalus aberrans Brooks, 1978 ex *Siren lacertina*; USA
Proteocephalus ambloplitis (Leidy, 1887) Benedict, 1900 ex *Ambloplites rupestris*; North America
Proteocephalus amphiumicola Brooks, 1978 ex *Amphiuma means*; North America
Proteocephalus australis Chandler, 1935 ex *Lepisosteus osseus*; North America
Proteocephalus bagri Spector & Garzon, 1988 ex *Rhamdia sapo* (= *Rhamdia quelen*); Uruguay (redecription: Gil de Pertierra [2002])
Proteocephalus beauchampi Furhmann & Baer, 1925 ex *Chrysichthys* sp.; Democratic Republic of the Congo
Proteocephalus bivitellatus Woodland, 1937 ex *Tilapia* sp.; North Africa
Proteocephalus brooksi García-Prieto, Rodríguez & Pérez-Ponce de León, 1996 ex *Rhamdia guatemalensis*; Mexico
Proteocephalus buplanensis Mayes, 1976 ex *Semotilus atromaculatus*; North America
Proteocephalus cernuae (Gmelin, 1790) La Rue, 1911 ex *Gymnocephalus cernua*; Europe
Proteocephalus chamelensis Pérez-Ponce de León, Brooks & Berman, 1995 ex *Gobiomorus maculatus*; Mexico
Proteocephalus chologasteri Whittaker & Hill, 1968 ex *Forbesichthys agassizi*; North America
Proteocephalus coregoni Wardle, 1932 ex *Coregonus clupeaformis*; North America
Proteocephalus criticum (Mpoame & Landers, 1981) **n. comb.** ex *Ptychocheilus lucius*; North America
Proteocephalus cunningtoni Furhmann & Baer, 1925 ex *Dinotopterus cunningtoni*; Tanzania
***Proteocephalus demshini* Scholz, de Chambrier, Shimazu, Ermolenko & Waeschenbach, 2017** ex *Barbatula toni*; Russia
Proteocephalus dinotopteri Furhmann & Baer, 1925 ex *Dinotopterus cunningtoni*; Tanzania
Proteocephalus elongatus Chandler, 1935 ex *Lepisosteus osseus*; North America
Proteocephalus filicollis (Rudolphi, 1802) Weinland, 1858 ex *Pungitius pungitius*; Europe
Proteocephalus fluviatilis Bangham, 1925 ex *Micropterus dolomieu*; North America
Proteocephalus fossatus (Riggenbach, 1895) La Rue, 1911 ex *Luciopimelodus pati*; Brazil
Proteocephalus gaspari de Chambrier & Vaucher, 1984 ex *Atractosteus tropicus*; Nicaragua
Proteocephalus gibsoni Rego & Pavanelli, 1991 ex *Geophagus brasiliensis*; Brazil
Proteocephalus glanduligerus (Janicki, 1928) Fuhrmann, 1933 **(redescription: Scholz et al. [2009])** ex *Clarias anguilliaris*; Africa
Proteocephalus gobiorum Dogiel & Bychowsky, 1939 ex *Benthophilus macrophalus*; Europe
Proteocephalus hemioliopterus de Chambrier & Vaucher, 1997 ex *Phractocephalus hemioliopterus*; Brazil
Proteocephalus hemispherous Rahemo & Al Niaeemi, 2001 ex *Silurus glanis*; Iraq
Proteocephalus hobergi de Chambrier & Vaucher, 1999 ex *Oxydoras kneri*; Paraguay
Proteocephalus kashmirensis Dhar & Raina, 1983 ex *Triplophysa kashmirensis*; India
Proteocephalus kuyukuyu Woodland, 1935 ex *Oxydoras niger*; Brazil
Proteocephalus longicollis (Zeder, 1800) Nufer, 1905 ex *Salmo trutta*; Europe
Proteocephalus luciopercae Wardle, 1932 ex *Sander vitreum*; North America
Proteocephalus macrocephalus (Creplin, 1825) Nufer, 1905 ex *Anguilla anguilla*; Europe
Proteocephalus macrophallus (Diesing, 1850) La Rue, 1914 ex *Cichla ocellaris*; Brazil
Proteocephalus mahnerti de Chambrier & Vaucher, 1999 ex *Hoplerythrinus unitaeniatus*; Paraguay
Proteocephalus manjuariphilus Vigueras, 1936 ex *Atractosteus tristoechus*; Cuba
Proteocephalus membranacei Troncy, 1978 **(new synonymy and redescription: de Chambrier et al. [2011b**]) ex *Synodontis membranaceus*; Chad
Proteocephalus microscopicus Woodland, 1935 ex *Cichla ocellaris*; Brazil
Proteocephalus midoriensis Shimazu, 1990 ex *Lefua echigonia*; Japan **(redescription: Scholz et al. [2017])**
***Proteocephalus misgurni* Scholz, de Chambrier, Shimazu, Ermolenko & Waeschenbach, 2017** ex *Misgurnus anguillicaudatus*; Russia
Proteocephalus osburni Bangham, 1925 ex *Micropterus dolomieu*; North America
Proteocephalus parasiluri Yamaguti, 1934 ex *Parasilurus asotus*; Japan
Proteocephalus pearsei La Rue, 1919 ex *Perca flavescens*; North America
Proteocephalus pentastomus (Klaptocz, 1906) La Rue, 1911 ex *Polypterus bichir*; Sudan
Proteocephalus percae (Müller, 1780) Railliet, 1899 ex *Perca fluviatilis*; Europe
Proteocephalus perplexus La Rue, 1911 ex *Amia calva*; North America
Proteocephalus pilarensis de Chambrier & Vaucher, 1999 ex *Paraloricaria* sp.; Paraguay
Proteocephalus pimelodi (Gil de Pertierra, 1995) de Chambrier & Vaucher, 1997 ex *Pimelodus maculatus*; Argentina
Proteocephalus pinguis La Rue, 1911 ex *Esox niger*; North America

Proteocephalus platystomi Lynsdale, 1959 ex *Pseudoplatystoma* sp.; Brazil
Proteocephalus plecoglossi Yamaguti, 1934 ex *Plecoglossus altivelis*; Japan
Proteocephalus poulsoni Whittaker & Zober, 1978 ex *Amblyopsis spelaea*; North America
Proteocephalus pugetensis Hoff & Hoff, 1929 ex *Gasterosteus aculeatus*; North America
Proteocephalus regoi de Chambrier, Scholz & Vaucher, 1996 ex *Hoplias malabaricus*; Paraguay
Proteocephalus renaudi de Chambrier & Vaucher, 1994 ex *Platydoras costatus*; Paraguay
Proteocephalus rhamdiae Spector & Garzon, 1988 ex *Rhamdia quelen*; Uruguay (redescription: Gil de Pertierra [2002])
Proteocephalus sagittus (Grimm, 1872) La Rue, 1911 ex *Barbatula barbatula*; Europe
Proteocephalus serrasalmus Rego & Pavanelli, 1990 ex *Serrasalmus spilopleura*; Brazil
Proteocephalus singularis La Rue, 1911 ex *Lepisosteus platostomus*; North America
Proteocephalus sinocyclocheili Nie, 1997 ex *Synocyclocheilus tingi*; China
Proteocephalus sireni Brooks & Buckner, 1976 ex *Siren intermedia*; North America
Proteocephalus soniae de Chambrier & Vaucher, 1994 ex *Platydoras costatus*; Paraguay
Proteocephalus sophiae de Chambrier & Rego, 1994 ex *Zungaro jahu*; Paraguay
Proteocephalus stizostethi Hunter & Bangham, 1933 ex *Perca flavescens*; North America
Proteocephalus sulcatus (Klaptocz, 1906) La Rue, 1911 ex *Clarotes laticeps*; Sudan
Proteocephalus synodontis Woodland, 1925 **(redescription: de Chambrier et al. [2011b])** ex *Synodontis schall*; Sudan
Proteocephalus tetrastomus (Rudolphi, 1810) Willemse, 1969 ex *Osmerus eperlanus*; Europe
Proteocephalus thymalli (Annenkova-Chlopina, 1923) Gvosdev, 1950 ex *Thymallus baicalensis*; Russia
Proteocephalus torulosus (Batsch, 1786) Nufer, 1905 ex *Leuciscus idus*; Europe
Proteocephalus vazzolerae Pavanelli & Takemoto, 1995 ex *Piaractus mesopotamicus*; Brazil
Proteocephalus vitellaris Verma, 1928 ex *Bagarius yarrellii*; India
Proteocephalus vladimirae de Chambrier & Vaucher, 1999 ex *Pinirampus pirinampu*; Paraguay
Pseudocrepidobothrium Rego & Ivanov, 2001
Pseudocrepidobothrium eirasi (Rego & de Chambrier, 1995) Rego & Ivanov, 2001 (type) ex *Phractocephalus hemioliopterus*; Brazil
Pseudocrepidobothrium chanaorum Arredondo, de Chambrier & Gil de Pertierra, 2014 ex *Pseudoplatystoma corruscans*; Argentina
***Pseudocrepidobothrium ludovici* Ruedi & de Chambrier, 2012** ex *Phractocephalus hemioliopterus*; Brazil
Scholzia de Chambrier, Rego & Gil de Pertierra, 2005
Scholzia emarginata (Diesing, 1850) de Chambrier, Rego & Gil de Pertierra, 2005 (type) ex *Phractocephalus hemioliopterus*; Brazil
Tejidotaenia Freze, 1965 (revised diagnosis: Rego & de Chambrier [2000])
Tejidotaenia appendiculatus (Baylis, 1947) Freze, 1965 (type) ex *Tupinambis teguixin*; Surinam
Thaumasioscolex Cañeda-Guzmán, de Chambrier & Scholz, 2001
Thaumasioscolex didelphidis Cañeda-Guzmán, de Chambrier & Scholz, 2001 (type) ex *Didelphis marsupialis*; Mexico
Travassiella Rego & Pavanelli, 1987
Travassiella jandia (Woodland, 1934) **de Chambrier, Scholz & Kuchta, 2014** (type) **(redescription: de Chambrier et al. (2014); new synonymy: de Chambrier et al. [2014])** ex *Zungaro zungaro*; Brazil

SUBFAMILY RUDOLPHIELLINAE WOODLAND, 1935
Rudolphiella Fuhrmann, 1916 (revised diagnosis: Gil de Pertierra & de Chambrier [2000])
Rudolphiella lobosa (Riggenbach, 1895) Fuhrmann, 1916 (type) ex "*Pimelodus pati*" (probably *Megalonema platanum*); Paraguay
Rudolphiella myoides (Woodland, 1934) Woodland, 1935 ex *Pinirampus pirinampu*; Brazil
Rudolphiella piracatinga (Woodland, 1935) Gil de Pertierra & de Chambrier, 2000 ex *Calophysus macropterus*; Brazil
Rudolphiella piranabu (Woodland, 1934) Woodland, 1935 ex *Pinirampus pirinampu*; Brazil
Rudolphiella szidati Gil de Pertierra & de Chambrier, 2000 ex *Luciopimelodus pati*; Argentina

SUBFAMILY SANDONELLINAE KHALIL, 1960
Sandonella Khalil, 1960 **(revised diagnosis: de Chambrier et al. [2008])**
Sandonella sandoni (Lynsdale, 1960) Khalil, 1960 (type) ex *Heterotis niloticus*; Sudan **(redescription: de Chambrier et al., 2008)**

SUBFAMILY TESTUDOTAENIINAE DE CHAMBRIER, COQUILLE, MARIAUX & TKACH, 2009
Testudotaenia Freze, 1965 (revised diagnosis: de Chambrier et al. [2009a])
Testudotaenia testudo (Magath, 1924) Freze, 1965 (type) ex *Apalone spinifera*; USA

SUBFAMILY ZYGOBOTHRIINAE WOODLAND, 1933*
Amphoteromorphus Diesing, 1850 (revised diagnosis: Carfora et al. [2003])
Amphoteromorphus peniculus Diesing, 1850 (type) ex *Brachyplatystoma rousseauxii*; Brazil
Amphoteromorphus ninoi Carfora, de Chambrier & Vaucher, 2003 ex *Brachyplatystoma vaillanti*; Brazil

Amphoteromorphus ovalis Carfora, de Chambrier & Vaucher, 2003 ex *Brachyplatystoma* sp.; Brazil
Amphoteromorphus parkamoo Woodland, 1935 ex *Zungaro zungaro*; Brazil
Amphoteromorphus piraeeba Woodland, 1934 ex *Brachyplatystoma filamentosum*; Brazil
Amphoteromorphus piriformis Carfora, de Chambrier & Vaucher, 2003 ex *Brachyplatystoma rousseauxii*; Brazil
Brooksiella Rego, Chubb & Pavanelli, 1999 (revised diagnosis: de Chambrier et al. [2004c])
Brooksiella praeputialis (Rego, Santos & Silva, 1974) Rego, Chubb & Pavanelli, 1999 (type) ex *Cetopsis coecutiens*; Brazil
Gibsoniela Rego, 1984
Gibsoniela mandube (Woodland, 1935) Rego, 1984 (type) ex *Ageneiosus brevifilis* (= *Ageneiosus inermis*); Brazil
Gibsoniela meursaulti de Chambrier & Vaucher, 1999 ex *Ageneiosus brevifilis* (= *Ageneiosus inermis*); Brazil
Harriscolex Rego, 1987 (revised diagnosis: de Chambrier & Vaucher [1999])
Harriscolex kaparari (Woodland, 1935) Rego, 1987 (type) **(redescription: Gil de Pertierra & de Chambrier [2013])** ex *Pseudoplatystoma tigrinum*; Brazil
***Harriscolex nathaliae* Gil de Pertierra & de Chambrier, 2013** ex *Pseudoplatystoma corruscans*; Paraguay
Harriscolex piramutab (Woodland, 1933) **de Chambrier, Kuchta & Scholz, 2015** ex *Brachyplatystoma vaillanti*; Brazil
Houssayela Rego, 1987 (revised diagnosis: de Chambrier & Scholz [2005])
Houssayela sudobim (Woodland, 1935) Rego, 1987 (type) ex *Pseudoplatystoma fasciatum*; Brazil
Nomimoscolex Woodland, 1934 (revised diagnosis: de Chambrier & Vaucher [1997])
Nomimoscolex piraeeba Woodland, 1934 (type) ex *Brachyplatystoma filamentosum*; Brazil
Nomimoscolex admonticellia Woodland, 1935 ex *Pinirampus pirinampu*; Amazon River, Brazil
Nomimoscolex alovarius Brooks & Deardorff, 1980 ex *Pimelodus clarias* (= *P. blochii*?); Colombia
Nomimoscolex chubbi (Pavanelli & Takemoto, 1995) de Chambrier & Vaucher, 1997 ex *Gymnotus carapo*; Brazil
Nomimoscolex dechambrieri Gil de Pertierra, 2003 ex *Gymnotus carapo*; Argentina
Nomimoscolex dorad Woodland, 1935 ex *Brachyplatystoma rousseauxii*; Brazil
Nomimoscolex guillermoi Gil de Pertierra, 2003 ex *Gymnotus carapo*; Argentina
Nomimoscolex lenha (Woodland, 1933) Woodland, 1935 ex *Sorubimichthys planiceps*; Brazil
Nomimoscolex lopesi Rego, 1989 ex *Pseudoplatystoma fasciatum*; Brazil
Nomimoscolex magna Rego, Santos & Silva, 1974 ex ex *Pimelodus clarias* (= *P. blochii*?); Brazil
Nomimoscolex matogrossensis Rego & Pavanelli, 1990 ex *Hoplias malabaricus*; Brazil
Nomimoscolex microacetabula Gil de Pertierra, 1995 ex *Pimelodus maculatus*; Argentina
Nomimoscolex pertierrae de Chambrier, Takemoto & Pavanelli, 2006 ex *Pseudoplatystoma corruscans*; Brazil
Nomimoscolex semenasae Gil de Pertierra, 2002 ex *Olivaichthys viedmensis*; Argentina
Nomimoscolex sudobim Woodland, 1935 ex *Pseudoplatystoma fasciatum*; Brazil
Nomimoscolex suspectus Zehnder, de Chambrier, Vaucher & Mariaux, 2000 ex *Brachyplatystoma filamentosum*; Brazil
Nomimoscolex touzeti de Chambrier & Vaucher, 1992 ex *Ceratophrys cornuta*; Ecuador
Postgangesia Akhmerov, 1969 (revised diagnosis: de Chambrier et al. [2003])
Postgangesia orientalis Akhmerov, 1969 (type) **(new synonymy: Ash et al. [2015])** ex *Silurus soldatovi*; Russia
Postgangesia inarmata de Chambrier, Al-Kallak & Mariaux, 2003 ex *Silurus glanis*; Iraq
Vaucheriella de Chambrier, 1987
Vaucheriella bicheti de Chambrier, 1987 (type) ex *Tropidophis taczanowskyi*; Ecuador
Zygobothrium Diesing, 1850
Zygobothrium megacephalum Diesing, 1850 (type) ex *Phractocephalus hemioliopterus*; Brazil

SPECIES INQUIRENDAE

Acanthotaenia multitesticulata Shah, Baz & Khan, 1968; type host unknown; India
Gangesia pseudobagrae Chen Yen-hsin, 1962 ex *Parasilurus soldatovi*; China
Monticellia diesingii (Monticelli, 1891) La Rue, 1911 ex "*Silurus dargado*;" type locality unknown, probably South America (Brazil)
Monticellia macrocotylea (Monticelli, 1891) La Rue, 1911; "*Silurus megacephalus*;" type locality unknown, probably South America (Brazil)
Nomimoscolex arandasregoi Fortes, 1981 ex *Genidens barbus*; Brazil
Nomimoscolex shrotrii Mathur & Srivastav, 2000 ex *Heteropneustes fossilis*; India
Ophiotaenia amphiboluri Nybelin, 1917 **(redescription: de Chambrier & de Chambrier [2010])** ex *Pogona barbata*; Australia
Ophiotaenia fixa Meggitt, 1927 ex *Amphiesma stolatum*; India
Ophiotaenia junglensis (Srivastava & Capoor, 1980) Schmidt, 1986 ex *Hoplobatrachus tigrinus*; India
Ophiotaenia lactea (Leidy, 1855) La Rue, 1911 ex *Nerodia sipedon*; USA
Ophiotaenia longmani Johnston, 1916 **(redescription: de Chambrier & de Chambrier [2010]**) ex *Aspidites ramsayi*; Australia

Ophiotaenia meggitti Hilmy, 1936 ex *Atheris chloroechis*; Africa
Ophiotaenia monnigi Fuhrmann, 1924 ex *Crotaphopeltis hotamboeia*; South Africa
Ophiotaenia pigmentata (von Linstow, 1908) La Rue, 1911 ex *Psammodynastes pulverulentus*; Indonesia
Ophiotaenia punica (Cholodkowsky, 1980) La Rue, 1911 ex *Canis familiaris* (?); Tunisia
Ophiotaenia russelli Beddard, 1913 ex *Daboia russelli*; India
Ophiotaenia striata (Johnston, 1914) Wardle & McLeod, 1952 **(redescription: de Chambrier & de Chambrier [2010])** ex *Lialis burtonis*; Townsville, Australia
Ophiotaenia trionychium Lönnberg ex *Apalone ferox*; North America
Proteocephalus esocis Schneider, 1905 ex *Esox lucius*; Estonia
Proteocephalus fragile Essex, 1929 ex *Ictalurus punctatus*; North America
Proteocephalus microcephalus Haderlie, 1953 ex *Micropterus dolomieu*; North America
Proteocephalus micropteri Leidy, 1887 ex *Micropterus nigricans*; North America
Proteocephalus nematosoma Leidy, 1890 ex *Esox reticulatus*; North America
Proteocephalus salmonisumblae Zschokke, 1884 ex *Salvelinus umbla*; Europe
Proteocephalus salvelini Linton, 1897 ex *Salvelinus namaycush*; North America
Proteocephalus simplicissimus Leidy, 1887 ex *Gadus collaris* (?); North America
Vermaia sorrakowahi Zaidi & Khan, 1979 ex *Scoliodon sorrakowah*; “Arabic Sea off Pakistan”

15 Onchoproteocephalidea II

Caira, Jensen, Waeschenbach, Olson & Littlewood, 2014

By
Janine N. Caira[1], Kirsten Jensen, and Verónica A. Ivanov

Our handling of the Onchoproteocephalidea in this Special Publication differs from that of all 18 other cestode orders in that this order is treated in two chapters. The taxa that primarily parasitize freshwater fishes, frogs, snakes, and lizards (i.e., those formerly assigned to the Proteocephalidea) are covered in Chapter 14 of this volume as the Onchoproteocephalidea I (de Chambrier et al., 2017). Here we focus on the elasmobranch-hosted (i.e., batoid- and shark-hosted), primarily hook-bearing members of the order. Although historically considered members of the family Onchobothriidae Braun, 1900 within the order Tetraphyllidea, the hooked taxa treated here are neither close relatives of the other hooked genera once also assigned to that family, which remain as "tetraphyllidean" relics (see Chapter 20 this volume, Caira et al., 2017) nor do they mutually represent a monophyletic group. In fact, substantial evidence suggests they represent a series of independent lineages subtending a crown group composed of the Onchoproteocephalidea I (Fig. 1). Nonetheless, considering them separately here greatly facilitates discussion of various aspects of their biology, and specifically their host associations and geographic distributions, as well as predictions of diversity.

ONCHOPROTEOCEPHALIDEA II AS THEY WERE KNOWN PRIOR TO THE PBI PROJECT

Diversity and Classification. Historically, the hooked elasmobranch-hosted taxa now assigned to the Onchoproteocephalidea were classified in the family Onchobothriidae within the order Tetraphyllidea. Braun (1900) considered the family to include the genera: *Onchobothrius* [sic] de Blainville, 1828, *Acanthobothrium* Blanchard, 1848 (see Machado and Marques [2012] for a history of this name), *Calliobothrium* van Beneden, 1850, *Ceratobothrium* Monticelli, 1892, *Cylindrophorus* Diesing, 1863, *Phoreiobothrium* Linton, 1889, *Platybothrium* Linton, 1890, *Prosthecobothrium* Diesing, 1863, and *Thysanocephalum* Linton, 1890. The family was originally characterized by their possession of an armed scolex with weakly stalked or sessile bothridia with or without apical suckers and/or facial loculi, pronounced segmentation, and proglottids that drop from the strobila before or with maturity (Braun, 1900). For decades thereafter, the family diagnosis deviated relatively little from Braun's (1900) original concept (e.g., Southwell, 1925; Fuhrmann, 1931; Wardle and McLeod, 1952; Yamaguti, 1959; Schmidt, 1986; Euzet, 1994).

As fieldwork expanded to include collections from localities beyond the Mediterranean Sea and eastern Atlantic Ocean, and, in particular to include regions of the Indo-Pacific Ocean,

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[1] Corresponding author (janine.caira@uconn.edu)

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additional genera consistent with the original concept of the family were discovered and added as members. By the late 1970s the following 12 genera had been added to the family and were considered valid by at least several authors: *Pedibothrium* Linton, 1909, *Balanobothrium* Hornell, 1912, *Uncibilocularis* Southwell, 1925, *Spiniloculus*, Southwell, 1925, *Yorkeria* Southwell, 1927, *Acrobothrium* Baer, 1948, *Dicranobothrium*, Euzet, 1953, *Pinguicollum* Riser, 1955, *Megalonchos* Baer & Euzet, 1962, *Pachybothrium* Baer & Euzet, 1962, *Potamotrygonocestus* Brooks & Thorson, 1976, and *Acanthobothroides* Brooks, 1977.

Two relatively modern synthetic treatments of the family have appeared. They differed somewhat in terms of the subset of genera that were considered valid and included in the family. Schmidt (1986) recognized 16 valid onchobothriid genera: *Acanthobothrium*, *Acanthobothroides*, *Calliobothrium*, *Ceratobothrium*, *Cylindrophorus*, *Oncobothrium* [sic], *Pachybothrium*, *Pedibothrium*, *Phoreiobothrium*, *Pinguicollum*, *Platybothrium*, *Potamotrygonocestus*, *Spiniloculus*, *Thysanocephalum*, *Uncibilocularis*, and *Yorkeria*. Following Yamaguti (1959), he treated *Balanobothrium* Hornell, 1911 in the Balanobothriidae Pintner, 1928 within the order Lecanicephalidea. He considered *Dicranobothrium* and *Prosthecobothrium* to be synonyms of *Acanthobothrium*, and *Megalonchos* to be a synonym of *Uncibilocularis*. He also did not include *Acrobothrium* which had earlier convincingly been synonymized with *Acanthobothrium* by Yamaguti (1959).

Euzet (1994) recognized a slightly different collection of 15 genera as valid members of the family. These were: *Acanthobothrium*, *Acanthobothroides*, *Balanobothrium*, *Calliobothrium*, *Dicranobothrium*, *Megalonchos*, *Onchobothrium*, *Pachybothrium*, *Pedibothrium*, *Phoreiobothrium*, *Platybothrium*, *Potamotrygonocestus*, *Spiniloculus*, *Uncibilocularis*, and *Yorkeria*. He considered *Ceratobothrium* and *Thysanocephalum* as members of the Phyllobothriidae Braun, 1900 because they lacked scolex armature. He considered *Cylindrophorus* as a *nomen nudum* and *Pinguicollum* as a synonym of *Acanthobothrium*. Unlike Schmidt (1986), however, he considered *Dicranobothrium* and *Megalonchos* to be valid. Following Perrenoud (1931), Wardle and McLeod (1952), and Baer and Euzet (1962), he treated *Balanobothrium* as an onchobothriid.

Perhaps the most intriguing genus assigned to the Onchobothriidae is *Prosobothrium* Cohn, 1902 because, while it bears proglottids that resemble those of some onchobothriids, it possesses a scolex with acetabula in the form of musculo-glandular pads rather than muscular bothridia, and completely lacks armature. Cohn (1902) originally placed it in the Tetrabothriidea. Southwell (1925) considered it a member of the Cyclophyllidea. When Yamaguti described a second species in 1934, he treated *Prosobothrium* as an aberrant member of the Tetraphyllidea, with affinities to the phyllobothriids. Wardle and McLeod (1952) included it as a *genus inquirendum* within the Lecanicephala. It was Baer and Euzet (1955) who first drew attention to the remarkable strobilar similarities between *Prosobothrium* and the onchobothriid genera *Platybothrium* and *Dicranobothrium*, and to a lesser extent *Phoreiobothrium*. They erected the family Prosobothriidae Baer & Euzet, 1955 to house all four genera. A few years later, Euzet (1959) erected a superfamily Prosobothrioidea Baer & Euzet, 1955 and the new family Phoreiobothriidae Euzet, 1959 for *Phoreiobothrium* (and several phyllobothriid genera), retaining Prosobothriidae for the three remaining genera. Although Yamaguti (1959) and Schmidt (1986) retained *Prosobothrium* in the Proteocephalidea, in his synthetic treatment of elasmobranch-hosted cestodes, Euzet (1994) treated it as a member of the Tetraphyllidea.

Prior to the PBI project in 2008, the generic constituency of the Onchobothriidae had only slightly changed from that of Euzet (1994). The validity of *Pinguicollum* was confirmed by Caira and Keeling (1996). Healy (2003) presented convincing evidence that *Dicranobothrium* is, indeed, a synonym of *Platybothrium*. Two new genera were added to the family: Nasin et al.

(1997) erected the monotypic *Biloculuncus* Nasin, Caira & Euzet, 1997, which was subsequently expanded to house two additional species by Caira et al. (2007). Healy et al. (2001) erected the monotypic *Erudituncus* Healy, Scholz & Caira, 2001. By 2008, the family was considered to house the following 17 valid genera: *Acanthobothrium*, *Acanthobothroides*, *Balanobothrium*, *Biloculuncus*, *Calliobothrium*, *Erudituncus*, *Megalonchos*, *Onchobothrium*, *Pachybothrium*, *Pedibothrium*, *Phoreiobothrium*, *Pinguicollum*, *Platybothrium*, *Potamotrygonocestus*, *Spiniloculus*, *Uncibilocularis*, and *Yorkeria.*

The magnitude of species level diversity in the family has varied with generic membership. Only a few authors have tackled assessments of species diversity in the family overall. Most notably, Yamaguti (1959) recognized 67 valid species—but recognized only ten genera in the family. Schmidt (1986) provided a list of 120 valid species across the 16 genera he considered valid; by far the majority of these (i.e., 71) belonged to the speciose genus *Acanthobothrium*. Between 1986 and the inception of the PBI project, diversity in the family had more than doubled—again much of that novelty was associated with *Acanthobothrium*, with 70 new species described in this genus between 1987 and 2008. This was primarily due to concerted collecting efforts by the following teams in selected regions: Marques and colleagues in Central and South America (Marques et al., 1995, 1997a, b), Caira and colleagues in the Gulf of California (Caira and Burge, 2001; Caira and Zahner, 2001; Ghoshroy and Caira, 2001), Caira, Jensen, and colleagues in Borneo (Fyler and Caira, 2006; Reyda and Caira, 2006), and most prominently by Campbell and Beveridge in Australia, who alone described 27 species new to science (Campbell and Beveridge, 2002). Ghoshroy and Caira (2001) developed a strategy to help overcome the challenge of working with this highly diverse genus, which in 2001 they estimated included at least 100 species worldwide. Their strategy involved categorizing each species into one of nine formal Categories based on its possession of the combination of one of two states for each of the following four characters: total length (≤ 15 mm vs. > 15 mm), number of proglottids (≤ 50 vs. > 50), number of testes (≤ 80 vs. > 80), and ovary symmetry (lobes symmetrical or asymmetrical). Once categorized, a species need be compared only to the subset of species with the same category designation to confirm its novelty.

Notable additions to other genera are as follows: two species of *Megalonchos* by Caira et al. (2007), five species of *Phoreiobothrium* by Caira et al. (2005a), five species of *Platybothrium* by Healy (2003), four species of *Potamotrygonocestus* by Marques and collaborators (Marques et al., 2003; Luchetti et al., 2008), and four species of *Uncibilocularis* by Jensen and Caira (2008). By the beginning of the PBI project in 2008, the 17 genera assigned to the Onchobothriidae were composed of approximately 275 valid species, by far the majority of which (i.e., 163 species) were members of *Acanthobothrium*.

MORPHOLOGY. Their possession of a scolex consisting of four, hooked, muscular bothridia was regarded to unite members of the Onchobothriidae. Thus, the muscular nature of the bothridial extensions seen in *Ceratobothrium* and *Thysanocephalum* led to the elimination of both genera from the family (see Euzet, 1994; Caira et al., 1999, 2001). Among onchobothriids, a wide array of hook morphologies was recognized. These included one (e.g., *Uncibilocularis*) or two (e.g., *Calliobothrium*) pairs of hooks; unipronged (e.g., *Potamotrygonocestus*), bipronged (e.g., *Acanthobothrium*), tripronged (e.g., *Phoreiobothrium*) hooks, or one bipronged and one tripronged (e.g., *Erudituncus*) hook; symmetrical (e.g., *Megalonchos*) or asymmetrical (e.g., *Acanthobothroides*) hooks in a pair, with our without an accessory piece between the bases of hooks in a pair (see Caira et al., 1999, 2001 for a detailed treatment of hook characters). Most taxa exhibit an apical modification of each bothridium as an apical pad, with or without an accessory sucker. In some taxa, one or two horizontal septa divide the bothridia into two or three loculi and the posterior loculus in some is subdivided by vertical septa. Members are generally considered to be euapolytic (i.e., drop mature proglottids from the stobila), but hyperapolysis (i.e., the dropping of immature proglottids) is known in some genera (e.g., some species of *Yorkeria*). Proglottid anatomy typically includes multiple testes, a posterior ovary, and vitelline follicles arranged in two lateral bands, one on each side of the proglottid. Because the morphological concept of the family is obviously tied to its membership, and thus the concept changed substantially with the erection of the order Onchoproteocephalidea, we have refrained from providing more detail here, and instead direct readers to the description of the morphology provided in the post-PBI section below.

PHYLOGENETIC RELATIONSHIPS. Few explicit comprehensive phylogenetic works focused on the Onchobothriidae appeared prior to 2008. The morphology-based analyses of Caira et al. (1999, 2001), which included 14 species in 13 of the 17 genera and 32 species in 14 of the 17 genera, respectively, regarded then as onchobothriids, yielded trees that supported the monophyly of the family as circumscribed by Euzet (1994), including his exclusion of *Prosobothrium* as a member. Among the four genera represented by four or more species included in the expanded analysis of Caira et al. (2001), species of *Platybothrium* were consistently recovered as a monophyletic group; *Phoreiobothrium* was either monophyletic or its relationships relative to a diversity of the hooked taxa unresolved, depending on the analysis. Despite their overall uniform scolex morphology, the five species of *Acanthobothrium* included in the analyses of Caira et al. (2001) were not recovered as monophyletic. In all cases, two clades of *Calliobothrium* were recovered; one composed of the two large, laciniate species, and the other composed of the four small, non-laciniate species included in the analyses. This supported the results of an earlier phylogenetic analysis by Nasin et al. (1997) focused on *Calliobothrium*. We would note that the complexity of hooks seen across these genera resulted in what may have been an overemphasis on hook features in the analyses of Caira et al. (1999, 2001).

In terms of other studies, Healy (2003) conducted a morphological phylogenetic analysis of species of *Platybothrium* and found support for the monophyly of that genus relative to a clade consisting of exemplars of four of the other onchobothriid genera also included in her analysis (i.e., *Biloculuncus*, *Calliobothrium*, *Erudituncus*, and *Pedibothrium*); the relationship of *Phoreiobothrium* was unresolved with respect to these two clades. The cophylogenetic analysis of onchobothriids and their elasmobranch hosts of Caira and Jensen (2001) relied on a cestode tree derived from the Caira et al. (2001) and thus is not an independent assessment of onchobothriid interrelationships.

In contrast, the monophyly of the Onchobothriidae as broadly circumscribed by either Schmidt (1986) or Euzet (1994) has failed to be supported in trees resulting from all molecular analyses conducted prior to 2008, even in cases in which taxon sampling of the family was limited. The analyses of Olson and Caira (1999), based on complete 18S rDNA and partial Ef-1α sequence data, which included an exemplar each of *Calliobothrium* and *Platybothrium*, did not consistently support a sister-group relationship between these two taxa, rather, the relationships of both genera were labile relative to the non-onchobothriid taxa across analyses and data partitions. In all cases, at least one of these species grouped with the proteocephalidean exemplar included in the analyses. Even more intriguing were the results of Olson et al. (1999) based on partial 18S rDNA sequence data, which supported the monophyly of the exemplar species of the four putative onchobothriid genera included in their study (i.e., *Acanthobothrium*, *Calliobothrium*, *Phoreiobothrium*, and *Platybothrium*) only if *Prosobothrium armigerum* Cohn, 1902 was also included in the clade—in fact, among these genera, the latter taxon grouped robustly as the sister to *Platybothrium*. The sister-group relationship between *Prosobothrium* and *Platybothrium* was also highly supported by all of the analyses conducted by Olson et al. (2001), based on complete 18S rDNA and partial 28S rDNA sequence data. In addition to support for a sister-group relationship between these two genera, with *Phoreiobothrium* as their closest relative, the analyses of Caira et al. (2005b), based on partial 18S rDNA and partial 28S rDNA sequence data, yielded trees indicating that this clade was sister to a clade comprised of taxa then classified as proteocephalideans and *Acanthobothrium*. Based on analyses of complete 18S rDNA and complete 28S rDNA sequence data, Waeschenbach et al. (2007) also found *Acanthobothrium* to be more closely related to the proteocephalidean species included in the analyses than to *Pachybothrium*, the other onchobothriid exemplar included in their analyses.

By the inception of the PBI project the interrelationships among the genera assigned to the Onchobothriidae were uncertain and the monophyly of the family overall was in doubt. As a consequence, investigation of onchobothriid interrelationships became one of the primary goals of our PBI efforts.

HOST ASSOCIATIONS. All 17 of the genera putatively assigned to the Onchobothriidae up to the inception of the PBI project in 2008 were known only from elasmobranchs. Species in 11 of these genera were exclusively parasites of sharks, species in five were exclusively parasites of batoids, and one (i.e., *Acanthobothrium*) included a majority of species that parasitize batoids and some that parasitize sharks (Fig. 1). Among the shark-hosted taxa, species in six genera parasitize the Carcharhiniformes (the ground sharks) and species in five genera parasitize the Orectolobiformes (carpet sharks). Among the batoid-hosted taxa, the Myliobatiformes (stingrays) were emphasized as hosts, but the monotypic *Pinguicollum* was known only from the Rajiformes (skates). Species of *Acanthobothrium* had been reported only from batoids of the orders Myliobatiformes, Rajiformes, Rhinopristiformes (guitarfish and their kin), and Torpediniformes (electric rays), as well as sharks of the orders Carcharhiniformes, Orectolobiformes, Heterodontiformes (bull sharks), and the occasional member of the Squaliformes (dogfish sharks) (see Euzet, 1994).

GEOGRAPHIC DISTRIBUTION. The 17 genera assigned to the Onchobothriidae in 2008 had collectively been reported from the following countries: Antarctica, Argentina, Australia, Belgium, Brazil, Chile, China, Colombia, Costa Rica, Ecuador, England, France, French Polynesia, Iceland, India, Italy, Japan, Indonesia, Madagascar, Malaysia, Mexico, New Zealand, Pakistan, Peru, Romania (Black Sea), Senegal, Sri Lanka, Taiwan, Thailand, USA (both coasts), Uruguay, and Venezuela. The family was primarily known from coastal regions in the tropics, subtropics, and to a lesser extent in temperate regions. In addition, it was one of the few families known from the river systems of South America (e.g., Brooks and Thorson, 1976; Mayes et al., 1981; Marques et al., 2003; Ivanov, 2005; Luchetti et al., 2008) and Malaysian Borneo (e.g., Fyler and Caira, 2006; Reyda and Caira, 2006). In addition, several species of *Acanthobothrium* have been reported from as far north as Iceland (e.g., Manger, 1972). The largest gaps in our knowledge of the distribution of onchobothriids in 2008 included much of the coasts of South America and Africa, as well as the Arabian Peninsula, all of which had been very poorly sampled.

CURRENT STATUS OF THE ONCHOPROTEOCEPHALIDEA II

Insights obtained largely from molecular phylogenetic work conducted as a result of PBI project efforts resulted in substantial revisions to the ordinal assignments of many of the 17 genera considered to belong to the Onchobothriidae in 2008. Thus, we will begin with a discussion of phylogenetic relationships to provide the justification for these major revisions. This will also provide the context needed to understand the changes that have occurred in assessments of diversity, morphology, host associations, and geographic distribution of the elasmobranch-hosted members of the Onchoproteocephalidea.

PHYLOGENETIC RELATIONSHIPS. The body of molecular phylogenetic work published since 2008 leaves little doubt that a subset of the genera previously assigned to the tetraphyllidean family Onchobothriidae are the closest relatives of the group previously recognized at the ordinal level as the Proteocephalidea. Although their work focused on rhinebothriidean interrelationships and thus had limited representation of hooked elasmobranch-hosted taxa, Healy et al. (2009) found support for affinities between *Acanthobothrium*, *Phoreiobothrium*, and *Platybothrium*, and the three proteocephalidean examplars (i.e., 2 species of *Proteocephalus* Weinland, 1858 and 1 species of *Gangesia* Woodland, 1924) included in their analyses of complete 18S rDNA and partial 28S rDNA data. Similarly, in their analyses based on data for a large fragment of the mitochondrial genome, in addition to portions of 28S rDNA and 18S rDNA genes, Waeschenbach et al. (2012) found the exemplar of *Acanthobothrium* and the exemplar of *Proteocephalus* to group as sister taxa across all analyses of all data partitions. However, it was the work of Caira et al. (2014) that provided the most compelling evidence confirming the close affinities between the proteocephalideans and a subset of hooked elasmobranch-hosted genera. Their study included 134 species in 97 genera across 15 of the eucestode orders recognized at that time. Representation of elasmobranch-hosted taxa was especially extensive. In terms of hooked taxa, their analyses included 12 of the 17 genera assigned to the family in 2008 (i.e., all but *Biloculuncus*, *Erudituncus*, *Acanthobothroides*, *Onchobothrium*, and *Pinguicollum*), as well as a representative of the newly described genus *Triloculatum* Caira & Jensen, 2009 and an undescribed taxon they referred to as New genus 8. Their results expanded the set of genera exhibiting proteocephalidean affinities beyond *Acanthobothrium*, *Phoreiobothrium*, *Platybothrium*, and *Prosobothrium* to also include *Potamotrygonocestus*, *Triloculatum*, *Uncibilocularis*, New genus 8, and possibly also *Megalonchos*. Their results also confirmed the extremely close affinities between *Prosobothrium* and *Platybothrium*.

While the monophyly of a crown group consisting of taxa previously assigned to the Proteocephalidea was supported by the results of the analyses of Caira et al. (2014), the monophyly of the eight to nine elasmobranch-hosted genera with close affinities to that crown group was not. Instead, these genera grouped as several independent lineages subtending the crown group (Fig. 1). Unfortunately, continued recognition of the Proteocephalidea at the ordinal level would relegate their elasmobranch-hosted close relatives to a paraphyletic group. This led to what was arguably the most radical (and controversial) taxonomic action to result from the PBI project—erection of the order Onchoproteocephalidea to accommodate all of the genera previously assigned to the Proteocephalidea *and* a subset of hooked genera hosted by elasmobranchs (as well as *Prosobothrium*). This action had two major consequences. First, it subdivided the heretofore iconic Onchobothriidae by reassigning a subset of as many as 12 of its genera to the new order Onchoproteocephalidea leaving the remaining five genera family-less in the "Tetraphyllidea" relics (see Chapter 20 this volume, Caira et al., 2017). Second, it changed the ordinal designation of the taxa that primarily parasitize freshwater fishes, snakes, lizards, frogs, and the exceptional mammal from the Proteocephalidea to the Onchoproteocephalidea (see Chapter 14 this volume, de Chambrier et al., 2017). The end result was an order that included both cestodes of elasmobranchs and cestodes of freshwater fishes and some tetrapods.

An unexpected, but intriguing, result of the analyses of Caira et al. (2014) was that the six of the 17 onchobothriid genera that did not group among the Onchoproteocephalidea emerged as two independent clades each with non-hooked taxa as their closest relatives. One

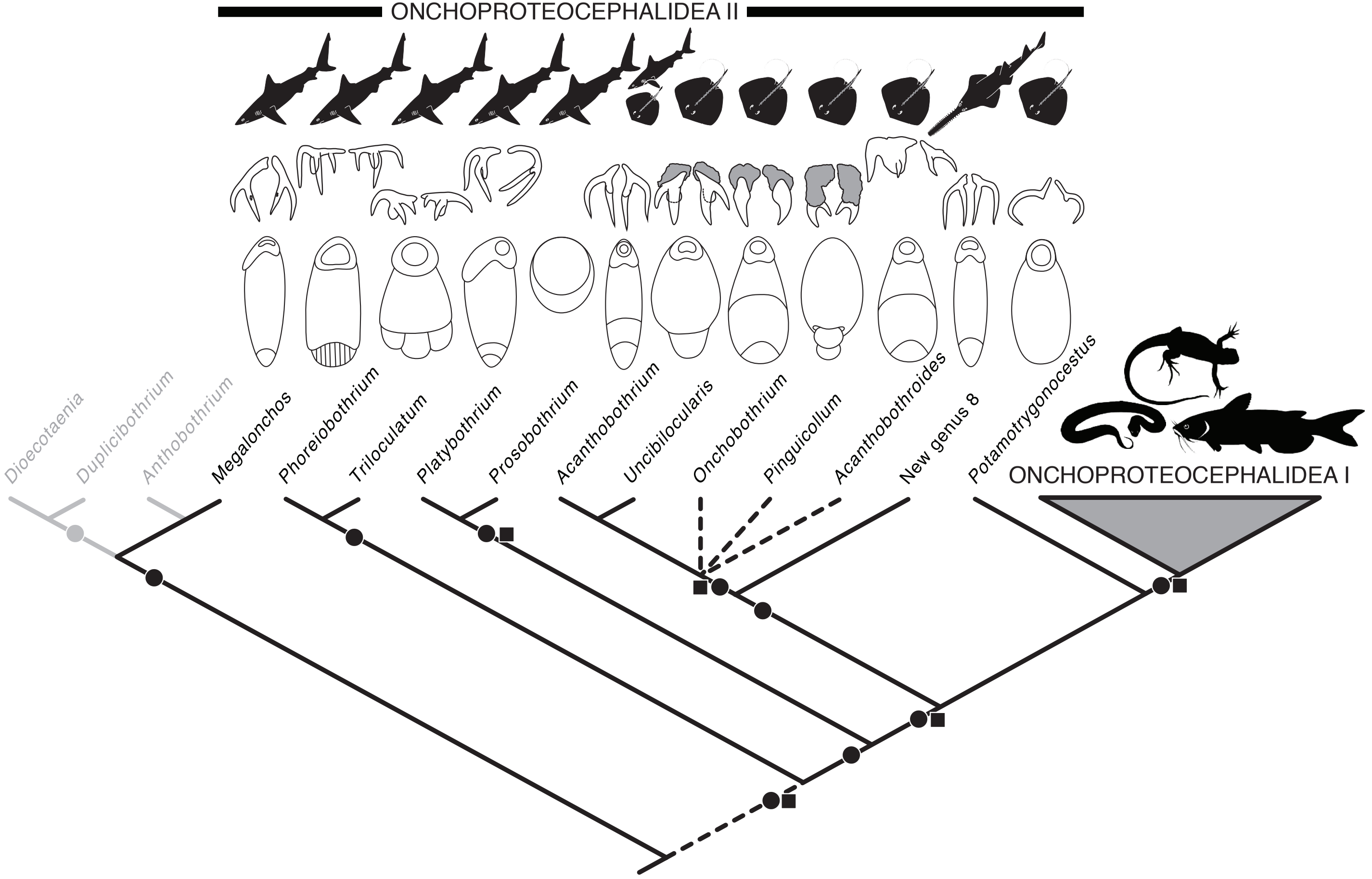


FIGURE 1. Schematic representation of the phylogenetic position of elasmobranch-hosted genera relative to "terrestrial" genera of Onchoproteocephalidea in the molecular phylogeny of Caira et al. (2014). Nodal support is indicated with solid circles in cases of those with posterior probabilities of 0.95 or greater from Bayesian Inference and solid squares in cases of those with bootstrap values 75% or greater from maximum likelihood analysis. For each genus, morphology of one bothridium and its pair of bothridial hooks are illustrated; general host associations are indicated with black icons.

of these clades consisted of the five hooked genera that parasitize orectolobiform sharks (i.e., *Balanobothrium*, *Pachybothrium*, *Pedibothrium*, *Spiniloculus*, and *Yorkeria*); the other consisted of two species of *Calliobothrium.* Beyond noting that Caira et al. (2014) predicted that *Biloculuncus* and *Erudituncus* would ultimately be found to belong to the latter clade, nothing further will be said of these genera here. Readers interested in the fate of these genera are referred to Chapter 20 of this volume (Caira et al., 2017).

However, the Onchoproteocephalidea have not been universally adopted (e.g., Arredondo et al., 2013; de Chambrier et al., 2015). The resistance, not unexpectedly, has come from those working on the taxa previously assigned to the Proteocephalidea. The latter group is generally considered to be a highly cohesive collection of taxa. Morphologically, their scolex is typically simple, bearing four round or elongate, unarmed acetabula, which may be divided into two or three loculi; many possess an apical organ that may or may not be armed in the adult stage. Most members parasitize freshwater fishes, snakes, or lizards—a fact that led de Chambrier et al. (2015) to refer to them as the "terrestrial" members. By far the biggest point of contention, however, surrounds the identification of a morphological feature uniting both suites of genera. Caira et al. (2014) proposed that the presence of gladiate spinitriches throughout the length of the strobila, rather than restricted to the scolex, held some promise as a diagnostic feature for the new order. However, this feature remains to be explored in more detail in the "terrestrial" (*sensu* de Chambrier et al. [2015]) onchoproteocephalidean taxa, many of which, as noted by Caira et al. (2014), have either not yet been characterized with scanning electron microscopy (SEM), or have been examined in the proliferation zone, but not the strobila.

Despite these issues, there remains consistent and convincing molecular support for the monophyly of the Onchoproteocephalidea and no molecular support for the reciprocal monophyly of the elasmobranch-hosted onchobothriid genera independent of the "terrestrial" genera. Moreover, morphological similarities do in fact exist between both suites of genera. The basic proglottid anatomy of many of the "terrestrial" genera is very much like that of the elasmobranch-hosted genera (see de Chambrier et al., 2009; Gil de Pertierra and de Chambrier, 2013; Scholz et al., 2013). These features include: proglottids that house numerous testes, a posterior H-shaped ovary that is usually bilobed in cross-section, as well as vitelline follicles arranged in two lateral bands in most genera, and lateral genital pores that irregularly alternate along the length of the strobila. As was noted by de Chambrier et al. (1999) when they described the catfish-hosted *Euzetiella tetraphylliformis* de Chambrier, Rego & Vaucher, 1999, with elongate proglottids and very weakly developed inner longitudinal musculature, the similarity between this species and elasmobranch-hosted genera is striking. The species *Margaritaella gracilis* Arredondo & Gil de Pertierra, 2012, described as a proteocephalidean by Arredondo and Gil de Pertierra (2012) from a siluriform fish in Argentina, also exhibits these features.

Given the generic focus of PBI project molecular phylogenetic work on the elasmobranch-hosted onchoproteocephalidean taxa, taxon sampling within most genera has been extremely limited. The exception was the dissertation work carried out by Carrie Fyler (Fyler, 2009) who conducted phylogenetic analyses on newly generated partial 28S rDNA and 16S rDNA sequence data for 53 species of *Acanthobothrium*, over half of which were undescribed. Her work provided some important first insights into the interrelationships of this speciose genus. For example, she demonstrated that species of *Acanthobothrium* parasitizing the same host species are not necessarily each others' closest relatives in *Urogymnus acanthobothrium* Last, White & Kyne (as *Himantura* sp.) (see Fyler et al., 2009) and *Rhynchobatus laevis* (Bloch & Schneider) (see Fyler and Caira, 2010). She also provided preliminary evidence that shark associations of members of the genus likely represent host-switching events, and she detected a strong geographic, rather than cophylogenetic, signal between host and cestode trees.

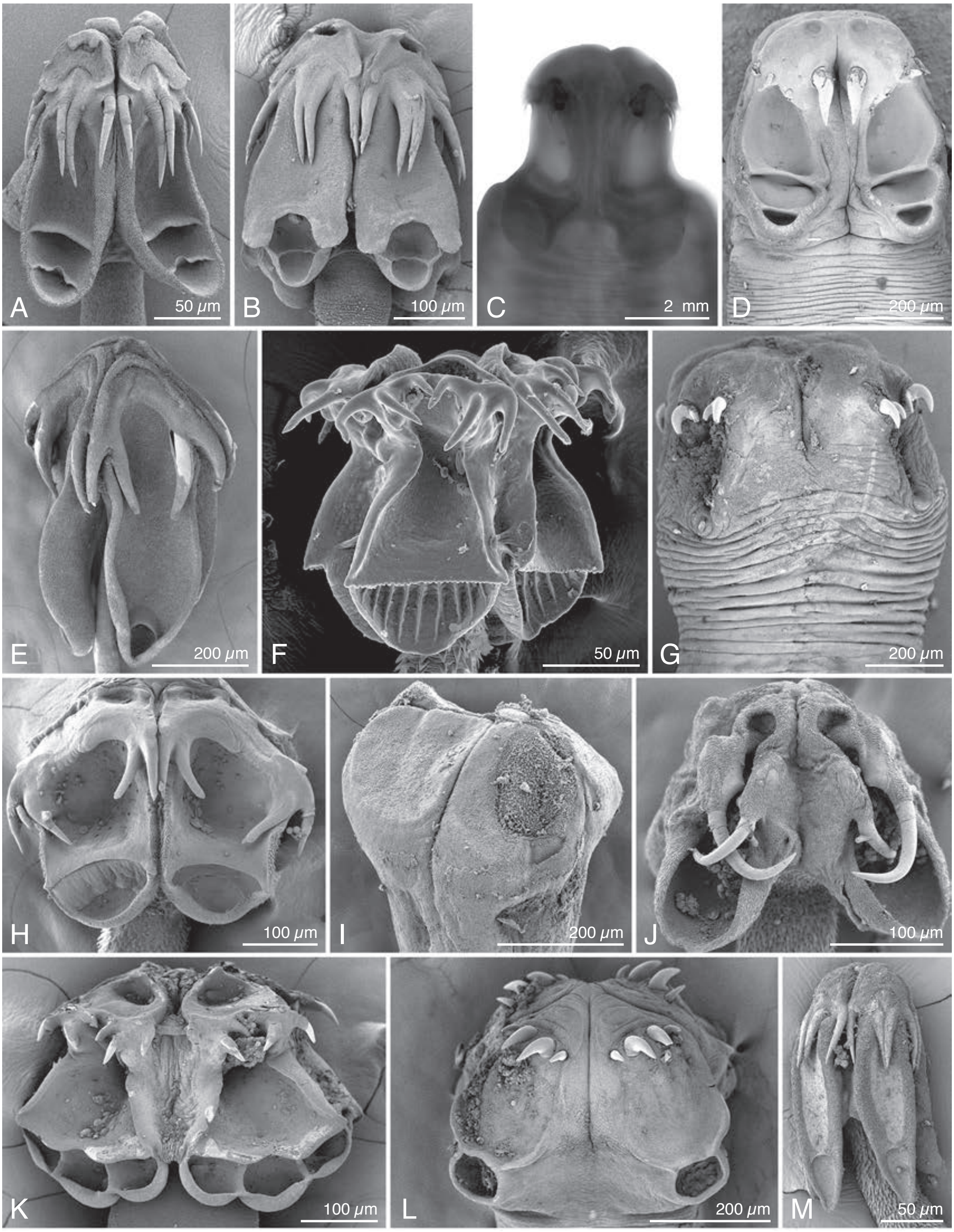
In terms of published analyses, even the relatively comprehensive analyses of Caira et al. (2014) included no more than two species of any genus. As a consequence, the interrelationships among genera and, in most cases, the monophyly of individual genera have not been formally assessed and remain to be explored in substantially more detail.

Diversity and Classification. Eight elasmobranch-hosted genera included in the analyses of Caira et al. (2014) robustly grouped with the "terrestrial" taxa *sensu* de Chambrier et al. (2015) (i.e., *Acanthobothrium* [Fig. 2A–C], *Phoreiobothrium* [Fig. 2F], *Platybothrium* [Fig. 2H], *Potamotrygonocestus* [Fig. 2J], *Prosobothrium* [Fig. 2I], *Triloculatum* [Fig. 2K], *Uncibilocularis* [Fig. 2L], and New genus 8 of Caira et al. [2014] [Fig. 2M]) and were thus assigned to the Onchoproteocephalidea with confidence. Despite its labile position across analyses, *Megalonchos* (Fig. 2E) was also provisionally assigned to the order based on its morphological resemblance to *Platybothrium*. Based on morphological grounds alone, Caira et al. (2014) also included *Acanthobothroides* (Fig. 2D), *Onchobothrium*, and *Pinguicollum* (Fig. 2G) in the order. Thus, in addition to all genera previously assigned to the Proteocephalidea (treated as Onchoproteocephalidea I in Chapter 14 this volume, de Chambrier et al., 2017), the Onchoproteocephalidea include 12 elasmobranch-hosted genera.

The ordinal reclassification also has major implications for the membership of the Onchobothriidae. If familial monophyly is to be maintained, the Onchobothriidae should be reconfigured to include only *Onchobothrium* and its close relatives. Curiously, *Onchobothrium* remains the most poorly known of the 12 elasmobranch-hosted genera of Onchoproteocephalidea. No new specimens were collected over the course of the PBI project, a representative has yet to be included in a molecular analysis, and the type material of most of its six valid species is unavailable for study. Nonetheless, it is provisionally considered valid here until it can be examined in more detail. Regardless, until its placement relative to the other genera can be determined with some confidence, the 12 elasmobranch-hosted genera remain essentially without family designations (see Table 3).

PBI project contributions to diversity in the elasmobranch-hosted genera included erection of the new genus *Triloculatum* by Caira and Jensen (2009) for a series of hooked species that parasitize carcharhinid sharks, and discovery and description of a total of 25 new species (see Table 3). These include 17 of the 24 species of *Acanthobothrium* described since 2008 (see Fyler et al., 2009; Fyler and Caira, 2010; Fyler, 2011; Zschoche et al., 2011; Maleki et al., 2013, 2015). The remaining seven new species were collectively described by Tazerouti et al. (2009), Vardo-Zalik and Campbell (2011), and Yang et al. (2016). The project also resulted in the description of the eight new species described across the other 11 elasmobranch-hosted genera, which consisted of five new species of *Triloculatum* (see Caira and Jensen, 2009) and three new species of *Phoreiobothrium* (see Caira and Jensen, 2015). At present, the total count of valid elasmobranch-hosted species in the Onchoproteocephalidea in the 11 described valid genera is 246. Of this total, 188 species are members of *Acanthobothrium.*

However, additional material collected over the course of the PBI project includes nearly 70 new species that we have not yet had an opportunity to examine in detail or describe. These species were included in the counts in Tables 1 and 2, not only to provide a picture of the full extent of the elasmobranch groups that host the order, but also so that they could be used to inform our prediction of the total global diversity of the order in elasmobranchs. Based on the diversity and host associations of the 246 described and nearly 70 undescribed species, we currently have evidence of a worldwide fauna of 316 species. Given the known host associations of these species and the known number of species in each elasmobranch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genus, we estimate the global fauna of Onchoproteocephalidea hosted by elasmobranchs to be greater than 1,150 species (Tables 1 and 2); more than 260 in sharks and more than 880 in batoids. If our estimate is correct, substantial work remains to be done in this order!

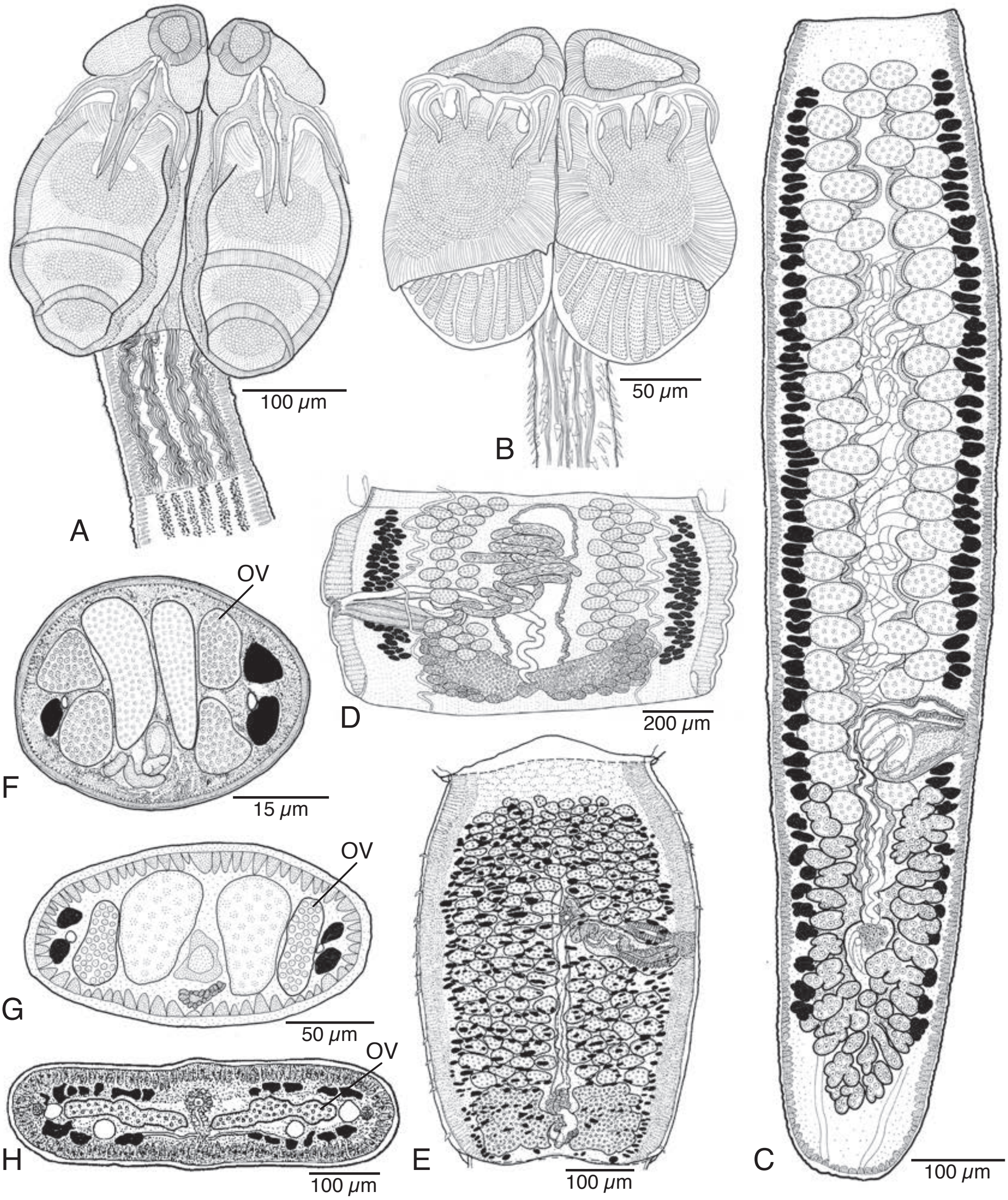
MORPHOLOGY. Once *Balanobothrium*, *Pachybothrium*, *Pedibothrium*, *Spiniloculus*, *Yorkeria*, and *Calliobothrium* are removed from consideration—an action that is also supported by the lack of homology in hook proteins between these genera and those of the genera hosted by elasmobranchs assigned to Onchoproteocephalidea (see Caira and Jensen, 2014)—the morphology of the latter is much more uniform. They can generally be characterized as possessing bothridia with two (5 genera; Fig. 1 and Fig. 2E, F, K, L, M) or three (5 genera; Fig. 2A–D, G, H) facial loculi. The exceptions are *Potamotrygonocestus* with only a single loculus (Fig. 2J) and the enigmatic *Prosobothrium*, with acetabula in the form of musculo-glandular pads (Fig. 2I) rather than muscular bothridia. Most species with muscular bothridia bear an anterior modification of the bothridium in the form of a muscular pad with or without an accessory sucker.

Hook morphology of the constituent genera is also now more consistent (Fig. 1). The bothridia of all genera but *Prosobothrium* bear only a single pair of hooks, and the hooks in a pair are generally bipronged; an accessory piece is present between the bases of the hooks in some. The exceptions are *Phoreiobothrium* and *Triloculatum*, which usually exhibit tripronged hooks, and *Onchobothrium* and *Potamotrygonocestus* in which the hooks are unipronged. The subdivision of the posterior loculus in *Triloculatum* and *Phoreibothrium* into subloculi appears to be a synapomorphy uniting these two genera.

The boundary between the cephalic peduncle and strobila is indistinct in many of the 12 elasmobranch-hosted genera assigned to the Onchoproteocephalidea largely because the gladiate spinitriches, which are often conspicuous in size, extend from the scolex (Fig. 3B) throughout the length of the strobila (Fig. 3E), but also because of the configuration of the muscle bundles (see Caira et al., 1999 for discussion of cephalic peduncle criteria). It was this spinithrix feature that Caira et al. (2014) identified as a potential distinguishing characteristic for the Onchoproteocephalidea overall, for it is also seen in many of the "terrestrial" (i.e., formerly proteocephalidean) taxa that have been examined with SEM in the post-scolex regions of the body (see Caira et al., 2014). Although unknown in any other order of cestodes, not all species of the 12 elasmobranch-hosted genera (or the "terrestrial" taxa) appear to possess this feature. Thus, although the presence of this feature solidly identifies a taxon as a member of the Onchoproteocephalidea, its absence does not eliminate a species from membership. Clearly this feature requires further investigation.

Not unexpectedly given its diversity, much of the variation in size seen across the elasmobranch-hosted onchoproteocephalideans is exhibited by members of *Acanthobothrium*. This genus includes species such as *Acanthobothrium gnomus* Reyda & Caira, 2006, which can be less than a millimeter in length with only seven proglottids (see Reyda and Caira, 2006) and

◄—FIGURE 2. Scanning electron micrographs of scoleces of Onchoproteocephalidea that parasitize elasmobranchs. **(A)** *Acanthobothrium brevissime* ex *Hypanus say* from the Gulf of Mexico. **(B)** *Acanthobothrium margieae* ex *Orectolobus japonicus* from Taiwan. **(C)** *Acanthobothrium* cf. *microcephalum* ex *Myliobatis californica* from the Gulf of California. **(D)** *Acanthobothroides thorsoni* ex *Styracura schmardae* from Colombia (modified from Caira et al. [2001]). **(E)** *Megalonchos sumansinghai* ex *Hemipristis elongata* from Australia. **(F)** *Phoreiobothrium jahki* ex *Rhizoprionodon* cf. *acutus* 3 *sensu* Naylor et al. (2012a) from Borneo. **(G)** *Pinguicollum pinguicollum* ex *Raja asterias* from California, USA (modified from Caira et al. [2001]). **(H)** *Platybothrium spinulifera* ex *Galeocerdo cuvier* from Australia. **(I)** *Prosobothrium armigerum* ex *Prionace glauca* from Montauk, USA (modified from Caira et al. [2001]). **(J)** *Potamotrygonocestus* n. sp. ex *Potamotrygon aiereba* in Peru. **(K)** *Triloculatum andersonorum* ex *Negaprion acutidens* in Australia. **(L)** *Uncibilocularis okei* ex *Pastinachus ater* in Australia. **(M)** New genus 8 *sensu* Caira et al. (2014) ex *Pristis clavata* from Australia.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species such as *Acanthobothrium bajaensis* Appy & Dailey, 1973, which attains a length of over 22 cm and can have up to 500 proglottids (see Appy and Dailey, 1993).

Nonetheless, proglottid anatomy among members of the 12 genera of Onchoproteocephalidea hosted by elasmobranchs is relatively uniform. With the exception of only a few taxa (e.g., Fig. 3D), proglottids are conspicuously longer than wide (e.g., Fig. 3C, E), house numerous testes that are usually, but not always (e.g., *Acanthobothrium saliki* Fyler & Caira, 2006), pre-ovarian. The cirrus is armed with spinitriches. The ovary is located at the posterior of the proglottid and is usually H-shaped in frontal view and bilobed in cross-section (Fig. 3G, H), although tetralobed ovaries in cross-section are known in some taxa (e.g., Fig. 3F; *Acanthobothrium marymichaelorum* Twohig, Caira & Fyler, 2008). The vitellarium is follicular; vitelline follicles are arranged in two lateral bands in most genera (e.g., Fig. 3C, D, G); the exceptions are *Platybothrium* (Fig. 3E, H) and *Prosobothrium*, in which the vitelline follicles are circum-medullary. The genital pores are lateral in position (Fig. 3C–E) and usually irregularly alternate along the length of the strobila. Species in most genera are euapolytic (i.e., mature proglottids drop from strobila), although there is a tendency towards hyperapolysis (i.e., immature proglottids drop from strobila) in *Yorkeria*, *Megalonchos*, *Phoreiobothrium*, and some species of *Acanthobothrium* (e.g., *A. margieae* Fyler, 2011).

HOST ASSOCIATIONS. With the elimination of *Balanobothrium*, *Pachybothrium*, *Pedibothrium*, *Spiniloculus*, *Yorkeria*, and *Calliobothrium* from the "group" as a result of the reclassification of orders, the primary shark taxa hosted by members of the group shifted from the order Orecolobiformes towards members of the order Carcharhiniformes. This fact does little to alter pre-PBI knowledge of batoid hosts parasitized by members of the order because *Acanthobothrium* was retained in the "group" and by far the majority of its many species parasitize batoids.

The new material of onchoproteocephalideans examined over the course of the PBI project greatly expands the known host associations of the order. Published reports from this new material now include an additional nine species and one genus; added were the batoid species *Rhynchobatus laevis* (e.g., Fyler and Caira, 2010) and the recently described dasyatid species *Urogymnus acanthobothrium* (see Fyler et al., 2009), as well as the sharks *Orectolobus japonicus* Regan (see Fyler, 2011) and several undescribed species of *Rhizoprionodon* Whitley (see Caira and Jensen, 2015); the latter also represents a new host genus record for the order.

The majority of the undescribed material is of *Acanthobothrium*. This material further expands the known host associations of the order to include 12 additional genera of elasmobranchs. Six of these are sharks (i.e., *Brachaelurus* Ogilby, *Chiloscyllium* Müller & Henle, *Holohalaelurus* Fowler, *Lamiopsis* Gill, *Paragaleus* Budker, and *Squaliolus* Smith) and six are batoids (i.e., *Acroteriobatus* Giltay, *Fontitrygon* Last, Naylor & Manjaji-Matsumoto, *Maculabatis*

◄—FIGURE 3. Line drawings of morphology and anatomy of selected elasmobranch-hosted Onchoproteocephalidea. **(A)** Scolex of *Acanthobothrium romanowi* ex *Urogymnus acanthobothrium* from Australia (modified from Fyler et al. [2009]). **(B)** Scolex of *Phoreiobothrium jahki* ex *Rhizoprionodon* cf. *acutus* 3 *sensu* Naylor et al. (2012a) from Borneo (modified from Caira and Jensen [2015]). **(C)** Mature terminal proglottid of *Acanthobothrium romanowi* ex *Urogymnus acanthobothrium* from Australia (modified from Fyler et al. [2009]). **(D)** Mature proglottid of *Acanthobothrium maryanskii* ex *Diplobatis ommata* from the Gulf of California (modified from Caira and Burge [2001]). **(E)** Mature proglottid of *Platybothrium angelbahiense* ex *Carcharhinus leucas* from the Gulf of California (modified from Healy [2003]). **(F)** Cross-section through mature proglottid of *Acanthobothrium marymichaelorum* ex *Brevitrygon heterura* from Malaysia (modified from Twohig et al. [2008]). **(G)** Cross-section through mature proglottid of *Acanthobothrium bobconniorum* ex *Rhynchobatus laevis* from Australia (modified from Fyler and Caira [2010]). **(H)** Cross-section through mature proglottid of *Platybothrium angelbahiense* ex *Carcharhinus leucas* from the Gulf of California (modified from Healy [2003]). *Abbreviations*: OV, ovary.

Last, Naylor & Manjaji-Matsumoto, *Taeniurops* Garman, *Trygonoptera* Müller & Henle, and *Zanobatus* Garman).

The described and undescribed new material expands known host associations of the order to include an additional 48 elasmobranch species. This information has been incorporated into the host records provided in Tables 1 and 2. In summary, the number of new host species records for each genus are: *Acroteriobatus* (1 sp.), *Aetobatus* Blainville (1 sp.), *Aetomylaeus* Garman (2 spp.), *Aptychotrema* Norman (1 sp.), *Brachaelurus* (1 sp.), *Carcharhinus* Blainville (3 spp.), *Chiloscyllium* (3 spp.), *Dasyatis* Rafinesque (2 spp.), *Dipturus* Rafinesque (1 sp.), *Fontitrygon* (1 sp.), *Glaucostegus* Bonaparte (1 sp.), *Gymnura* van Hasselt (3 spp.), *Himantura* Müller & Henle (3 spp.), *Holohalaelurus* (1 sp.), *Lamiopsis* (1 sp.), *Maculabatis* (1 sp.), *Neotrygon* Castelnau (2 spp.), *Paragaleus* (1 sp.), *Parascyllium* Gill (1 sp.), *Pastinachus* Rüppell (1 sp.), *Pateobatis* Last, Naylor & Manjaji-Matsumoto (1 sp.), *Potamotrygon* Garman (1 sp.), *Raja* L. (3 spp.), *Rhinobatos* Linck (1 sp.), *Rhizoprionodon* Ogilby (3 spp.), *Rostroraja* Hulley (1 sp.), *Squaliolus* (1 sp.), *Taeniurops* (1 sp.), *Torpedo* Dumeril (1 sp.), *Trygonoptera* (1 sp.), *Urogymnus* Müller & Henle (1 sp.), *Urotrygon* Gill (1 sp.), *Zanobatus* (1 sp.), and *Zapteryx* Jordan & Gilbert (1 sp.). The new material includes new records for three species of whaler sharks (i.e., *Carcharhinus* Blainville).

Our current understanding of the host associations of the elasmobranch-hosted Onchoproteocephalidea (see Tables 1 and 2) is thus as follows. Of the eight orders of sharks, species of this cestode order commonly parasitize the Carcharhiniformes (15 of 52 genera), the Heterodontiformes (its only genus), the Orectolobiformes (6 of 13 genera), and the Pristiophoriformes (1 of 2 genera); they are found to a much lesser extent in the Squaliformes (2 of 23 genera). Onchoproteocephalideans have yet to be reported from the Hexanchiformes (sixgill sharks), Lamniformes (mackerel sharks), or Squatiformes (angelsharks) and given that we have examined a diversity of members of these orders to date, we have no reason to believe these orders will be found to host onchoproteocephalideans in the future. Among the carcharhiniforms, onchoproteocephalideans are especially diverse in requiem sharks (Carcharhinidae Jordan & Evermann), weasel sharks (Hemigaleidae Compagno, 1984), and hammerhead sharks (Sphyrnidae Gill). In fact, it is not uncommon for individual species of carcharhinids and sphyrnids to host one or more species of *Phoreiobothrium* and *Platybothrium*, and, in the cases of larger carcharhinid shark species, also *Triloculatum*. Hemigaleids typically host species of *Megalonchos*. Records from the remaining carcharhiniform families, as well as all of those from the heterodontiforms and squaliforms, consist entirely of species of *Acanthobothrium*.

Onchoproteocephalideans are also known from all four orders of batoids (Table 2). However, this breadth is largely a result of the host associations of *Acanthobothrium*—the host associations of the other five genera that parasitize batoids are very restricted. *Potamotrygonocestus* and *Acanthobothroides* are known only from species of Potamotrygonidae Garman (as the family was recently reconfigured by de Carvalho et al., 2016); the former genus parasitizes freshwater members of the family and the latter marine species of *Styracura* de Carvalho, Loboda & Da Silva. *Onchobothrium* and *Pinguicollum* are, primarily in the former case and entirely in the latter case, parasites of skates. *Uncibilocularis* is known only from the stingray genus *Pastinachus* Rüppell and one species of *Himantura* (see Jensen and Caira, 2008). New genus 8, although not formally established, is important because it is the only genus of the order that parasitizes the sawfishes (i.e., Pristidae Bonaparte). In contrast, species of *Acanthobothrium* are known from all but four of the 25 families across the four orders of batoids. The exceptions are the leg skates (Anacanthobatidae von Bonde), the pygmy skates (Gurgesiellidae De Buen), the devil rays (Mobulidae Gill), and the cownose rays (Rhinopteridae

Jordan & Evermann), none of which have been reported to host onchoproteocephalideans to date. The lack of records from the former two families is likely attributable to a lack of sampling. Both of these groups are not very speciose, limited in distribution, and occur in relatively deep waters and are thus difficult to collect. In contrast, the lack of onchoproteocephalideans from the latter two families is likely to be real; we have examined multiple specimens of multiple species and have yet to encounter a member of the order.

GEOGRAPHIC DISTRIBUTION. The elasmobranch-hosted Onchoproteocephalidea are essentially cosmopolitan in distribution. Prior to the PBI project, they were known from ten of Spalding et al.'s (2007) 12 marine realms of the world. As a result of collections conducted over the course of the PBI project, the distribution of the order was expanded to include the Temperate Southern Africa realm, with collections on the *RS Africana* off South Africa. Within the Western Indo-Pacific realm, distributions were expanded to include the waters off Mozambique and Iran; within the Central Indo-Pacific realm to include Vietnam, Taiwan, and the Solomon Islands; within the Tropical Atlantic realm to include Trinidad and Tobago, Senegal, Belize and Panama; within the Temperate Northern Atlantic realm to include Algeria; and within the Tropical Eastern Pacific realm to include Panama. All but the records from Algeria and Iran, which come from Tazerouti et al. (2009) and Maleki et al. (2013, 2015), respectively, have yet to be published. Although the order has not been reported from the Arctic realm, there is no reason to believe its members do not occur there, particularly in light of Manger's (1972) report of two species of *Acanthobothrium* from western Iceland. We believe sampling effort in the Arctic realm focused on skates is likely to yield specimens of the order. Additional collections from multiple localities in river systems throughout Brazil, Colombia, Peru, and Venezuela by F. P. L. Marques, F. B. Reyda, and colleagues substantially expanded our understanding of the distribution of the order in the freshwater elasmobranchs of South America (e.g., Reyda and Marques, 2011; Marques and Reyda, 2015). No new records from freshwater elasmobranchs outside of South America, beyond the existing ones from Malaysian Borneo (i.e., Fyler and Caira, 2006; Reyda and Caira, 2006), were found.

CONCLUSIONS

The elasmobranch-hosted members of the Onchoproteocephalidea now number 246 valid species and 11 valid genera (assuming the hypothesized affinities of *Megalonchos* can be confirmed), in addition to the undescribed New genus 8 of Caira et al. (2014) (see Table 3). *Acanthobothrium* is by far the most speciose of these 12 elasmobranch-hosted genera, with 188 (i.e., approx. 76%) of the described species. PBI collecting efforts led to the erection of one new genus and the descriptions of 25 new species, as well as material of tens of additional undescribed new species. Host associations span the Elasmobranchii overall, but this is largely a result of the host associations of the highly speciose *Acanthobothrium*, which remains the only acetabulate genus of elasmobranch-hosted cestodes known to parasitize both batoids and sharks. Host associations of most other genera are restricted to one or two families of either sharks or batoids. In such cases, species and genera that have not yet been examined are most likely to be found to host additional diversity, as are geographic regions home to such taxa that have not yet been explored. Based on existing host data, the order is estimated to be found to include more than 800 additional species parasitizing elasmobranchs (Tables 1 and 2). Collectively, the elasmobranch-hosted members of the order are cosmopolitan in distribution with the majority of species parasitizing marine elasmobranchs and a handful parasitizing stingrays of the rivers of South America and Borneo. In combination, these 12 elasmobranch-hosted genera do not comprise a monophyletic group rather they represent a series of independent, early diverging lineages subtending a clade consisting of the "terrestrial" taxa previously assigned to the Proteocephalidea. The presence of gladiate spinitriches throughout the length of the strobila has potential as a synapomorphy for the order Onchoproteocephalidea. It is doubtful that the close affinities between the elasmobranch-hosted genera of onchoproteocephalideans and those parasitizing "terrestrial" hosts will be refuted by future work. Dedicated effort to identify shared morphological similarities across the members of the group would be highly productive.

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Table 1. Expected global shark associations of onchoproteocephalidean species (in yellow). Number of shark species per genus given in parentheses (includes known undescribed shark species). First column: number of onchoproteocephalidean species parasitizing each shark taxon as of 2017 (includes known undescribed cestode species); second column: predicted total number of onchoproteocephalidean species parasitizing each shark taxon globally. Quotes indicate non-monophyletic taxa (Naylor et al., 2012b). Question marks indicate genera not yet examined for cestodes. * Designation New genus D is for *Scyliorhinus torazame* (Tanaka).

	Onchoproteocephalidea spp.	
	2017	ESTIM.
SELACHOIDEA		
Carcharhiniformes	**57**	**200**
Carcharhinidae	**37**	**108**
Carcharhinus (44 spp.)	19	70
Galeocerdo (2 spp.)	1	2
Glyphis (6 spp.)	0	3
Isogomophodon (1 sp.)	?	1
Lamiopsis (2 spp.)	3	6
Loxodon (2 spp.)	0	2
Nasolamia (1 sp.)	?	1
Negaprion (2 spp.)	7	8
Prionace (1 sp.)	3	3
Rhizoprionodon (10 spp.)	4	10
Scoliodon (3 spp.)	0	1
Triaenodon (1 sp.)	0	1
Hemigaleidae	**4**	**10**
Chaenogaleus (2 spp.)	?	2
Hemigaleus (2 spp.)	1	2
Hemipristis (1 sp.)	2	2
Paragaleus (4 spp.)	1	4
Leptochariidae	**0**	**0**
Leptocharias (1 sp.)	0	0
Pentanchidae	**1**	**42**
Apristurus (46 spp.)	0	15
Asymbolus (9 spp.)	0	3
Cephalurus (1 sp.)	?	0
Galeus (18 spp.)	0	5
Halaelurus (7 spp.)	0	7
Haploblepharus (4 spp.)	0	4
Holohalaelurus (5 spp.)	1	5
Parmaturus (11 spp.)	?	3
Pentanchus (1 sp.)	?	0
Proscylliidae	**0**	**0**
Ctenacis (1 sp.)	?	0
Eridacnis (3 spp.)	0	0
Proscyllium (3 spp.)	?	0
Pseudotriakidae	**0**	**0**
Gollum (2 spp.)	?	0
Planonasus (1 sp.)	?	0
Pseudotriakis (1 sp.)	0	0
"Scyliorhinidae"	**1**	**9**
Atelomycterus (6 spp.)	0	0
Aulohalaelurus (2 spp.)	?	0
Bythaelurus (11 spp.)	?	3
Cephaloscyllium (18 spp.)	0	0
Figaro (3 spp.)	?	1
New genus D* (1 sp.)	0	0
Poroderma (2 spp.)	0	0
Schroederichthys (5 spp.)	?	0
Scyliorhinus (15 spp.)	1	5
Sphyrnidae	**9**	**19**
Eusphyra (1 sp.)	1	1
Sphyrna (12 spp.)	8	18
Triakidae	**5**	**12**
Furgaleus (1 sp.)	0	0
Galeorhinus (1 sp.)	0	0
Gogolia (1 sp.)	?	0
Hemitriakis (8 spp.)	0	0
Hypoglaeus (1 sp.)	?	0
Iago (5 spp.)	0	0
Mustelus (30 spp.)	4	10
Scylliogaleus (1 sp.)	?	0
Triakis (5 spp.)	1	2
Heterodontiformes	**5**	**13**
Heterodontidae	**5**	**13**
Heterodontus (10 spp.)	5	13
Hexanchiformes	**0**	**0**
Lamniformes	**0**	**0**
Orectolobiformes	**10**	**30**
Brachaeluridae	**1**	**2**
Brachaelurus (2 spp.)	1	2
Ginglymostomatidae	**1**	**1**
Ginglymostoma (2 spp.)	1	1
Nebrius (1 sp.)	0	0
Pseudoginglymostoma (1 sp.)	0	0
Hemiscylliidae	**3**	**9**
Chiloscyllium (9 spp.)	3	9
Hemiscyllium (9 spp.)	0	0
Orectolobidae	**3**	**12**
Eucrossorhinus (1 sp.)	0	1
Orectolobus (10 spp.)	2	10
Sutorectus (1 sp.)	1	1
Parascylliidae	**2**	**6**
Cirrhoscyllium (3 spp.)	0	1
Parascyllium (5 spp.)	2	5
Rhincodontidae	**0**	**0**
Rhincodon (1 sp.)	0	0
Stegostomatidae	**0**	**0**
Stegostoma (1 sp.)	0	0
Pristiophoriformes	**2**	**14**
Pristiophoridae	**2**	**14**
Pliotrema (1 sp.)	0	0
Pristiophorus (7 spp.)	2	14
Squaliformes	**3**	**12**
Centrophoridae	**0**	**0**
Centrophorus (16 spp.)	0	0
Deania (6 spp.)	0	0
Dalatiidae	**1**	**2**
Dalatias (1 sp.)	0	0
Euprotomicroides (1 sp.)	?	0
Euprotomicrus (1 sp.)	0	0
Heteroscymnoides (1 sp.)	?	0
Isistius (2 spp.)	?	0
Mollisquama (1 sp.)	?	0
Squaliolus (2 spp.)	1	2
Echinorhinidae	**0**	**0**
Echinorhinus (3 spp.)	0	0
Etmopteridae	**0**	**0**
Aculeola (1 sp.)	?	0
Centroscyllium (7 spp.)	0	0
Etmopterus (39 spp.)	0	0
Trigonognathus (1 sp.)	?	0
Oxynotidae	**0**	0
Oxynotus (5 spp.)	0	0
Somniosidae	**0**	**0**
Centroscymnus (2 spp.)	0	0
Centroselachus (1 sp.)	0	0
Scymnodalatias (4 spp.)	?	0
Scymnodon (4 spp.)	0	0
Somniosus (5 spp.)	0	0
Zameus (1 sp.)	?	0
Squalidae	**2**	**10**
Cirrhigaleus (2 spp.)	?	0
Squalus (41 spp.)	2	10
Squatiniformes	**0**	**0**
SHARK TOTAL	**77**	**269**

Table 2. Expected global batoid associations of onchoproteocephalidean species (in yellow). Number of batoid species per genus given in parentheses (includes known undescribed batoid species). First column: number of onchoproteocephalidean species parasitizing each batoid taxon as of 2017 (includes known undescribed cestode species); second column: predicted total number of onchoproteocephalidean species parasitizing each batoid taxon globally. Quotes indicate non-monophyletic taxa (Naylor et al., 2012b; Last et al., 2016a, b). Question marks indicate genera not yet examined for cestodes. Estimated total number of onchoproteocephalidean species parasitizing elasmobranchs globally given at bottom of Table.

	Onchoproteocephalidean spp.	
	2017	ESTIM.
BATOIDEA		
Myliobatiformes	**149**	**433**
Aetobatidae	**9**	**21**
Aetobatus (7 spp.)	9	21
Dasyatidae	**85**	**275**
"*Bathytoshia*" (3 spp.)	3	9
Brevitrygon (5 spp.)	3	7
Dasyatis (5 spp.)	3	15
Fluvitrygon (3 spp.)	2	3
Fontitrygon (4 spp.)	1	4
Hemitrygon (10 spp.)	8	30
Himantura (8 spp.)	9	24
Hypanus (12 spp.)	13	36
Maculabatis (13 spp.)	6	39
Makararaja (1 sp.)	?	1
Megatrygon (1 sp.)	0	3
Neotrygon (13 spp.)	4	26
Pastinachus (6 spp.)	10	20
Pateobatis (7 spp.)	6	21
Pteroplatytrygon (1 sp.)	2	2
Taeniura (5 spp.)	0	0
Taeniurops (2 spp.)	1	2
"*Telatrygon*" (4 spp.)	3	12
Urogymnus (7 spp.)	11	21
Gymnuridae	**8**	**20**
Gymnura (15 spp.)	8	20
Hexatrygonidae	**1**	**1**
Hexatrygon (1 sp.)	1	1
Mobulidae	**0**	**0**
Mobula (8 spp.)	0	0
Myliobatidae	**13**	**29**
Aetomylaeus (9 spp.)	4	9
Myliobatis (11 spp.)	9	20
Plesiobatidae	**0**	**1**
Plesiobatis (1 sp.)	0	1
Potamotrygonidae	**19**	**37**
Heliotrygon (2 spp.)	**0**	1
Styracura (2 spp.)	4	4
Paratrygon (1 sp.)	1	1
Plesiotrygon (2 spp.)	2	4
Potamotrygon (27 spp.)	12	27
Rhinopteridae	**0**	**0**
Rhinoptera (8 spp.)	0	0
Urolophidae	**8**	**31**
Spinilophus (1 sp.)	?	1
Trygonoptera (6 spp.)	1	6
Urolophus (21 spp.)	7	24
Urotrygonidae	**6**	**18**
Urobatis (6 spp.)	3	6
Urotrygon (12 spp.)	3	12
Rhinopristiformes	**38**	**117**
Glaucostegidae	**3**	**14**
Glaucostegus (9 spp.)	3	14
Platyrhinidae	**1**	**3**
Platyrhina (5 spp.)	0	2
Platyrhinoidis (1 sp.)	1	1
"Pristidae"	**3**	**5**
Anoxypristis (1 sp.)	0	0
Pristis (5 spp.)	3	5
Rhinidae	**13**	**36**
Rhina (1 sp.)	0	1
Rhynchobatus (8 spp.)	12	34
Rhynchorhina (1 sp.)	?	1
"Rhinobatidae"	**8**	**40**
Acroteriobatus (8 spp.)	1	7
Pseudobatos (8 spp.)	4	16
Rhinobatos (16 spp.)	3	16
Trygonorrhinidae	**10**	**17**
Aptychotrema (3 spp.)	5	8
Trygonorrhina (2 spp.)	3	6
Zapteryx (3 spp.)	2	3
Zanobatidae	**1**	**2**
Zanobatus (2 spp.)	1	2
Torpediniformes	**15**	**82**
Hypnidae	**1**	**1**
Hypnos (1 sp.)	1	1
Narcinidae	**8**	**56**
Benthobatis (4 spp.)	?	2
Diplobatis (4 spp.)	3	3
Discopyge (2 spp.)	0	1
Narcine (15 spp.)	5	45
Narcinops (5 spp.)	0	5
Narkidae	**2**	**8**
Crassinarke (1 sp.)	?	1
Electrolux (1 sp.)	?	1
Heteronarce (4 spp.)	?	1
Narke (3 spp.)	2	3
Temera (1 sp.)	?	1
Typhlonarke (1 sp.)	0	1
Torpedinidae	**4**	**17**
Tetronarce (9 spp.)	0	5
Torpedo (12 spp.)	4	12
Rajiformes	**35**	**253**
Anacanthobatidae	**0**	**0**
Anacanthobatis (1 sp.)	?	0
Indobatis (1 sp.)	?	0
Schroederobatis (1 sp.)	?	0
Sinobatis (8 spp.)	?	0
Springeria (2 spp.)	?	0
Arhynchobatidae	**5**	**104**
Arhynchobatis (1 sp.)	?	1
Atlantoraja (3 spp.)	1	3
Bathyraja (57 spp.)	2	57
Brochiraja (9 spp.)	0	5
Insentiraja (2 spp.)	?	2
Irolita (2 spp.)	?	2
Notoraja (12 spp.)	?	12
Pavoraja (6 spp.)	?	6
Psammobatis (8 spp.)	1	8
Pseudoraja (1 sp.)	?	1
Rhinoraja (3 spp.)	?	3
Rioraja (1 sp.)	0	1
Sympterygia (4 spp.)	1	4
Gurgesiellidae	**0**	**0**
Cruriraja (8 spp.)	0	0
Fenestraja (8 spp.)	?	0
Gurgesiella (3 spp.)	?	0
Rajidae	**30**	**149**
Amblyraja (9 spp.)	0	5
Beringraja (6 spp.)	2	6
Breviraja (5 spp.)	?	3
Dactylobatus (2 spp.)	?	1
Dentiraja (11 spp.)	?	11
Dipturus (52 spp.)	4	52
Hongeo (1 sp.)	?	1
Leucoraja (13 spp.)	2	13
Malacoraja (4 spp.)	0	2
Neoraja (5 spp.)	?	2
Okamejei (12 spp.)	0	6
Orbiraja (3 spp.)	0	1
Raja (17 spp.)	17	26
Rajella (20 spp.)	0	9
Rostroraja (10 spp.)	4	10
Spiniraja (1 sp.)	1	1
BATOID TOTAL	**237**	**885**
ELASMOBRANCH TOTAL	**314**	**1,154**

TABLE 3. List of onchoproteocephalidean II taxa with their type hosts. New taxa and taxonomic actions resulting from PBI project activities indicated in bold. * Host identification requiring confirmation.

VALID TAXA

Acanthobothrium Blanchard, 1848 (syns. *Petalocephalus* van Lidth de Jeude, 1829; *Petalostoma* van Lidth de Jeude, 1829; *Prosthecobothrium* Diesing, 1863; *Acrobothrium* Baer, 1948)
Acanthobothrium coronatum (Rudolphi, 1819) Blanchard, 1848 (type) ex *Raja batis*
Acanthobothrium adlardi Campbell & Beveridge, 2002 ex *Pristiophorus cirratus*
Acanthobothrium aetiobatis (Shipley, 1900) Southwell, 1925 ex *Aetobatus ocellatus** (as *Aetiobatis narinari*)
Acanthobothrium amazonensis Mayes, Brooks & Thorson, 1978 ex *Potamotrygon circularis*
Acanthobothrium americanum Campbell, 1969 ex *Hypanus americanus* (as *Dasyatis americana*)
Acanthobothrium angelae Campbell & Beveridge, 2002 ex *Hypnos monopterygius*
Acanthobothrium annapinkiensis Carvajal & Goldstein, 1971 *ex Dipturus chilensis* (as *Raja chilensis*)
Acanthobothrium arlenae Campbell & Beveridge, 2002 ex *Aetobatus ocellatus* (as *Aetobatus narinari*)
Acanthobothrium asnihae Fyler & Caira, 2006 ex *Urogymnus polylepis* (as *Himantura chaophraya*)
***Acanthobothrium asriniae* Maleki, Malek & Palm, 2015** ex *Rhynchobatus djiddensis* or *R. laevis** (as *Rhynchobatus* cf. *djiddensis*)
Acanthobothrium atahualpai Marques, Brooks & Barriga, 1997 ex *Gymnura afuerae*
Acanthobothrium australis Robinson, 1965 ex *Squalus megalops*
Acanthobothrium bajaense Appy & Dailey, 1973 ex *Heterodontus francisci*
Acanthobothrium bartonae Campbell & Beveridge, 2002 ex *Rhynchobatus palpebratus* or *R. australiae** (as *Rhynchobatus djiddensis*)
Acanthobothrium batailloni Euzet, 1955 ex *Myliobatis aquila*
Acanthobothrium benedeni Lönnberg, 1889 ex *Raja clavata*
Acanthobothrium bengalense Baer & Euzet, 1962 ex *Pastinachus sephen** (as *Trygon sephen*)
Acanthobothrium blairi Campbell & Beveridge, 2002 ex *Spiniraja whitleyi* (as *Raja whitleyi*)
***Acanthobothrium bobconniorum* Fyler & Caira, 2010** ex *Rhynchobatus laevis**
Acanthobothrium brachyacanthum Riser, 1955 ex *Raja montereyensis*
Acanthobothrium brayi Campbell & Beveridge, 2002 ex *Sutorectus tentaculatus*
Acanthobothrium brevissime Linton, 1908 ex *Hypanus say* (as *Dasyatis say*)
Acanthobothrium bullardi Ghoshroy & Caira, 2001 ex *Hypanus dipterurus* (as *Dasyatis brevis*)
Acanthobothrium cairae Vardo-Zalik & Campbell, 2011 ex *Bathytoshia centroura* (as *Dasyatis centroura*)
Acanthobothrium campbelli Marques, Brooks & Monks, 1995 ex *Urotrygon chilensis*
Acanthobothrium cannoni Campbell & Beveridge, 2002 ex *Himantura uarnak**
Acanthobothrium cartagenensis Brooks & Mayes, 1980 ex *Urobatis jamaicensis* (as *Urolophus jamaicensis*)
Acanthobothrium cestraciontis Yamaguti, 1934 ex *Heterodontus japonicus* (as *Cestracion japonicus*)
Acanthobothrium chengi Cornford, 1974 ex *Bathytoshia lata* (as *Dasyatis lata*)
Acanthobothrium chilensis Rego, Vincente & Herrera, 1968 ex *Sarda chilensis* (Perciformes)
Acanthobothrium chisholmae Campbell & Beveridge, 2002 ex *Pastinachus ater* (as *Pastinachus sephen*)
Acanthobothrium cimari Marques, Brooks & Monks, 1995 ex *Hypanus longus* (as *Dasyatis longa*)
Acanthobothrium clarkeae Campbell & Beveridge, 2002 ex *Urolophus paucimaculatus*
Acanthobothrium cleofanus Monks, Brooks & Ponce de Leon, 1996 ex *Hypanus longus* (as *Dasyatis longa*)
Acanthobothrium colombianum Brooks & Mayes, 1980 ex *Aetobatus narinari*
Acanthobothrium confusum Baer & Euzet, 1962 ex *Neotrygon kuhlii** (as *Trygon kuhli*)
Acanthobothrium coquimbensis Carvajal & Jeges, 1980 ex *Myliobatis chilensis*
Acanthobothrium costarricense Marques, Brooks & Monks, 1995 ex *Hypanus longus* (as *Dasyatis longa*)
Acanthobothrium crassicolle Wedl, 1855 ex *Dasyatis pastinaca* (as *Trygon pastinaca*)
Acanthobothrium cribbi Campbell & Beveridge, 2002 ex *Gymnura australis*
Acanthobothrium dasi Ghoshroy & Caira, 2001 ex *Hypanus dipterurus* (as *Dasyatis brevis*)
Acanthobothrium dasybati Yamaguti, 1934 ex *Hemitrygon akajei* (as *Dasybatus akajei*)
Acanthobothrium dighaensis Srivastava & Capoor, 1980 ex *Himantura marginata* (as *Trygon marginatus*)
Acanthobothrium dollyae Caira & Burge, 2001 ex *Diplobatis ommata*
Acanthobothrium dujardini van Beneden, 1850 ex *Raja clavata* (as *Raia clavata*)
Acanthobothrium dysbiotos (MacCallum, 1921) Williams, 1969 ex *Aetobatus ocellatus** (as *Aetobatis narinari*)
Acanthobothrium edmondsi Campbell & Beveridge, 2002 ex *Parascyllium ferrugineum*
Acanthobothrium edwardsi Williams, 1969 ex *Leucoraja fullonica* (as *Raja fullonica*)
Acanthobothrium electricolum Brooks & Mayes, 1978 ex *Narcine brasiliensis*

Acanthobothrium elongatum Subhapradha, 1955 ex *Rhynchobatus djiddensis**
Acanthobothrium etini Fyler & Caira, 2006 ex *Urogymnus polylepis* (as *Himantura chaophraya*)
Acanthobothrium filicolle (Zschokke, 1888) Yamaguti, 1959 ex *Torpedo marmorata*
Acanthobothrium floridensis Goldstein, 1964 ex *Raja eglanteria*
Acanthobothrium fogeli Goldstein, 1964 ex *Gymnura micrura*
Acanthobothrium foulki Reyda & Caira, 2006 ex *Pateobatis uarnacoides* (as *Himantura uarnacoides*)
Acanthobothrium franus Marques, Centritto & Stewart, 1997 ex *Narcine entemedor*
***Acanthobothrium fylerae* Maleki, Malek & Palm, 2015** ex *Rhynchobatus djiddensis* or *R. laevis** (as *Rhynchobatus* cf. *djiddensis*)
Acanthobothrium gasseri Campbell & Beveridge, 2002 ex *Pastinachus ater* (as *Pastinachus sephen*)
Acanthobothrium gibsoni Campbell & Beveridge, 2002 ex *Rhynchobatus palpebratus* or *R. australiae** (as *Rhynchobatus djiddensis*)
Acanthobothrium giganticum Sanaka, Vijaya Lakshmi & Hanumantha Rao, 1993 ex *Gymnura micrura**
Acanthobothrium gloveri Campbell & Beveridge, 2002 ex *Trygonorrhina fasciata*
Acanthobothrium gnomus Reyda & Caira, 2006 ex *Pateobatis uarnacoides* (as *Himantura uarnacoides*)
Acanthobothrium goldsteini Appy & Dailey, 1973 ex *Platyrhinoidis triseriata*
Acanthobothrium gonzalesmugaburoi Severino & Sarmiento, 1979 ex *Myliobatis peruvianus*
Acanthobothrium gracile Yamaguti, 1952 ex *Narke japonica*
Acanthobothrium grandiceps Yamaguti, 1952 ex *Telatrygon zugei* (as *Dasybatus zugei*)
Acanthobothrium guanghaiense Yang, Sun, Zhi, Iwaki, Reyda & Yang, 2016 ex *Hemitrygon akajei* (as *Dasyatis akajei*)
Acanthobothrium hanumantharaoi Rao, 1977 ex *Aetomylaeus nichofii* (as *Myliobatus nieuhofii*)
Acanthobothrium herdmani Southwell, 1912 ex *Neotrygon kuhlii** (as *Trygon kuhli*)
Acanthobothrium heterodonti Drummond, 1937 ex *Heterodontus portusjacksoni* (as *Heterodontus philippi*)
Acanthobothrium himanturi Brooks, 1977 ex *Styracura schmardae* (as *Himantura schmardae*)
Acanthobothrium hispidum Riser, 1955 ex *Tetronarce californica*
Acanthobothrium holorhini Alexander, 1953 ex *Myliobatis californica* (as *Holorhinus californicus*)
***Acanthobothrium hypermekkolpos* Fyler & Caira, 2010** ex *Rhynchobatus laevis**
Acanthobothrium icelandicum Manger, 1972 ex *Raja batis*
Acanthobothrium ijimai Yoshida, 1917 ex *Hemitrygon akajei* (as *Dasyatis akaei* [sic])
Acanthobothrium inbiorium Marques, Centritto, & Stewart, 1997 ex *Narcine entemedor*
Acanthobothrium incognita (MacCallum, 1921) Wardle & McLeod, 1952 ex *Dasyatis pastinaca* (as *Dasybatus pastinacus*)
Acanthobothrium indicum Subhapradha, 1955 ex *Narcine brasiliensis* (as *Narcine braunii*)
Acanthobothrium intermedium Perrenoud, 1931 ex *Dasyatis pastinaca* (as *Trygon pastinaca*)
***Acanthobothrium jalalii* Maleki, Malek & Palm, 2013** ex *Pastinachus* cf. *sephen**
***Acanthobothrium jamesi* Maleki, Malek & Palm, 2015** ex *Rhynchobatus djiddensis* or *R. laevis** (as *Rhynchobatus* cf. *djiddensis*)
***Acanthobothrium janineae* Maleki, Malek & Palm, 2015** ex *Rhynchobatus djiddensis* or *R. laevis** (as *Rhynchobatus* cf. *djiddensis*)
***Acanthobothrium jeanneae* Fyler & Caira, 2010** ex *Rhynchobatus laevis**
Acanthobothrium jonesi Campbell & Beveridge, 2002 ex *Dasyatis* sp.*
Acanthobothrium karachiense Bilqees, 1980 ex *Mustelus manazo* (as *Myrmillo manazo*)
Acanthobothrium larsoni Reyda & Caira, 2006 ex *Himantura uarnacoides*
Acanthobothrium lasti Campbell & Beveridge, 2002 ex *Rhynchobatus palpebratus* or *R. australiae** (as *Rhynchobatus djiddensis*)
Acanthobothrium latum Yamaguti, 1952 ex *Hemitrygon akajei* (as *Dasybatus akajei*)
Acanthobothrium laurenbrownae Campbell & Beveridge, 2002 ex *Pastinachus ater* (as *Pastinachus sephen*)
Acanthobothrium lentiginosum Vardo-Zalik & Campbell, 2011 ex *Pseudobatos lentiginosus* (as *Rhinobatos lentiginosus*)
Acanthobothrium lepidum Reyda & Caira, 2006 ex *Pateobatis uarnacoides* (as *Himantura uarnacoides*)
Acanthobothrium lilium Baer & Euzet, 1962 ex *Dasyatis* sp.* (as *Dasybatus* sp.)
Acanthobothrium lineatum Campbell, 1969 ex *Hypanus americanus* (as *Dasyatis americana*)
Acanthobothrium lintoni Goldstein, Henson & Schlicht, 1968 ex *Narcine brasiliensis*
Acanthobothrium longipedunculata Uma Maheswari, Vijaya Lakshmi & Hanumantha Rao, 1985 ex *Himantura uarnak** (as *Dasyatis uarnak*)
Acanthobothrium lusarmientoi Severino & Verano, 1980 ex *Sympterygia brevicaudata* (as *Psammobatis caudispina*)
Acanthobothrium macracanthum Southwell, 1925 ex *Urogymnus* sp. (as "*Urogymnus* sp. (*asperrimus*?)")
Acanthobothrium macrocephalum Wang & Yang, 2001 ex *Hemitrygon akajei* (as *Dasyatis akajei*)
Acanthobothrium maculatum Riser, 1955 ex *Myliobatis californica* (as *Aetobatus californicus*)
Acanthobothrium magnum Euzet, 1959 ex *Pteroplatytrygon violacea* (as *Dasyatis violacea*)
Acanthobothrium manteri Hassan, 1983 ex *Pastinachus sephen** (as *Dasyatis sephen*)
***Acanthobothrium margieae* Fyler, 2011** ex *Orectolobus japonicus*

Acanthobothrium marplatensis Ivanov & Campbell, 1998 ex *Atlantoraja castelnaui* (as *Rioraja castelnaui*)
Acanthobothrium martini Campbell & Beveridge, 2002 ex *Myliobatis australis*
Acanthobothrium maryanskii Caira & Burge, 2001 ex *Diplobatis ommata*
Acanthobothrium marymichaelorum Twohig, Caira and Fyler, 2008 ex *Brevitrygon heterura* (as *Himantura walga*)
Acanthobothrium masnihae Fyler & Caira, 2006 ex *Urogymnus polylepis* (as *Himantura chaophraya*)
Acanthobothrium mathiasi Euzet, 1959 ex *Mustelus mustelus*
***Acanthobothrium matttaylori* Fyler & Caira, 2010** ex *Rhynchobatus laevis**
Acanthobothrium micracantha Yamaguti, 1952 ex *Hemitrygon akajei* (as *Dasybatus akajei*)
Acanthobothrium microcephalum Alexander, 1953 ex *Myliobatis californica* (as *Holorhinus californicus*)
Acanthobothrium minus Tazerouti, Kechemir-Issad & Euzet, 2009 ex *Raja asterias*
Acanthobothrium minusculus Marques, Brooks & Barriga, 1997 ex *Urobatis tumbesensis* (as *Urolophus tumbesensis*)
Acanthobothrium monksi Marques, Brooks & Barriga, 1997 ex *Aetobatus narinari* (as *Aetobatis narinari*)
Acanthobothrium mooreae Campbell & Beveridge, 2002 ex *Trygonorrhina fasciata*
Acanthobothrium mujibi Bilqees, 1980 ex *Mustelus manazo* (as *Myrmillo manazo*)
Acanthobothrium musculosum (Baer, 1948) Yamaguti, 1959 ex *Pteroplatytrygon violacea* (as *Dasyatis violacea*)
Acanthobothrium myliomaculata Srivastav, Shweta & Noopur, 1995 ex *Aetomylaeus maculatus* (as *Myliobatis maculata*)
***Acanthobothrium nanogravidum* Zschoche, Caira & Fyler, 2011** ex *Pastinachus ater* (as *Pastinachus atrus*)
Acanthobothrium nicoyaense Brooks & McCorquodale, 1995 ex *Aetobatus narinari*
Acanthobothrium ningdense Yang, Sun, Zhi, Iwaki, Reyda & Yang, 2016 ex *Hemitrygon akajei* (as *Dasyatis akajei*)
Acanthobothrium obuncus Marques, Brooks & Barriga, 1997 ex *Hypanus longus* (as *Dasyatis longa*)
Acanthobothrium ocallaghani Campbell & Beveridge, 2002 ex *Aptychotrema vincentiana*
***Acanthobothrium oceanharvestae* Fyler, Caira & Jensen, 2009** ex *Urogymnus acanthobothrium* (as *Himantura* sp.)
Acanthobothrium odonoghuei Campbell & Beveridge, 2002 ex *Urolophus expansus*
Acanthobothrium olseni Dailey & Mudry, 1968 ex *Pseudobatos productus* (as *Rhinobatos productus*)
Acanthobothrium parviuncinatum Young, 1954 ex *Urobatis halleri*
Acanthobothrium parvum Manger, 1972 ex *Raja batis*
Acanthobothrium paulum Linton, 1890 ex *Bathytoshia centroura* (as *Trygon centrura*)
Acanthobothrium pearsoni Williams, 1962 ex *Orectolobus maculatus*
Acanthobothrium peruviense Reyda, 2008 ex *Potamotrygon motoro*
Acanthobothrium pichelinae Campbell & Beveridge, 2002 ex *Myliobatis australis*
Acanthobothrium pintanensis Wang, 1984 ex *Neotrygon kuhlii** (as *Dasyatis kuhlii*)
Acanthobothrium polytesticularis Wang & Yang, 2001 ex *Squalus* sp.
Acanthobothrium ponticum Léon-Borcea, 1934 ex *Raja clavata*
***Acanthobothrium popi* Fyler, Caira & Jensen, 2009** ex *Urogymnus acanthobothrium* (as *Himantura* sp.)
Acanthobothrium psammobati Carvajal & Goldstein, 1969 ex *Psammobatis scobina*
Acanthobothrium puertecitense Caira & Zahner, 2001 ex *Heterodontus francisci*
Acanthobothrium puntarenasense Marques, Brooks & Monks, 1995 ex *Hypanus longus* (as *Dasyatis longa*)
Acanthobothrium quadripartitum Williams, 1968 ex *Leucoraja naevus* (as *Raja naevus*)
Acanthobothrium quinonesi Mayes, Brooks & Thorson, 1978 ex *Potamotrygon magdalenae*
Acanthobothrium rajaebatis (Rudolphi, 1810) Euzet, 1959 ex *Dipturus oxyrinchus** (as *Raja bati*)
Acanthobothrium rajivi Ghoshroy & Caira, 2001 ex *Hypanus dipterurus* (as *Dasyatis brevis*)
Acanthobothrium ramiroi Ivanov, 2005 ex *Potamotrygon motoro*
Acanthobothrium regoi Brooks, Mayes & Thorson, 1981 ex *Potamotrygon hystrix*
Acanthobothrium rhinobati Alexander, 1953 ex *Pseudobatos productus* (as *Rhinobatos productus*)
Acanthobothrium robertsoni Campbell & Beveridge, 2002 ex *Trygonorrhina fasciata*
Acanthobothrium robustum Alexander, 1953 ex *Pseudobatos productus* (as *Rhinobatos productus*)
***Acanthobothrium rodmani* Fyler, Caira & Jensen, 2009** ex *Urogymnus acanthobothrium* (as *Himantura* sp.)
Acanthobothrium rohdei Campbell & Beveridge, 2002 ex *Urolophus lobatus*
***Acanthobothrium romanowi* Fyler, Caira & Jensen, 2009** ex *Urogymnus acanthobothrium* (as *Himantura* sp.)
Acanthobothrium rotundum Subhapradha, 1955 ex *Rhynchobatus djiddensis**
Acanthobothrium royi Caira & Burge, 2001 ex *Diplobatis ommata*
Acanthobothrium rubrum Bilqees, 1980 ex *Mustelus manazo* (as *Myrmillo manazo*)
Acanthobothrium saliki Fyler & Caira, 2006 ex *Urogymnus polylepis* (as *Himantura chaophraya*)
Acanthobothrium santarosaliense Caira & Zahner, 2001 ex *Heterodontus mexicanus*
Acanthobothrium satyanarayanaraoi Sanaka, Vijaya Lakshmi & Hanumantha Rao, 1993 ex *Glaucostegus granulatus* (as *Rhinobatus granulatus*)
Acanthobothrium schalli Vardo-Zalik & Campbell, 2011 ex *Mustelus canis* (as *Mustelus canis canis*)
Acanthobothrium semnovesiculum Verma, 1928 ex *Pastinachus sephen** (as *Hypolophus sephen*)
Acanthobothrium septentrionale Baer & Euzet, 1962 ex *Raja batis*

Acanthobothrium soberoni Ghoshroy & Caira, 2001 ex *Hypanus dipterurus* (as *Dasyatis brevis*)
Acanthobothrium southwelli Subhapradha, 1955 ex *Rhinobatos schlegelii* (as *Rhinobatus schlegelii*)
***Acanthobothrium sphaera* Maleki, Malek & Palm, 2013** ex *Pastinachus* cf. *sephen**
Acanthobothrium stevensi Campbell & Beveridge, 2002 ex *Trygonorrhina fasciata*
Acanthobothrium tasajerasi Brooks, 1977 ex *Styracura schmardae* (as *Himantura schmardae*)
Acanthobothrium terezae Rego & Dias, 1976 ex *Potamotrygon motoro* (as *Paratrygon motoro*)
Acanthobothrium tetabuanense Reyda & Caira, 2006 ex *Pateobatis uarnacoides* (as *Himantura uarnacoides*)
Acanthobothrium thomasae Campbell & Beveridge, 2002 ex *Aptychotrema vincentiana*
Acanthobothrium tortum (Linton, 1916) Baer & Euzet, 1962 ex *Aetobatus narinari* (as *Aetobatis narinari*)
Acanthobothrium triacis Yamaguti, 1952 ex *Triakis scyllium* (as *Triacis scyllium*)
Acanthobothrium tripartitum Williams, 1969 ex *Raja microocellata* (as *Raja micro-ocellata*)
Acanthobothrium ulmeri Vardo-Zalik & Campbell, 2011 ex *Rostroraja texana* (as *Raja texana*)
Acanthobothrium unilateralis Alexander, 1953 ex *Myliobatis californica* (as *Holorhinus californicus*)
Acanthobothrium urogymni (Hornell, 1912) Southwell, 1925 ex *Urogymnus asperrimus*
Acanthobothrium urolophi Schmidt, 1973 *ex Urolophus testaceus*
Acanthobothrium urotrygoni Brooks & Mayes, 1980 ex *Urotrygon venezuelae*
Acanthobothrium vargasi Marques, Brooks & Monks, 1995 ex *Hypanus longus* (as *Dasyatis longa*)
Acanthobothrium walkeri Campbell & Beveridge, 2002 ex *Pastinachus ater* (as *Pastinachus sephen*)
Acanthobothrium waltairensis Uma Maheswari, Sanaka, Vijaya Lakshmi & Hanumantha Rao, 1987 ex *Himantura uarnak** (as *Dasyatis uarnak*)
Acanthobothrium wedli Robinson, 1959 ex *Dipturus nasuta* (as *Raja nasuta*)
Acanthobothrium westi Vardo-Zalik & Campbell, 2011 ex *Rostroraja texana* (as *Raja texana*)
Acanthobothrium woodsholei Baer, 1948 ex *Bathytoshia centroura* (as *Dasyatis centrura* [sic])
Acanthobothrium xiamenensis Yang & Lin, 1994 ex *Rhynchobatus djiddensis**
Acanthobothrium zainali Fyler & Caira, 2006 ex *Urogymnus polylepis* (as *Himantura chaophraya*)
Acanthobothrium zapterycum Núñez, 1971 ex *Zapteryx brevirostris*
***Acanthobothrium zimmeri* Fyler, Caira & Jensen, 2009** ex *Urogymnus acanthobothrium* (as *Himantura* sp.)
Acanthobothrium zschokkei Baer, 1948 ex *Torpedo torpedo* (as *Torpedo ocellata*)
Acanthobothroides Brooks, 1977
Acanthobothroides thorsoni Brooks, 1977 (type) ex *Styracura schmardae* (as *Himantura schmardae*)
Acanthobothroides pacificus Marques, Brooks & Ureña, 1996 ex *Styracura pacifica* (as *Himantura pacifica*)
Megalonchos Baer & Euzet, 1962
Megalonchos mandleyi (Southwell, 1927) Baer & Euzet, 1962 (type) ex *Chaenogaleus macrostoma* (as *Hemigaleus balfouri*)
Megalonchos shawae Caira, Reyda & Mega, 2007 ex *Hemipristis elongatus*
Megalonchos sumansinghai Caira, Reyda & Mega, 2007 ex *Hemipristis elongatus*
New genus 8 *sensu* Caira et al. (2014)
New genus 8 n. sp. 1 *sensu* Caira et al. (2014) ex *Pristis clavata*
Onchobothrium de Blainville, 1828
Onchobothrium pseudouncinatum de Beauchamp, 1905 (type) ex *Raja asterias* (as *Raja punctata*)
Onchobothrium antarcticum Wojciechowska, 1990 ex *Bathyraja eatonii*
Onchobothrium convolutum (Yoshida, 1917) Southwell, 1925 ex *Mustelus manazo*
Onchobothrium farmeri (Southwell, 1911) Southwell, 1930 ex *Brevitrygon walga** (as *Himantura walga*)
Onchobothrium magnum Campbell, 1977 ex *Bathyraja richardsoni*
Onchobothrium schizacanthium Lönnberg, 1893 ex "Hai" [likely *Ginglymostoma* or *Chiloscyllium*]
Phoreiobothrium Linton, 1889
Phoreiobothrium lasium Linton, 1889 (type) ex *Carcharhinus obscurus* (as *Carcharias obscurus*)
Phoreiobothrium anticaporum Caira, Richmond & Swanson, 2005 ex *Negaprion brevirostris*
Phoreiobothrium blissorum Caira, Richmond & Swanson, 2005 ex *Carcharhinus plumbeus*
Phoreiobothrium exceptum Linton, 1924 ex *Sphyrna zygaena* (as *Cestracion zygaena*)
***Phoreiobothrium jahki* Caira & Jensen, 2015** ex *Rhizoprionodon* cf. *acutus* 3 *sensu* Naylor et al. (2012a)
Phoreiobothrium lewinense Caira, Richmond & Swanson, 2005 ex *Sphyrna lewini* 1 *sensu* Naylor et al. (2012a)
Phoreiobothrium manirei Caira, Healy & Swanson, 1996 ex *Sphyrna mokarran*
***Phoreiobothrium nadiae* Caira & Jensen, 2015** ex *Rhizoprionodon* cf. *acutus* 1 *sensu* Naylor et al. (2012a)
Phoreiobothrium pectinatum Linton, 1924 ex *Sphyrna zygaena* (as *Cestracion zygaena*)
Phoreiobothrium perilocrocodilus Caira, Richmond & Swanson, 2005 ex *Negaprion acuteness*
Phoreiobothrium puriensis Srivastav & Capoor, 1982 ex *Eusphyra blochii* (as *Zygaena blochii*)
Phoreiobothrium robertsoni Caira, Richmond & Swanson, 2005 ex *Carcharhinus brachyurus*
***Phoreiobothrium swaki* Caira & Jensen, 2015** ex *Rhizoprionodon* cf. *acutus* 2 *sensu* Naylor et al. (2012a)
Phoreiobothrium tiburonis Cheung, Nigrelli & Ruggieri, 1982 ex *Sphyrna tiburo*

Pinguicollum Riser, 1955
  Pinguicollum pinguicollum (Sleggs, 1927) Riser, 1955 (type) ex "skate"
Platybothrium Linton, 1890 (syn. *Dicranobothrium* Euzet, 1953)
  Platybothrium cervinum Linton, 1890 (type) ex *Carcharhinus obscurus*
  Platybothrium angelbahiense Healy, 2003 ex *Carcharhinus leucas*
  Platybothrium auriculatum Yamaguti, 1952 ex *Prionace glauca*
  Platybothrium coshtaprum Healy, 2003 ex *Carcharhinus plumbeus*
  Platybothrium harpago (Euzet, 1953) Healy, 2003 ex *Negaprion brevirostris*
  Platybothrium hypoprioni Potter, 1937 ex *Negaprion brevirostris* (as *Hypoprion brevirostris*)
  Platybothrium jondoeorum Healy, 2003 ex *Carcharhinus melanopterus*
  Platybothrium kirstenae Healy, 2003 ex *Carcharhinus obscurus*
  Platybothrium spinulifera Southwell, 1912 ex *Galeocerdo cuvier*
  Platybothrium tantulum Healy, 2003 ex *Sphyrna lewini*
Potamotrygonocestus Brooks & Thorson, 1976
  Potamotrygonocestus magdalenensis Brooks & Thorson, 1976 (type) ex *Potamotrygon magdalenae*
  Potamotrygonocestus amazonensis Mayes, Brooks & Thorson, 1981 ex *Potamotrygon orbignyi* (as *Potamotrygon circularis*)
  Potamotrygonocestus chaoi Marques, Brooks & Araujo, 2003 ex *Plesiotrygon iwamae*
  Potamotrygonocestus fitzgeraldae Marques, Brooks & Araujo, 2003 ex *Paratrygon aiereba*
  Potamotrygonocestus marajoara Luchetti, Marques & Charvet-Almeida, 2008 ex *Plesiotrygon iwamae*
  Potamotrygonocestus maurae Marques, Brooks & Araujo, 2003 ex *Potamotrygon orbignyi*
  Potamotrygonocestus orinocoensis Brooks, Mayes & Thorson, 1981 ex *Potamotrygon orbignyi* (as *Potamotrygon reticulatus*)
  Potamotrygonocestus travassosi Rego, 1979 ex *Potamotrygon orbignyi* (as *Paratrygon hystrix* [sic])
Prosobothrium Cohn, 1902 (syn. *Ichthyotaenia* Linton, 1924; *Lintoniella* Woodland, 1927)
  Prosobothrium armigerum Cohn, 1902 (type) ex *Squalus acanthias**
  Prosobothrium adherens (Linton, 1924) Riser, 1955 ex *Sphyrna zygaena* (as *Cestracion zygaena*)
  Prosobothrium japonicum Yamaguti, 1934 ex *Prionace glauca*
***Triloculatum* Caira & Jensen, 2009**
  Triloculatum triloculatum (Linton, 1901) **Caira & Jensen, 2009** (type) ex *Carcharhinus obscurus*
  ***Triloculatum andersonorum* Caira & Jensen, 2009** ex *Negaprion acutidens*
  ***Triloculatum bullardi* Caira & Jensen, 2009** ex *Carcharhinus brevipinna*
  ***Triloculatum geeceearelensis* Caira & Jensen, 2009** ex *Carcharhinus isodon*
  ***Triloculatum jodyi* Caira & Jensen, 2009** ex *Carcharhinus acronotus*
  ***Triloculatum oregontwoae* Caira & Jensen, 2009** ex *Carcharhinus plumbeus*
Uncibilocularis Southwell, 1925
  Uncibilocularis trygonis (Shipley & Hornell, 1906) Southwell, 1925 (type) ex *Brevitrygon walga** (as *Trygon walga*)
  Uncibilocularis loreni Jensen & Caira, 2008 ex *Pastinachus ater* (as *Pastinachus* cf. *sephen*)
  Uncibilocularis okei Jensen & Caira, 2008 ex *Pastinachus ater* (as *Pastinachus* cf. *sephen*)
  Uncibilocularis sidocymba Jensen & Caira, 2008 ex *Himantura australis* (as *Himantura uarnak*)
  Uncibilocularis squireorum Jensen & Caira, 2008 ex *Himantura australis* (as *Himantura uarnak*)

SPECIES *INCERTAE SEDIS*

  Uncibilocularis aurangabadensis Deshmukh & Shinde, 1975 ex *Stromateus* sp. (Perciformes)
  Uncibilocularis indiana Jadhav, Shinde, Muralidhar & Mohekar, 1989 ex *Telatrygon zugei* (as *Trygon zugei*)
  Uncibilocularis indica Subhapradha, 1955 ex *Chiloscyllium griseum*
  Uncibilocularis plagiosumae Dhole, Waghmare, Chavan, & Abdar, 2012 ex *Chiloscyllium plagiosum*
  Uncibilocularis somnathii Deshmukh, 1979 ex *Gymnura micrura** (as *Pteroplatea micrura*)

16 Phyllobothriidea
Caira, Jensen, Waeschenbach, Olson & Littlewood, 2014

By
Timothy R. Ruhnke[1], Janine N. Caira, and Maria Pickering

PHYLLOBOTHRIIDEA AS THEY WERE KNOWN PRIOR TO THE PBI PROJECT

Diversity and Classification. The formal taxonomic concept of the Phyllobothriidea did not exist prior to the initiation of the PBI project in 2008, which somewhat complicates discussion of the nature of this order prior to 2008. Nonetheless, because the Phyllobothriidea were essentially born out of the tetraphyllidean family Phyllobothriidae Braun, 1900, the history of this family is relevant to the history of the order. The group has its origin with van Beneden's (1850; pg. 182) section Phyllobothriens, which he established for tetraphyllideans with conspicuous, unarmed "Bothridies molles" (i.e., soft bothridia). The group was treated as the subfamily Phyllobothidea [sic] Carus, 1863 by Carus (1863; pg. 481) to house tetraphyllideans with "Saugnäpfe sind stets weich und haben weder Stacheln noch Haken" (i.e., with bothridia that are soft and unarmed). In the last volume of his 1894–1900 treatment of cestodes, Braun (1900; pg. 1701) elevated the group to family level as the Phyllobothriidae, which he diagnosed as follows: "Scolex unbewaffnet, mit vier meist gestielten oder auch sessilen Bothridien, welche einfach oder in Areolen getheilt oder mit accessorischen Saugnäpfen besetzt sein können. Hals vorhanden oder fehlend. Genitalpori randständing, einseitig oder alternirend. Eier oft spindelförmig." Essentially, Braun considered the group to house tetraphyllideans with stalked or sessile bothridia that were either simple, divided into loculi (in various ways), or that possessed accessory suckers. A neck was present or not. The genital pores were marginal and unilateral or alternating.

Braun's (1900) extremely broad concept of the family was somewhat problematic because the variety of scolex forms on which his concept was based applied to many of the genera parasitizing elasmobranchs. Linton (1924; pg. 15) noted this issue stating "In common with others who attempted to classify Selachian Cestodes I have experienced much difficulty with those genera of the Phyllobothriidae which are characterized by having a scolex with four unarmed bothridia, each provided with an auxiliary sucker at its anterior end, and without costae." Southwell (1925; pg. 144) provided the first comprehensive review of the family, with the following familial diagnosis (essentially translated from Braun [1900]): "Head unarmed, with four pedunculated or sessile bothridia, which are simple, complicated, or divided up into areolae, or furnished with accessory suckers. Neck present or absent. Genital pores marginal, unilateral, or regularly or irregularly alternating; eggs often spindle-shaped; segments frequently separate from the chain before maturity." Southwell (1925) recognized

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[1] Corresponding author (ruhnketr@wvstateu.edu)

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TABLE 1. Comparison of Phyllobothriidae/Phyllobothriidea generic membership across studies. * *Sensu* Caira et al. (2014).

Euzet (1959)	**Yamaguti (1959)**	**Schmidt (1986)**	**Euzet (1994)**	**Ruhnke (2011)**	**Caira et al. (2014)**	**This chapter**
Anthobothrium	*Anthobothrium*	*Anthobothrium*	*Anthobothrium*	*Bibursibothrium*	*Alexandercestus*	*Alexandercestus*
Calyptrobothrium	*Aocobothrium*	*Aocobothrium*	*Calyptrobothrium*	*Calyptrobothrium*	*Bibursibothrium*	*Bibursibothrium*
Caulobothrium	*Carpobothrium*	*Carpobothrium*	*Carpobothrium*	*Cardiobothrium*	*Calyptrobothrium*	*Bilocularia*
Ceratobothrium	*Cyatocotyle*	*Caulobothrium*	*Caulobothrium*	*Chimaerocestos*	*Cardiobothrium*	*Calyptrobothrium*
Clydonobothrium	*Dinobothrium*	*Clydonobothrium*	*Ceratobothrium*	*Clistobothrium*	*Chimaerocestos*	*Cardiobothrium*
Crossobothrium	*Echeneibothrium*	*Cyatocotyle*	*Clistobothrium*	*Crossobothrium*	*Clistobothrium*	*Chimaerocestos*
Dinobothrium	*Gastrolecithus*	*Duplicibothrium*	*Clydonobothrium*	*Doliobothrium*	*Crossobothrium*	*Clistobothrium*
Echeneibothrium	*Marsupiobothrium*	*Echeneibothrium*	*Crossobothrium*	*Flexibothrium*	*Flexibothrium*	*Crossobothrium*
Monorygma	*Monorygma*	*Gastrolecithus*	*Dinobothrium*	*Marsupiobothrium*	*Marsupiobothrium*	*Doliobothrium*
Orygmatobothrium	*Myzophyllobothrium*	*Glyphobothrium*	*Duplicibothrium*	*Monorygma*	*Nandocestus*	*Flexibothrium*
Phyllobothrium	*Orygmatobothrium*	*Marsupiobothrium*	*Echeneibothrium*	*Nandocestus*	*Orectolobicestus*	*Guidus*
Rhabdotobothrium	*Pelichnibothrium*	*Mixophyllobothrium*	*Gastrolecithus*	*Orectolobicestus*	*Orygmatobothrium*	*Hemipristicola*
Rhinebothrium	*Phyllobothrium*	*Monorygma*	*Glyphobothrium*	*Orygmatobothrium*	*Paraorygmatobothrium*	*Marsupiobothrium*
Scyphophyllidium	*Pithophorus*	*Myzophyllobothrium*	*Marsupiobothrium*	*Paraorygmatobothrium*	*Pelichnibothrium*	*Monorygma*
Sphaerobothrium	*Pseudanthobothrium*	*Orygmatobothrium*	*Monorygma*	*Phyllobothrium*	*Phyllobothrium*	*Nandocestus*
Thysanocephalum	*Reesium*	*Pelichnibothrium*	*Myzocephalus*	*Ruhnkecestus*	*Ruhnkecestus*	*Orectolobicestus*
Tritaphros	*Rhodobothrium*	*Phormobothrium*	*Myzophyllobothrium*	*Scyphophyllidium*	*Scyphophyllidium*	*Orygmatobothrium*
	Scyphophyllidium	*Phyllobothrium*	*Orygmatobothrium*	*Thysanocephalum*	*Thysanocephalum*	*Paraorygmatobothrium*
		Pithophorus	*Pentaloculum*		New genus 10*	*Pelichnibothrium*
		Pseudanthobothrium	*Phormobothrium*			*Phyllobothrium*
		Reesium	*Phyllobothrium*			*Ruhnkecestus*
		Rhabdotobothrium	*Pithophorus*			*Scyphophyllidium*
		Rhinebothrium	*Pseudanthobothrium*			*Thysanocephalum*
		Rhinebothroides	*Rhabdotobothrium*			*Trilocularia*
		Rhodobothrium	*Rhinebothrium*			New genus 10*
		Scyphophyllidium	*Rhinebothroides*			New genus 18
		Spongiobothrium	*Rhodobothrium*			New genus 20
			Scyphophyllidium			
			Thysanocephalum			
			Trilocularia			
			Tritaphros			
			Zyxibothrium			

species from 28 genera as members of the family. However, he distilled those 28 genera through synonymization into the following eight genera: *Anthobothrium* van Beneden, 1850, *Aocobothrium* Mola, 1907, *Carpobothrium* Shipley & Hornell, 1906, *Echeneibothrium* van Beneden, 1850, *Myzophyllobothrium* Shipley & Hornell, 1906, *Orygmatobothrium* Diesing, 1863, *Phyllobothrium* van Beneden, 1850, and *Pithophorus* Southwell, 1925. In truth, Southwell's fevered lumping hindered a better understanding of the Phyllobothriidae for several decades because the original 28 genera were each clearly diagnosable. Wardle and McLeod (1952) recognized 11 genera within the Phyllobothriidae. They made no mention of *Aocobothrium*, and, beyond the remaining seven genera recognized by Southwell (1925), they included *Dinobothrium* van Beneden, 1889, *Myzophorus* Woodland, 1934 (actually an onchoproteocephalidean), *Pelichnibothrium* Monticelli, 1889, and *Scyphophyllidium* Woodland, 1927 in the family. Subsequent treatments returned to a less expansive concept of individual genera in favor of recognition of more genera. Euzet (1959) recognized 17 genera in four subfamilies: the Phyllobothriinae, Echeneibothriinae de Beauchamp, 1905, Rhinebothriinae Euzet, 1953, and Thysanocephalinae Euzet, 1953. Yamaguti (1959) recognized 18 genera. Several decades later Schmidt (1986) recognized 27 genera. In the most recent comprehensive treatment of the family prior to 2008, Euzet (1994) considered 32 genera as valid members of the Phyllobothriidae, and organized them into the five subfamilies Echeneibothriinae, Phyllobothriinae, Rhinebothriinae, Thysanocephalinae, and Triloculariinae Yamaguti, 1959. As can be seen from Table 1, the selection of genera considered to belong to the family has differed substantially over time with only six genera (i.e., *Anthobothrium*, *Echeneibothrium*, *Monorygma*, *Orygmatobothrium*, *Phyllobothrium*, and *Scyphophyllidium*) unanimously considered to belong to the Phyllobothriidae by Euzet (1959), Yamaguti (1959), Schmidt (1986), and Euzet (1994).

An additional 14 genera were assigned to the Phyllobothriidae between Euzet's (1994) work and 2008. In chronological order, these are *Anthocephalum* Linton 1890 (resurrected by Ruhnke [1994a] from synonymy with *Phyllobothrium*); *Paraorygmatobothrium* Ruhnke, 1994 erected by Ruhnke (1994b); *Bibursibothrium* McKenzie & Caira, 1998, *Cardiobothrium* McKenzie & Caira, 1998, and *Flexibothrium* McKenzie & Caira, 1998 erected by McKenzie and Caira (1998); *Pararhinebothroides* Zamparo, Brooks & Barriga erected by Zamparo et al. (1999); *Anindobothrium* Marques, Brooks & Lasso, 2001 erected by Marques et al. (2001); *Notomegarhynchus* Ivanov & Campbell, 2002 erected by Ivanov and Campbell (2002); *Scalithrium* Ball, Neifar & Euzet, 2003 erected by Ball et al. (2003); *Orectolobicestus* Ruhnke, Caira & Carpenter, 2006 erected by Ruhnke et al. (2006a); *Guidus* Ivanov, 2006 erected by Ivanov (2006); *Ruhnkecestus* Caira & Durkin, 2006 erected by Caira and Durkin (2006); and *Nandocestus* Reyda, 2008 erected by Reyda (2008) for a species originally assigned to *Anindobothrium*. Establishment of *Prionacestus* Mete & Euzet, 1996 for adult worms collected from the blue shark, *Prionace glauca* (L.), by Mete and Euzet (1996) helped resolve the long-standing issue of the identity of *Pelichnibothrium* Monticelli, 1889, which Euzet (1994), like others before him, was unable to assign to a described adult form because it was known only from plerocercoids taken from the longsnouted lancetfish *Alepisaurus ferox* Lowe in Madeira. Scholz et al. (1998) synonymized these two genera, retaining *Pelichnibothrium* as the senior name. By 2008, the family was generally considered to house 46 valid genera.

We note that at the inception of the PBI project, all taxa included in the classification schemes of the Phyllobothriidae were distinguished from the other tetraphyllideans, and, also united by, their lack of bothridial hooks. Such groups were termed "not-A" groups by Eldredge and Cracraft (1980), who noted that such groups should always be suspected to be paraphyletic or polyphyletic.

MORPHOLOGY. As noted above, the pre-PBI project morphological concept of the Phyllobothriidae was rather broad, particularly with respect to bothridial morphology. Given the substantial reconfiguration of this group over the course of the PBI project, we believe a detailed treatment of the morphology of genera once considered to belong to the family is of limited value. However, a few examples of this morphological breadth are as follows. Bothridial variation included: simple with single loculus lacking an apical sucker as in *Anthobothrium* (see Ruhnke and Caira, 2009); simple with single loculus and an anterior sucker as in *Paraorygmatobothrium* (see Ruhnke, 1994b); simple with single loculus, an anterior sucker, and a central accessory organ, as in *Orygmatobothrium* (see Euzet, 1959); simple with single loculus, marginal loculi, and an anterior sucker as in *Anthocephalum* (see Ruhnke, 1994a); extensively foliose, posteriorly bifid single loculus with an anterior sucker as in *Phyllobothrium* (see Euzet, 1959); and stalked and facially loculated as in *Rhinebothrium* Linton, 1890 (see Euzet, 1959) and *Echeneibothrium* (see Euzet, 1959). Whereas taxa such as the latter genus exhibited a scolex with an apical myzorhynchus in the adult form, the members of most other genera did not. Proglottid anatomy was similarly variable. Testes number ranged from two, for example in *Rhinebothrium ditesticulum* Appy & Dailey, 1977 (see Appy and Dailey, 1977), to over 450, for example in *Orygmatobothrium juani* Ivanov, 2008 (see Ivanov, 2008). Genital pore position ranged in position from the anterior quarter of the proglottid in species such as *Paraorygmatobothrium exiguum* (Yamaguti, 1935) Ruhnke, 1994 (see Ruhnke, 1994b) to the posterior quarter of the proglottid as in taxa such as *Rhinebothroides campbelli* Ivanov, 2004 (see

Ivanov, 2004). The ovary was tetralobed in cross-section in taxa such as *Anthocephalum alicae* Ruhnke, 1994 (see Ruhnke, 1994a) but bilobed in taxa such as *Clistobothrium montaukensis* Ruhnke, 1993 (see Ruhnke, 1993).

PHYLOGENETIC RELATIONSHIPS. Prior to the PBI project, phylogenetic analyses of phyllobothriid taxa were limited. Caira et al. (1999, 2001) provided rigorous morphological phylogenetic assessments of targeted tetraphyllidean taxa, but their results were inconclusive in terms of the phylogenetic cohesion of the phyllobothriids. Ruhnke et al. (2006a) noted that the presence of unique types of spinitriches (i.e., serrate or gongylate gladiate spinitriches *sensu* Chervy [2009]) on the proximal and/or distal bothridial surfaces as seen with scanning electron microscopy was indicative of close affinities among *Orectolobicestus*, *Paraorygmatobothrium*, *Ruhnkecestus*, *Thysanocephalum* Linton, 1890, and perhaps also *Orygmatobothrium* and *Phyllobothrium squali* Yamaguti, 1952. The only molecular phylogenetic studies that included more than a single representative of the family were those of Olson and Caira (1999) and Olson et al. (1999). The former study, which was based on 18S rDNA and Ef1-α sequence data, included only a single species each of *Anthobothrium* and *Rhinebothrium.* No support for close affinities between these two genera was found in trees resulting from any of the analyses of any data partitions. The analyses of Olson et al. (1999), which were based on 18S rDNA data for one or more species of nine genera assigned to the Phyllobothriidae at that time, yielded trees in which phyllobothriid genera were distributed among genera then assigned to several other unrelated families. Their results did, however, suggest the existence of shark-hosted and ray-hosted clades of tetraphyllideans, each of which included representatives of the Phyllobothriidae.

HOST ASSOCIATIONS. Given the broad definition of the Phyllobothriidae at the inception of the PBI project, it is not surprising that members of the family had been reported from a wide array of elasmobranch taxa. Based on Euzet's (1994) concept of the family and its 32 genera, phyllobothriids had been reported from members of the shark orders Carcharhiniformes, Hexanchiformes, Lamniformes, Orectolobiformes, and Squaliformes, as well as from the batoid orders Myliobatiformes, Rajiformes, Rhinopristiformes, and Torpediniformes. With their erection of three new genera from the longnose sawshark, *Pristiophorus cirratus* (Latham), McKenzie and Caira (1998) added the Pristiophoriformes to the list of shark orders reported to host phyllobothriids. It is of particular note that Marques et al.'s (2001) erection of *Anindobothrium* expanded the limited selection of myliobatiform batoids known to host species then assigned to the Phyllobothriidae to include freshwater stingrays (Potamotrygonidae Garman). Once again, given the substantial reconfiguration of this group that occurred over the course of the PBI project, a detailed treatment of the host associations of genera once considered to belong to the family is of limited value. Nonetheless it was becoming clear by 2008 that phyllobothriid species generally exhibit oioxenous specificity (*sensu* Euzet and Combes [1980]) for their elasmobranch hosts.

GEOGRAPHIC DISTRIBUTION. Prior to 2008, the Phyllobothriidae as a group was considered to have a cosmopolitan distribution, with one or more species having been reported from 11 of Spalding et al.'s (2007) 12 marine realms of the world. The exception was Temperate Southern Africa, which had been essentially unexplored by those interested in the cestodes of elasmobranchs prior to the PBI project. In fact, the Southern Hemisphere in general had received relatively little attention. As noted by Schmidt in 1986, the majority of the records of phyllobothriids then known came from the Northern Hemisphere. However, once again, a detailed treatment of the geographic distribution of taxa once assigned to the family is of limited use given that many of these taxa no longer belong to the group.

CURRENT STATUS OF THE PHYLLOBOTHRIIDEA

Diversity and Classification. Substantial reconfiguration of the classification of the order Tetraphyllidea as a whole took place over the course of the PBI project. This work had a profound impact on the membership and taxonomic status of the Phyllobothriidae. Among the most consequential of these efforts was establishment of the order Rhinebothriidea by Healy et al. (2009) for a selection of phyllobothriid genera possessing stalked bothridia, parasitic in batoids. Among described genera, Healy et al. (2009) advocated that *Anthocephalum*, *Echeneibothrium*, *Rhabdotobothrium* Euzet, 1953, *Rhinebothrium*, *Rhinebothroides* Mayes, Brooks & Thorson, 1981, *Rhodobothrium* Linton, 1889, *Scalithrium*, and *Spongiobothrium* Linton, 1889 be transferred from the Phyllobothriidae to their new order, noting that *Clydonobothrium* Euzet, 1959, *Phormobothrium* Alexander, 1963, *Pseudanthobothrium* Baer, 1946, and *Tritaphros* Lönnberg, 1889 were likely to also be found to belong to the order. The Rhinebothriidea have been expanded further since to include a number of additional genera. Readers are referred to Ruhnke et al. (2017) (Chapter 17 this volume) for a more complete treatment of the Rhinebothriidea.

Membership in the Phyllobothriidae was further refined by Ruhnke (2011) in his monograph on the family. In that work, he examined all genera ever placed in the Phyllobothriidae and determined that only the type genus, *Phyllobothrium*, should be considered unambiguously as a valid member of the family. However, he treated *Bibursibothrium*, *Calyptrobothrium*, *Cardiobothrium*, *Clistobothrium* Ruhnke, 1993, *Crossobothrium* Linton, 1889, the then newly described *Doliobothrium* Caira, Malek & Ruhnke, 2011 (see below), *Flexibothrium*, *Marsupiobothrium* Yamaguti, 1952, *Monorygma* Diesing, 1863, *Nandocestus*, *Orectolobicestus*, *Orygmatobothrium*, *Paraorygmatobothrium*, *Ruhnkecestus*, *Scyphophyllidium* Woodland, 1927, and *Thysanocephalum* as provisional members of the family. Ruhnke (2011) treated *Chimaerocestos* Williams & Bray, 1984 as an *incertae sedi*s member of the family. Ruhnke's (2011) monograph also served to highlight the fact that sharks play a much more important role as hosts to phyllobothriids than do batoids.

Three genera discovered over the course of the PBI project (2 as part of the project) were established in the Phyllobothriidae. These are *Doliobothrium* erected by Caira et al. (2011), *Hemipristicola* Cutmore, Theiss, Bennett & Cribb, 2011 erected by Cutmore et al. (2011), and *Alexandercestus* Ruhnke & Workman, 2013 erected by Ruhnke and Workman (2013). Ruhnke (2011) had already included the first of these in the Phyllobothriidae. Ruhnke and Workman (2013) subsequently provided molecular phylogenetic evidence in the form of partial 28S rDNA sequence data for the provisional inclusion of both *Alexandercestus* and *Hemipristicola* in the family.

In 2014, inspired in part by the work of Ruhnke (2011), but also by the novel results from their molecular work, Caira et al. (2014) erected the order Phyllobothriidea to house a series of phyllobothriid genera with simple bothridia bearing an apical sucker that chiefly parasitize sharks. Their list of genera for definitive or potential inclusion in the new order included *Phyllobothrium* and 14 of the 16 genera provisionally assigned to the Phyllobothriidae by Ruhnke (2011). In fact, the concepts of Ruhnke (2011) and Caira et al. (2014) differed essentially only in that Caira et al. (2014) did not recognize *Doliobothrium* or *Monorygma* as members of the Phyllobothriidea, but unlike Ruhnke (2011), they included *Pelichnibothrium* and *Alexandercestus* in the group. The analyses of Caira et al. (2014) also included a specimen of an undescribed genus from a hammerhead shark, which they referred to as New genus 10. That taxon is also considered here to belong to the order.

Here we expand the concept of the Phyllobothriidea somewhat further. We consider it to include all genera assigned, either formally or provisionally, to the Phyllobothriidae by Ruhnke (2011) (including *Doliobothrium* and *Monorygma*) and Ruhnke and Workman (2013) (i.e., to include *Alexandercestus* and *Hemipristicola*), as well as *Pelichnibothrium* following Caira et al. (2014). Moreover, the poorly known *Bilocularia* Obersteiner, 1914, considered a *genus inquirendum* by Euzet (1994), is also here considered a member of the order because new material collected as part of PBI fieldwork in the Azores confirms its validity. In addition, *Trilocularia* and *Guidus*, both of which have been assigned to the Phyllobothriidae by previous authors (Euzet, 1994 and Ivanov, 2006, respectively), but were treated as *incertae sedis* in terms of their membership in the Phyllobothriidae by Ruhnke (2011), are treated here at least as provisional members of the order.

In summary, in terms of the fates of the 46 genera assigned to the Phyllobothriidae at the inception of the PBI project, 14 are now members of the Rhinebothriidea (see Chapter 17 this volume, Ruhnke et al., 2017) and 13 are considered among the "tetraphyllidean" relics (see Chapter 20 this volume, Caira et al., 2017). With the addition of five newly described or resurrected genera, the Phyllobothriidea now houses 24 described and three undescribed genera (see below and Tables 1 and 4). We note that the issues surrounding the phylogenetic relationships and possibly also the monophyly of the Phyllobothriidea as treated here may ultimately lead to further reconfiguration of the order.

Fieldwork conducted as part of the PBI project led to the discovery of multiple new species of phyllobothriideans, eight of which were described over the course of the project. These consisted of two new species of *Alexandercestus* (see Ruhnke and Workman, 2013), two new species of *Crossobothrium* (see Ivanov, 2009), one new species of *Doliobothrium* (see Caira et al., 2011), two new species of *Paraorygmatobothrium* (see Malek et al., 2010), and one new species of *Trilocularia* (see Pickering and Caira, 2012). In addition, although not formally part of the project, in 2011, Cutmore and colleagues described a new species of *Hemipristicola*. In total, the 24 described genera of phyllobothriideans now house a total of 69 valid species (see Table 4). Among these, the genus *Paraorygmatobothrium*, whose members parasitize carcharhiniform sharks, is by far the most speciose with 21 valid species.

Material of tens of additional new species of phyllobothriideans was collected as a result of PBI fieldwork but has not yet been investigated in detail; many of these taxa are also members of *Paraorygmatobothrium*. Given the host associations of the various phyllobothriidean genera, we predict the latter genus will remain the most speciose in the order given that tens of species of carcharhinid sharks have yet to be examined for cestodes. However, numerous new species were also discovered parasitizing genera of elasmobranchs not previously reported to host phyllobothriideans. These are treated below in the section on host associations.

An additional 29 species are treated here as *incertae sedis* because, although we have evidence that they represent unique species, each is not currently assigned to the appropriate genus, or possibly even order. We note that all but nine of these species are currently assigned to *Phyllobothrium*; it seems likely that many of these species, and especially many of those that parasitize batoids, will ultimately be found to belong to genera in the Rhinebothriidea.

In combination, morphological and molecular work conducted on newly collected material of adult cestodes supports the existence of several additional undescribed genera of phyllobothriideans. These include New genus 10 of Caira et al. (2014; fig. 1F) from hammerhead sharks, New genus 18 which includes the species previously described as *Phyllobothrium squali* Yamaguti, 1952 (Fig. 1K) and its relatives from squaliform sharks, and New genus 20 (Fig. 1L) from skates. Moreover, work conducted in the Azores and Madeira yielded larval and juvenile cestodes that appear to represent additional novel genera, for they differ from known adult phyllobothriidean taxa based on sequence data for the D1–D3 region of the 28S rDNA gene, and in most cases also in terms of scolex morphology. However, as noted below, substantial uncertainty remains concerning the monophyly and phylogenetic relationships of the phyllobothriideans. We have therefore refrained from formally establishing these additional new genera and also from developing a family-level classification scheme for the order at this time. In order to achieve a classification based on monophyletic groups it would seem prudent to formalize the phylogenetic relationships and membership of the order before proceeding with such an endeavor.

MORPHOLOGY. The relatively simple configuration of the bothridia (Fig. 1) persists as a feature that is shared by phyllobothriideans. However, the possibility that this represents an ancestral similarity, and thus should not be used to unite members of the order, remains to be investigated in more detail. The bothridia are unarmed and the anterior margin of each typically bears a sucker (e.g., *Doliobothrium*) or a loculus (e.g., *Monorygma*). While the bothridia of many genera are round to oval and relatively flat (e.g., *Orygmatobothrium*, Fig. 1G; *Paraorygmatobothrium*, Fig. 1H; New genus 18, Fig. 1K), those of other groups are highly foliose (e.g., *Clistobothrium*, Fig. 1B; *Phyllobothrium*, Fig. 1I; New genus 20, Fig. 1L) or pouch-like (e.g., *Guidus*, see Ivanov, 2006, fig. 15; *Doliobothrium* Fig. 1D). In the latter case, the pouches bear proximal openings and actually constitute tubes (see Caira et al., 2011, figs. 1–3). The bothridia of some taxa even bear marginal (e.g., *Chimaerocestus*, Fig. 1A; *Orectolobicestus*, Fig. 1F; New genus 20, Fig. 1L) or facial (e.g., *Trilocularia*, Fig. 1J) loculi. The presence of serrate or gongylate gladiate spinitriches on the scolex and scutes comprised of densely packed capilliform filitriches on the cephalic peduncle remain features uniting a subset of phyllobothriidean genera that is now known to include *Doliobothrium*, *Hemipristicola*, *Nandocestus*, *Paraorygmatobothrium*, *Orectolobicestus*, *Orygmatobothrium*, *Ruhnkecestus*, *Thysanocephalum*, and possibly also *Alexandercestus*. It is intriguing that the close affinities of the majority of these genera were also supported by molecular phylogenetic analyses (see below). Laciniate proglottids are found in a few taxa (e.g., *Chimaerocestus*, Fig. 1A; *Crossobothrium*). Most taxa are euapolytic or anapolytic in terms of the developmental stage at which their proglottids drop from the strobila; *Trilocularia* is exceptional in being hyperapolytic. In general, the proglottids possess numerous testes; a post-poral field of testes is nearly always present (Fig. 2). The genital pore is lateral and is almost always located in the anterior half of the proglottid. The vagina opens into the genital atrium anterior to the cirrus-sac. The vitellarium is follicular; the vitelline follicles are generally arranged in two lateral fields of multiple columns. In a few cases, the vitelline fields may encroach on the mid-line of the proglottid (e.g., *Paraorygmatobothrium janineae* Ruhnke, Healy & Shapero, 2006 and *P. kirstenae* Ruhnke, Healy & Shapero, 2006; see Ruhnke et al., 2006b, figs. 3 and 8, respectively). In rare cases, the vitelline follicles are circum-medullary (e.g., *Nandocestus guariticus* [Marques, Brooks & Lasso, 2001] Reyda, 2008; see Reyda, 2008, fig. 2). Most phyllobothriideans are less than 30 mm in length, but a few species, such as *Phyllobothrium riseri* Ruhnke, 1996, can attain a length of over 10 cm (Ruhnke, 2011). Linton (1890) reported specimens of *Thysanocephalum thysanocephalum* (Linton, 1890) Braun, 1900 that were over 1 m in length! Readers are directed to the monograph of Ruhnke (2011) for more detailed treatments of the morphology of phyllobothriidean genera and species.

PHYLOGENETIC RELATIONSHIPS. The analyses of Caira et al. (2014), which were based on complete 18S rDNA and partial (D1–D3) 28S rDNA sequence data, serve as the most comprehensive investigation of phyllobothriidean interrelationships published to date. Their

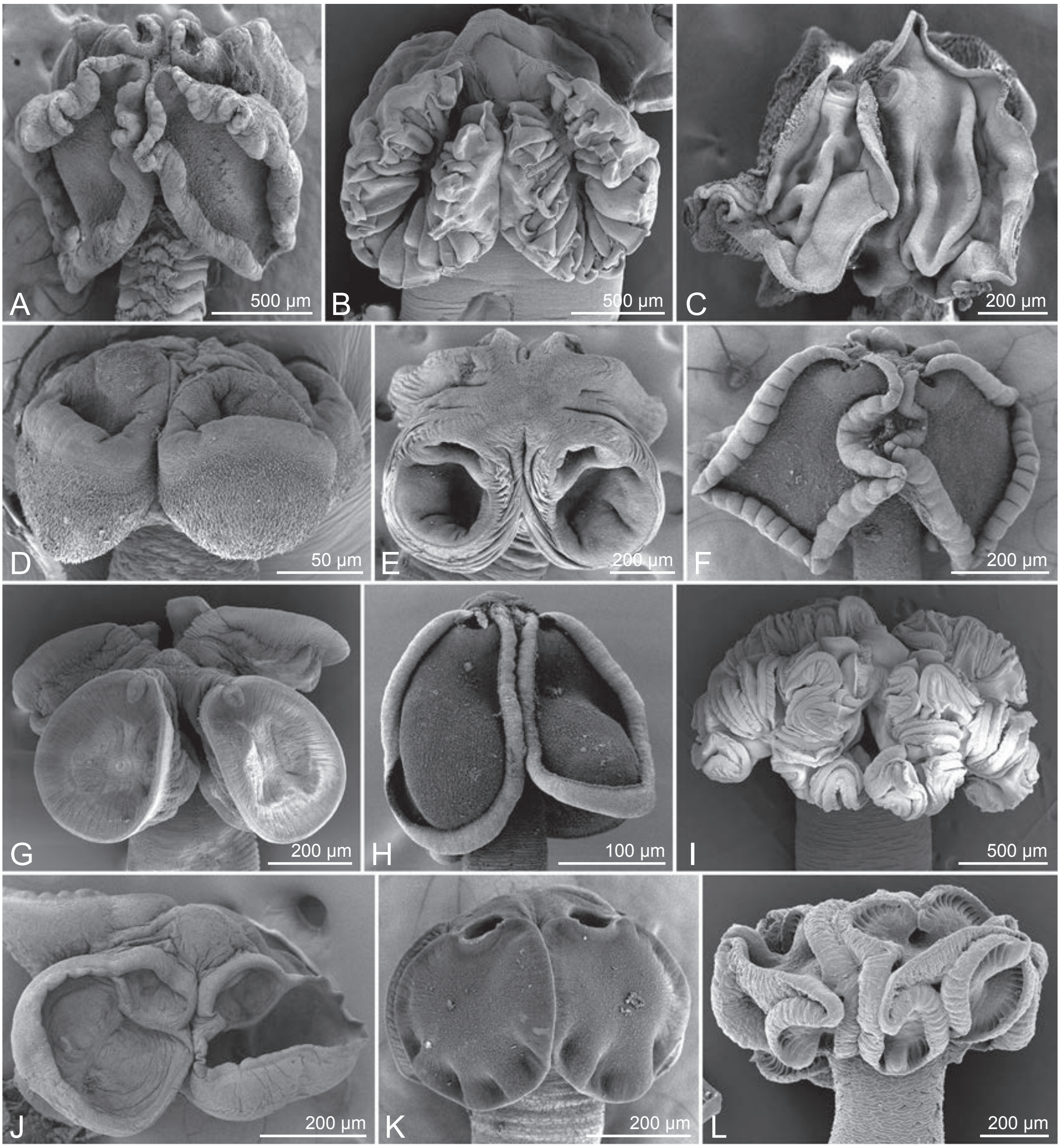

FIGURE 1. Scanning electron micrographs of scoleces of selected phyllobothriidean genera. **(A)** *Chimaerocestos* sp. ex *Rhinochimaera pacifica* from New Zealand. **(B)** *Clistobothrium montaukensis* ex *Isurus oxyrinchus* from Montauk, USA. **(C)** *Crossobothrium laciniatum* ex *Carcharias taurus* from the eastern Atlantic Ocean. **(D)** *Doliobothrium musculosum* ex *Rhizoprionodon* cf. *acutus* 2 (*sensu* Naylor et al. [2012a]) from Fog Bay, Australia. **(E)** *Monorygma* sp. ex *Centroscymnus coelolepis* from the Azores. **(F)** *Orectolobicestus randyi* ex *Chiloscyllium hasselti* from Mukah, Borneo. **(G)** *Orygmatobothrium* sp. ex *Mustelus asterias* from the North Sea. **(H)** *Paraorygmatobothrium* sp. ex *Carcharhinus amblyrhynchoides* from the Timor Sea, Australia. **(I)** *Phyllobothrium* sp. ex *Mustelus asterias* from the North Sea. **(J)** *Trilocularia gracilis* ex *Squalus acanthias* off Rhode Island, USA. **(K)** New genus 18 *squali* ex *Squalus acanthias* off Rhode Island, USA. **(L)** New genus 20 n. sp. 1 ex *Dipturus chilensis* from Chiloé, Chile.

analyses included one or two representatives of 14 of the 24 described phyllobothriidean genera, as well as a species assigned to a taxon they referred to as New genus 10. Based on the results of their analyses, relatively high support was found for a group consisting of the following 12 genera: *Calyptrobothrium*, *Chimaerocestos*, a taxon they referred to as *Marsupiobothrium* (but that remains to be confirmed as a member of that genus), *Nandocestus*, *Orectolobicestus*, *Orygmatobothrium*, *Paraorygmatobothrium*, *Phyllobothrium*, *Ruhnkecestus*, *Scyphophyllidium*, *Thysanocephalum*, and New genus 10 (*sensu* Caira et al. {2014]). Support for inclusion of *Clistobothrium*, *Trilocularia*, and *Crossobothrium* in the order was less convincing, particularly since the latter two genera grouped with members of the tetraphyllidean family Calliobothriidae (see Chapter 20 this volume, Caira et al., 2017), although with low support. The close affinities among *Alexandercestus*, *Hemipristicola*, and *Paraorygmatobothrium*, reported by Ruhnke and Workman (2013), were also supported.

However, a series of unpublished Bayesian and maximum likelihood analyses conducted over the course of the PBI project, some elements of which were the result of dissertation work by the third author of this chapter (see Pickering, 2012), reveal potential additional instability in the phyllobothriidean relationships presented by Caira et al. (2014). These new analyses included substantially more comprehensive taxon coverage than that of the Caira et al. (2014) study, both in terms of genera and species. Perhaps most importantly, novel sequence data were generated for representatives of *Bilocularia* and *Monorygma* as well as for specimens of New genus 18 (this study) from squaliform sharks and New genus 20 (this study) from skates. Sequence data for *Alexandercestus* and *Hemipristicola* from Ruhnke and Workman (2013) were also included. The sequence data on which these analyses were based were, however, more limited than those used by Caira et al. (2014) in that they consisted of only partial (D1–D3) 28S rDNA sequence data. As a consequence, the results of our new analyses, which are summarized below, should be viewed with caution. Nonetheless, they are important to consider here for they bolster the case that future work may lead to some reconfiguration of the Phyllobothriidea.

Our new preliminary phylogenetic results suggest the following: (1) *Trilocularia* and *Crossobothrium* remain among the most problematic genera and, although never highly supported, they routinely group with the tetraphyllidean hooked family Calliobothriidae, rather than with the other phyllobothriideans. (2) *Monorygma, Bilocularia*, and *Calyptrobothrium* were typically found to group with several undescribed genera from sharks and skates; *Chimaerocestus* most commonly grouped as the sister taxon to this clade. (3) A clade consisting of *Alexandercestus*, *Hemipristicola*, *Nandocestus*, *Orectolobicestus*, *Paraorygmatobothrium*, *Ruhnkecestus*, *Scyphophyllidium*, *Thysanocephalum*, and the taxon referred to as *Marsupiobothrium* by Caira et al. (2014) was routinely recovered. (4) The relationships of *Orygmatobothrium*, *Phyllobothrium*, and *Clistobothrium* (including a species newly collected from the crocodile shark, *Pseudocarcharias kamoharai* [Matsubara]) were generally unresolved with respect to the other phyllobothriidean taxa and also relative to one another.

In terms of how best to proceed with resolving the interrelationships of the Phyllobothriidea, more dense taxon sampling of all included genera is likely to improve the situation, as is the addition of representatives of the six genera (i.e., *Bibursibothrium*, *Cardiobothrium*, *Doliobothrium*, *Flexibothrium*, *Guidus*, and *Pelichnibothrium*) currently assigned to the order for which material preserved properly for molecular work has not yet been collected. Nonetheless, data from additional molecular markers are likely to be required to fully resolve these relationships. We note that, although we could have chosen to retain a number of the more problematic phyllobothriidean genera in the category of “tetraphyllidean”

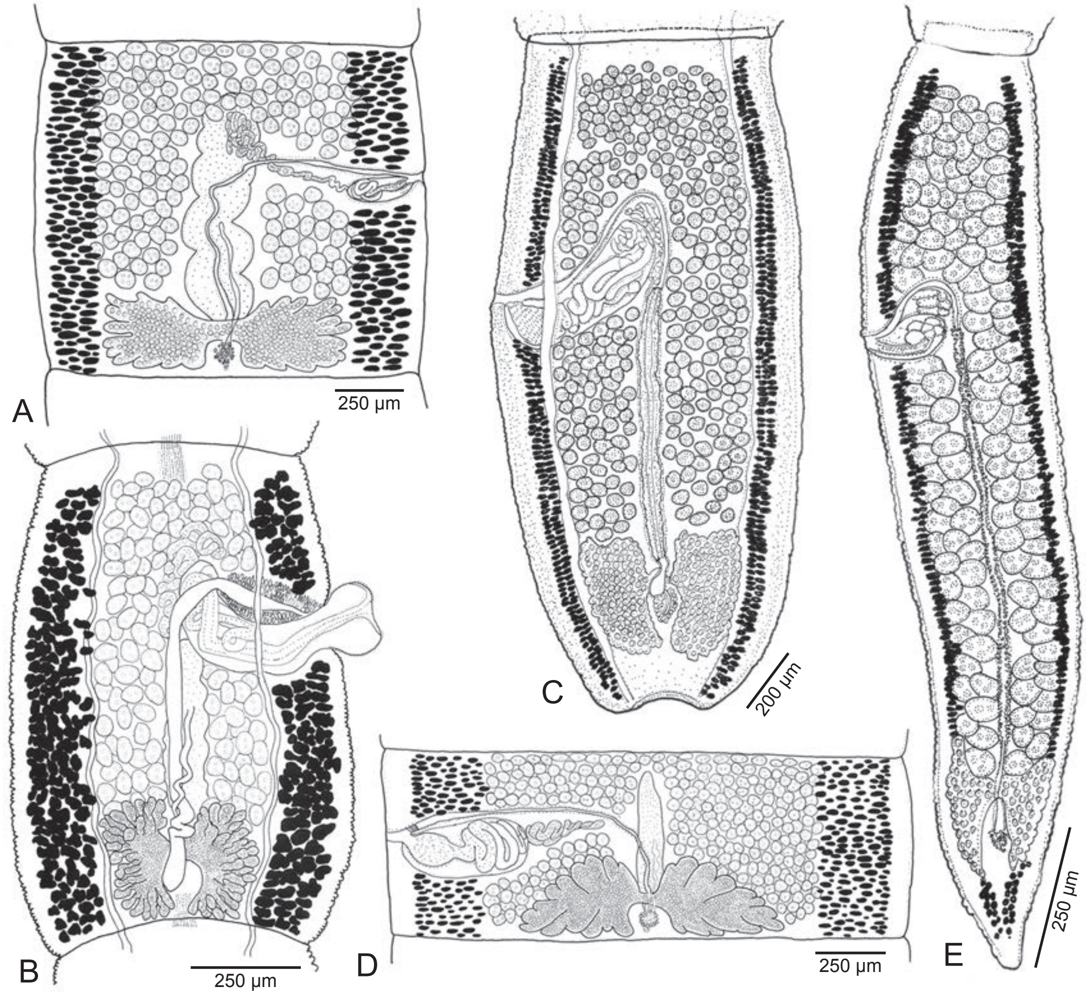

FIGURE 2. Line drawings of proglottid anatomy of selected phyllobothriidean genera. **(A)** New genus 18 *squali* (redrawn from Euzet [1959]). **(B)** *Clistobothrium carcharodoni* ex *Carcharodon carcharias (*redrawn from Dailey and Vogelbein [1990]). **(C)** *Orygmatobothrium juani* ex *Mustelus fasciatus (*redrawn from Ivanov [2008]). **(D)** *Phyllobothrium lactuca* ex *Mustelus mustelus* (redrawn from Euzet [1959]). **(E)** *Paraorygmatobothrium roberti* ex *Negaprion brevirostris* (redrawn from Ruhnke and Thompson [2006]).

relics, we have not done so. This is because we believe the morphology and host associations of the genera treated here are sufficient to consider them members of the Phyllobothriidea, despite the uncertainty surrounding the results of existing molecular analyses.

HOST ASSOCIATIONS. In total, 34 of the 69 valid phyllobothriidean species (i.e., ~50%), belonging to ten of the 24 valid phyllobothriidean genera parasitize carcharhiniform sharks (collectively in the genera *Carcharhinus* Blainville, *Galeocerdo* Müller & Henle, *Galeus* Schaeffer, *Hemigaleus* Bleeker, *Hemipristis* Agassiz, *Mustelus* Linck, *Negaprion* Whitley, *Prionace* Cantor, *Rhizoprionodon* Whitley, *Scoliodon* Müller & Henle, and *Triakis* Müller & Henle); this number is 35 if New genus 10 n. sp. 1 (*sensu* Caira et al. [2014]) is included for that species parasitizes the hammerhead shark, *Sphyrna lewini* 1 (*sensu* Naylor et al. [2012a]). Beyond carcharhiniform sharks, seven species in four genera of phyllobothriideans parasitize lamniform sharks (of the genera *Alopias* Rafinesque, *Carcharodon* Smith in Müller & Henle, *Isurus* Rafinesque, and *Odontaspis* Agassiz) and seven species, six of which are members of *Orectolobicestus* and one of *Paraorygmatobothrium*, parasitize orectolobiform sharks (*Chiloscyllium* Müller & Henle and *Orectolobus* Bonaparte). Squaliform sharks (of the genera *Centrophorus* Müller & Henle, *Somniosus* Lesueur, and *Squalus* L.) host a total of six species in three described phyllobothriidean genera. A single species of the Pristiophoriformes hosts three species, each of which belongs to a monotypic genus. Collectively, four of the five species of *Crossobothrium* parasitize all three genera of hexanchiform sharks; this is the only genus of phyllobothriideans that parasitizes this order of sharks. In contrast, only seven of the 69 valid species of phyllobothriideans parasitize batoids. The monotypic *Nandocestus* parasitizes a species of freshwater stingray (Potamotrygonidae Garman, Myliobatiformes); all three species of *Calyptrobothrium* parasitize electric rays (Torpediniformes), and all three species of *Guidus* parasitize skates of the genus *Bathyraja* Ishiyama (Rajiformes).

The host associations of the species considered *incertae sedis* (Table 4) have the potential to substantially expand the repertoire of viable hosts for phyllobothriideans if they are ultimately all determined to belong to the order. In terms of shark taxa, carcharhiniform host genera would include *Cephaloscyllium* Gill, *Eusphyra* Gill, and *Scyliorhinus* Blaineville; lamniform host genera would include *Mitsukurina* Jordan; hexanchiform host genera would be expanded to include *Chlamydoselachus* Garman; orectolobiform genera would include *Nebrius* Rüppell; and the order Heterodontiformes would also be added to the list of hosts. In terms of batoids, the type hosts of the species considered *incertae sedis* would be expanded as follows: Rajiform genera would be expanded to include *Amblyraja* Malm, *Beringraja* Ishihara, *Leucoraja* Malm, and *Raja* L. In the Rhinopristiformes, *Rhynchobatus* Müller & Henle would be added to the list of genera. However, the remaining published records of phyllobothriideans from batoids are more highly suspect. For example, Linton's (1897) report of *Orygmatobothrium crenulatum* Linton, 1897 from *Bathytoshia centroura* (Mitchill) (as *Dasyatis centrura* [sic] [Mitchill]) and Yamaguti's (1934) report of *Phyllobothrium dasybati* Yamaguti, 1934 from *Hemitrygon akajei* (Müller & Henle) (as *Dasyatis akajei* [Müller & Henle]) likely represent accidental infections or incorrect host identifications. Nonetheless, for our purposes here they have been included in the diversity data presented in Tables 2 and 3.

Assuming that *Chimaerocestos* is ultimately confirmed to belong to the Phyllobothriidea, the order should also be considered to include members parasitizing holocephalans. Beyond the original report of *Chimaerocestos prudhoei* Williams & Bray, 1984 (see Williams and Bray, 1984) from *Rhinochimaera atlantica* Holt & Byrne, our examination of new material revealed a second, as-of-yet undescribed member of this genus in *Rhinochimaera pacifica* (Mitsukuri) off the Chatham Rise in New Zealand (see Caira et al., 2014). It seems likely that the third member of this holocephalan genus, *Rhinochimaera africana* Compagno, Stehmann & Ebert, is likely to host yet another undescribed species of *Chimaerocestos*. The other genera of Rhinochimaridae are also candidate hosts. We are less certain of the suitability of members of the Callorhinchidae and Chimaeridae to serve as hosts for this genus because examination of multiple specimens, and in some cases even species, of *Callorhinchus* Lacepède, *Harriotta* Goode, and *Hydrolagus* Gill failed to yield specimens of *Chimaerocestos*.

There is a strong degree of concordance between phyllobothriidean genera and elasmobranch host families or genera. For example, species of the type genus of the order, *Phyllobothrium*, parasitize sharks of the family Triakidae Gray (see Ruhnke, 1996); species of *Clistobothrium* parasitize sharks of the family Lamnidae Müller & Henle (see Ruhnke, 1993).

Species of *Orectolobicestus* are known only from species of *Chiloscyllium* Müller & Henle (see Ruhnke et al., 2006a), and species of *Orygmatobothrium* parasitize only sharks of the genus *Mustelus* Link (see Euzet, 1959; Ivanov, 2008). Table 4 provides additional examples. A few notable exceptions include *Crossobothrium*, three species of which parasitize hexanchiform sharks of the family Hexanchidae Gray, but one of which parasitizes the lamniform shark *Odontaspis taurus* (Rafinesque). Also intriguing is the breadth of the host associations of *Paraorygmatobothrium*; although the majority of species parasitize carcharhinid sharks, other species are known from lamniform sharks (e.g., *P. exiguum* [Yamaguti, 1935] Ruhnke, 1994; see Ruhnke (1994b), and others from orectilobiform sharks (e.g., *P. orectolobi* [Butler, 1987] Ruhnke, 2011; see Ruhnke, 2011).

One of the main aims of the PBI project was to explore host taxa that had not previously been examined for cestodes. In the case of elasmobranchs, substantial effort was thus placed on examining some of the deeper water species, and in particular dogfish sharks (i.e., Squaliformes) and cat sharks (i.e., Pentanchidae Smith and "Scyliorhinidae" Gill). These efforts not only led to the discovery of substantial undescribed novelty and new host associations, but also provided compelling evidence that the cestode faunas of these deeper water elasmobranchs are particularly depauperate (e.g., see Caira and Pickering, 2013). In terms of novelty from other shark taxa, phyllobothriidean species preliminarily assigned to the Phyllobothriidea were discovered in each of the following genera for the first time: *Apristurus* Garman, *Centroscymnus* Barbosa du Bocage & Brito Capello, *Dalatias* Rafinesque, *Galeus* Cuvier, *Halaelurus* Gill, *Holohalaelurus* Fowler, New genus D (for S*cyliorhinus torazame* [Tanaka] [unpubl. data]), *Pseudocarcharias* Cadenat, *Rhincodon* Smith, *Stegostoma* Müller & Henle, and *Triaenodon* Müller & Henle. Prevously unexamined species of *Carcharhinus* Blainville, *Hexanchus* Rafinesque, *Isurus* Rafinesque, *Mustelus* Linck, and *Squalus* L., were also discovered to host phyllobothriideans. In all cases, the phyllobothriideans involved appear to represent novel species, and in some instances even genera. The presence of specimens preliminarily assigned to the Phyllobothriidea were also found in some batoids. Newly collected material of New genus 20 from *Dipturus* suggests that *Guidus* is not the only genus of phyllobothriidean that parasitizes skates and also suggests that the records of many of the species *incertae sedis* in Table 4 from skate genera may actually be valid. Given that myliobatiform elasmobranchs are among the most well sampled order of batoids, the discovery of additional phyllobothriidean species from this order is not anticipated. Across these genera, however, by far the greatest new diversity was found in carcharhiniform sharks. The dogfish and cat sharks were also discovered to be relatively productive sources of novel taxa.

The host associations of all known phyllobothriidean taxa are presented in Table 2 for sharks and Table 3 for batoids and holocephalans. The data in these tables come from (1) described species, (2) species *incertae sedis* from Table 4, which although they are currently assigned to incorrect genera, are likely to remain in the Phyllobothriidea, and (3) novel undescribed species discovered over the course the PBI project. Also presented in these tables are the total numbers of phyllobothriidean species predicted to parasitize sharks, batoids, and holocephalans globally, based on extrapolations from known diversity in each host group. At present, an estimated 144 species of phyllobothriideans (only 69 of which have been described) are known to parasitize elasmobranchs globally; by far the majority of these, 118 (i.e., 82%) parasitize sharks and 26 parasitize batoids, and two parasitize holocephalans. Based on these data (Tables 2 and 3), we predict the total number of phyllobothriidean species globally to be 669, 473 of which parasitize sharks and the remainder batoids and holocephalans. If these predictions are correct, only approximately 22% of the global phyllobothriidean fauna has been described!

The predictions made above were largely made possible because phyllobothriideans in general exhibit oioxenous specificity (*sensu* Euzet and Combes [1980]) for their elasmobranch hosts. However, a few exceptions do exist. For example, work on the genus *Paraorygmatobothrium* appears to illustrate more relaxed host specificity in some cases. Jensen and Bullard (2010) provided molecular evidence to suggest that a number of undescribed species of *Paraorygmatobothrium* each appear to be hosted by multiple species of carcharhinid sharks. For example, their *Paraorygmatobothrium* sp. 3 is hosted by *Carcharhinus limbatus* (Müller & Henle) and *Rhizoprionodon terranovae* (Richardson); whereas their *Paraorygmatobothrium* sp. 5 is hosted by *Carcharhinus brevipinna* (Müller & Henle), C. *isodon* (Müller & Henle), *C. limbatus*, and *R. terranovae* (see Jensen and Bullard, 2010). Interestingly, all of these examples of more relaxed host specificity were discovered as a result of more comprehensive collections of shark species from the Gulf of Mexico (see Jensen and Bullard, 2010). Given that the sampling density for most phyllobothriidean species is low, strict host specificity may be found to be violated for other taxa as a result of future collections involving higher numbers of individual host species.

GEOGRAPHIC DISTRIBUTION. Interestingly, the substantially revised configuration of the Phyllobothriidea presented here does little to change the known geographic distribution of the Phyllobothriidea, largely because the genera responsible for extremes in geographic distribution (e.g., *Monorygma*, *Bibusibothrium*, *Guidus*, etc.) remain members of the order. However, the addition of *Trilocularia* to the order, in combination with Pickering and Caira's (2012) description of a new member of this genus from South Africa, extends the distribution to include the Temperate Southern African marine realm and thus the order is now known from all 12 of Spalding et al.'s (2007) marine realms of the world. The erection of *Doliobothrium* and the description of new species of *Paraorygmatobothrium* by Caira et al. (2011) and Malek et al. (2010), respectively, extended the distribution of the order to include Iranian waters. Records of the genera *Alexandercestus* were added from the Bahamas and Australia (see Ruhnke and Workman, 2013), and records of *Hemipristicola* and *Paraorygmatobothrium* were added from Australia (see Cutmore et al., 2009, 2011). Phyllobothriideans remain known chiefly from the Northern Hemisphere, with 73% of described species known only from localities north of the equator. Additional future collections from the Southern Hemisphere are required to determine whether this is an artifact of sampling intensity or of the substantial difference in landmass distribution between these two hemispheres.

CONCLUSIONS

Work completed over the course of the PBI project has substantially reshaped our understanding of the Phyllobothriidea. Indeed, this taxonomic entity was created as a result of PBI work. Members of the order share simple, unarmed bothridia that bear apical suckers. Since 2008, three new genera of phyllobothriideans were erected, eight new species were described and eight new combinations were made. The order now includes 24 described genera and 69 described species; all but eight of these species parasitize sharks. This is the only order of cestodes that includes taxa that parasitize holocephalans and elasmobranchs. The cosmopolitan nature of the order was confirmed; the distribution was expanded to include the Bahamas, South Africa, and Iran. Morphological novelty was found in the tubular bothridial construction of species of *Doliobothrium*. A family-level classification of the order remains to be established. Perhaps most importantly, work completed over the course of the PBI project provided initial estimates for the phylogenetic positions of a number of genera allocated to the order. Phyllobothriideans are for the most part found in carcharhiniform sharks and nearly three quarters of phyllobothriidean species have been collected from the Northern Hemisphere. However, new collections suggest that dogfish and cat sharks are likely to also be productive hosts to explore for additional diversity in the order. In total, 144 species of phyllobothriideans are known, only about half of which have been formally described; 82% of these parasitize sharks. The prediction of global diversity in the order is approximately 669 species, suggesting that nearly 78% of the global fauna has yet to be discovered.

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TABLE 2. Expected global shark associations of phyllobothriidean species (in yellow). Number of shark species per genus given in parentheses (includes known undescribed shark species). First column: number of phyllobothriidean species parasitizing each shark taxon as of 2017 (includes known undescribed cestode species); second column: predicted total number of phyllobothriidean species parasitizing each shark taxon globally. Quotes indicate non-monophyletic taxa (Naylor et al., 2012b). Question marks indicate genera not yet examined for cestodes. * Designation New genus D is for *Scyliorhinus torazame* (Tanaka).

	Phyllobothriidean spp.	
	2017	**ESTIM.**
SELACHOIDEA		
CARCHARHINIFORMES	**62**	**283**
Carcharhinidae	**21**	**100**
Carcharhinus (44 spp.)	7	64
Galeocerdo (2 spp.)	2	4
Glyphis (6 spp.)	0	6
Isogomophodon (1 sp.)	?	1
Lamiopsis (2 spp.)	1	2
Loxodon (2 spp.)	0	2
Nasolamia (1 sp.)	?	1
Negaprion (2 spp.)	4	4
Prionace (1 sp.)	2	2
Rhizoprionodon (10 spp.)	2	10
Scoliodon (3 spp.)	2	3
Triaenodon (1 sp.)	1	1
Hemigaleidae	**4**	**12**
Chaenogaleus (2 spp.)	?	2
Hemigaleus (2 spp.)	2	4
Hemipristis (1 sp.)	2	2
Paragaleus (4 spp.)	0	4
Leptochariidae	**0**	**0**
Leptocharias (1 sp.)	0	0
Pentanchidae	**8**	**51**
Apristurus (46 spp.)	5	23
Asymbolus (9 spp.)	0	4
Cephalurus (1 sp.)	?	0
Galeus (18 spp.)	1	8
Halaelurus (7 spp.)	1	7
Haploblepharus (4 spp.)	0	4
Holohalaelurus (5 spp.)	1	5
Parmaturus (11 spp.)	?	0
Pentanchus (1 sp.)	?	0
Proscylliidae	**0**	**0**
Ctenacis (1 sp.)	?	0
Eridacnis (3 spp.)	0	0
Proscyllium (3 spp.)	?	0
Pseudotriakidae	**0**	**0**
Gollum (2 spp.)	?	0
Planonasus (1 sp.)	?	0
Pseudotriakis (1 sp.)	0	0
"Scyliorhinidae"	**6**	**35**
Atelomycterus (6 spp.)	0	0
Aulohalaelurus (2 spp.)	?	0
Bythaelurus (11 spp.)	?	5
Cephaloscyllium (18 spp.)	1	12
Figaro (3 spp.)	?	1
New genus D* (1 sp.)	1	1
Poroderma (2 spp.)	0	1
Schroederichthys (5 spp.)	?	0
Scyliorhinus (15 spp.)	4	15
Sphyrnidae	**3**	**13**
Eusphyra (1 sp.)	1	1
Sphyrna (12 spp.)	2	12
Triakidae	**20**	**72**
Furgaleus (1 sp.)	0	0
Galeorhinus (1 sp.)	1	2
Gogolia (1 sp.)	?	1
Hemitriakis (8 spp.)	0	8
Hypoglaeus (1 sp.)	?	1
Iago (5 spp.)	0	5
Mustelus (30 spp.)	15	45
Scylliogaleus (1 sp.)	?	1
Triakis (5 spp.)	4	9
HETERODONTIFORMES	**1**	**5**
Heterodontidae	**1**	**5**
Heterodontus (10 spp.)	1	5
HEXANCHIFORMES	**9**	**12**
Chlamydoselachidae	**1**	**2**
Chlamydoselachus (2 spp.)	1	2
Hexanchidae	**8**	**10**
Heptranchias (1 sp.)	2	2
Hexanchus (3 spp.)	4	6
Notorynchus (1 sp.)	2	2
LAMNIFORMES	**15**	**12**
Alopiidae	**5**	**8**
Alopias (3 spp.)	5	8
Cetorhinidae	**0**	**0**
Cetorhinus (1 sp.)	0	0
Lamnidae	**7**	**7**
Carcharodon (1 sp.)	2	2
Isurus (2 spp.)	3	3
Lamna (2 spp.)	2	2
Megachasmidae	**0**	**0**
Megachasma (1 sp.)	0	0
Mitsukurinidae	**1**	**1**
Mitsukurina (1 sp.)	1	1
Odontaspididae	**1**	**3**
Carcharias (1 sp.)	1	1
Odontaspis (2 spp.)	0	2
Pseudocarcharhiidae	**1**	**1**
Pseudocarcharias (1 sp.)	1	1
ORECTOLOBIFORMES	**10**	**28**
Brachaeluridae	**0**	**0**
Brachaelurus (2 spp.)	0	0
Ginglymostomatidae	**1**	**1**
Ginglymostoma (2 spp.)	0	0
Nebrius (1 sp.)	1	1
Pseudoginglymostoma (1 sp.)	0	0
Hemiscylliidae	**6**	**13**
Chiloscyllium (9 spp.)	6	13
Hemiscyllium (9 spp.)	0	0
Orectolobidae	**1**	**12**
Eucrossorhinus (1 sp.)	0	1
Orectolobus (10 spp.)	1	10
Sutorectus (1 sp.)	0	1
Parascylliidae	**0**	**0**
Cirrhoscyllium (3 spp.)	0	0
Parascyllium (5 spp.)	0	0
Rhincodontidae	**1**	**1**
Rhincodon (1 sp.)	1	1
Stegostomatidae	**1**	**1**
Stegostoma (1 sp.)	1	1
PRISTIOPHORIFORMES	**3**	**21**
Pristiophoridae	**3**	**21**
Pliotrema (1 sp.)	0	0
Pristiophorus (7 spp.)	3	21
SQUALIFORMES	**16**	**93**
Centrophoridae	**1**	**8**
Centrophorus (16 spp.)	1	8
Deania (6 spp.)	0	0
Dalatiidae	**1**	**2**
Dalatias (1 sp.)	1	1
Euprotomicroides (1 sp.)	?	0
Euprotomicrus (1 sp.)	0	0
Heteroscymnoides (1 sp.)	?	0
Isistius (2 spp.)	?	2
Mollisquama (1 sp.)	?	0
Squaliolus (2 spp.)	0	0
Echinorhinidae	**0**	**0**
Echinorhinus (3 spp.)	0	0
Etmopteridae	**0**	**0**
Aculeola (1 sp.)	?	0
Centroscyllium (7 spp.)	0	0
Etmopterus (39 spp.)	0	0
Trigonognathus (1 sp.)	?	0
Oxynotidae	**0**	0
Oxynotus (5 spp.)	0	0
Somniosidae	**4**	**19**
Centroscymnus (2 spp.)	1	2
Centroselachus (1 sp.)	0	1
Scymnodalatias (4 spp.)	?	4
Scymnodon (4 spp.)	0	4
Somniosus (5 spp.)	3	7
Zameus (1 sp.)	?	1
Squalidae	**10**	**64**
Cirrhigaleus (2 spp.)	?	3
Squalus (41 spp.)	10	61
SQUATINIFORMES	**2**	**11**
Squatinidae	2	11
Squatina (23 spp.)	2	11
SHARK TOTAL	**118**	**473**

TABLE 3. Expected global batoid and holocephalan associations of phyllobothriidean species (in yellow). Number of batoid and holocephalan species per genus given in parentheses (includes known undescribed batoid species). First column: number of phyllobothriidean species parasitizing each batoid or holocephalan taxon as of 2017 (includes known undescribed cestode species); second column: predicted total number of phyllobothriidean species parasitizing each batoid and holocephalan taxon globally. Quotes indicate non-monophyletic taxa (Naylor et al., 2012b; Last et al., 2016a, b). Question marks indicate genera not yet examined for cestodes. Estimated total number of phyllobothriidean species parasitizing elasmobranchs and holocephalans globally given at bottom of Table.

	Phyllobothriidean spp.	
	2017	**ESTIM.**
BATOIDEA		
MYLIOBATIFORMES	**3**	**9**
Aetobatidae	**0**	**0**
Aetobatus (7 spp.)	0	0
Dasyatidae	**2**	**8**
“*Bathytoshia*” (3 spp.)	1	3
Brevitrygon (5 spp.)	0	0
Dasyatis (5 spp.)	0	0
Fluvitrygon (3 spp.)	0	0
Fontitrygon (4 spp.)	0	0
Hemitrygon (10 spp.)	1	5
Himantura (8 spp.)	0	0
Hypanus (12 spp.)	0	0
Maculabatis (13 spp.)	0	0
Makararaja (1 sp.)	?	0
Megatrygon (1 sp.)	0	0
Neotrygon (13 spp.)	0	0
Pastinachus (6 spp.)	0	0
Pateobatis (7 spp.)	0	0
Pteroplatytrygon (1 sp.)	0	0
Taeniura (5 spp.)	0	0
Taeniurops (2 spp.)	0	0
“*Telatrygon*” (4 spp.)	0	0
Urogymnus (7 spp.)	0	0
Gymnuridae	**0**	**0**
Gymnura (15 spp.)	0	0
Hexatrygonidae	**0**	**0**
Hexatrygon (1 sp.)	0	0
Mobulidae	**0**	**0**
Mobula (8 spp.)	0	0
Myliobatidae	**0**	**0**
Aetomylaeus (9 spp.)	0	0
Myliobatis (11 spp.)	0	0
Plesiobatidae	**0**	**0**
Plesiobatis (1 sp.)	0	0
Potamotrygonidae	**1**	**1**
Heliotrygon (2 spp.)	0	0
Styracura (2 spp.)	0	0
Paratrygon (1 sp.)	1	1
Plesiotrygon (2 spp.)	0	0
Potamotrygon (27 spp.)	0	0
Rhinopteridae	**0**	**0**
Rhinoptera (8 spp.)	0	0
Urolophidae	**0**	**0**
Spinilophus (1 sp.)	?	0
Trygonoptera (6 spp.)	0	0
Urolophus (21 spp.)	0	0
Urotrygonidae	**0**	**0**
Urobatis (6 spp.)	0	0
Urotrygon (12 spp.)	0	0
RHINOPRISTIFORMES	**6**	**15**
Glaucostegidae	**2**	**6**
Glaucostegus (9 spp.)	2	6
Platyrhinidae	**0**	**0**
Platyrhina (5 spp.)	0	0
Platyrhinoidis (1 sp.)	0	0
“Pristidae”	**2**	**5**
Anoxypristis (1 sp.)	0	0
Pristis (5 spp.)	2	5
Rhinidae	**2**	**4**
Rhina (1 sp.)	0	0
Rhynchobatus (8 spp.)	2	4
Rhynchorhina (1 sp.)	?	0
“Rhinobatidae”	**0**	**0**
Acroteriobatus (8 spp.)	0	0
Pseudobatos (8 spp.)	0	0
Rhinobatos (16 spp.)	0	0
Trygonorrhinidae	**0**	**0**
Aptychotrema (3 spp.)	0	0
Trygonorrhina (2 spp.)	0	0
Zapteryx (3 spp.)	0	0
Zanobatidae	**0**	**0**
Zanobatus (2 spp.)	0	0
TORPEDINIFORMES	**3**	**21**
Hypnidae	**0**	**0**
Hypnos (1 sp.)	0	0
Narcinidae	**0**	**0**
Benthobatis (4 spp.)	?	0
Diplobatis (4 spp.)	0	0
Discopyge (2 spp.)	0	0
Narcine (15 spp.)	0	0
Narcinops (5 spp.)		
Narkidae	**0**	**0**
Crassinarke (1 sp.)	?	0
Electrolux (1 sp.)	?	0
Heteronarce (3 spp.)	?	0
Narke (3 spp.)	0	0
Temera (1 sp.)	?	0
Typhlonarke (1 sp.)	0	0
Torpedinidae	**3**	**21**
Tetronarce (9 spp.)	2	9
Torpedo (12 spp.)	1	12
HOLOCEPHALI		
CHIMAERIFORMES	**2**	**8**
Callorhinchidae	**0**	**0**
Callorhinchus (3 spp.)	0	0
Chimaeridae	**0**	**0**
Chimaera (16 spp.)	0	0
Hydrolagus (23 spp.)	0	0
Rhinochimaridae	**2**	**8**
Harriotta (2 spp.)	0	2
Neoharriotta (3 spp.)	0	3
Rhinochimaera (3 spp.)	2	3
HOLOCEPHALAN TOTAL	**2**	**8**
RAJIFORMES	**14**	**151**
Anacanthobatidae	**0**	**0**
Anacanthobatis (6 spp.)	?	0
Indobatis (1 sp.)	?	0
Schroederobatis (1 sp.)	?	0
Sinobatis (9 spp.)	?	0
Springeria (2 spp.)	?	0
Arhynchobatidae	**3**	**56**
Arhynchobatis (1 sp.)	?	0
Atlantoraja (3 spp.)	0	0
Bathyraja (56 spp.)	3	56
Brochiraja (9 spp.)	0	0
Insentiraja (2 spp.)	?	0
Irolita (2 spp.)	?	0
Notoraja (12 spp.)	?	0
Pavoraja (6 spp.)	?	0
Psammobatis (8 spp.)	0	0
Pseudoraja (1 sp.)	?	0
Rhinoraja (3 spp.)	?	0
Rioraja (1 sp.)	0	0
Sympterygia (4 spp.)	0	0
Gurgesiellidae		
Cruriraja (8 spp.)	0	0
Fenestraja (8 spp.)	?	0
Gurgesiella (3 spp.)	?	0
Rajidae	**11**	**95**
Amblyraja (19 spp.)	1	11
Beringraja (2 spp.)	1	2
Breviraja (5 spp.)	?	0
Dactylobatus (2 spp.)	?	0
Dentiraja (11 spp.)	?	0
Dipturus (52 spp.)	5	52
Hongeo (1 sp.)	?	0
Leucoraja (13 spp.)	2	13
Malacoraja (4 spp.)	0	0
Neoraja (5 spp.)	?	0
Okamejei (13 spp.)	0	0
Orbiraja (3 spp.)	0	0
Raja (17 spp.)	2	17
Rajella (20 spp.)	0	0
Rostroraja (10 spp.)	0	0
Spiniraja (1 sp.)	0	0
BATOID TOTAL	**26**	**196**
ELASMOBRANCH TOTAL	**144**	**669**

Table 4. List of phyllobothriidean taxa. New taxa and taxonomic actions resulting from PBI project activities indicated in bold. * Host identifications requiring confirmation.

VALID TAXA

- **_Alexandercestus_ Ruhnke & Workman, 2013**
  - **_Alexandercestus gibsoni_ Ruhnke & Workman, 2013** (type) ex *Negaprion acutidens*
  - **_Alexandercestus manteri_ Ruhnke & Workman, 2013** ex *Negaprion brevirostris*
- *Bibursibothrium* McKenzie & Caira, 1998
  - *Bibursibothrium gouldeni* McKenzie & Caira, 1998 (type) ex *Pristiophorus cirratus*
- *Bilocularia* Obersteiner, 1914
  - *Bilocularia hyperapolytica* Obersteiner, 1914 (type) ex *Centrophorus granulosus*
- *Calyptrobothrium* Monticelli, 1893
  - *Calyptrobothrium riggii* Monticelli, 1893 (type) ex *Torpedo marmorata*
  - *Calyptrobothrium minus* Linton, 1907 ex *Tetranarce occidentalis*
  - *Calyptrobothrium occidentale* Linton, 1900 ex *Tetranarce occidentalis*
- *Cardiobothrium* McKenzie & Caira, 1998
  - *Cardiobothrium beveridgei* McKenzie & Caira, 1998 (type) ex *Pristiophorus cirratus*
- *Chimaerocestos* Williams & Bray, 1984
  - *Chimaerocestos prudhoei* Williams & Bray, 1984 (type) ex *Rhinochimaera atlantica*
- *Clistobothrium* Dailey & Vogelbein, 1990
  - *Clistobothrium carcharodoni* Dailey & Vogelbein, 1990 (type) ex *Carcharodon carcharias*
  - *Clistobothrium montaukensis* Ruhnke, 1993 ex *Isurus oxyrinchus*
  - *Clistobothrium tumidum* (Linton, 1922) Ruhnke, 1993 ex *Carcharodon carcharias*
- *Crossobothrium* Linton, 1889
  - *Crossobothrium laciniatum* Linton, 1889 (type) ex *Odontaspis taurus* (as *Odontaspis littoralis*)
  - **_Crossobothrium antonioi_ Ivanov, 2009 ex _Notorynchus cepedianus_**
  - *Crossobothrium campanulatum* Klaptocz, 1906 ex *Hexanchus griseus* (as *Notidanus griseus*)
  - *Crossobothrium dohrni* (Örley, 1885) Ruhnke, 1996 ex *Heptranchias perlo* (as *Heptanchus cinereus*)
  - **_Crossobothrium pequeae_ Ivanov, 2009** ex *Notorynchus cepedianus*
- **_Doliobothrium_ Caira, Malek & Ruhnke, 2011**
  - **_Doliobothrium haselii_ Caira, Malek & Ruhnke, 2011** (type) ex *Carcharhinus dussumeri* (as *Carcharhinus* cf. *dussumeri*)
  - _Doliobothrium musculosum_ (Subhapradha, 1955) **Caira, Malek & Ruhnke, 2011** ex _Rhizoprionodon acutus_* (as _Carcharias acutus_)
- *Flexibothrium* McKenzie & Caira, 1998
  - *Flexibothrium ruhnkei* McKenzie & Caira, 1998 (type) ex *Pristiophorus cirratus*
- *Guidus* Ivanov, 2006
  - *Guidus argentinense* Ivanov, 2006 (type) ex *Bathyraja brachyurops*
  - *Guidus antarcticus* (Wojciechowska, 1991) Ivanov, 2006 ex *Bathyraja maccaini*
  - *Guidus awii* (Rocka & Zdzitowiecki, 1998) Ivanov, 2006 ex *Bathyraja maccaini*
- *Hemipristicola* Cutmore, Theiss, Bennett & Cribb, 2011
  - *Hemipristicola gunterae* Cutmore, Theiss, Bennett & Cribb, 2011 (type) ex *Hemipristis elongata*
- *Marsupiobothrium* Yamaguti, 1952
  - *Marsupiobothrium alopias* Yamaguti, 1952 (type) ex *Alopias vulpinus*
- *Monorygma* Diesing, 1863
  - *Monorygma perfectum* (van Beneden, 1853) Diesing, 1863 (type) ex *Somniosus microcephalus*
  - *Monorygma macquariae* Johnston, 1937 ex *Somniosus* sp.
  - *Monorygma magnum* (Hart, 1936) Williams, 1968 ex *Somniosus pacificus* (as *Somniosus microcephalus*)
- *Nandocestus* Reyda, 2008
  - *Nandocestus guariticus* (Marques, Brooks & Lasso, 2001) Reyda, 2008 (type) ex *Paratrygon aiereba*
- **New genus 10 _sensu_ Caira et al. (2014)**
  - **New genus 10 n. sp. 1** ex *Sphyrna lewini* 1 (*sensu* Naylor et al. [2012a])
- **New genus 18 (this study)**
  - **New genus 18 _squali_ (Yamaguti, 1952)** ex *Squalus suckleyi* (as *S. sucklii*)
- **New genus 20 (this study)**
  - **New genus 20 n. sp. 1** ex *Dipturus chilensis*

- *Orectolobicestus* Ruhnke, Caira & Carpenter, 2006
  - *Orectolobicestus tyleri* Ruhnke, Caira & Carpenter, 2006 (type) ex *Chiloscyllium punctatum*
  - *Orectolobicestus chiloscyllii* (Subhapradha, 1955) Ruhnke, Caira & Carpenter, 2006 ex *Chiloscyllium griseum*
  - *Orectolobicestus kelleyae* Ruhnke, Caira & Carpenter, 2006 ex *Chiloscyllium indicum*
  - *Orectolobicestus lorettae* Ruhnke, Caira & Carpenter, 2006 ex *Chiloscyllium* cf. *punctatum*
  - *Orectolobicestus mukahensis* Ruhnke, Caira & Carpenter, 2006 ex *Chiloscyllium indicum*
  - *Orectolobicestus randyi* Ruhnke, Caira & Carpenter, 2006 ex *Chiloscyllium hasselti*
- *Orygmatobothrium* Diesing, 1863
  - *Orygmatobothrium musteli* (van Beneden, 1850) Diesing, 1863 (type) ex *Mustelus mustelus* (as *Mustelus vulgaris*)
  - *Orygmatobothrium juani* Ivanov, 2008 ex *Mustelus fasciatus*
  - *Orygmatobothrium schmittii* Suriano & Labiola, 2001 ex *Mustelus schmitti*
- *Paraorygmatobothrium* Ruhnke, 1994
  - *Paraorygmatobothrium prionacis* (Yamaguti, 1934) Ruhnke, 1994 (type) ex *Prionace glauca*
  - *Paraorygmatobothrium angustum* (Linton, 1889) **Ruhnke, 2011** ex *Carcharhinus obscurus* (as *Carcharias obscurus*)
  - *Paraorygmatobothrium arnoldi* Ruhnke & Thompson, 2006 ex *Negaprion acutidens*
  - *Paraorygmatobothrium bai* Ruhnke & Carpenter, 2008 ex *Mustelus mustelus*
  - *Paraorygmatobothrium barberi* Ruhnke, 1994 ex *Triakis semifasciata*
  - *Paraorygmatobothrium exiguum* (Yamaguti, 1935) Ruhnke, 1994 ex *Alopias vulpinus*
  - *Paraorygmatobothrium filiforme* (Yamaguti, 1952) Ruhnke, 1996 ex *Alopias vulpinus*
  - *Paraorygmatobothrium floraformis* (Southwell, 1912) **Ruhnke, 2011** ex *Carcharhinus sorrah* (as *Carcharias bleekeri*)
  - *Paraorygmatobothrium janineae* Ruhnke, Healy & Shapero 2006 ex *Hemipristis elongate*
  - *Paraorygmatobothrium kirstenae* Ruhnke, Healy & Shapero, 2006 ex *Hemigaleus microstoma*
  - *Paraorygmatobothrium leuci* (Watson & Thorson, 1976) **Ruhnke, 2011** ex *Carcharhinus leuci*
  - ***Paraorygmatobothrium mobedii* Malek, Caira, & Haseli 2010** ex *Carcharhinus* cf. *dussumieri*
  - *Paraorygmatobothrium nicaraguensis* (Watson & Thorson, 1976) **Ruhnke, 2011** ex *Carcharhinus leuci*
  - *Paraorygmatobothrium orectolobi* (Butler, 1987) **Ruhnke, 2011** ex *Orectolobus maculatus*
  - *Paraorygmatobothrium paulum* (Linton, 1897) **Ruhnke, 2011** ex *Galeocerdo cuvier* (as *Galeocerdo tigrinus*)
  - *Paraorygmatobothrium roberti* Ruhnke & Thompson, 2006 ex *Negaprion brevirostris*
  - *Paraorygmatobothrium rodmani* Ruhnke & Carpenter, 2008 ex *Mustelus antarcticus*
  - ***Paraorygmatobothrium sinuspersicense* Malek, Caira, & Haseli 2010** ex *Carcharhinus* cf. *dussumieri*
  - *Paraorygmatobothrium taylori* Cutmore, Bennett & Cribb 2009 ex *Hemigaleus australiensis*
  - *Paraorygmatobothrium triacis* (Yamaguti, 1952) Ruhnke, 1996 ex *Triakis scyllium* (as *Triacis scyllium*)
  - *Paraorygmatobothrium typicum* (Subhapradha, 1955) **Ruhnke, 2011** ex *Rhizoprionodon acutus* (as *Carcharias acutus*)
- *Pelichnibothrium* Monticelli, 1889 (synonym: *Prionacestus* Mete & Euzet, 1996)
  - *Pelichnibothrium speciosum* Monticelli, 1889 (type) ex *Alepidosaurus ferox* (and *Prionace glauca*)
- *Phyllobothrium* van Beneden, 1850
  - *Phyllobothrium lactuca* van Beneden, 1850 (type) ex *Mustelus mustelus* (as *Mustelus vulgaris*)
  - *Phyllobothrium riseri* Ruhnke, 1996 ex *Triakis semifasciata*
  - *Phyllobothrium serratum* Yamaguti, 1952 ex *Triakis scyllium* (as *Triacis scyllium*)
- *Ruhnkecestus* Caira & Durkin, 2006
  - *Ruhnkecestus latipi* Caira & Durkin, 2006 (type) ex *Scoliodon macrorhynchos* (as *Scoliodon laticaudus*)
- *Scyphophyllidium* Woodland, 1927
  - *Scyphophyllidium giganteum* (van Beneden, 1858) Woodland, 1927 (type) ex *Galeorhinus galeus* (as milandre)
  - *Scyphophyllidium uruguayense* Brooks, Marques, Perroni & Sidagis, 1999 ex *Mustelus mento**
- *Thysanocephalum* Linton, 1890
  - *Thysanocephalum thysanocephalum* (Linton, 1890) Braun, 1900 (type) ex *Galeocerdo cuvieri*
- *Trilocularia* Olsson, 1867
  - *Trilocularia gracilis* Olsson, 1867 (type) ex *Squalus acanthias*
  - ***Trilocularia eberti* Pickering & Caira, 2012** ex *Squalus* cf. *mitsukurii*

SPECIES *INCERTAE SEDIS*

- *Anthobothrium pristis* Woodland, 1934 ex *Pristis microdon*
- *Crossobothrium longicolle* (Molin, 1858) Euzet, 1959 ex *Scyliorhinus stellaris*
- *Marsupiobothrium gobelinus* Caira & Runkle, 1993 ex *Mitsukurina owstoni*
- *Monorygma chlamydoselachi* Lönnberg, 1898 ex *Chlamydoselachus anguineus*
- *Monorygma megacotyla* Yamaguti, 1952 ex *Cephaloscyllium umbratile*
- *Orygmatobothrium crenulatum* Linton, 1897 ex *Bathytoshia centroura* (as *Dasyatis centrura* [sic])
- *Orygmatobothrium forte* Linton, 1924 ex *Sphyrna zygaena* (as *Cestracion zygaena*)

Orygmatobothrium velamentum Yoshida, 1917 ex *Mustelus manazo*
Phyllobothrium arctowskii Wojciechowska, 1991 ex *Bathyraja* sp. 2
Phyllobothrium blochii Srivastav & Srivastava, 1988 ex *Eusphyra blochii*
Phyllobothrium bombayensis Srivastava & Capoor, 1979 ex *Scoliodon laticaudus*
Phyllobothrium brittanicum Williams, 1968 ex *Raja montagui*
Phyllobothrium dasybati Yamaguti, 1934 ex *Hemitrygon akajei* (as *Dasyatis akajei*)
Phyllobothrium georgiense Wojciechowska, 1991 ex *Amblyraja georgiana*
Phyllobothrium loculatum Yamaguti, 1952 ex *Heterodontus zebra*
Phyllobothrium marginatum Yamaguti, 1934 ex *Squatina japonica*
Phyllobothrium microsomum Southwell & Hilmy, 1929 ex *Nebrius ferrugineus* (as *Ginglymostoma concolor*)
Phyllobothrium minimum Subhapradha, 1955 ex *Rhynchobatus djiddensis*
Phyllobothrium piriei Williams, 1968 ex *Leucoraja naevus* (as *Raja naevus*)
Phyllobothrium pristis Watson & Thorson, 1976 ex *Pristis microdon*
Phyllobothrium radioductum Kay, 1942 ex *Beringraja binoculata* (as *Raja binoculata*)
Phyllobothrium rakusai Wojciechowska, 1991 ex *Bathyraja maccaini*
Phyllobothrium siedleckii Wojciechowska, 1991 ex *Bathyraja eatonii*
Phyllobothrium sinuosiceps Williams, 1959 ex *Hexanchus griseus*
Phyllobothrium spini Pramanik & Manna, 2009 ex *Carcharhinus sorrah*
Phyllobothrium thridax van Beneden, 1850 ex *Squatina squatina*
Phyllobothrium vagans Haswell, 1902 ex *Heterodontus portjacksoni*
Phyllobothrium williamsi Schmidt, 1986 ex *Leucoraja fullonica* (as *Raja fullonica*)
Pithophorus vulpeculae Yamaguti, 1952 ex *Alopias vulpinus*

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Rhinebothriidea

Healy, Caira, Jensen, Webster & Littlewood, 2009

By
Timothy R. Ruhnke[1], Florian B. Reyda, and Fernando P. L. Marques

RHINEBOTHRIIDEA AS THEY WERE KNOWN PRIOR TO THE PBI PROJECT

Diversity and Classification. The hypothesis that many of the genera now assigned to this order represented a clade distinct from the Tetraphyllidea was developed largely through the dissertation work of Claire Healy at the University of Connecticut. In addition to careful morphological work and a substantial amount of molecular work, done in collaboration with Bonnie Webster and Timothy Littlewood at the Natural History Museum in London, UK, Healy (2006a) made a convincing case for the existence of the Rhinebothriidae Euzet, 1953 as a diverse, but cohesive subgroup among a non-monophyletic Tetraphyllidea. However, because the action to formally elevate this group to ordinal status was not taken until a few years later (Healy et al., 2009), the Rhinebothriidea did not formally exist prior to the initiation of the PBI project in 2008. Nonetheless, it is useful to trace the taxonomic history of those taxa which ultimately became its members.

Rhinebothriideans have historically been housed in the order Tetraphyllidea. A thorough account of the convoluted taxonomic history of the Tetraphyllidea is beyond the scope of this contribution; readers are referred to Chapter 20 on the "Tetraphyllidea" relics (Caira et al., 2017a) in this volume for a more complete treatment of the current status of that order. The reader is also referred to Schmidt (1986) and Euzet (1994), and references therein, for more details on individual species and genera. The genera that now comprise the Rhinebothriidea were historically members of the family Phyllobothriidae Braun, 1900 (see Schmidt, 1986; Euzet, 1994). Euzet's (1994) phyllobothriid classification scheme included five subfamilies: Echeneibothriinae de Beauchamp, 1905, Phyllobothriinae, Rhinebothriinae, Thysanocephalinae Euzet, 1953, and Triloculariinae Yamaguti, 1959. In essence, the rhinebothriideans were born out of the species allocated to the Rhinebothriinae and Echeneibothriinae. Euzet (1994) included the following genera in the Echeneibothriinae: *Pseudanthobothrium* Baer, 1956, *Clydonobothrium* Euzet, 1959, *Phormobothrium* Alexander, 1963, *Tritaphros* Lönnberg, 1889, and *Echeneibothrium* van Beneden, 1850. Genera included in the Rhinebothriinae by Euzet (1994) were *Duplicibothrium* Williams & Campbell, 1978, *Caulobothrium* Baer, 1948, *Glyphobothrium* Williams & Campbell, 1977, *Rhabdotobothrium* Euzet, 1953, *Rhinebothrium* Linton, 1889, and *Rhinebothroides* Mayes, Brooks & Thorson, 1981.

Morphology. Given that rhinebothriidean taxa prior to the initiation of the PBI project were assigned either to the Echeneibothriinae or the Rhinebothriinae, we will restrict

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[1] Corresponding author (ruhnketr@wvstateu.edu)

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discussion of morphological diversity here to genera placed in those two subfamilies. With the exception of *Pseudanthobothrium*, the majority of genera assigned to these subfamilies bear bothridia with some form of facial and/or marginal loculi, and typically possess proglottids that lack post-vaginal testes. Euzet's (1994) Echeneibothriinae housed species with an adult form in which the scolex possessed an apical myzorhynchus; his Rhinebothriinae housed species with an adult form in which the scolex lacked a myzorhynchus.

In her dissertation, Healy (2006a) emphasized the importance of septal construction for the identification of rhinebothriid genera, noting that the architecture of the underlying musculature (as observed in histological section) may represent a diagnostic character for at least the rhinebothriids that possess facial loculi. She did, however, note that the ubiquity of this feature required confirmation with additional comparative work. Healy (2006a) also suggested that the insertion of the vas deferens into the anterior rather than medial margin of the cirrus-sac might represent a character uniting these genera. This feature, however, also required confirmation in terms of its presence across all candidate genera.

PHYLOGENETIC RELATIONSHIPS. Prior to 2008, very little was known about the phylogenetic relationships of the genera now housed in the Rhinebothriidea. The results of Olson et al.'s (1999) molecular phylogenetic analyses of partial 18S rDNA sequence data yielded a clade of genera including *Anthocephalum* Linton, 1890, *Echeneibothrium*, *Rhinebothrium*, *Rhodobothrium* Linton, 1890, and *Spongiobothrium* Linton, 1889. In the trees resulting from these same analyses, the genera *Dioecotaenia* Schmidt, 1969 and *Duplicibothrium* comprised a second, independent clade, and *Caulobothrium* formed another independent clade along with the lamniform-hosted genera *Ceratobothrium* Monticelli, 1892 and *Litobothrium* Dailey, 1969. Brooks and Barriga (1995) noted the similarities between *Dioecotaenia*, *Duplicibothruim*, *Glyphobothrium*, and *Serendip* Brooks & Barriga, 1995, placing the latter three genera in the Serendipidae Brooks & Barriga, 1995. Ruhnke et al. (2000) cited the results of Olson et al. (1999) to argue for a sister-group relationship between *Dioecotaenia* and *Duplicibothrium*. As a consequence, the work of Olson et al. (1999), while providing phylogenetic evidence for a kinship between echeneibothriines and a subset of rhinebothriines, nonetheless failed to support the monophyly of the Rhinebothriinae as envisioned by Euzet (1994). Their analyses also provided evidence for the inclusion of the genera *Anthocephalum* (considered by Euzet [1994] as a synonym of *Phyllobothrium* van Beneden, 1850), *Rhodobothrium* (considered by Euzet [1994] as a genus in the Phyllobothriinae), and *Spongiobothrium* (considered by Euzet [1994] as a *genus inquirendum* of the Phyllobothriinae) as candidates for inclusion in the Rhinebothriinae. In their molecular phylogenetic study based on sequence data for the complete 18S rDNA gene and partial (D1–D3) 28S rDNA gene, Olson et al. (2001) found molecular phylogenetic evidence for a close relationship between *Rhabdotobothrium* and *Rhinebothrium*.

Caira et al. (1999, 2001) provided morphological phylogenetic assessments of the relationships among species of the Echeneibothriinae and Rhinebothriinae. The results of their analyses provided evidence of monophyly for the echeneibothriine species, but not for the rhinebothriine species included. They also failed to find support for close affinities bewteen the Echeneibothriinae and the Rhinebothriinae. Healy (2006a) completed a rigorous taxonomic study of selected species of the Rhinebothriinae, in addition to morphological and molecular phylogenetic assessments of previously known and new species. As in the study of Olson et al. (1999), she found no evidence for the inclusion of *Caulobothrium* within the Rhinebothriinae, but did find evidence to suggest that species of *Rhinebothrium*, *Rhinebothroides*, *Spongiobothrium*, *Scalithrium* Neifar & Euzet, 2003, *Rhabdotobothrium*, and a number of new species she believed represented new genera belonged in the subfamily. As a consequence, the work of Healy (2006a) served as the critical foundation for the eventual establishment of the Rhinebothriidea based on additional morphological and phylogenetic work by her and her colleagues (Healy et al., 2009).

HOST ASSOCIATIONS. Species assigned to the genera included in the Echeneibothriinae and the Rhinebothriinae by Euzet (1994) parasitize only batoid elasmobranchs. Furthermore, rhinebothriidean genera were known to be associated with specific groups of batoid hosts. For example, species of *Echeneibothrium* are restricted to skates (see Euzet, 1959; Campbell, 1977) and species of *Rhinebothrium* are, with a few exceptions, parasites of stingrays (see Euzet, 1959; Campbell, 1970).

GEOGRAPHIC DISTRIBUTION. Rhinebothriideans were known to be cosmopolitan in distribution prior to the initiation of the PBI project, with species having been reported from the coasts of every continent including Antarctica (e.g., Wojciechowska, 1991), and Oceania (Williams, 1964; Butler, 1987), as well as from freshwater habitats, primarily in South America (Brooks et al., 1981), but also from Borneo (Healy, 2006b). Prior to the PBI project, the majority of rhinebothriideans had been reported from North and South American, and European coastal waters.

CURRENT STATUS OF THE RHINEBOTHRIIDEA

DIVERSITY AND CLASSIFICATION. Diversity in the Rhinebothriidea was substantially expanded at all taxonomic levels over the course of the PBI project. As a result of PBI project efforts, 25 new species were described, five new genera were erected, two subfamilies were elevated to family level, and two new families were established. These numbers do not include the non-PBI funded efforts of Tan et al. (2009) establishing *Biotobothrium* Tan, Zhou & Yang, 2009, Ruhnke and Seaman (2009) describing three new species of *Anthocephalum*, or Kornyushin and Polyakova (2012) erecting *Cairaeanthus* Kornyushin & Polyakova, 2012 and its two new species.

When Healy et al. (2009) established the order Rhinebothriidea, they included the following known genera: *Anthocephalum*, *Echeneibothrium*, *Rhabdotobothrium*, *Rhinebothrium*, *Rhinebothroides*, *Rhodobothrium*, *Scalithrium*, and *Spongiobothrium*. Also recognized within the Rhinebothriidea were members of what Healy et al. (2009) identified as four new genera (as New genus 1 through 4) as well as a taxon they referred to as "Rhinebothriinae n. sp." (see Table 1). Their analyses of complete 18S rDNA and partial 28S rDNA sequence data revealed this group of taxa to be phylogenetically distinct relative to the other genera considered to be tetraphyllideans at that time. Healy et al. (2009) identified the following additional genera as candidates for possible future inclusion in the order: *Clydonobothrium*, *Escherbothrium* Berman & Brooks, 1994, *Glyphobothrium*, *Notomegarhynchus* Ivanov & Campbell, 2002, *Phormobothrium*, *Pseudanthobothrium*, *Serendip*, and *Tritaphros* (see Table 1). Ruhnke (2011) subsequently considered the following genera as possible additional members of the Rhinebothriidea: *Biotobothrium*, *Notomegarhynchus*, *Pararhinebothroides* Zamparo, Brooks & Barriga, 1999, and *Pentaloculum* Alexander, 1963.

Since Healy et al.'s (2009) work, much progress has been made towards further improving the classification of the Rhinebothriidea. A series of later studies have addressed the composition of the Rhinebothriidea, while also testing some of the predictions made by Healy et al. (2009) with respect to membership in the order. These studies have also expanded the diversity of the order. Below, we will highlight those contributions and discuss points that remain to be better elucidated by future research.

TABLE 1. Development of the classification of Rhinebothriidea during the PBI project. * As referred to by Healy et al. (2009).

Healy et al. (2009)	Caira et al. (2014)	Ruhnke et al. (2015)
Anthocephalum	*Anthocephalum*	**Rhinebothriidae**
Echeneibothrium	*Echeneibothrium*	*Rhinebothrium*
Rhabdotobothrium	*Rhabdotobothrium*	*Rhabdotobothrium*
Rhinebothroides	*Rhinebothroides*	*Rhinebothroides*
Rhinebothrium	*Rhinebothrium*	*Rhodobothrium*
Rhodobothrium	*Rhodobothrium*	*Scalithrium*
Scalithrium	*Scalithrium*	*Spongiobothrium*
Spongiobothrium	*Spongiobothrium*	**Tentative members:**
New genus 1* (*Divaricobothrium*)	New genus 1* (*Divaricobothrium*)	*Crassuseptum*
New genus 2* (*Barbeaucestus*)	New genus 2* (*Barbeaucestus*)	*Biotobothrium*
New genus 3* (*Stillabothrium*)	New genus 3* (*Stillabothrium*)	
New genus 4* (*Sungaicestus*)	New genus 4* (*Sungaicestus*)	**Echeneibothriidae**
Rhinebothriinae n. sp.* (New genus 11)	*Pseudanthobothrium*	*Echeneibothrium*
		Pseudanthobothrium
Tentative members:	**Tentative members:**	*Clydonobothrium*
Pseudanthobothrium	*Clydonobothrium*	*Phormobothrium*
Clydonobothrium	*Phormobothrium*	*Tritaphros*
Phormobothrium	*Tritaphros*	*Notomegarhynchus*
Tritaphros	*Notomegarhynchus*	
Notomegarhynchus	*Escherbothrium*	**Anthocephaliidae**
Escherbothrium	*Zyxibothrium*	*Anthocephalum*
Serendip	*Biotobothrium*	New genus 1* (*Divaricobothrium*)
Glyphobothrium		New genus 2* (*Barbeaucestus*)
		New genus 4* (*Sungaicestus*)
		Cairaeanthus
		Escherbothriidae
		Escherbothrium
		New genus 3* (*Stillabothrium*)
		Included without familial placement:
		New genus 11 (Rhinebothriinae n. sp.*)

Caira et al. (2014) provided the first robust test of the monophyly of the Rhinebothriidea since its erection in 2009. Their phylogenetic analyses were based on complete 18S rDNA and full or partial 28S rDNA (D1–D3) sequence data for a total of 134 terminals representing 97 genera in 15 orders of eucestodes, 23 genera of which were considered members of the Rhinebothriidea. Their study produced the most taxonomically comprehensive phylogenetic hypothesis for eucestodes published to date—in particular shedding some light on the generic composition of the Rhinebothriidea. Not only did they corroborate most of the predictions of group membership suggested by Healy et al. (2009) (see Table 1), but they also refuted the inclusion of some taxa that exhibit apparent stalks. For instance, the inclusion of a representative of *Pseudanthobothrium* in their study confirmed the close affinities between the latter genus and *Echeneibothrium* in a clade characterized by their possession of an apical modification of the scolex proper in the form of a myzorhynchus that persists into the adult stage. On the other hand, several genera also possessing stalks (i.e., *Anthobothrium* van Beneden, 1850, *Carpobothrium* Shipley & Hornell, 1906, and *Clistobothrium* Dailey & Vogelbein, 1990) nested elsewhere in the trees resulting from their phylogenetic analyses. Readers are referred to Chapter 16 on the Phyllobothriidea (Ruhnke et al., 2017) and Chapter 20 on the "Tetraphyllidea" relics (Caira et al., 2017a) in this volume for more detailed treatments of, and current thoughts on, the affinities of these genera. Based on their possession of a myzorhynchus on the adult scolex, Caira et al. (2014) considered the remaining members of the Echeneibothriinae (i.e., *Clydonobothrium*, *Notomegarhynchus*, *Phormobothrium*, and *Tritaphros*) to also belong in the Rhinebothriidea. They indicated that the genera *Escherbothrium*, *Biotobothrium*, and *Zyxibothrium* Hayden & Campbell, 1981 were candidates for membership in the order (see Table 1), in addition to an undescribed genus which they referred to as New genus 7 and *Pentaloculum*.

Ruhnke et al. (2015) subsequently conducted a phylogenetic study based on partial 28S rDNA (D1–D3) and complete 18S rDNA sequence data in which they described eight new species of *Anthocephalum* and provided an infraordinal classification for the order (Table 1). Their dataset contained all rhinebothriideans from Caira et al.'s (2014) study including five undescribed species of Healy et al.'s (2009) New genus 3 (now *Stillabothrium* Healy & Reyda, 2016; Reyda et al., 2016), and one species each of Healy et al.'s (2009) New genus 1, 2 and 4 (now *Divaricobothrium* Caira, Healy, Marques & Jensen, 2017, *Barbeaucestus* Caira, Healy, Marques & Jensen, 2017, and *Sungaicestus* Caira, Healy, Marques & Jensen, 2017, respectively; Caira et al., 2017b), as well as "Rhinebothriinae n. sp." of Healy et al. (2009) which Ruhnke et al. (2015) referred to as New genus 11. Ruhnke et al. (2015) expanded this dataset to include an additional 14 species of *Anthocephalum* and one species of *Escherbothrium*. Based on their results, they recognized four families in the Rhinebothriidea, two of which were new: Anthocephaliidae Ruhnke, Caira & Cox, 2015, Echeneibothriidae, Escherbothriidae Ruhnke, Caira & Cox, 2015, and Rhinebothriidae.

The composition of the Rhinebothriidea as suggested by Ruhnke et al. (2015) is, in many respects, similar to that suggested by Caira et al. (2014). Based on morphological grounds, Ruhnke et al. (2015) tentatively assigned *Biotobothrium* and *Crassuseptum* Eyring, Healy & Reyda, 2012 to the Rhinebothriidae; *Clydonobothrium*, *Notomegarhynchus*, *Phormobothrium*, and *Tritaphros* were assigned to the Echeneibothriidae; and *Cairaeanthus* and *Pararhinebothroides* were tentatively assigned to the newly erected Anthocephaliidae. However, the rhinebothriidean affinities of Caira et al.'s (2014) New genus 7 and *Pentaloculum* hypothesized by Caira et al. (2014) were not supported in the results of the analyses of Ruhnke et al. (2015). The 18 described genera and five undescribed genera assigned to the order by Ruhnke et al. (2015) are summarized in Table 1.

The final set of contributions to our understanding of diversity and classification of the Rhinebothriidea from the PBI project spawned from three very recent publications. Marques and Caira (2016) provided molecular evidence that *Pararhinebothroides hobergi* Zamparo, Brooks & Barriga, 1999, the type and only known member of its genus, should be considered a member of *Anthocephalum* (as *Anthocephalum hobergi* [Zamparo, Brooks & Barriga, 1999] Marques & Caira, 2016) as had been predicted by Ruhnke and Seaman (2009) and Ruhnke et al. (2015). As noted above, Reyda et al. (2016) erected *Stillabothrium* for Healy et al.'s (2009) New genus 3, which Ruhnke et al. (2015) assigned to the Escherbothriidae (see Table 1). Caira et al. (2017b) erected three new genera to house the genera originally referred to by Healy et al. (2009) as New genus 1, 2, and 4; these were *Divaricobothrium*, *Barbeaucestus*, and *Sungaicestus*, respectively (see Table 1).

Although our understanding of the composition of the Rhinebothriidea has been greatly expanded, there is still much to be done. Presently, the Rhinebothriidea are composed of 136 valid species in 22 described genera and four families (Table 3). Of these 136 species, the familial assignments of *Anindobothrium anacolum* (Brooks, 1977) Marques, Brooks &

Lasso, 2001 and *A. lisae* Marques, Brooks & Lasso, 2001 remain to be determined, as does the assignment of the undescribed taxon from *Prisitis clavata* Garman, mentioned above, referred to as "Rhinebothriinae n. sp." by Healy et al. (2009) and New genus 11 by Ruhnke et al. (2015). Likewise, several of the recently established genera include a number of known, but as-of-yet undescribed species. For example, when they erected *Stillabothrium*, Reyda et al. (2016) included descriptions of five new species and revised generic assignments for two previously described species, but also made reference to specimens of multiple potentially new species that could be the focus of future research.

Further work is also needed to address the membership of the 36 species recognized here (see Table 3) within the Rhinebothriidea as *incertae sedis*. We believe it is likely that all of these species are valid. In some cases, the species are consistent with the concept of the Rhinebothriidea but are currently assigned to genera outside of the Rhinebothriidea (e.g., *Anthobothrium* [16 spp.], *Phyllobothrium* [10 spp.]). In other cases, species are currently assigned to the incorrect rhinebothriidean genera (e.g., *Echeneibothrium* [9 spp.]). In these cases generic reassignments will require careful study if these species are to be properly incorporated into the current classification of this order. Finally, the known host associations of the Rhinebothriidea point to the fact that a substantial amount of the diversity in this order has yet to be discovered (see below and Table 2).

MORPHOLOGY. Healy et al. (2009) identified the presence of stalked bothridia as a putative morphological synapomorphy for the Rhinebothriidea. Subsequent work (Caira et al., 2014; Ruhnke et al., 2015; Marques and Caira, 2016) has provided strong molecular support for the monophyly of the order with its expanded generic membership. However, this work has not led to the identification of additional morphological synapomorphies for the order. A number of the most conspicuous features shared by rhinebothriideans are also found in many other elasmobranch-hosted taxa. These include a follicular vitellarium, a posterior ovary, and a cirrus armed with spinitriches. Healy's (2006a) suggestion that the vas deferens entering the anterior margin of the cirrus-sac is a diagnostic character for the group is supported by work on a number of genera that have received attention in recent morphological studies (e.g., *Anthocephalum*, *Barbeaucestus*, *Crassuseptum*, *Divaricobothrium*, *Rhinebothrium*, *Scalithrium*, *Stillabothrium*, and *Sungaicestus*). But this feature remains to be confirmed in other genera (e.g., *Cairaeanthus*).

The scoleces of rhinebothriideans represent a spectacular amount of morphological diversity. The PBI project brought this to light with the discovery of new genera and new species, and with new collections of previously documented but poorly known species. Figure 1 illustrates some of the morphological variation seen in scolex morphology among representatives of 14 genera, including representatives of each of the four families. Many species in the order possess bothridia that are longer than wide (e.g., Fig. 1J), but some possess bothridia that are wider than long, the most notable of which is *Barbeaucestus* (Fig. 1B). The bothridia of many rhinebothriideans tend to be flimsy (e.g., Fig. 1J). Those of some are flat (e.g., Fig. 1M), but those of others are highly folded (e.g., Fig. 1N). In some the bothridia are laterally constricted (Fig. 1I); the bothridia of most members bear a conspicuous, membranous rim. The exceptions are the bothridia of *Echeneibothrium* and *Pseudanthobothrium*, which are thick (e.g., Fig. 1E) and deep, or even cup-shaped (e.g., Fig. 1F). The bothridia of *Divaricobothium* (Fig. 1C) are unusual in that they are bifid posteriorly. Some genera, such as *Anthocephalum*, clearly possess apical suckers on their bothridia (e.g., Fig. 1A), others, such as *Stillabothrium* lack suckers (e.g., Fig. 1G). The order includes a few members that lack, rather than possess, facial loculi (e.g., *Pseudanthobothrium*). The variation seen in the configuration of

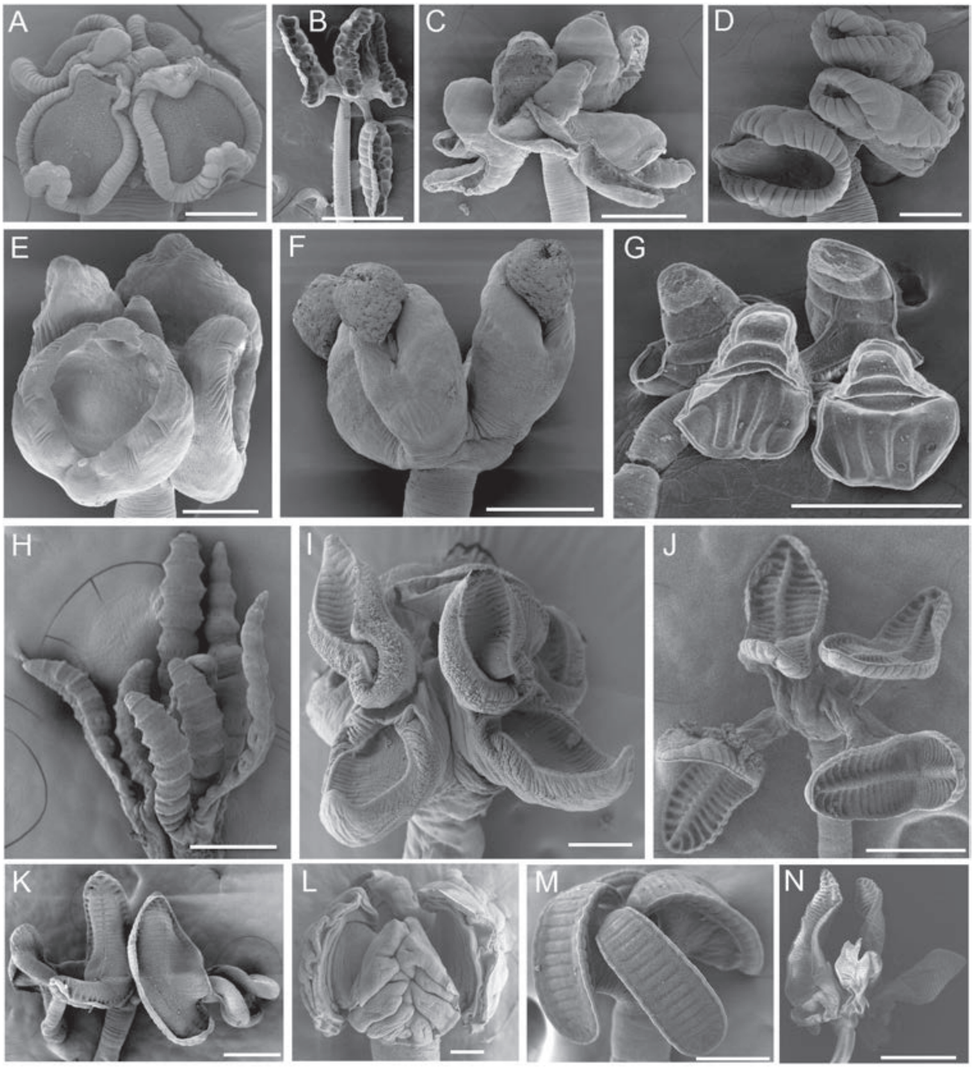

FIGURE 1. Scanning electron micrographs of the scoleces of representative genera of the four families of Rhinebothriidea. **(A–D)** ANTHOCEPHALIIDAE: **(A)** *Anthocephalum jensenae* from *Pateobatis jenkensii* from the Arafura Sea. **(B)** *Barbeaucestus jockuschae* from *Neotrygon orientale* from the South China Sea (modified from Caira et al. [2017b]). **(C)** *Divaricobothrium tribelum* from *Maculabatis* cf. *gerrardi* 2 (as *Himantura* cf. *gerrardi* 2 *sensu* Naylor et al. [2012a]) from the South China Sea (modified from Caira et al. [2017b]). **(D)** *Sungaicestus kinabatanganensis* from *Urogymnus polylepis* from the Kinabatangan River, Malaysian Borneo (modified from Caira et al. [2017b]). **(E–F)** ECHENEIBOTHRIIDAE: **(E)** *Echeneibothrium williamsi* from *Dipturus chilensis* off Chile (modified from Bueno and Caira [2017]). **(F)** *Pseudanthobothrium hanseni* from *Amblyraja radiata* off Massachusetts, USA. **(G)** ESCHERBOTHRIIDAE: *Stillabothrium cadenati* from *Zanobatus schoenleinii* off Senegal (modified from Reyda et al. [2016]). **(H–N)** RHINEBOTHRIIDAE: **(H)** *Crassuseptum pietrafacei* from *Mobula kuhlii* from the South China Sea. **(I)** *Rhabdotobothrium anterophallum* from *Mobula hypostoma* from the Gulf of Mexico. **(J)** *Rhinebothrium paratrygoni* from *Potamotrygon falkneri* from the Paraná River, Brazil. **(K)** *Rhinebothroides* sp. from *Paratrygon aiereba* from the Madre de Dios River, Peru. **(L)** *Rhodobothrium paucitesticulare* from *Rhinoptera* cf. *steindachneri sensu* Naylor et al. (2012a) in the Gulf of Mexico (modified from Jensen and Bullard [2010]). **(M)** *Scalithrium* sp. from *Glaucostegus typus* from Heron Island, Australia (modified from Healy [2006a]). **(N)** *Spongiobothrium* sp. from *Hypanus guttatus* off Belize. *Scale bars*: A, D, E, H, I, and M, 100 μm; C, F, G, J, K, and L, 200 μm; B and N, 500 μm.

facial septa and loculi is striking. In *Anthocephalum* (Fig. 1A) and in *Echeneibothrium* (Fig. 1E) the loculi are confined to the margins of the bothridia. Numerous genera possess bothridia in which the entire distal surface is covered with loculi, but the orientation and extent of the loculi and septa vary. In *Crassuseptum* (Fig. 1H), *Scalithrium* (Fig. 1M), and in at least one species of *Rhabdotobothrium* (Fig. 1I), only transverse septa are present, resulting in distal bothridial surfaces that are completely covered with transversely oriented loculi. The distal bothridial surfaces of *Sungaicestus* (Fig. 1D), *Rhinebothrium* (Fig. 1J), *Rhinebothroides* (Fig. 1K), and *Spongiobothrium* (Fig. 1N) are also completely covered with transverse septa, but the presence of single median longitudinal septum divides the transversely oriented loculi into two columns. Species of *Rhinebothroides* (Fig. 1K) and some species of *Rhinebothrium* possess marginal loculi in addition to transverse loculi. Species of *Barbeaucestus* (Fig. 1B), *Escherbothrium*, and *Stillabothrium* (Fig. 1G) possess different combinations of transversely and longitudinally oriented loculi and septa, resulting in configurations of loculi that are completely unlike those previously mentioned. Several genera and species of rhinebothriids, such as species of *Rhodobothrium* (Fig. 1L) possess bothridia that are apparently weakly loculated, but further study is needed to clarify this.

Reyda et al.'s (2016) erection of *Stillabothrium*, which included the description of multiple new species, serves to illustrate the extensive variation of bothridial morphologies seen even within a genus. In their treatment of a total of seven species, the monophyly of the group was confirmed with phylogenetic analyses based on sequence data for the D1–D3 region of the 28S rDNA gene. Reyda et al. (2016; fig. 1) provided diagrammatic illustrations of the remarkable facial loculus variation seen across species. Although each species of the genus possesses both longitudinally and transversely oriented loculi, the configuration of the loculi varies from species to species (see fig. 1; Reyda et al. [2016]). The species also vary greatly in terms of proglottid features, such as vaginal course and vitelline follicle arrangement.

During the relatively short history of the Rhinebothriidea, we have also learned that taxa across the order vary substantially in their proglottid anatomy. For example, most species of anthocephaliids (e.g., Fig. 2A) and escherbothriids possess vitelline follicles that are interrupted by the ovary, whereas species of echeneibothriids and rhinebothriids generally possess vitelline follicles that overlap the ovary (e.g., Fig. 2B). Most species in the order possess numerous testes (e.g., Fig. 2A, C), but there are at least three species of *Rhinebothrium* that possess only two testes (e.g., Fig. 2B). Members of the order also vary in the presence or absence of an external seminal vesicle, vaginal sphincter, as well as in terms of ovarian symmetry. Some groups exhibit symmetrical ovaries (e.g., Fig. 2A), while those of others are asymmetrical (e.g., Fig. 2C); furthermore, whereas in some species the ovary is bilobed in cross-section, in others it is tetralobed. At least four genera (i.e., *Rhabdotobothrium*, *Rhinebothrium*, *Rhodobothrium*, and *Stillabothrium)* include species with greatly expanded genital atria (e.g., Fig. 2D), however, this is unusual among members of the order. Nonetheless, the genital pore is usually in the posterior half of the proglottid and the cirrus-sac is usually tilted or bent posteriorly. In summary, the order Rhinebothriidea serves as an example of a monophyletic group of morphologically diverse cestodes that, with each new study, challenges the limits of our imagination.

Phylogenetic Relationships. All existing comprehensive phylogenetic hypotheses of rhinebothriidean interrelationships were generated as a result of PBI project efforts. Thus, we are beginning to more fully understand the relationships among members of this order and the composition of its subgroups. Ruhnke et al. (2015) found the Anthocephaliidae to be sister to the Escherbothriidae; in the trees resulting from their analyses, this clade was the

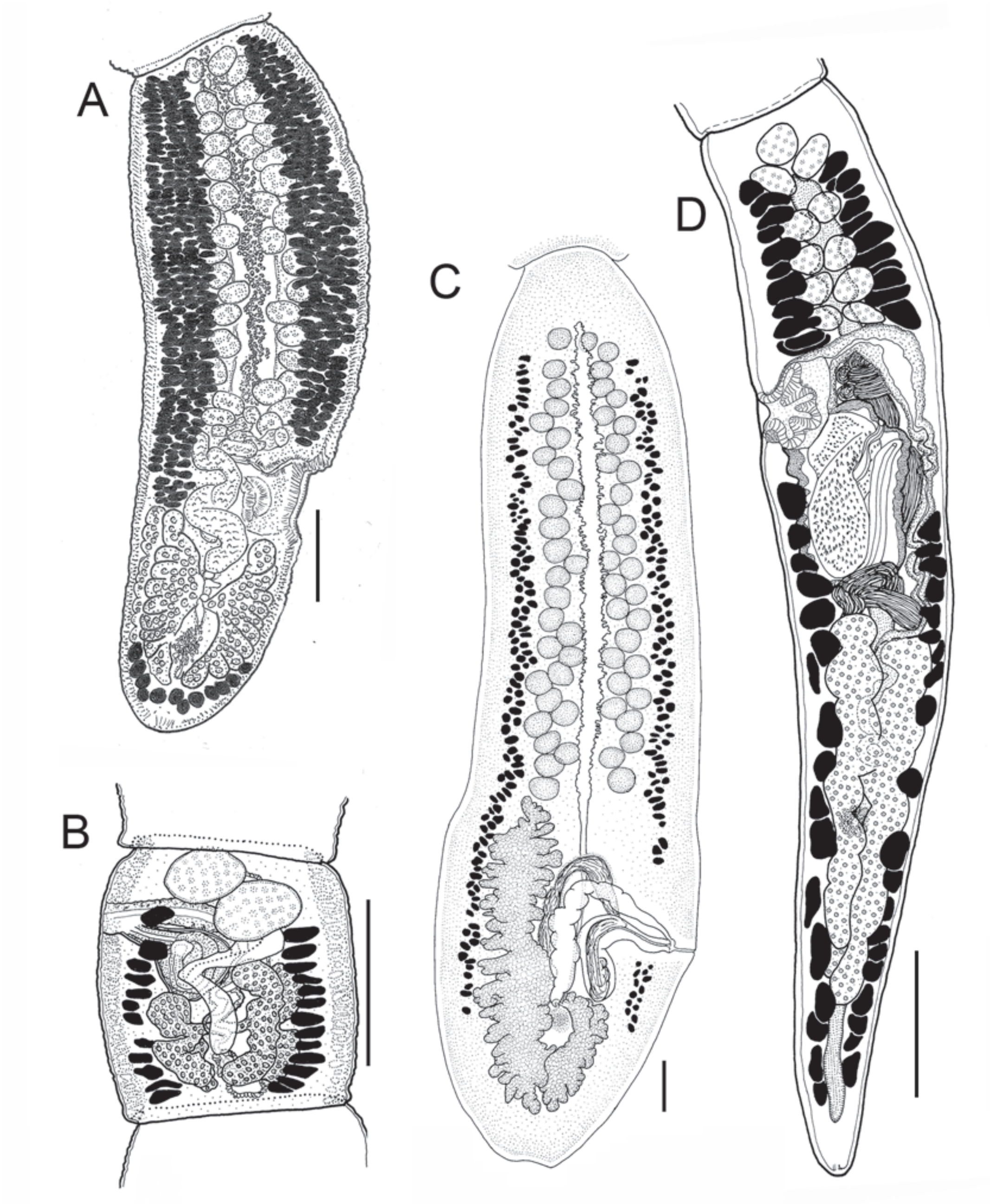

Figure 2. Line drawings of selected rhinebothriideans. **(A)** Terminal proglottid of *Anthocephalum healyae* from *Neotrygon australiae* from the Gulf of Carpentaria, Australia (modified from Ruhnke et al. [2015]). **(B)** Mature proglottid of *Rhinebothrium fulbrighti* from *Potamotrygon orbignyi* from the Amazon River, Brazil (modified from Reyda and Marques [2011]). **(C)** Terminal proglottid of *Rhinebothroides freitasi* from *Potamotrygon constellata* from the Itacuaí River, Brazil (modifed from Marques and Brooks [2003]). **(D)** *Stillabothrium cadenati* from *Zanobatus schoenleinii* off Senegal (modified from Reyda et al. [2016]). *Scale bars*: A, 200 μm; B–D, 100 μm.

sister taxon of an unresolved clade comprising New genus 11, the Echeneibothriidae, and the Rhinebothriidae (Fig. 3A). Marques and Caira (2016) also recovered the clade Anthocephaliidae + Escherbothriidae, but their results (Fig. 3B) suggested that the Echeneibothriidae were the sister taxon of that clade, and that the Rhinebothriidae were sister to the clade composed of the three other familes. According to the topology recovered by Marques and Caira (2016) (Fig. 3B), New genus 11 diverged from all other lineages early in the diversification of the order.

There are many factors that could explain the differences between these two hypotheses, despite the fact that Marques and Caira (2016) used the same dataset as Ruhnke et al. (2015) with the only difference being the addition of four terminals representing *Anthocephalum hobergi*. The most obvious one is the optimality criterion employed. The topology presented by Ruhnke et al. (2015) was inferred using Bayesian analysis, whereas Marques and Caira (2016) presented a phylogenetic hypothesis using maximum parsimony. Both studies, however, also analyzed the data under maximum likelihood, in which case both studies recovered the same phylogenetic pattern as their primary optimality criteria. This observation suggests that optimality criterion might not be the sole cause for these differences. Most likely, sequence alignment strategies contributed to the discrepancies observed. Both studies adopted different alignment procedures (see Ruhnke et al. [2015] and Marques and Caira [2016] for details), and phylogenetic results are known to be more sensitive to alignment than to optimality criteria (see Morrison [2009] and references therein). Be that as it may, both studies found relatively weak support for the nodes related to the relationships among families, indicating that those internal nodes are not all that well supported by 28S rDNA (D1–D3) and complete 18S rDNA sequence data. Therefore, a more robust proposal for the phylogenetic relationships among families of Rhinebothriidea awaits future research and additional data.

The results of Ruhnke et al. (2015) and Marques and Caira (2016) provide some guidance as to directions of future research if a more robust classification for the Rhinebothriidea is to be achieved. First, the as-of-yet undescribed New genus 11 likely represents a unique lineage within the Rhinebothriidea that should be assigned to its own family. This assertion is based not only on its unique morphology (see Healy [2006a] and fig. 6 of Healy et al. [2009]), but also on its substantial nucleotide divergence relative to the other rhinebothriidean taxa (see Marques and Caira, 2016). Both of these previous studies indicate that additional revision of the classification of the Rhinebothriidae is warranted, especially with respect to the circumscription of *Rhinebothrium*, which was found to be polyphyletic in both studies (Fig. 3C, D)—a hypothesis that has also been voiced by previous authors (e.g., Reyda and Marques, 2011). Furthermore, it is possible that some genera within this family (e.g., *Rhinebothroides* and *Scalithrium*) will be found to be junior synonyms of *Rhinebothrium*. However, in order to test these predictions, *Rhinebothrium flexile* Linton, 1890—the type species of the genus—must be included in future phylogenetic studies. In addition, the morphology of taxa presently attributed to *Rhinebothrium* should be studied in more detail. Such studies are likely to reveal a diversity of cohesive but as-of-yet unrecognized morphological subgroups that could justify the erection of new genera to resolve the non-monophyly of *Rhinebothrium*. Further work on the genus could also shed light on the intriguing question of the identity of the marine sister taxon of the seven species of *Rhinebothrium* that parasitize South American freshwater stingrays (see Reyda and Marques, 2011). Finally, within the Anthocephaliidae (Fig. 3E, F), the unstable phylogenetic position of an undescribed species of *Anthocephalum* from *Himantura leoparda* Manjaji-Matsumoto & Last from the Indo-Pacific Ocean (identified as *Anthocephalum* n. sp. 1 [LRP 8505] by Ruhnke et al. [2015]), would be extremely interesting to investigate further. As things stand, its phylogenetic position seems to be contingent on

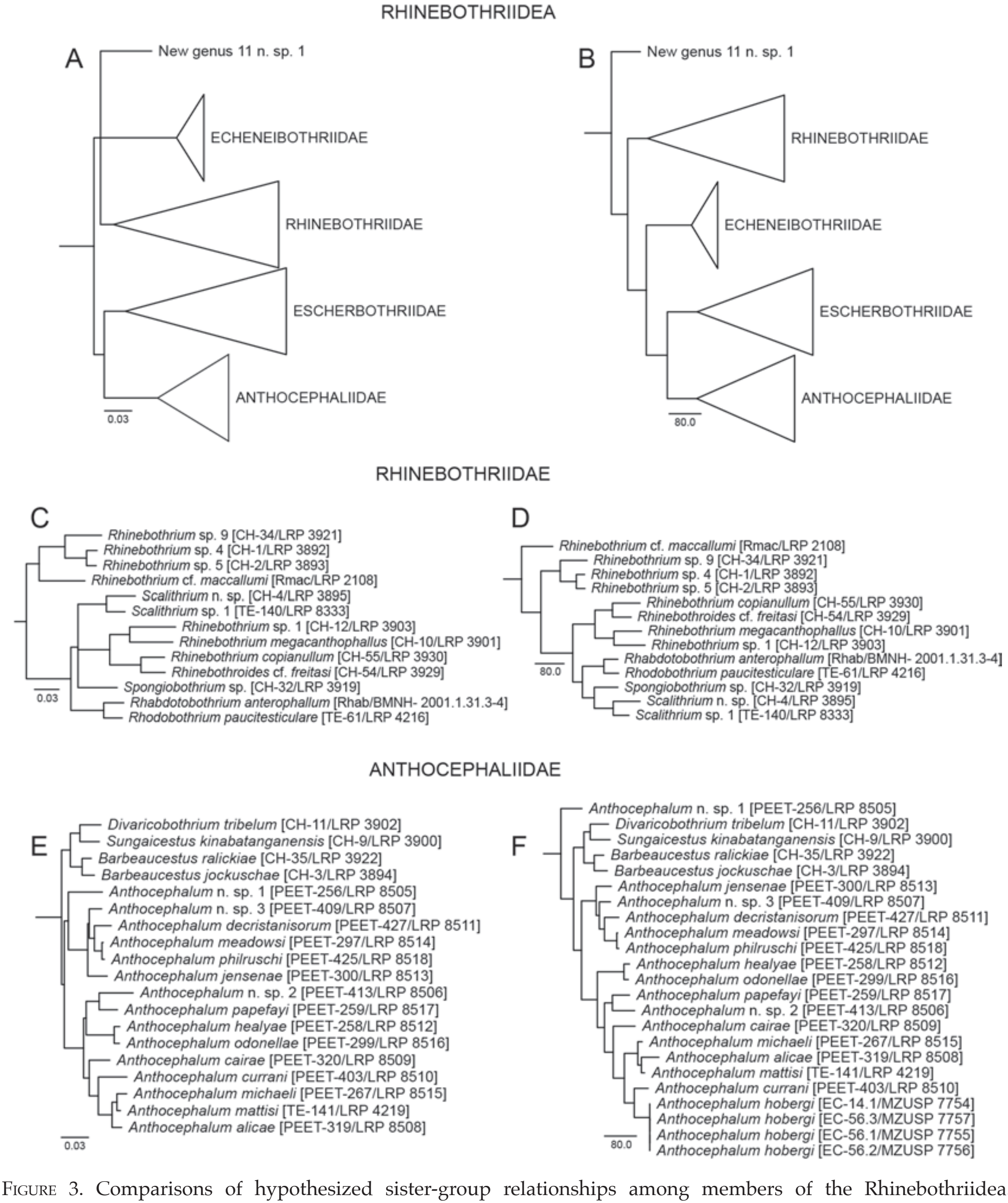

Figure 3. Comparisons of hypothesized sister-group relationships among members of the Rhinebothriidea. **(A, C, E)** From Ruhnke et al. (2015). **(B, D, F)** From Marques and Caira (2016). Figures modified from original studies to reflect the recently named genera *Divaricobothrium*, *Sungaicestus*, and *Barbeaucestus* (see Caira et al., 2017b).

the optimality criterion and/or alignment employed in phylogenetic analyses.

Host Associations. The duration of the PBI project represents a particularly productive period in the history of elasmobranch systematics and biodiversity. Over that time, substantial progress was made in the molecular systematics of elasmobranchs, including the development of molecular methods to assist with the identification of elasmobranchs (e.g., Naylor et al., 2012a). Phylogenetic analyses with broad representation across elasmobranchs are also now available (e.g., Naylor et al., 2012b). Elasmobanch classifications have been refined so as to bring major taxonomic categories into line with assessments of phylogenetic relationships. However, the new understanding of elasmobranch diversity has raised significant uncertainty in terms of past host identifications, calling into question many previous host records and necessitating the development of a more careful and tractable approach to host identifications involving digital photographs and DNA vouchering, as well as vouchering of elasmobranch specimens when possible (see Caira and Jensen, 2014).

Existing records indicate that the degree of host specificity exhibited by rhinebothriideans is very strict and predominantly oioxenous (*sensu* Euzet and Combes [1980]). Of the 31 rhinebothriidean species described over the course of the PBI period, only four were found to parasitize more than one host species. Of the 136 valid species in the order, only 13 have been reported to parasitize more than one host species. Hence, by far the majority of species have been reported only from their type host. Nonetheless, the exceptions to oioxeny are worth noting. The rhinebothriidean parasites of potamotrygonid stingrays (i.e., South American freshwater stingrays) are conspicuous exceptions to this general pattern of strict host specificity (see Marques and Brooks, 2003; Reyda and Marques, 2011). All five species of *Rhinebothroides* (see Table 3) parasitize more than one potamotrygonid species (Marques and Brooks, 2003). Of the seven species of *Rhinebothrium* described from potamotrygonids, five parasitize more than one host species; two of these, *Rhinebothrium copianullum* Reyda, 2008 and *Rhinebothrium paratrygoni* Rego & Dias, 1976, have been reported from eight and seven potamotrygonid species, respectively (Reyda and Marques, 2011). Whereas it has been suggested that the relaxed host specificity of rhinebothriideans from potamotrygonids may be associated with the unique nature of that freshwater elasmobranch hosted cestode system (Reyda and Marques, 2011), there are also exceptions to oioxeny among strictly marine rhinebothriideans. The recent study by Reyda et al. (2016) reported that two of the seven species of *Stillabothrium* had somewhat relaxed levels of host specificity; *Stillabothrium davidcynthiaorum* Daigler & Reyda, 2016 was reported from four species of dasyatids which are now, following Last et al. (2016a), considered to be members of the genera *Brevitrygon* Last, Naylor & Manjaji-Matsumoto, *Himantura* Müller & Henle, and *Maculabatis* Last, Naylor & Manjaji-Matsumoto, and *Stillabothrium cadenati* (Euzet, 1954) Healy & Reyda, 2016 was reported from two species of batoids from different families. The question of host specificity is an intriguing one that should be further studied. At this time, it can be stated that species of rhinebothriideans are generally strictly host specific (i.e., oioxenous), with some interesting exceptions.

The host associations of existing and known undescribed adult rhinebothriideans are summarized in Table 2. It is clear from an examination of these associations that rhinebothriideans are exclusively parasites of batoid elasmobranchs, with the exception of *Rhodobothrium enigmaticum* (Gallien, 1949) Carvajal & Campbell, 1979, which is known only from its larval stages in the surf clam *Spisula solida* (L.). Of the 136 species currently included in the Rhinebothriidea, approximately 65% parasitize Myliobatiformes (stingrays and eagle rays) and approximately 29% parasitize Rajiformes (skates). Although these two host orders collectively include almost 80% of known batoid species, our knowledge of the diversity of the rhinebothriideans they host comes from a very small subset of members of both groups. At present, 86 species of rhinebothriideans have been reported from 46 of the 324 species of myliobatiforms and 39 species of rhinebothriideans have been reported from 20 of the 317 species of Rajiformes. These numbers suggest that our understanding of rhinebothriidean diversity comes from studies of 14.2% of stingray and 6.3% of skate diversity. Overall, only 10% of batoid species account for the known diversity of rhinebothriidean species. One specific notable new association reported recently is the occurrence of *Biotobothrium platyrhina* Tan, Zhou & Yang, 2009 from *Platyrhina sinensis* (Bloch & Schneider), representing the first report of a rhinebothriidean from a fanray.

In terms of future discovery of rhinebothriideans, we predict that the most profitable host taxa to sample for new rhinebothriidean taxa will be members of the family Dasyatidae Jordan and members of the order Rajiformes (skates). Dasyatids include 110 species, of which only 28 (24%) have been reported to host 55 species of rhinebothriideans. We predict that more than 75% of the richness of rhinebothriideans in dasyatids remains to be described. The Rajiformes contains 324 species, and only 32 rhinebothriideans have been described from 20 species (~7%) of that rich group of batoids to date. For these hosts, we predict that more than 350 species remain to be described; in other words, we estimate that only approximately 10% of the diversity of rhinebothriideans from Rajiformes is known. For instance, we estimate that *Bathyraja* Ishiyama and *Dipturus* Rafinesque—two of the most speciose genera of the order, with 56 and 59 described species, respectively—are likely parasitized by more than 240 species of rhinebothriideans. In other words, we estimate that only 4.5% of the rhinebothriidean species diversity from these two rajiform genera is known at this time.

GEOGRAPHIC DISTRIBUTION. The compilation of the type localities of members of the Rhinebothriidea reveals a worldwide distribution for the order (Fig. 4). All families are known to have representatives in most oceans, but some interesting patterns are emerging. For instance, whereas members of the Anthocephaliidae and the Rhinebothriidae are found in both temperate and tropical waters, members of the Echeneibothriidae seem to be restricted to temperate waters, and representatives of the Escherbothriidae are found only in tropical waters. The two genera of escherbothriids have non-overlapping distributions: *Escherbothrium* is known only to occur in the Western Hemisphere, whereas *Stillabothrium* only occurs in the Eastern Hemisphere. Also, within the Rhinebothriidae there are 12 species restricted to Neotropical freshwater systems (5 and 7 species of *Rhinebothroides* and *Rhinebothrium*, respectively); the only other known species of freshwater rhinebothriids are the three that occur in Borneo (Healy, 2006b).

The greatest contribution to our knowledge of the geographic distributions of rhinebothriideans resulting from PBI project efforts was the characterization of new genera and species from the Central Indo-Pacific marine realm (*sensu* Spalding et al. [2007]). Seventeen of the 25 species of rhinebothriideans described during the PBI project were from those waters, with most of those having been reported from the western Pacific Ocean portions of that region. Figure 4 also serves to illustrate the gaps that remain in our knowledge of the geographic distribution of the order. There are several regions from which only a few species of rhinebothriideans have been described. For example, only two species of escherbothriids have been described from the eastern Atlantic Ocean off coastal Africa; only one rhinebothriid species and one echeneibothriid species have been described from the western Atlantic Ocean off Brazil and Argentina, respectively. Given the diversity of potential hosts known from these regions, it is safe to say that the diversity of rhinebothriideans will increase by work focused in these areas. Other striking gaps in our knowledge of the diversity of this order are the Western Indo-Pacific and Temperate Australasian realms of Spalding et al. (2007). These areas, with the exceptions of the descriptions of few species of rhinebothriids from India and Sri Lanka, and one description from New Zealand, are almost certainly home to a great diversity of species of this group, awaiting discovery.

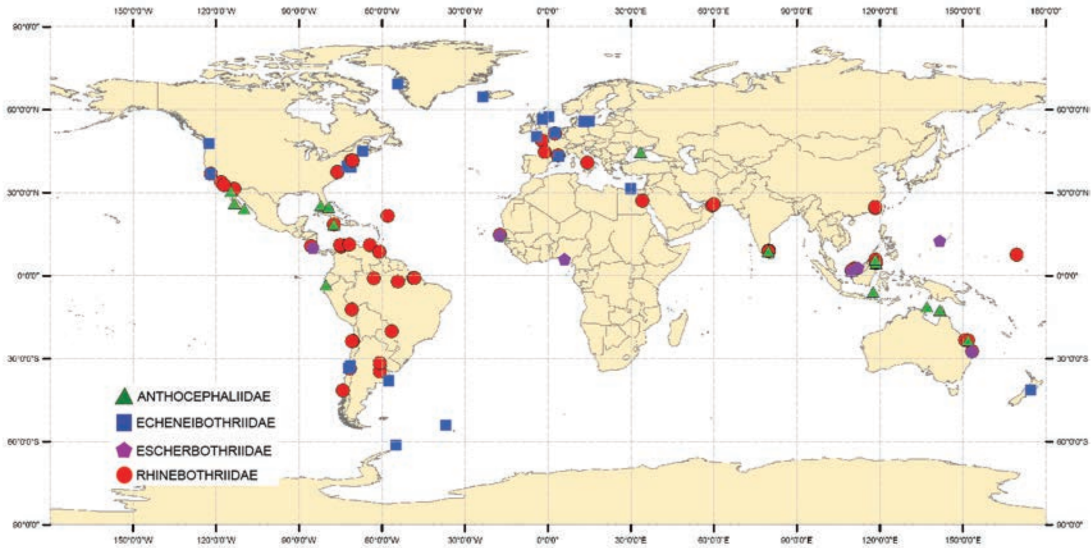

FIGURE 4. Distribution of rhinebothriideans by family (points based on type localities of valid species either provided in the original descriptions or estimated based on locality information).

CONCLUSIONS

Collections and taxonomic work associated with the PBI project have contributed to our knowledge of species diversity and higher-level taxonomic organization, as well as to our knowledge of host use, host specificity, geographic variation, and perhaps most notably, morphological variation in scoleces that is unrivaled by other cestode orders. The remarkable diversity in form across the order is exemplified by its extensive variation in bothridial architecture, which spans an astonishing range of shapes and septal configurations. PBI project efforts increased the number of valid rhinebothriidean species by 25, bringing the total number of valid species in the order to 136. In addition, six new genera, five resulting from PBI project efforts, were erected during the PBI period. Perhaps of greater importance, a familial level classification for the order was established. Thirty-five species designated as *incertae sedis* have been identified that should be incorporated into the classification of the Rhinebothriidea once their generic assignments have been reassessed. In terms of host specificity, most members of the order exhibit strict host specificity (i.e., oioxenous), but notable exceptions come from species parasitizing South American freshwater stingrays, and from escherbothriids (i.e., *Stillabothrium*). The geographic distribution of the order was expanded with the discovery of new species to include northern Australia, Malaysian and Indonesian Borneo, and Senegal. The order is now known from 11 of Spalding et al.'s (2007) 12 marine realms; the exception is Temperate Southern Africa. There are many regions of the planet that remain unexplored for rhinebothriideans. There is no doubt that rhinebothriidean diversity is greatly underestimated globally. This statement is based on both current patterns of geographic distribution and host use. With respect to the latter, we predict that examination of the many as-of-yet unexamined species of dasyatids will result in the discovery of more than 210 new rhinebothriidean species. Likewise, we predict that exploration of members of two of the four families of skates will lead to the discovery of an estimated 270 new rhinebothriideans. In total, we predict a total of approximately 790 rhinebothriideans globally.

As much as we have progressed in our understanding of the diversity, interrelationships, and morphological variation of this group, many areas of inquiry remain unexplored. The instability and relatively low support for internal nodes in previous phylogenetic studies indicates the need for the refinement of phylogenetic hyphotheses based on additional data and greater taxanomic representation. The distinct improvements in our knowledge of the evolutionary history of these intriguing parasites in just a few short years of the PBI project, however, can serve as a springboard for additional studies that will continue to contribute substantially to the field of cestodology.

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Table 2. Expected global elasmobranch associations of rhinebothriidean species (in yellow). Number of batoid species per genus given in parentheses (includes known undescribed batoid species). First column: number of rhinebothriidean species parasitizing each batoid taxon as of 2017 (includes known undescribed cestode species); second column: predicted total number of rhinebothriidean species parasitizing each batoid taxon globally. Quotes indicate non-monophyletic taxa (Naylor et al., 2012b; Last et al., 2016a, b). Question marks indicate genera not yet examined for cestodes. Estimated total number of rhinebothriidean species parasitizing elasmobranchs globally given at bottom of Table.

	Rhinebothriidean spp.	
	2017	ESTIM.
BATOIDEA		
Myliobatiformes	**116**	**424**
Aetobatidae	**0**	**0**
Aetobatus (7 spp.)	0	0
Dasyatidae	**82**	**298**
“*Bathytoshia*” (3 spp.)	8	15
Brevitrygon (5 spp.)	3	15
Dasyatis (5 spp.)	4	20
Fluvitrygon (3 spp.)	5	9
Fontitrygon (4 spp.)	5	8
Hemitrygon (10 spp.)	3	20
Himantura (8 spp.)	3	24
Hypanus (12 spp.)	13	48
Maculabatis (13 spp.)	7	39
Makararaja (1 sp.)	?	0
Megatrygon (1 sp.)	0	2
Neotrygon (13 spp.)	5	22
Pastinachus (6 spp.)	2	12
Pateobatis (7 spp.)	2	21
Pteroplatytrygon (1 sp.)	2	3
Taeniura (5 spp.)	8	16
Taeniurops (2 spp.)	1	2
“*Telatrygon*” (4 spp.)	2	8
Urogymnus (7 spp.)	9	14
Gymnuridae	**0**	**0**
Gymnura (15 spp.)	0	0
Hexatrygonidae	**0**	**0**
Hexatrygon (1 sp.)	0	0
Mobulidae	**2**	**8**
Mobula (8 spp.)	2	8
Myliobatidae	**4**	**15**
Aetomylaeus (9 spp.)	0	0
Myliobatis (11 spp.)	4	15
Plesiobatidae	**0**	**0**
Plesiobatis (1 sp.)	**0**	**0**
Potamotrygonidae	**17**	**65**
Heliotrygon (2 spp.)	**0**	0
Styracura (2 spp.)	4	4
Paratrygon (1 sp.)	2	2
Plesiotrygon (2 spp.)	0	0
Potamotrygon (25 spp.)	11	59
Rhinopteridae	**1**	**8**
Rhinoptera (8 spp.)	1	8
Urolophidae	**0**	**0**
Spinilophus (1 sp.)	?	0
Trygonoptera (6 spp.)	0	0
Urolophus (22 spp.)	0	0
Urotrygonidae	**10**	**30**
Urobatis (6 spp.)	9	18
Urotrygon (12 spp.)	1	12
Rhinopristiformes	**8**	**47**
Glaucostegidae	**3**	**14**
Glaucostegus (9 spp.)	3	14
Platyrhinidae	**1**	**5**
Platyrhina (5 spp.)	1	5
Platyrhinoidis (1 sp.)	0	0
“Pristidae”	**0**	**0**
Anoxypristis (1 sp.)	0	0
Pristis (5 spp.)	0	0
Rhinidae	**0**	**0**
Rhina (1 sp.)	0	0
Rhynchobatus (8 spp.)	0	0
Rhynchorhina (1 sp.)	?	0
“Rhinobatidae”	**2**	**24**
Acroteriobatus (8 spp.)	1	8
Pseudobatos (8 spp.)	1	8
Rhinobatos (16 spp.)	0	8
Trygonorrhinidae	**1**	**3**
Aptychotrema (3 spp.)	1	3
Trygonorrhina (2 spp.)	0	0
Zapteryx (3 spp.)	0	0
Zanobatidae	**1**	**1**
Zanobatus (1 sp.)	1	1
Torpediniformes	**1**	**12**
Hypnidae	**0**	**0**
Hypnos (1 sp.)	0	0
Narcinidae	**0**	**0**
Benthobatis (4 spp.)	?	0
Diplobatis (4 spp.)	0	0
Discopyge (2 spp.)	0	0
Narcine (15 spp.)	0	0
Narcinops (5 spp.)	0	0
Narkidae	**0**	**0**
Crassinarke (1 sp.)	?	0
Electrolux (1 sp.)	?	0
Heteronarce (3 spp.)	?	0
Narke (3 spp.)	0	0
Temera (1 sp.)	?	0
Typhlonarke (1 sp.)	0	0
Torpedinidae	**1**	**12**
Tetronarce (9 spp.)	0	0
Torpedo (12 spp.)	1	12
Rajiformes	**39**	**309**
Anacanthobatidae	**0**	**0**
Anacanthobatis (6 spp.)	?	0
Indobatis (1 sp.)	?	0
Schroederobatis (1 sp.)	?	0
Sinobatis (9 spp.)	?	0
Springeria (2 spp.)	?	0
Arhynchobatidae	**7**	**103**
Arhynchobatis (1 sp.)	?	0
Atlantoraja (3 spp.)	1	3
Bathyraja (57 spp.)	3	84
Brochiraja (9 spp.)	0	0
Insentiraja (2 spp.)	?	0
Irolita (2 spp.)	?	0
Notoraja (12 spp.)	?	0
Pavoraja (6 spp.)	?	0
Psammobatis (8 spp.)	1	8
Pseudoraja (1 sp.)	?	0
Rhinoraja (3 spp.)	?	0
Rioraja (1 sp.)	0	0
Sympterygia (4 spp.)	2	8
Gurgesiellidae	**0**	**0**
Cruriraja (8 spp.)	0	0
Fenestraja (8 spp.)	?	0
Gurgesiella (3 spp.)	?	0
Rajidae	**32**	**206**
Amblyraja (9 spp.)	5	18
Beringraja (6 spp.)	0	0
Breviraja (6 spp.)	?	0
Dactylobatus (2 spp.)	?	0
Dentiraja (11 spp.)	?	0
Dipturus (52 spp.)	8	104
Hongeo (1 sp.)	?	0
Leucoraja (13 spp.)	5	26
Malacoraja (4 spp.)	1	4
Neoraja (5 spp.)	?	0
Okamejei (12 spp.)	0	0
Orbiraja (3 spp.)	0	0
Raja (17 spp.)	12	34
Rajella (20 spp.)	1	20
Rostroraja (10 spp.)	0	0
Spiniraja (1 sp.)	0	0
BATOID TOTAL	**164**	**792**
SHARK TOTAL	**0**	**0**
ELASMOBRANCH TOTAL	**164**	**792**

Table 3. List of rhinebothriidean valid taxa, taxa *incertae sedis*, and their type hosts. New taxa and taxonomic actions resulting from PBI project activities indicated in bold. * Host identifications requiring confirmation. † Replacement name.

VALID TAXA

- Family Anthocephaliidae Ruhnke, Caira & Cox, 2015
  - *Anthocephalum* Linton, 1890 (syn. *Pararhinebothroides* Zamparo, Brooks & Barriga, 1999)
    - *Anthocephalum gracile* Linton, 1890 (type) ex *Bathytoshia centroura* (as *Trygon centrura* [sic])
    - *Anthocephalum alicae* Ruhnke, 1994 ex *Hypanus americanus* (as *Dasyatis americana*)
    - *Anthocephalum cairae* Ruhnke, 1994 ex *Hypanus americanus* (as *Dasyatis americana*)
    - *Anthocephalum currani* Ruhnke & Seaman, 2009 ex *Hypanus dipterura* (as *Dasyatis brevis*)
    - ***Anthocephalum decrisantisorum* Ruhnke, Caira & Cox, 2015** ex *Pateobatis uarnacoides* (as *Himantura uarnacoides*)
    - *Anthocephalum duszynskii* Ruhnke, 1994 ex *Urobatis halleri* (as *Urolophus halleri*)
    - ***Anthocephalum healyae* Ruhnke, Caira & Cox, 2015** ex *Neotrygon australiae* (as *Neotrygon kuhlii* 4 *sensu* Naylor et al. [2012a])
    - *Anthocephalum hobergi* (Zamparo, Brooks & Barriga, 1999) **Marques & Caira, 2016** ex *Urobatis tumbesensis*
    - ***Anthocephalum jensenae* Ruhnke, Caira & Cox, 2015** ex *Pateobatis jenkinsii* (as *Himantura jenkinsii*)
    - *Anthocephalum kingae* (Schmidt, 1978) Ruhnke & Seaman, 2009 ex *Urobatis jamaicensis* (as *Urolophus jamaicensis*)
    - *Anthocephalum lukei* Ruhnke & Seaman, 2009 ex *Hypanus longus* (as *Dasyatis longus*)
    - ***Anthocephalum mattisi* Ruhnke, Caira & Cox, 2015** ex *Dasyatis* sp.*
    - ***Anthocephalum meadowsi* Ruhnke, Caira & Cox, 2015** ex *Himantura leoparda*
    - *Anthocephalum michaeli* Ruhnke & Seaman, 2009 ex *Hypanus longus* (as *Dasyatis longus*)
    - ***Anthocephalum odonnellae* Ruhnke, Caira & Cox, 2015** ex *Neotrygon orientale* (as *Neotrygon kuhlii* 1 *sensu* Naylor et al. [2012a])
    - ***Anthocephalum papefayei* Ruhnke, Caira & Cox, 2015** ex *Fontitrygon margaritella* (as *Dasyatis margaritella*)
    - ***Anthocephalum philruschi* Ruhnke, Caira & Cox, 2015** ex *Himantura australis* (as *Himantura uarnak* 2 *sensu* Naylor et al. [2012a])
    - ***Anthocephalum wedli* Ruhnke, 2011†** ex *Torpedo marmorata*
  - ***Barbeaucestus* Caira, Healy, Marques & Jensen, 2017**
    - ***Barbeaucestus jockuschae* Caira, Healy, Marques & Jensen, 2017** (type) ex *Neotrygon orientale*
    - ***Barbeaucestus ralickiae* Caira, Healy, Marques & Jensen, 2017** ex *Taeniura lymma* 1 *sensu* Naylor et al. (2012a)
    - *Barbeaucestus shipleyi* (Southwell, 1912) **Caira, Healy, Marques & Jensen, 2017** ex *Neotrygon kuhlii** (as *Trygon kuhli*)
    - *Barbeaucestus sexorchidum* (Williams, 1964) **Caira, Healy, Marques & Jensen, 2017** ex *Taeniura lymma** (as *Taeniura lymna* [sic])
  - *Cairaeanthus* Kornyushin & Polyakova, 2012
    - *Cairaeanthus ruhnkei* Kornyushin & Polyakova, 2012 (type) ex *Dasyatis pastinaca*
    - *Cairaeanthus healyae* Kornyushin & Polyakova, 2012 ex *Dasyatis pastinaca*
  - ***Divaricobothrium* Caira, Healy, Marques & Jensen, 2017**
    - ***Divaricobothriurn tribelum* Caira, Healy, Marques & Jensen, 2017** (type) ex *Maculabatis gerrardi* (as *Himantura gerrardi*)
    - *Divaricobothrium trifidum* (Shipley & Hornell, 1906) **Caira, Healy, Marques & Jensen, 2016** ex *Brevitrygon walga** (as *Trygon walga*)
  - ***Sungaicestus* Caira, Healy, Marques & Jensen, 2017**
    - *Sungaicestus kinabatanganensis* (Healy, 2006) **Caira, Healy, Marques & Jensen, 2017** (type) ex *Urogymnus polylepis* (as *Himantura chaophraya*)
- Family Echeneibothriidae de Beauchamp, 1905
  - *Echeneibothrium* van Beneden, 1850 (syn. *Discobothrium* van Beneden, 1871)
    - *Echeneibothrium variabile* van Beneden, 1850 (type) ex *Raja clavata* (as *Raia clavata*)
    - *Echeneibothrium abyssorum* Campbell, 1977 ex *Amblyraja radiata* (as *Raja radiata*)
    - *Echeneibothrium bathyphilum* Campbell, 1975 ex *Rajella bathyphila* (as *Raja bathyphila*)
    - *Echeneibothrium beauchampi* Euzet, 1959 ex *Raja clavata*
    - *Echeneibothrium canadensis* Keeling & Burt, 1996 ex *Amblyraja radiata* (as *Raja radiata*)
    - *Echeneibothrium demeusiae* Euzet, 1959 ex *Dipturus batis* (as *Raja batis*)
    - *Echeneibothrium dolichoophorum* Riser, 1955 ex *Raja rhina*
    - *Echeneibothrium dubium* van Beneden, 1861 ex *Dipturus batis* (as *Raia batis*)
    - *Echeneibothrium elongatum* Williams, 1966 ex *Leucoraja circularis* (as *Raja circularis*)

  - *Echeneibothrium fallax* (van Beneden, 1871) Woodland, 1927 ex *Raja clavata*
  - *Echeneibothrium faxanum* Manger, 1972 ex *Dipturus batis* (as *Raja batis*)
  - *Echeneibothrium gracile* Zschokke, 1889 ex *Raja clavata* (as *Dasibatis* [sic] *clavata*)
  - *Echeneibothrium julievansium* Woodland, 1927 ex *Raja montagui* (as *Raia maculata*)
  - *Echeneibothrium macrascum* Riser, 1955 ex *Raja montereyensis**
  - *Echeneibothrium maculatum* Woodland, 1927 ex *Raja montagui* (as *Raia maculata*)
  - *Echeneibothrium megalosoma* Carvajal & Dailey, 1975 ex *Dipturus chilensis* (as *Raja chilensis*)
  - *Echeneibothrium minutum* Williams, 1966 ex *Dipturus batis* (as *Raja batis*)
  - *Echeneibothrium multiloculatum* Carvajal & Dailey, 1975 ex *Dipturus chilensis* (as *Raja chilensis*)
  - *Echeneibothrium myzorhynchum* Hart, 1936 ex *Beringraja binoculata* (as *Raja binoculata*)
  - *Echeneibothrium octorchis* Riser, 1955 ex *Raja montereyensis**
  - *Echeneibothrium pollonae* Campbell, 1977 ex *Bathyraja richardsoni*
  - *Echeneibothrium sobrinum* Campbell, 1975 ex *Leucoraja erinacea* (as *Raja erinacea*)
  - *Echeneibothrium vernetae* Euzet, 1956 ex *Leucoraja erinacea* (as *Raja erinacea*)
  - *Echeneibothrium williamsi* Carvajal & Dailey, 1975 ex *Dipturus chilensis* (as *Raja chilensis*)
- *Clydonobothrium* Euzet, 1959
  - *Clydonobothrium elegantissimum* (Lönnberg, 1889) Euzet, 1959 (type) ex *Dipturus batis* (as *Raja batis*)
  - *Clydonobothrium leioformum* Alexander, 1963 ex *Dipturus nasutus* (as *Raja nasuta*)
- *Notomegarhynchus* Ivanov & Campbell, 2002
  - *Notomegarhynchus navonae* Ivanov & Campbell, 2002 (type) ex *Atlantoraja castelnaui*
  - *Notomegarhynchus shetlandicum* (Wojciechowska, 1990) Ivanov & Campbell, 2002 ex *Bathyraja eatonii*
- *Phormobothrium* Alexander, 1963
  - *Phormobothrium affine* (Olsson, 1866) Alexander, 1963 (type) ex *Amblyraja radiata* (as *Raja radiata*)
- *Pseudanthobothrium* Baer, 1956
  - *Pseudanthobothrium hanseni* Baer, 1956 (type) ex *Amblyraja radiata* (as *Raja radiata*)
  - *Pseudanthobothrium aegyptiacus* (Hassan, 1982) Jensen, 2005 ex *Leucoraja circularis* (as *Raja circularis*)
  - *Pseudanthobothrium minutum* Wojciechowska, 1991 ex *Bathyraja eatonii*
  - *Pseudanthobothrium notogeorgianum* Wojciechowska, 1990 ex *Amblyraja georgiana* (as *Raja georgiana*)
  - *Pseudanthobothrium purtoni* Randhawa, Saunders, Scott & Burt, 2008 ex *Leucoraja erinacea*
- *Tritaphros* Lönnberg, 1889
  - *Tritaphros retzii* Lönnberg, 1889 (type) ex *Raja clavata*

Family Escherbothriidae Ruhnke, Caira & Cox, 2015

- *Escherbothrium* Berman & Brooks, 1994
  - *Escherbothrium molinae* Berman & Brooks, 1994 (type) ex *Urotrygon chilensis*
- ***Stillabothrium* Healy & Reyda, 2016**
  - ***Stillabothrium ashleyae* Willsey & Reyda, 2016** (type) ex *Telatrygon biasa* (as *Dasyatis biasa*)
  - *Stillabothrium amuletum* (Butler, 1987) **Healy & Reyda 2016,** ex *Glaucostegus typus* (as *Rhinobatus armatus*)
  - *Stillabothrium cadenati* (Euzet, 1954) **Healy & Reyda, 2016** ex *Zanobatus schoenleinii*
  - ***Stillabothrium campbelli* Delgado, Dedrick & Reyda, 2016** ex *Maculabatis* cf. *pastinacoides* (as *Himantura* cf. *pastinacoides sensu* Naylor et al. [2012a])
  - ***Stillabothrium davidcynthiaorum* Daigler & Reyda, 2016** ex *Brevitrygon heterura* (as *Himatura heterura*)
  - ***Stillabothrium hyphantoseptum* Herzog, Bergman & Reyda, 2016** ex *Pastinachus solocirostris*
  - ***Stillabothrium jeanfortiae* Forti, Aprill & Reyda, 2016** ex *Himantura australis*

Family Rhinebothriidae Euzet, 1953

- *Biotobothrium* Tan, Zhou & Yang, 2009
  - *Biotobothrium platyrhina* Tan, Zhou & Yang, 2009 (type) ex *Platyrhina sinensis*
- ***Crassuseptum* Eyring, Healy & Reyda, 2012**
  - ***Crassuseptum pietrafacei* Eyring, Healy & Reyda, 2012** (type) ex *Mobula kuhlii*
- *Rhabdotobothrium* Euzet, 1953
  - *Rhabdotobothrium dollfusi* Euzet, 1953 (type) ex *Dasyatis pastinaca*
  - *Rhabdotobothrium anterophallum* Campbell, 1975 ex *Mobula hypostoma*
- *Rhinebothrium* Linton, 1890
  - *Rhinebothrium flexile* Linton, 1890 (type) ex *Bathytoshia centroura* (as *Trygon centrura* [sic])
  - *Rhinebothrium abaiensis* Healy, 2006 ex *Urogymnus polylepis* (as *Himantura chaophraya*)
  - *Rhinebothrium baeri* Euzet, 1959 ex *Pteroplatytrygon violacea*
  - *Rhinebothrium biorchidum* Huber & Schmidt, 1985 ex *Urobatis jamaicensis* (as *Urolophus jamaicensis*)
  - ***Rhinebothrium brooksi* Reyda & Marques, 2011** ex *Paratrygon aiereba*
  - *Rhinebothrium burgeri* Baer, 1948 ex *Bathytoshia centroura* (as *Dasyatis centrura* [sic])

- *Rhinebothrium chilensis* Euzet & Carvajal, 1973 ex *Sympterygia lima* (as *Psammobatis lima*)
- *Rhinebothrium chollaensis* Friggens & Duszynski, 2005 ex *Urobatis halleri*
- *Rhinebothrium copianullum* Reyda, 2008 ex *Paratrygon aiereba*
- ***Rhinebothrium corbatai* Menoret & Ivanov, 2011** ex *Potamotrygon motoro*
- *Rhinebothrium corymbum* Campbell, 1975 ex *Hypanus americanus* (as *Dasyatis americana*)
- *Rhinebothrium devaneyi* Brooks & Deardorff, 1988 ex *Urogymnus asperrimus*
- *Rhinebothrium ditesticulum* Appy & Dailey, 1977 ex *Urobatis halleri* (as *Urolophus halleri*)
- *Rhinebothrium euzeti* Williams, 1958 ex *Dasyatis* sp.* (as *Dasybatis* sp.)
- ***Rhinebothrium fulbrighti* Reyda & Marques, 2011** ex *Potamotrygon orbignyi*
- *Rhinebothrium ghardaguensis* Ramadan, 1984 ex *Taeniura lymma*
- *Rhinebothrium gravidum* Friggens & Duszynski, 2005 ex *Urobatis halleri*
- *Rhinebothrium hawaiiensis* Cornford, 1974 ex *Bathytoshia lata* (as *Dasyatis lata*)
- *Rhinebothrium himanturi* Williams, 1964 ex *Urogymnus granulatus* (as *Himantura granulata*)
- ***Rhinebothrium jaimei* Marques & Reyda, 2015** ex *Potamotrygon orbignyi*
- ***Rhinebothrium kruppi* Golestaninasab & Malek, 2015** ex *Glaucostegus granulatus*
- *Rhinebothrium leiblei* Euzet & Carvajal, 1973 ex *Sympterygia lima* (as *Psammobatis lima*)
- *Rhinebothrium lintoni* Campbell, 1970 ex *Hypanus americanus* (as *Dasyatis americana*)
- *Rhinebothrium maccallumi* Linton, 1924 ex *Bathytoshia centroura* (as *Dasybatis centrura*)
- *Rhinebothrium margaritense* Mayes & Brooks, 1981 ex *Hypanus guttatus* (as *Dasyatis guttata*)
- *Rhinebothrium megacanthophallus* Healy, 2006 ex *Urogymnus polylepis* (as *Himantura chaophraya*)
- ***Rhinebothrium mistyae* Menoret & Ivanov, 2011** ex *Potamotrygon motoro*
- *Rhinebothrium monodi* Euzet, 1954 ex *Taeniurops grabata* (as *Taeniura grabata*)
- ***Rhinebothrium paranaensis* Menoret & Ivanov, 2009 ex *Potamotrygon falkneri***
- *Rhinebothrium paratrygoni* Rego & Dias, 1976 ex *Potamotrygon* sp.
- *Rhinebothrium pearsoni* Butler, 1987 ex *Aptychotrema rostrata* (as *Aptychotrema banskii*)
- ***Rhinebothrium persicum* Golestaninasab & Malek, 2015** ex *Glaucostegus granulatus*
- *Rhinebothrium rhinobati* Dailey & Carvajal, 1976 ex *Pseudobatus planiceps* (as *Rhinobatos planiceps*)
- *Rhinebothrium scobinae* Euzet & Carvajal, 1973 ex *Psammobatis scobina*
- *Rhinebothrium setiensis* Euzet, 1955 ex *Myliobatis aquila*
- *Rhinebothrium spinicephalum* Campbell, 1970 ex *Hypanus americanus* (as *Dasyatis americana*)
- *Rhinebothrium taeniuri* Ramadan, 1984 ex *Taeniura lymma*
- *Rhinebothrium tetralobatum* Brooks, 1977 ex *Styracura schmardae* (as *Himantura schmardae*)
- *Rhinebothrium urobatidium* (Young, 1955) Appy & Dailey, 1977 ex *Urobatis halleri*
- *Rhinebothrium walga* (Shipley & Hornell, 1906) Euzet, 1953 ex *Brevitrygon walga* (as *Trygon walga*)
- *Rhinebothrium xiamenensis* Wang & Yang, 2001 ex *Telatrygon zugei* (as *Dasyatis zugei*)

- *Rhinebothroides* Mayes, Brooks & Thorson, 1981
  - *Rhinebothroides moralarai* (Brooks & Thorson, 1976) Mayes, Brooks & Thorson, 1981 (type) ex *Potamotrygon magdelaenae*
  - *Rhinebothroides campbelli* Ivanov, 2004 ex *Potomotrygon motoro*
  - *Rhinebothroides freitasi* (Rego, 1979) Brooks, Mayes & Thorson, 1981 ex *Potamotrygon hystrix*
  - *Rhinebothroides glandularis* Brooks, Mayes & Thorson, 1981 ex *Potamotrygon hystrix*
  - *Rhinebothroides scorzai* (Lopez-Neyra & Diaz-Ungria, 1958) Mayes, Brooks & Thorson, 1981 ex *Potamotrygon hystrix*
- *Rhodobothrium* Linton, 1890 (syn. *Inermiphyllidium* Riser, 1955; *Proboscidosaccus* Gallien, 1949; *Sphaerobothrium* Euzet, 1959)
  - *Rhodobothrium pulvinatum* Linton, 1890 (type) ex *Bathytoshia centroura* (as *Trygon centroura*)
  - *Rhodobothrium brachyascum* (Riser, 1955) Campbell & Carvajal, 1979 ex *Myliobatis californica* (as *Aetobatus californicus*)
  - *Rhodobothrium enigmaticum* (Gallien, 1949) Carvajal & Campbell, 1979 ex *Spisula solida* (as *Mactra solida*) (Bivalvia)
  - *Rhodobothrium lubeti* (Euzet, 1959) Campbell & Carvajal, 1979 ex *Myliobatis aquila*
  - *Rhodobothrium mesodesmatum* (Bahamonde & Lopez, 1962) Campbell & Carvajal, 1979 ex *Myliobatis chilensis*
  - *Rhodobothrium paucitesticulare* Mayes & Brooks, 1981 ex *Rhinoptera bonasus*
- *Scalithrium* Ball, Neifar & Euzet, 2003
  - *Scalithrium minimum* (van Beneden, 1850) Ball, Neifar & Euzet, 2003 (type) ex *Dasyatis pastinaca* (as *Trygon pastinaca*)
  - *Scalithrium bilobatum* (Young, 1955) Ball, Neifar & Euzet, 2003 ex *Urobatis halleri* (as *Urolophus halleri*)
  - *Scalithrium geminum* (Marques, Brooks & Ureña, 1996) Ball, Neifar & Euzet, 2003 ex *Styracura pacifica* (as *Himantura pacifica*)
  - *Scalithrium magniphalum* (Brooks, 1977) Ball, Neifar & Euzet, 2003 ex *Styracura schmardae* (as *Himantura schmardae*)

Scalithrium palombii (Baer, 1948) Ball, Neifar & Euzet, 2003 ex *Pteroplatytrygon violacea* (as *Dasyatis violacea)*
Scalithrium rankini (Baer, 1948) Ball, Neifar & Euzet, 2003 ex *Bathytoshia centroura* (as *Dasyatis centrura* [sic])
Scalithrium trygonis (Shipley & Hornell, 1906) Ball, Neifar & Euzet, 2003 ex *Neotrygon kuhlii** (as *Dasyatis kuhlii*)
Spongiobothrium Linton, 1889
Spongiobothrium variabile Linton, 1889 (type) ex *Bathytoshia centroura* (as *Trygon centrura* [sic])

FAMILY PLACEMENT UNCERTAIN
Anindobothrium Marques, Brooks & Lasso, 2001
Anindobothrium anacolum (Brooks, 1977) Marques, Brooks & Lasso, 2001 (type) ex *Styracura schmardae* (as *Himantura schmardae*)
Anindobothrium lisae Marques, Brooks & Lasso, 2001 ex *Potamotrygon orbignyi*
New genus 11 *sensu* Ruhnke et al. (2015) (= Rhinebothriinae *sensu* Healy et al. [2009])
New genus 11 n. sp. 1 *sensu* Ruhnke et al. (2015) ex *Pristis clavata*

SPECIES *INCERTAE SEDIS*

INCERTAE SEDIS WTH RESPECT TO GENERIC PLACEMENT
Echeneibothrium ceylonicum Shipley & Hornell, 1906 ex *Brevitrygon walga** (as *Trygon walga*)
Echeneibothrium filamentosum Subhapradha, 1955 ex *Glaucostegus granulatus* (as *Rhinobatus granulatus*)
Echeneibothrium oligotesticularis Subramaniam, 1940 ex *Glaucostegus granulatus* (as *Rhinobatus granulatus*)
Echeneibothrium rhinobati Yamaguti, 1960 ex *Rhinobatos schlegelii* (as *Rhinobatus schlegeli*)
Echeneibothrium shindei Bhaware, 1993 ex *Rhynchobatus djiddensis** (as *Rhynchobatus djeddensis*)
Echeneibothrium simplex Shipley & Hornell, 1906 ex *Brevitrygon walga** (as *Trygon walga*)
Echeneibothrium singhi Bhaware, Motunge & Shinde, 1992 ex *Rhynchobatus djiddensis** (as *Rhynchobatus djeddensis*)
Echeneibothrium verticillatum Subhapradha, 1955 ex *Rhynchobatus djiddensis** (as *Rhynchobatus djeddensis*)
Rhinebothrium ceylonicum Shipley & Hornell, 1906 ex *Neotrygon kuhlii** (as *Trygon kuhli*)

INCERTAE SEDIS WTH RESPECT TO GENERIC AND ORDINAL PLACEMENT
Anthobothrium bifidum Yamaguti, 1952 ex *Hemitrygon akajei* (as *Dasybatus akajei*)
Anthobothrium crenulatum Subhapradha, 1955 ex *Glaucostegus halavi* (as *Rhinobatus halavi*)
Anthobothrium hickmani Crowcroft, 1947 ex *Narcine tasmaniensis* (as *Narcine tasmaniensis*)
Anthobothrium lilliiformis MacCallum, 1917
Anthobothrium loculatum Vijaya Lakshmi & Sanaka, 1993 ex *Himantura uarnak** (as *Dasyatis uarnak*)
Anthobothrium oligorchidum Young, 1954 ex *Urobatis halleri*
Anthobothrium panjadi Shipley, 1909 ex *Aetomylaeus maculatus* (as *Myliobatis maculata*)
Anthobothrium peruanum Rego, Vincente & Herrera, 1968 ex *Sarda chiliensis* (as *Sarda chilensis*) (Perciformes)
Anthobothrium pteroplateae Yamaguti, 1952 ex *Gymnura japonica* (as *Pteroplatea japonica*)
Anthobothrium quadribothria (MacCallum, 1921) Yamaguti, 1959 ex *Dasyatis pastinaca* (as *Dasybatus pastinacus*)
Anthobothrium rajae Yamaguti, 1952 ex *Okamejei kenojei* (as *Raja kenojei*)
Anthobothrium rugosum Shipley & Hornell, 1906 ex *Brevitrygon walga** (as *Trygon walga*)
Anthobothrium sasoonense Srivastav & Srivastava, 1988 ex *Glaucostegus granulatus* (as *Rhinobatus granulatus*)
Anthobothrium septatum Subhapradha, 1955 ex *Rhynchobatus djiddensis** (as *Rhynchobatus djeddensis*)
Anthobothrium taeniuri Saoud, 1963 ex *Taeniura lymma*
Anthobothrium veravalensis Shinde, Jadhav & Mohekar, 1981 ex *Rhynchobatus djiddensis** (as *Rhynchobatus djeddensis*)
Phyllobothrium auricula van Beneden, 1858 ex *Dasyatis pastinaca* (as *Trigon* [sic] *pastinaca*)
Phyllobothrium biacetabulatum Yamaguti, 1960 ex *Rhinobatos schlegelii* (as *Rhinobatus schlegeli*)
Phyllobothrium blakei Shipley & Hornell, 1906 ex *Neotrygon kuhlii** (as *Trygon kuhli*)
Phyllobothrium compactum Southwell & Prashad, 1920 ex *Neotrygon kuhlii** (as *Trygon kuhli*)
Phyllobothrium discopygi Campbell & Carvajal, 1987 ex *Discopyge tschudii* (as *Discopyge tschudi*)
Phyllobothrium foliatum Linton, 1890 ex *Bathytoshia centroura* (as *Trygon centrura* [sic])
Phyllobothrium hallericola Church & Schmidt, 1990 ex *Urobatis halleri* (as *Urolophus halleri*)
Phyllobothrium myliobatidis Brooks, Mayes & Thorson, 1981 ex *Myliobatis goodei* (as *Myliobatis goodei*)
Phyllobothrium pastinacae Mokhtar-Maamouri & Zamali, 1981 ex *Dasyatis pastinaca* (as *Dasyatis pastinaca*)
Phyllobothrium ptychocephalum Wang, 1984 ex *Neotrygon kuhlii** (as *Dasyatis kuhlii*)
Pillersium owenium Southwell, 1927 (type) ex *Urogymnus asperrimus* (as *Urogymnus asperimus* [sic])

18

Spathebothriidea Wardle & McLeod, 1952

By
Roman Kuchta and Tomáš Scholz[1]

SPATHEBOTHRIIDEA AS THEY WERE KNOWN PRIOR TO THE PBI PROJECT

Diversity and Classification. A total of 15 nominal species and seven nominal genera have been established since 1781 when the first species, *Taenia truncata* Pallas, 1781 (now *Cyathocephalus truncatus* [Pallas, 1781] Kessler, 1868), was described by Pallas (1781). The taxonomy and systematics of the group were reviewed by Nybelin (1922), Wardle and McLeod (1952), Burt and Sandeman (1969, 1974), Gibson (1994), and Protasova and Roitman (1995). Over time, two different genus-level classification schemes have been proposed. The broader of the two concepts, which was adopted by Gibson (1994) and Protasova and Roitman (1995), recognized four or five genera as valid. Under the narrower concept, which was embraced by Burt and Sandeman (1969, 1974), only *Bothrimonus* Duvernoy, 1842 (housing all forms with an anterior sucker-like attachment organ) and *Spathebothrium* Linton, 1922 (housing forms that lack an apical attachment organ) were considered to be valid. The members of this taxon have been considered as a subgroup within the order Pseudophyllidea by some authors (e.g., Nybelin, 1922; Joyeux and Baer, 1961; Dubinina, 1987), but as the independent order Spathebothriidea by others (e.g., Wardle and McLeod, 1952; Gibson, 1994).

Morphology. The morphology of the spathebothriideans is unique among almost all other cestodes in their possession of a relatively small, internally proglottized body with multiple genital complexes opening medially, but a total lack of external proglottization. In addition, spathebothriideans are unique in their possession of genital pores that either irregularly alternate dorsally and ventrally, or are entirely ventral (Gibson, 1994). The uterus opens between separate male and female pores. Scolex morphology differs across genera with some variation on a funnel-like scolex in most and the lack of a differentiated scolex in *Spathebothrium* (see Wardle and McLeod, 1952; Burt and Sandeman, 1974; Gibson, 1994). The eggs are operculated and may possess polar filaments in some species (Sandeman and Burt, 1972). The morphology of individual species was described in detail in several accounts (e.g., Wardle and McLeod, 1952; Burt and Sandeman, 1969, 1974; Sandeman and Burt, 1972), and in the monograph of Protasova and Roitman (1995), which also contained ultrastructural data (see also Davydov et al., 1997; Poddubnaya et al., 2005a, b). The karyotype of *Cyathocephalus truncatus* consists of nine pairs of chromosomes (2n = 18), which is the most common diploid chromosome number found among cestodes (Petkevičiūte, 1996).

Host Associations. Spathebothriideans have been reported from a diversity of unrelated families of teleosts, which include the Acipenseridae Bonaparte (Acipenseriformes), Soleidae Bonaparte (Pleuronectiformes), Salmonidae Cuvier (Salmoniformes), and Liparidae Gill (Scorpaeniformes) (see Protasova and Roitman, 1995). The first intermediate hosts are

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[1] Corresponding author (tscholz@paru.cas.cz)

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amphipods (Protasova and Roitman, 1995).

Geographic Distribution. Prior to the PBI project, spathebothriideans had been reported from numerous countries in the Palearctic realm, including Finland, Greenland, Italy, Romania (i.e., Black Sea), Russia, and Sweden, as well as from several localities in the USA (e.g., California, Massachusetts, New Hampshire, and Washington), and also Japan (Protasova and Roitman, 1995). Only two species exhibit a more southern distribution out of the Arctic and Subarctic: *Didymobothrium rudolphii* (Monticelli, 1890) Nybelin, 1912 occurs off the Atlantic coast of Europe and Africa (35–50°N) and in the Mediterranean Sea, whereas *Bothrimonus fallax* Lühe, 1900 has been reported from the Caspian Sea (Protasova and Roitman, 1995; Marques et al., 2007).

Phylogenetic Relationships. Molecular data, specifically sequence data for the 18S and 28S rRNA genes of four species, were available prior to 2008. The first sequence of a spathebothriidean—18S rDNA of *C. truncatus*—was published by Mariaux (1998). Later Olson and Caira (1999) added 18S rDNA and Ef-1α sequence data for *Spathebothrium simplex* Linton, 1922 and Olson et al. (2001) added 28S rDNA sequence data for the latter species, and also 28S rDNA and 18S rDNA data for *Cyathocephalus truncatus*. Marques et al. (2007) studied intraspecific genetic variation in *Did. rudolphii* using 28S rDNA and ITS2 sequence data, and detected the presence of two genetically distinct genotypes that may represent two cryptic species. However, these forms have not yet been formally described as separate species (Marques et al., 2007).

The phylogenetic position of the Spathebothriidea among the Eucestoda remains, however, unclear. Two possible scenarios have been proposed: (i) spathebothriideans represent the earliest diverging group of eucestodes (Olson and Caira, 1999; Kodedová et al., 2000); or (ii) they are among the earliest diverging lineages, but evolved more recently than the monozoic caryophyllideans (Olson et al., 2001; Waeschenbach et al., 2007).

CURRENT STATUS OF THE SPATHEBOTHRIIDEA

Diversity and Classification. The order was reviewed by Kuchta at al. (2014) who endorsed the classification of Gibson (1994). Thus, five genera of spathebothriideans are currently recognized (Table 1). Four of these are monotypic; the fifth genus, *Bothrimonus*, contains two species, including the type species *B. sturionis* Duvernoy, 1842 from *Acipenser oxyrhynchus* Mitchill—a spathebothriidean species of questionable validity. We concur with Protasova and Roitman (1995) that misidentification of *Diplocotyle olrikii* Krabbe, 1874 from an atypical host (sturgeon) is the most probable explanation of the only existing record of *B. sturionis* from the 19th century (Duvernoy, 1842). However, this assumption cannot be confirmed because the location of the type specimen of *B. sturionis* is unknown. Therefore, *B. sturionis*, which is the type species of the genus, is tentatively retained as valid. No new spathebothriidean taxa were discovered over the course of the PBI project.

Morphology. New data on the simple nature of the scolex morphology of five of the six species of the order, generated from examination of newly collected and extensive museum material using scanning electron microscopy (SEM) and histological sections were presented by Kuchta et al. (2014) (see Figs. 1 and 2 for micrographs of selected species). Those authors recognized four scolex conditions:

(1) Anterior end of the body not differentiated into a scolex: *Spathebothrium* Linton, 1922 (Figs. 1D, 2B).

(2) Scolex in form of a forwardly-directed, undivided, funnel-shaped organ: *Cyathocephalus* Kessler, 1868 (Fig. 1B).

(3) Scolex in form of a forwardly-directed organ with lumina separated internally by median septum into two sucker-like organs opening separately on the scolex surface: *Didymobothrium* Nybelin, 1922 and *Diplocotyle* Krabbe, 1874 (Figs. 1C, 2D).

(4) Scolex in form of a forwardly-directed sucker-like attachment organ with lumina partly separated by an incomplete septum at the base and a single opening on the scolex surface: *Bothrimonus* (Fig. 1A).

Kuchta et al. (2014) determined that the scoleces of the four spathebothriidean species they examined with SEM, including *B. fallax* and *S. simplex*, which had not previously been studied using SEM, as well as *Dip. olrikii* and *C. truncatus*, which had previously been examined (Marques et al., 2007; Levron et al., 2008), were uniformly covered with capilliform filitriches.

Using SEM to examine eggs liberated from the uterus of freshly collected specimens, Kuchta et al. (2014) also provided some insights into morphological differences between freshwater and marine species. They found that, whereas the eggs of the marine species *Dip. olrikii*, *S. simplex*, and *Did. rudolphii* (presented by Marques et al. [2007]) bear a tuft of terminal filaments, those of the freshwater species *B. fallax* and *C. truncatus* do not (Fig. 1E–H). Furthermore, they confirmed that the eggs of all spathebothriideans examined to date bear a large operculum and a surface that is smooth or slightly pitted.

Host Associations. The spathebothriideans have a relatively wide spectrum of fish hosts (see Protasova and Roitman, 1995), but we did not find any species over the course of the PBI project in higher host taxa (i.e., families or orders) that were not previously known to host

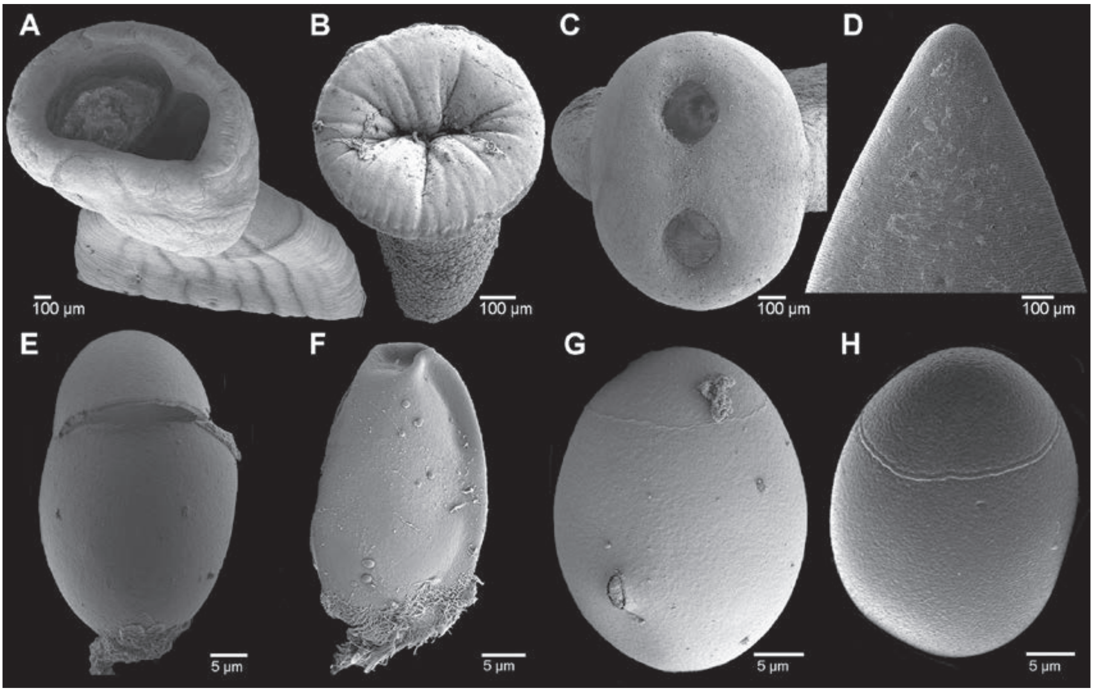

Figure 1. Scanning electron micrographs of scoleces (A–D) and eggs (E–H) of selected spathebothriidean cestodes. **(A, G)** *Bothrimonus fallax*. **(B, H)** *Cyathocephalus truncatus*. **(C, E)** *Diplocotyle olrikii*. **(D, F)** *Spathebothrium simplex*. Modified from Kuchta et al. (2014).

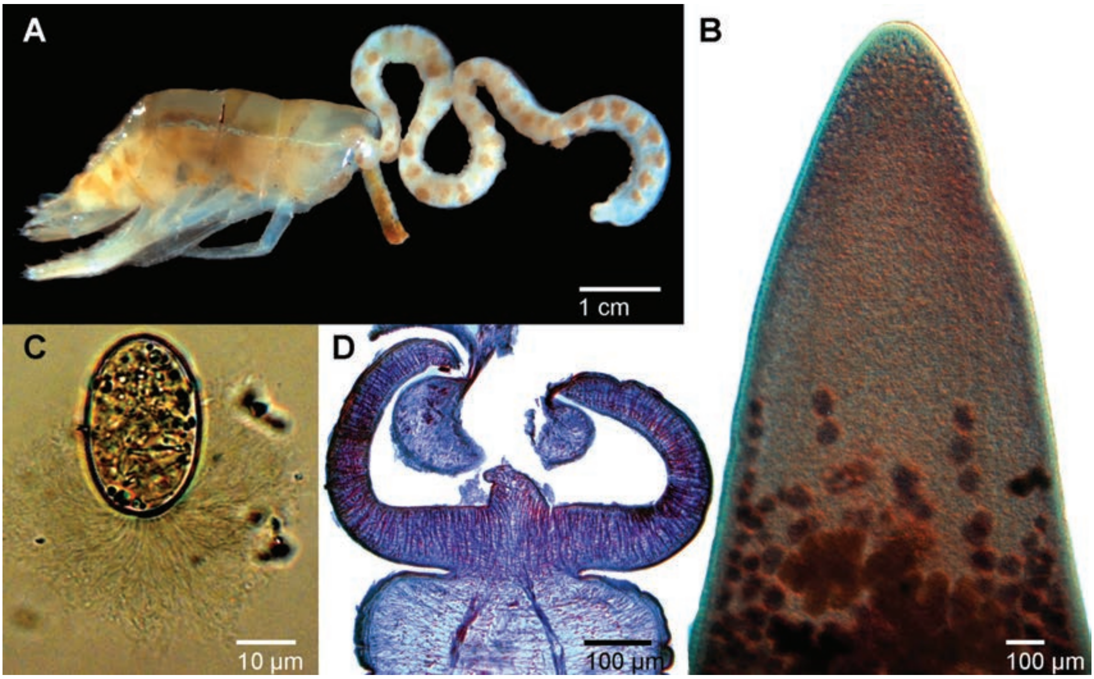

FIGURE 2. Photomicrographs of selected spathebothriideans. **(A, C)** Gravid specimen of *Diplocotyle olrikii* from body cavity of *Marinogammarus* sp. and egg free in water. **(B)** Anterior part of *Spathebothrium simplex*. **(D)** Histological section through the scolex of *Didymobothrium rudolphii* from *Pegusa lascaris*. Modified from Kuchta et al. (2014).

spathebothriideans. The genus *Bothrimonus* is specific to the Acipenseridae, *Spathebothrium* to the Liparidae, and *Didymobothrium* to the Soleidae. In contrast, *Diplocotyle* is widely distributed in several marine groups (except for the Pleuronectiformes) and *Cyathocephalus* is known from a wide spectrum of freshwater and anadromous fishes, especially salmonids (Salmoniformes). *Liparis fabricii* Krøyer (Scorpaeniformes: Liparidae) is a new definitive host for *S. simplex* and *Pegusa cadenati* Chabanaud (Pleuronectiformes: Soleidae) for *Did. rudolphii* (see Kuchta et al., 2014). However, records of *C. truncatus* from gadids (Gadidae), *Dip. olrikii* from eels (Anguillidae), and *S. simplex* from eelpouts (Zoarcidae) require verification, and may represent accidental infections, as suggested by their very low prevalence (see Protasova and Roitman, 1995; Kuchta et al., 2014).

Prevalence of infection may reach up to 100% in endemic areas, but generally fluctuates around 20%. New data on seasonality in the occurrence and maturation of spathebothriideans were not generated except for observations on the variation in prevalences of *Dip. olrikii* in *Gymnocanthus tricuspis* (Reinhardt) and *Myoxocephalus scorpius* (L.) in Svalbard, Norway across years (Kuchta et al., 2014). Data available indicate a tendency for the prevalence to decrease from mid-summer to early autumn for *Did. rudolphii* in the sand sole, *Pegusa lascaris* (Risso) (as *Solea lascaris*) (see fig. 9 in Marques et al. [2007]).

The first intermediate hosts of spathebothriideans are marine and freshwater gammarids, rarely mysids (both Amphipoda) (see Kuchta et al., 2014). Plerocercoids in amphipods can be progenetic (i.e., produce eggs) (Fig. 2A, C). This may represent a one-host life-cycle, similar to that seen in the caryophyllidean *Archigetes sieboldi* Leuckart, 1878 within oligochaetes (Protasova and Roitman, 1995; Kuchta et al., 2014).

Geographic Distribution. Three of five genera have an Arctic and subarctic distribution. However, *Bothrimonus* is endemic to the Caspian Sea (doubtful records from the Black Sea are not considered) and *Didymobothrium* occurs off the Atlantic coast of Europe. New geographic records include the southern-most occurrence of *Did. rudolphii* from the South Atlantic Ocean (off Cape Verde, Africa), and the occurrence of *S. simplex* off the Svalbard archipelago (subarctic Norway) (Kuchta et al., 2014).

Phylogenetic Relationships. The molecular phylogenetic analyses of Kuchta et al. (2014) provide some support for the validity of all five genera. The interrelationships of these genera based on the results of analyses of 28S rDNA sequence data by Kuchta et al. (2014) are illustrated in Figure 3. Based on their work, *Spathebothrium* is the sister taxon to the exemplars of the other four genera included in their analyses. Whereas *Dip. fallax* is the sister taxon to the clade comprising *Cyathocephalus* and the two genotypes of *Didymobothrium* (i.e., *Spathebothrium* (*Dip. olrikii* (*Didymobothrium* (*Cyathocephalus* + *Bothrimonus*)))) (Fig. 3). Analyses of ITS-2 sequence data, in which *Spathebothrium* was used as a functional outgroup, supported the same topology (i.e., (*Diplocotyle* (*Cyathocephalus* + *Didymobothrium*))) (Kuchta et al., 2014). These phylogenetic inferences suggest that spathebothriideans originated in marine hosts and thus their presence in freshwater hosts represents a derived condition. This

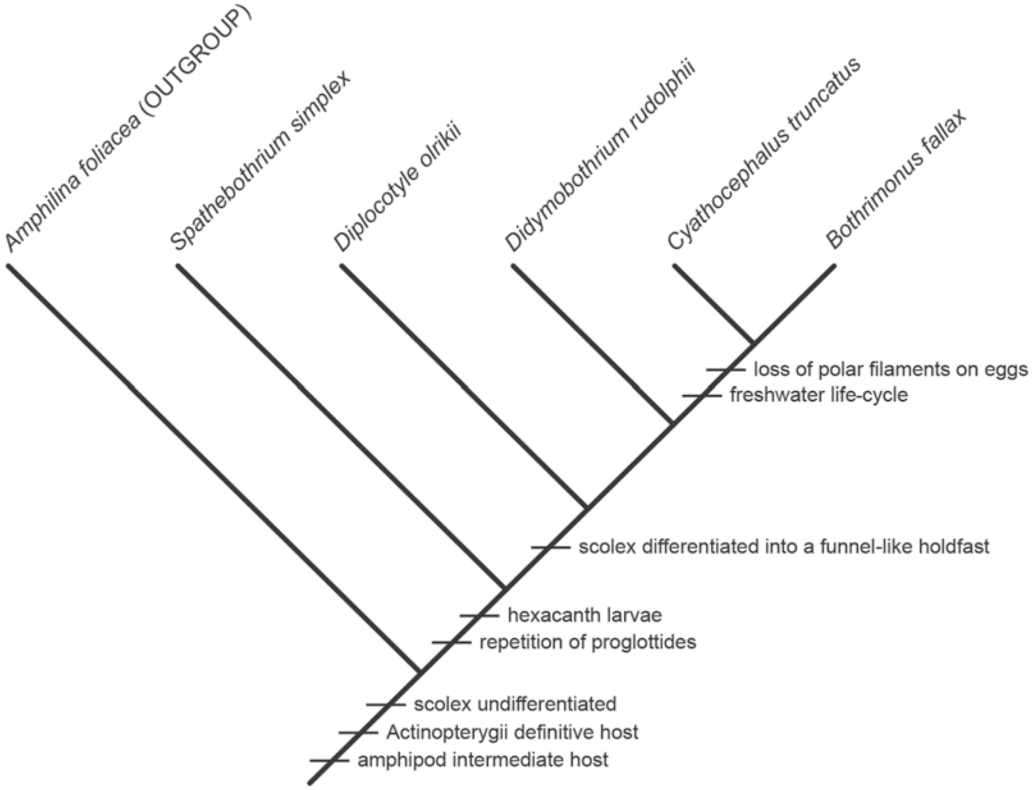

Figure 3. Summary tree showing putative morphological and life-cycle synapomorphies for various spathebothriidean genera. From Kuchta et al. (2014).

condition appears to be associated with the loss of polar filaments from their eggs (Kuchta et al., 2014).

The phylogenetic position of the Spathebothriidea within the Eucestoda remains unclear, but the most probable scenario is that spathebothriideans evolved more recently than the monozoic caryophyllideans as suggested by Waeschenbach et al. (2012).

CONCLUSIONS

The spathebothriideans are probably a relictual group now represented by a small number of species whose host associations and geographic distributions show little commonality (Kuchta et al., 2014). Together with the nippotaeniideans, also with only six valid species, the spathebothriideans are the least species-rich orders of the tapeworms, after the Haplobothriidea. The host spectrum of spathebothriideans is broad and includes several freshwater as well as marine fish groups, including ancient hosts (sturgeons; Acipenseridae). Spathebothriideans are widely distributed almost exclusively in Arctic and subarctic regions with the exception of *B. fallax* and *Dip. olrikii* reported from the Caspian Sea and the South Atlantic Ocean, respectively. Preliminary molecular phylogenetic analyses suggest that the monotypic marine genus *Spathebothrium*, which bears an undifferentiated scolex, represents the earliest diverging member of the order, while the freshwater *Cyathocephalus* and anadromous *B. fallax*, characterized by eggs without polar filaments, diverged most recently. The low number of species but relatively high amount of morphological diversity and broad host associations of the group suggest that current diversity represents only a small remainder of a previously much more species-rich and diverse group of cestodes. Due to new data generated as part of the PBI project and previous detailed studies mainly by Russian and Canadian authors, the present knowledge of the group is reasonably complete. Future directions should include: (i) Collection of fresh material of *Bothrimonus fallax* from sturgeons, because this unique and interesting species may well be on its way to extinction (Kuchta et al., 2014); (ii) a detailed study of the *Didymobothrium rudolphii* complex to formally describe the cryptic species; and (iii) life-cycle and ecological observations (ontogenetic development, seasonality of the occurrence and maturation, host-parasite relationships) for any members of this order.

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TABLE 1. List of valid spathebothriidean taxa with type hosts.

VALID TAXA

FAMILY ACROBOTHRIIDAE OLSSON, 1872
- *Bothrimonus* Duvernoy, 1842 (syn. *Disymphytobothrium* Diesing, 1854)
  - *Bothrimonus sturionis* Duvernoy, 1842 (type) ex *Acipenser oxyrhynchus*
  - *Bothrimonus fallax* Lühe, 1900 ex *Acipenser ruthenus*
- *Cyathocephalus* Kessler, 1868 (syn. *Acrobothrium* Olsson, 1872)
  - *Cyathocephalus truncatus* (Pallas, 1781) Kessler, 1868 (type) ex *Esox lucius*
- *Didymobothrium* Nybelin, 1922
  - *Didymobothrium rudolphii* (Monticelli, 1890) Nybelin, 1922 (type) ex *Solea solea*
- *Diplocotyle* Krabbe, 1874
  - *Diplocotyle olrikii* Krabbe, 1874 (type) ex *Salvelinus alpinus*

FAMILY SPATHEBOTHRIIDAE YAMAGUTI, 1934
- *Spathebothrium* Linton, 1922
  - *Spathebothrium simplex* Linton, 1922 (type) ex *Liparis liparis*

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Tetrabothriidea Baer, 1954

By
Jean Mariaux[1], Roman Kuchta, and Eric P. Hoberg

TETRABOTHRIIDEA AS THEY WERE KNOWN PRIOR TO THE PBI PROJECT

Diversity and Classification. The Tetrabothriidea are among the most overlooked groups of tapeworms. The type species of *Tetrabothrius* Rudolphi, 1819 was described at the end of 18th century as *Taenia immerina* Abildgaard, 1790 by Abildgaard (1790; pg. 62) from the aquatic bird "*Colymby Immeris*" (= *Gavia immer* [Brunnich]). This species was later redescribed by Rudolphi (1808, 1810) as *Bothriocephalus macrocephalus* Rudolphi, 1808. The genus *Bothriocephalus* Rudolphi, 1808 was subsequently divided by Rudolphi (1819) into four subgenera, including one named "*Tetrabothrii*" (with 4 species, including *B. macrocephalus*) (pg. 140). Diesing (1850) elevated each of Rudolphi's subgenera to the generic level, thereby establishing the genus *Tetrabothrius* Rudolphi, 1819. The first tetrabothriid species described from a cetacean was *Tetrabothrius triangularis* Diesing, 1850 (now valid as *Strobilocephalus triangularis* [Diesing, 1850] Baer, 1932) from the rough-toothed dolphin, *Steno bredanensis* (Cuvier) (as *Delphinus rostratus* Cuvier; Diesing, 1850; pg. 601). Although traditionally attributed to Linton (1891) as an etymological correction of the earlier name Tetrabothrida [sic] of Rudolphi and Diesing (see Wardle and McLeod [1952] for a historical summary), the family name Tetrabothriidae had been used earlier by Linton (1889) to include a number of elasmobranch-hosted cestode groups in addition to *Tetrabothrius*. Braun (1894–1900) recognized the Tetrabothriinae as a subfamily within the Taeniidae with *Tetrabothrius* as its only genus. Fuhrmann (1907) subsequently elevated the group to family rank. Wardle and McLeod (1952; pg. 333) incorrectly credited "Linton 1891, emended Fuhrmann, 1907" as the authorities of the family, and considered it to comprise nine genera.

Baer (1954) published the first detailed revision of the group and formally erected the order Tetrabothriidea. He recognized four genera, *Priapocephalus* Nybelin, 1922, *Strobilocephalus* Baer, 1932, *Tetrabothrius*, and *Trigonocotyle* Baer, 1932, and considered the order to house a total of 40 valid species. Yamaguti (1959) later recognized nine genera (4 exclusively in birds, 4 exclusively in mammals, and *Tetrabothrius* in both host groups). In addition to those recognized by Baer (1954), these genera were *Neotetrabothrius* Nybelin, 1929, *Paratetrabothrius* Yamaguti, 1940, *Porotaenia* Szpotanska, 1917 (all synonymized with *Tetrabothrius* by later authors), as well as *Anophryocephalus* Baylis, 1922 and *Chaetophallus* Nybelin, 1916. Yamaguti (1959) considered the order to comprise a total of 77 valid species.

Temirova and Skrjabin (1978) reviewed the order, which they treated as a suborder, retaining 52 species in five genera as valid. They divided the most species-rich genus *Tetrabothrius* into the four subgenera proposed by Murav'eva (1975) (i.e., *Biamniculus* Murav'eva, 1975, *Culmenamniculus* Murav'eva, 1975, *Uniamniculus* Murav'eva, 1975, and

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[1] Corresponding author (jean.mariaux@ville-ge.ch)

Mariaux, J., R. Kuchta, and E. P. Hoberg. 2017. Tetrabothriidea Baer, 1954. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 357–370.

Tetrabothrius) on the basis of the configuration of the genital atrium as seen in cross-section. In doing so they were following the informal subdivision of "Groupes A–D" proposed earlier by Baer (1954; pgs. 80–81).

Schmidt (1986), recognizing the group as a family in the Cyclophyllidea, considered it to include six genera (i.e., *Anophryocephalus*, *Chaetophallus*, *Priapocephalus*, *Strobilocephalus*, *Tetrabothrius*, and *Trigonocotyle*) and 60 valid species. The most recent revision of the order was that of Hoberg (1994), who recognized six genera (i.e., those recognized by Schmidt [1986], in addition to the four subgenera of *Tetrabothrius* proposed by Murav'eva [1975], although 3 of the putative subgenera were considered synonyms of existing taxa). A revision of the genus *Anophryocephalus*, which included a key to its seven species, was published by Hoberg and Measures in 1995.

A total of approximately ten species has been described in the genera *Tetrabothrius, Anophryocepahlus*, and *Trigonocotyle* since the review of Temirova and Skrjabin (1978). The most recent addition to the order was *Shindeobothrium* Shinde, Patel & Begum, 2000 proposed by Shinde et al. (2000) to accommodate *Shindeobothrium rehanae* Shinde, Patel & Begum, 2000 from *Rattus rattus* (L.) in India. Although the description is incomplete, the figures clearly show that this species does not belong to the Tetrabothriidea; it is more likely a species of cyclophyllidean. That having been said, *S. rehanae* is not a valid name because type material was not deposited in a public repository, no holotype was designated, and the genus was named after the first author of the taxon. As a consequence, the description violates both Articles 16.4.1 and 16.4.2 of the International Code of Zoological Nomenclature (ICZN, 1999).

MORPHOLOGY. The most typical characteristics of the order are the structure of the scolex, which generally bears four bothridia each with some sort of lateral, paired auricular appendages, and proglottids that house compact antero-ventral vitelline glands, and complex, unilateral genital atria (Figs. 1, 2). Other important characters are the absence of a rostellum from the adult scolex and the dorsal position of the uterus relative to the ovary. Genera are defined mainly by the shape of the scolex and bothridia, however the four subgenera of *Tetrabothrius* are characterized by the configuration of their genital atrium in cross-section, and, perhaps, more importantly, by the position of the genital apertures relative to the genital papilla. The first key to tetrabothriidean species was published by Baer (1954) and was based mainly on the number of testes, the size of the cirrus-sac, and the organization of the longitudinal musculature. This key was modified by Temirova and Skrjabin (1978) to accommodate the

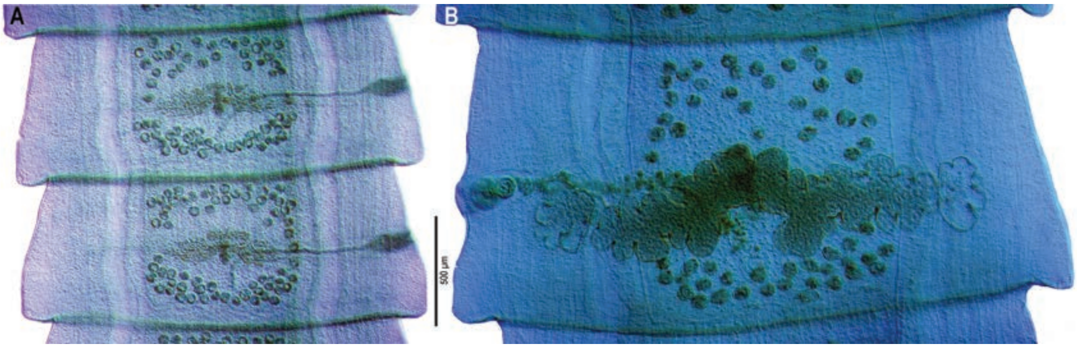

FIGURE 1. Photomicrographs of proglottids of *Tetrabothrius* (*Neotetrabothrius*) *eudyptidis* from *Eudyptes chrysocome* (Spheniscidae) from Phillip Island, Victoria, Australia. **(A)** Mature proglottids. **(B)** Young gravid proglottid.

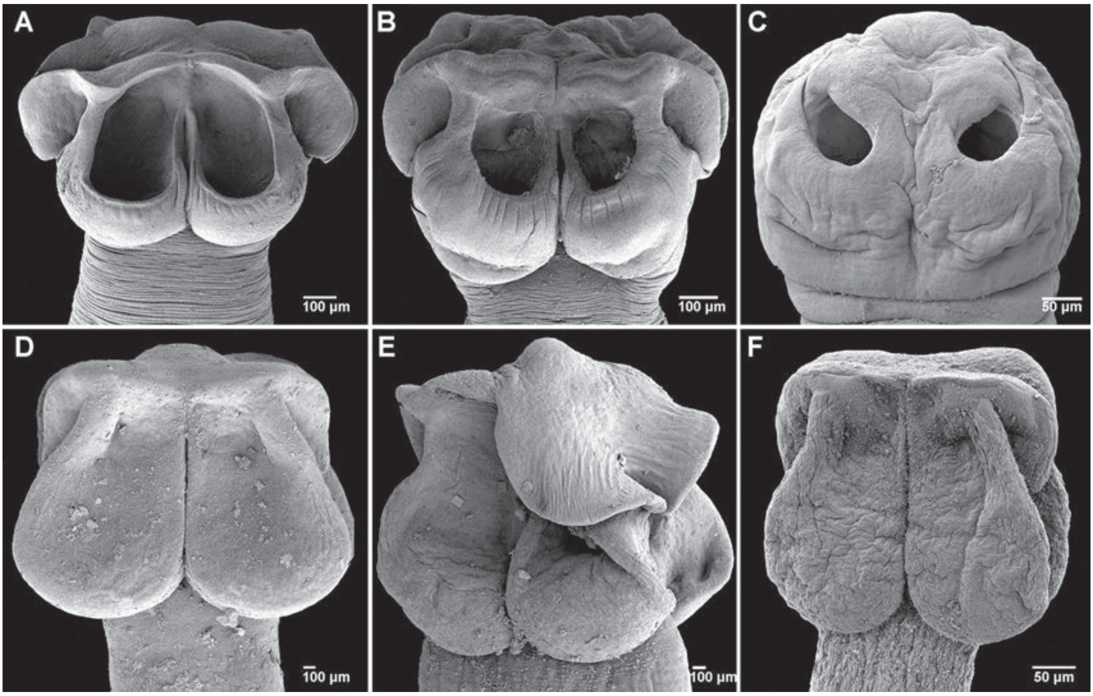

FIGURE 2. Scanning electron micrographs of scoleces of selected tetrabothriideans. **(A–B)** *Tetrabothrius* cf. *macrocephalus* ex *Gavia stellata* (Gaviidae) from Svalbard, Norway. **(C)** *Anophryocephalus* sp. ex *Zalophus californianus* (Otariidae) from California, USA. **(D–F)** *Tetrabothrius* cf. *cylindraceus*. **(D)** Ex *Hydroprogne caspia* (Sternidae) from Iran. **(E)** Ex *Larus dominicanus* (Laridae) from Chile. **(F)** Ex *Ardenna tenuirostris* (Procellariidae) from Australia.

species described between 1954 and 1978. However, Hoberg (1987a, 1994) observed that in some cases, the overlap in diagnostic features was extensive and morphometric characters may be dramatically influenced by individual variation and physiological condition (i.e., age) of the proglottids. He also pointed out that descriptions that directly account for ontogenetic variation in the structure of the genital atrium (and changing dimensions relative to stage of development from mature through post-mature and gravid proglottids), based on definable reference points involving the timing of the expansion of the tubular uterus (e.g., Hoberg, 1987a), are necessary in this group.

Detailed ultrastructural data, including scolex morphology and the first characterization of microthrix configuration in a tetrabothriidean using scanning electron microscopy (SEM), were provided by Hoberg et al. (1995). The first ultrastructural data on spermatozoon morphology and spermiogenesis in a tetrabothriidean were provided by Stoitsova et al. (1995).

HOST ASSOCIATIONS. Collectively, the tetrabothriideans are parasites of marine birds and both major groups of marine mammals (i.e., pinnipeds and cetaceans). Among the 66 species of tetrabothriideans recognized in 2008, 44 (67%) parasitize seabirds, 15 parasitize cetaceans, and seven parasitize pinnipeds. Among seabirds, most species parasitize Charadriformes of the genus *Larus* Linnaeus and Procellariformes, although a few species are also found in Pelecaniformes and Sphenisciformes. Those parasitizing mammals include *Priapocephalus* with three species in whales, *Anophyrocephalus* with seven species in Arctic pinnipeds, *Trigonocotyle* with three species in delphinids, and the monotypic *Strobilocephalus* reported from a diversity of cetacean species (Temirova and Skrjabin, 1978). The host associations of the order overall were studied by Hoberg (1987a, 1995, 1996) and Hoberg and Brooks (2008) who proposed that tetrabothriideans initially diversified in seabirds, following an event of host colonization from marine archosaurs, prior to the origin of modern birds and before the K-T boundary extinction event. Subsequent radiation of this marine fauna has been postulated to involve sequential and independent episodes of host-switching from marine birds to cetaceans and pinnipeds during the middle to late Tertiary. In contrast, Galkin (1987) supported cetaceans as the original hosts of tetrabothriideans.

No complete life-cycle is known for any member of the order. However, three hosts are likely involved. These include an invertebrate (crustacean or cephalopod) as the first intermediate host, a fish as the second intermediate (and / or paratenic) host, and a homeotherm as the definitive host (Baer, 1954; Hoberg, 1994). The metacestode has been demonstrated to be a type of plerocercoid with an apical acetabulum; at present, all that is known comes from post-larval stages found in the definitive hosts *Puffinus gravis* (O'Reilly) by Hoberg (1987b) and *Rissa tridactyla* (L.) by Galkin (1996). Although the ontogeny of tetrabothriideans remains incompletely characterized, a common pattern in which the development of the bothridia is delayed until the metacestodes are ingested by their definitive host seems to be the norm as established for selected species of *Tetrabothrius* and *Anophryocephalus* (see Hoberg et al., 1991; Hoberg and Measures, 1995; Chervy, 2002).

GEOGRAPHIC DISTRIBUTION. The tetrabothriideans are found worldwide. They are typically associated with marine pelagic environments in colder climates, mainly in Arctic, Antarctic, and subarctic regions, although, several species are known to parasitize seagulls (i.e., Laridae Vigors) in near-shore temperate environments (e.g., Hoberg, 1994, 1996). Among the six valid genera of tetrabothriideans, *Anophryocephalus* has the most restricted geographic distribution—it is currently known to occur only in the waters of the Holarctic realm. The historical biogeography of this genus was studied by Hoberg (1995). Additional global treatments of the order overall include those of Hoberg (1996), Hoberg and Adams (2000), and Hoberg and Brooks (2008).

PHYLOGENETIC RELATIONSHIPS. Historically, the phylogenetic affinities of the Tetrabothriidea relative to the other orders of cestodes have been unclear. At one time or another, they have been considered to be most closely allied with orders then known as the Pseudophyllidea and Proteocephalidea, as well as the Cyclophyllidea, or the Tetraphyllidea (see Hoberg, 1994). After reviewing previous hypotheses, Baer (1954) favored an origin of the group within the Ichthyotaenidea (= Proteocephalidea)—itself derived from the Tetraphyllidea. More recently, the tetrabothriideans have been most closely allied with the Cyclophyllidea (e.g., Schmidt, 1986; Hoberg et al., 1997) or the Tetraphyllidea (e.g., Temirova and Skrjabin, 1978; Hoberg 1987b, 1994; Brooks et al., 1991), depending on the weight given to genital anatomy or scolex morphology, respectively. Ultrastructural features of sperm have been equally ambiguous as a source of evidence for the phylogenetic affinities of the order (e.g., Stoitsova et al., 1995; Justine, 1998). Hoberg et al.'s (1997) morphological cladistic analysis clearly supported a close relationship between the Tetrabothriidea and the Cyclophyllidea. The close affinities between the Tetrabothriidea and Cyclophyllidea (and the Nippotaeniidea and Mesocestoididae) were confirmed by later, molecular phylogenetic studies (e.g., Mariaux, 1998; Olson et al., 2001; Waeschenbach et al., 2007). These affinities were also supported by the total evidence analyses of Hoberg et al. (2001).

Tetrabothriidean interrelationships are even less well understood. The only phylogenetic study aimed at resolving these relationships was that of Hoberg (1989), who, based on morphological data, explored the interrelationships among tetrabothriidean genera using single exemplars of each genus. His results indicated that *Tetrabothrius* (which includes species found in marine birds and species found in marine mammals) was the earliest diverging genus of the order, which includes a clade comprising the four genera that parasitize marine mammals exclusively.

CURRENT STATUS OF THE TETRABOTHRIIDEA

Diversity and Classification. No fieldwork specifically targeting the Tetrabothriidea was conducted over the course of the PBI project. As a consequence, the relatively limited new material obtained was generally the result of opportunistic collections focused on other cestode orders. This material did, however yield one new species, *Tetrabothrius* (*Tetrabothrius*) *hobergi* Nikolov, Cappozzo, Beron-Vera, Crespo, Raga & Fernandez, 2010, from a specimen of Hector's beaked Whale (*Mesoplodon hectori* [Gray]) stranded south of Mar del Plata, in Argentina and described by Nikolov et al. (2010). In that same contribution, two additional undetermined species of *Tetrabothrius*, both of which may also be new, were found: one in the same individual of Hector's beaked Whale, the other in a specimen of the spectacled porpoise, *Phocoena dioptrica* Lahille, also from Argentina. The final potentially novel species collected over the course of the PBI project was a species of *Anophryocephalus* (Fig. 2C) from a California sea lion, *Zalophus californianus* (Lesson), collected in 2013 off San Francisco, California, USA. Despite the relative abundance of this pinniped, it appears that tetrabothriideans have not previously been reported from this host species.

Other opportunistic collections were conducted in association with fieldwork focused on cyclophyllidean cestodes in Norway, Iran, Chile, and Australia. It is possible that this material includes additional novel taxa, but, in most cases, further study is required to confirm new species status. Nonetheless, the majority of the species encountered represent new host and/or locality records, mostly of species of the genus *Tetrabothrius* (see Table 1).

In total, six genera and 70 species of tetrabothriideans are currently recognized as valid (Table 2); 45 of these parasitize birds, 18 parasitize cetaceans, and seven parasitize seals. Of these 70 species, by far the large majority (i.e., 52) are members of the genus *Tetrabothrius* (42 in birds; 8 in cetaceans).

The validity and identities of subgenera of *Tetrabothrius* remain, however, very poorly understood. As a starting point, it remains to be confirmed that the work of Murav'eva (1975), published in a book of conference proceedings, is a validly published contribution. In view of the number of copies produced and its extensive distribution it should be considered available. However, Murav'eva's characterizations of the subgenera are suspect. Murav'eva (1975) based her definitions on Baer's (1954) A–D groups of species but did not designate type species for any of these new taxa. Specimens figured by Baer (1954) might provide evidence to help ground the identities of these taxa, but several figures, from different species, were used by Baer to illustrate his groups. In addition, Hoberg (1994) resurrected *Oriana* Leiper & Atkinson, 1914 as a subgenus with *Biamniculus* as its synonym, resurrected *Neotetrabothrius* Nybelin, 1931 with *Uniamniculus* as its synonym, leaving only *Culmenamniculus* Murav'eva, 1975 as potentially valid, but without a type species (although *Tetrabothrius* [*Culmenamniculus*] *cylindraceus* Rudolphi, 1819 is likely the best candidate) (Temirova and Skrjabin, 1978). In any case, the attribution of species of *Tetrabothrius* to any subgenus remains controversial, and impossible to determine until appropriate histological sections are available. This is the case for most species described in the last 40 years. What is now needed is the collection of new material adequately prepared for study and the generation of a robust phylogenetic framework for the groups based on molecular sequence data. Only then can the monophyly

TABLE 1. Summary of new tetrabothriidean material, including new host (*) and new locality (country) (†) records. Cestode intensities and prevalences were not available for all host species. ‡ Potentially new species.

Host Family Host Species	Locality	Intensity	Prevalence	Parasite Genus and Species	Publication
AVES					
Gaviidae					
Gavia stellata	Norway†	9–15	100 (2/2)	*Tetrabothrius* cf. *macrocephalus*	Unpublished
Lariidae					
*Hydroprogne caspia**	Iran† (Persian Gulf)	1–3	50 (2/4)	*Tetrabothrius* cf. *cylindraceus*	Unpublished
Larus dominicanus	Chile	4–22	100 (2/2)	*Tetrabothrius* cf. *cylindraceus*	Unpublished
*Larus heuglini**	Iran† (Persian Gulf)	2–3	20 (2/10)	*Tetrabothrius* cf. *cylindraceus*	Unpublished
Sulidae					
*Morus serrator**	Australia†	—	—	*Tetrabothrius* sp.	Unpublished
Procellariidae					
Ardenna tenuirostris	Australia	—	—	*Tetrabothrius* sp.	Unpublished
*Ardenna tenuirostris**	Australia†	—	—	*Tetrabothrius* cf. *cylindraceus*	Unpublished
*Eudyptes chrysocome**	Australia†	2	100 (1/1)	*Tetrabothrius eudyptidis*	Unpublished
Fulmarus glacialis	Norway†	15	100 (1/1)	*Tetrabothrius* cf. *erostris*	Unpublished
MAMMALIA					
Otariidae					
*Zalophus californianus**	USA†	6–45	29 (2/7)	*Anophryocephalus* sp.‡	Unpublished
Phocoenidae					
*Phocoena dioptrica**	Argentina	3	—	*Tetrabothrius* sp.‡	Nikolov et al. (2010)
Ziphiidae					
Mesoplodon hectori	Argentina	4	—	*Tetrabothrius* (*T.*) *hobergi* *Tetrabothrius* sp.‡	Nikolov et al. (2010)

and relationships of subgroups of *Tetrabothrius*, whether corresponding to the present subgenera or an alternative classification scheme, be assessed. In this contribution we opted for a pragmatic approach (Table 2). Species already attributed to a subgenus of *Tetrabothrius* are listed accordingly, and the others are simply not assigned to subgenera and instead are listed as *incertae sedis* in the order. It should be noted however that this is merely a temporary, pragmatic approach that does not reflect a stable classification.

MORPHOLOGY. Our understanding of the morphology and anatomy of the Tetrabothriidea has changed little over the course of the PBI project. The new collections did, however, provide an opportunity for the collection of material preserved for scanning electron microscopy (SEM). The SEM images in Figure 2 are the first SEMs of scoleces of *T.* cf. *macrocephalus*, *T.* cf. *cylindraceus*, and *Anophryocephalus* sp. Moreover, the copulatory apparatus (Korneva et al., 2015) and uterus (Korneva et al., 2014) of *Tetrabothrius erostris* were recently examined in detail using light and transmission electron microscopy.

HOST ASSOCIATIONS. With the exception of *Tetrabothrius cylindraceus* Rudolphi, 1819, which was already known from, among other hosts, the kelp gull, *Larus dominicanus* Lichtenstein, in Argentina, Chile, the Falkland Islands, and the Antarctic (Torres et al., 1991; Diaz et al., 2011), and *Tetrabothrius erostris* which was reported parasitizing, again, among other hosts, the Northern fulmar, *Fulmarus glacialis* (L.), in the Arctic Russian Islands by Galkin et al. (1994), all of the host associations listed in Table 1 are new records. *Tetrabothrius hobergi* is the second species of *Tetrabothrius* reported from Hector's beaked whale, *Mesoplodon hectori*. *Tetrabothrius forsteri* was reported by Baker et al. (2001) from this host in New Zealand. Although *T. cylindraceus* is known from a wide range of species in the family Laridae, it had not previously been reported from Heuglin's gull, *Larus heuglini* Bree, the Caspian tern, *Hydroprogne caspia* (Pallas), or the short-tailed shearwater, *Ardenna tenuirostris* (Temminck). Similarly *Tetrabothrius eudyptidis* (Lönnberg, 1896) Nybelin, 1929 had been reported from a number of penguin species, including members of *Eudyptes* Vieillot (see Szpotanska, 1929), but not previously from the southern rockhopper penguin, *Eudyptes chrysocome* (Forster). This is also the first report of a species of *Tetrabothrius* from the Australasian gannet, *Morus serrator* (Gray).

GEOGRAPHIC DISTRIBUTION. Although several taxa treated as part of this project were from countries from which they had not previously been reported (Table 1), no significant expansions of their distributions were observed. The most notable finding was the presence of several species of *Tetrabothrius* in larids from Iran (Persian Gulf); these findings were however not entirely unexpected given the global distribution of other species of tetrabothriideans in gulls (e.g., *T. cylindraceus*). Another significant result was the discovery of an as-of-yet unidentified tetrabothriidean from the South American fur seal, *Arctocephalus australis* (Zimmermann), in Patagonia (Hernández-Orts et al., 2013). This is the first record of a seal tetrabothriid from the Southern Hemisphere.

PHYLOGENETIC RELATIONSHIPS. In the most recent molecular survey of the Cestoda using nuclear rDNA gene sequence data and a contiguous fragment (> 4 kb) of mitochondrial DNA, Waeschenbach et al. (2012) confirmed the derived position of the Tetrabothriidea, together with the Nippotaeniidea, Cyclophyllidea, and Mesocestoididae—a result also obtained in the ultrastructural analysis of Levron et al. (2010). However, the exact position of the Tetrabothriidea within this assemblage remains ambiguous. Whereas the nuclear ribosomal RNA genes favor a sister-group relationship with the Cyclophyllidea, the mitochondrial data favor a sister-group relationship with the Nippotaeniidea. Although their taxon sampling for non-elasmobranch hosted cestode groups was limited, Caira et al.'s (2014) analyses of full 18S rDNA and partial 28S rDNA sequence data indicated that the two species of tetrabothriideans included in their analyses were sister taxa to the species of Mesocestoididae, and that this clade was sister to a clade consisting of the three nippotaeniids and two cyclophyllideans included in their analyses.

The monophyly of the order is well supported. That said, the phylogenetic relationships among the tetrabothriideans remain very poorly understood. In fact, the phylogenetic relationships among species in this order are arguably the most poorly known of the 19 orders of tapeworms. A molecular phylogenetic study of the order has yet to be conducted.

CONCLUSIONS

The Tetrabothriidea are a monophyletic group that parasitize marine homeotherms, specifically pinnipeds, cetaceans, and seabirds, primarily in cooler waters around the globe. At present, 70 species in six genera are recognized as valid. The validity of subgenera in the most speciose of these genera (i.e., *Tetrabothrius*) requires confirmation. Tetrabothriidean morphology is fairly well characterized. The scolex typically bears four bothridia which, in many species, bear anterolateral auricular appendages. Most conspicuously, tetrabothriideans exhibit a compact vitellarium located anteroventral to the ovary, and possess unilateral genital pores. Collections as part of the PBI project resulted in few novel taxa, but several new host and locality records. Nonetheless, the group remains one of the most poorly known orders of cestodes, with little attention having been paid to its members over the last two or so decades. Their phylogenetic interrelationships have yet to be examined in any detail.

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TABLE 2. List of valid tetrabothriidean taxa, including their hosts and geographic distributions. New taxa and locality records resulting from PBI project activities indicated in bold. See text for treatment of subgenera of *Tetrabothrius*. *Abbreviations:* B, birds; C, cetaceans; S, seals; TH, type host.

VALID TAXA

Anophryocephalus Baylis, 1922
  Anophryocephalus anophrys Baylis, 1922 (type)
    Hosts (S): *Cystophora cristata*, *Pusa hispida*? (TH)
    Distribution: Greenland Sea (Svalbard); Iceland; White Sea
  Anophryocephalus arcticensis Hoberg & Measures, 1995
    Hosts (S): *Pagophilus groenlandicus* (as *Phoca groenlandica*), *Pusa hispida* (as *Phoca hispida hispida*) (TH)
    Distribution: Canada (near Salluit, Sugluk Inlet, Hudson Strait, northern Quebec; St Lawrence River estuary, Sept-Isles, Quebec)
  Anophryocephalus eumetopii Hoberg, Adams & Rausch, 1991
    Host (S): *Eumetopias jubatus*
    Distribution: Bering Sea, Sea of Okhotsk
  Anophryocephalus inuitorum Hoberg & Measures, 1995
    Host (S): *Pusa hispida* (as *Phoca hispida hispida*)
    Distribution: Canada (northern Quebec)
  Anophryocephalus nunivakensis Hoberg, Adams & Rausch, 1991
    Host (S): *Phoca largha*
    Distribution: USA (Nunivak Island, eastern Bering Sea, Alaska)
  Anophryocephalus ochotensis Delyamure & Krotov in Delyamure, 1955
    Hosts (S): *Callorhinus ursinus*?, *Eumetopias jubatus* (TH)
    Distribution: Russia (Tulení Island, Sea of Okhotsk); Bering Sea; northern Gulf of Alaska
  Anophryocephalus skrjabini (Krotov & Delyamure in Delyamure, 1955) Murav'eva, 1969
    Hosts (S): *Histriophoca fasciata*, *Phoca vitulina*, *Phoca larga*, *Pusa hispida ochotensis* (TH)
    Distribution: Bering Sea; Chuckchi Sea; Russia (Sea of Okhotsk); western Arctic Ocean; Sea of Japan
Chaetophallus Nybelin, 1916
  Chaetophallus robustus Nybelin, 1916 (type)
    Host (B): *Thalassogeron chlororhynchus*
    Distribution: Angola
  Chaetophallus umbrella (Fuhrmann, 1899) Nybelin, 1916
    Hosts (B): *Diomedea* sp. (TH), *D. exulans*, *Macronectes giganteus*, *Phoebetria palpebrata*, *Procellaria cinerea*, *Thalassarche antarctica*, *T. chlororhynchos*
    Distribution: Antarctic
Priapocephalus Nybelin, 1922
  Priapocephalus grandis Nybelin, 1922 (type)
    Hosts (C): *Balaenoptera borealis*, *B. musculus intermedia* (as *B. intermedia*) (TH), *B. physalus*, *Eubalaena glacialis*, *Physeter catodon*
    Distribution: Azores Islands; South Africa (Saldanha Bay, Durban Bay); South Shetland Islands

Priapocephalus eschrichtii Murav'eva & Treshchev, 1970

Host (C): *Eschrichtius robustus*

Distribution: Russian Far East (around town Enurmino, Chukotka)

Priapocephalus minor Nybelin, 1928

Hosts (C): *Balaenoptera borealis* (TH), *B. physalus*

Distribution: Atlantic Ocean (west coast of Norway); Sea of Okhotsk (Kuril Islands); Antarctic

Strobilocephalus Baer, 1932

Strobilocephalus triangularis (Diesing, 1850) Baer, 1932 (type)

Hosts (C): *Cephalorhynchus commersonii*, *Delphinus* sp., *Hyperoodon ampullatus*, *Inia geoffrensis* (as *Delphinus rostratus*) (TH), *Lagenodelphis hosei*, *Lagenorhynchus acutus*, *Mesoplodon bidens*, *Stenella coeruleoalba*, *Steno bredanensis*, *Tursiops truncatus*

Distribution: Mediterranean Sea; eastern Atlantic Ocean (around Lisbon); western Atlantic Ocean (off Brazil and Patagonia); Pacific Ocean (Marshall Islands and Costa Rica)

Tetrabothrius Rudolphi, 1819

Subgenus *Culmenamniculus* Murav'eva, 1975

Tetrabothrius (*Culmenamniculus*) *cylindraceus* Rudolphi, 1819

Hosts (B): "*Lari Atricillae*" (Rudlophi, 1819, pg. 478) (TH), ***Ardenna tenuirostris***, *Chroicocephalus genei*, *Hydrocoloeus minutus*, ***Hydroprogne caspia***, *Ichthyaetus audouinii*, *I. hemprichii*, *I. melanocephalus*, *Larus argentatus*, *La. canus*, *La. crassirostris*, *La. dominicanus*, ***La. heuglini***, *La. hyperboreus*, *La. fuscus*, *La. marinus*, *La. michahellis michahellis*, *La. ridibundus*, *Leucophaeus atricillus*, *Le. modestus*, *Le. pipixcan*, *Puffinus puffinus*, *Rissa tridactyla*, *Stercorarius pomarinus*, *Stercorarius skua*, *Sterna hirundo*, *Thalasseus sandvicensis*, *T. maximus*, *Uria aalge*, *Xema sabini*

Distribution: North America (off Pacific and Atlantic between 35° N and around 30° S), Peru, Chile, Red Sea, Mediterranean Sea, Chafarinas Islands, Europe, Iraq, **Iran (Persian Gulf)**; Greenland; Russia (Barents Sea, Novaya Zemlya); Sea of Okhotsk (Kuril Islands); Japan; **Australia**; Antarctic

Tetrabothrius (*Culmenamniculus*) *drygalskii* Szpotanska, 1929

Host (B): *Sula* sp.

Distribution: Antarctic

Tetrabothrius (*Culmenamniculus*) *gracilis* Nybelin, 1916

Hosts (B): *Fulmarus glacialoides*, *Procellaria aequinoctialis* (as *Majaqueus aequinoctialis*) (TH)

Distribution: South Africa (Alexander Bay Harbour); Atlantic Ocean; South Pacific Ocean (Juan Fernandez Islands)

Tetrabothrius (*Culmenamniculus*) *laccocephalus* Spätlich, 1909

Hosts (B): *Puffinus* sp. (TH), *Ardenna creatopus*, *A. gravis*, *A. grisea*, *Calonectris borealis*, *C. diomedea*, *Fulmarus glacialis*, *F. glacialodes*, *Pagodroma nivea*, *Procellaria aequinoctialis*, *Puffinus lherminieri*

Distribution: North Atlantic Ocean, Kerguelen Is., Antarctic (South Atlantic Ocean, Scott Island), South Pacific (Juan Fernandez Islands)

Tetrabothrius (*Culmenamniculus*) *procerus* Spätlich, 1909

Hosts (B): *Ardenna creatopus*, *A. gravis*, *A. grisea*, *Calonectris borealis*, *Fulmarus glacialis*, *Puffinus* sp. (TH)

Distribution: Greenland; south Pacific Ocean (Juan Fernandez Islands)

Tetrabothrius (*Culmenamniculus*) *sarasini* Fuhrmann, 1918

Hosts (B): *Sterna paradisaea*, *Thalasseus bergii* (as *Sterna bergii*) (TH)

Distribution: Antarctic; New Caledonia

Tetrabothrius (*Culmenamniculus*) *torulosus* Linstow, 1888

Hosts (B): *Diomedea brachyura* (TH), *Diomedea exulans*, *Phoebastria albatrus*, *P. nigripes*

Distribution: north Pacific Ocean; South Polar ring area; Kerguelen Island

Subgenus *Neotetrabothrius* Nybelin, 1929 (syn. *Uniamniculus* Murav'eva, 1975)

Tetrabothrius (*Neotetrabothrius*) *pellucidus* Nybelin, 1929 (type of subgenus)

Hosts (B): *Spheniscus magellanicus* (TH)

Distribution: South Pacific Ocean (Robinson Crusoe Island; Juan Fernandez Islands)

Tetrabothrius (*Neotetrabothrius*) *eudyptidis* (Lönnberg, 1896) Nybelin, 1929

Hosts (B): *Ardenna creatopus*, ***Eudyptes chrysocome***, *Eudyptula minor*? (as "im Darm des blauen *Pinguins*, *Eudyptes catarractes*"; Lönnberg [1896], pg. 6) (TH), *Spheniscus humboldti*, *S. magellanicus*

Distribution: Chile; Falkland Islands; Antarctic; **Australia**

Tetrabothrius (*Neotetrabothrius*) *joubini* Railliet & Henry, 1912

Host (B): *Pygoscelis antarcticus*

Distribution: Antarctic

Tetrabothrius (*Neotetrabothrius*) *lutzi* Parona, 1901

Hosts (B): *Eudyptula minor*, *Pygoscelis papua*, *Spheniscus magellanicus* (TH)

Distribution: Tasmania, South Pacific (Juan Fernandez Islands), Antarctic

Tetrabothrius (*Neotetrabothrius*) *pauliani* Joyeux & Baer, 1954
Hosts (B): *Aptenodytes patagonicus*, *Pygoscelis adeliae*, *P. antarctica*, *P. papua* (TH)
Distribution: Antarctic
Tetrabothrius (*Neotetrabothrius*) *wrighti* Leiper & Atkinson, 1914
Hosts (B): *Aptenodytes forsteri*, *A. patagonicus*, *Pygoscelis adeliae* (TH), *P. papua*
Distribution: Antarctic
Subgenus *Oriana* Leiper & Atkinson, 1914 (syn. *Biamniculus* Muravijova, 1975)
Tetrabothrius (*Oriana*) *wilsoni* Leiper & Atkinson, 1914 (type of subgenus)
Host (C): *Balaenoptera borealis* (TH)
Distribution: Antarctic
Tetrabothrius (*Oriana*) *affinis* (Lönnberg, 1891) Lönnberg, 1892
Hosts (C): *Balaenoptera borealis* (TH), *B. musculus*, *Physeter catodon*
Distribution: Norway; South Africa; New Zealand; Antarctic; North Pacific Ocean
Tetrabothrius (*Oriana*) *arsenyevi* Delyamure, 1955
Host (C): *Balaenoptera borealis*
Distribution: Antarctic
Tetrabothrius (*Oriana*) *campanulatus* (Fuhrmann, 1899) Fuhrmann, 1908
Hosts (B): *Daption capense*, *Diomedea exulans*, *Fulmarus glacialoides*, *Macronectes giganteus*, *Pachyptila desolata*, *Pagodroma nivea*, *Procellaria aequinoctialis*, *Pr. cinerea*, *Procellaria* sp. (TH), *Thalassoica antarctica*
Distribution: Cape of Good Hope; Kerguelen Islands; South Georgia Island
Tetrabothrius (*Oriana*) *creani* Leiper & Atkinson, 1914
Host (B): *Aestrelata trinitatis* (TH), *Pterodroma arminjoniana*
Distribution: Trinidad; Kerguelen Islands
Tetrabothrius (*Oriana*) *egregius* Skrjabin & Murav'eva, 1971
Host (C): *Balaenoptera physalus*
Distribution: Antarctic, Ballen Island
Tetrabothrius (*Oriana*) *erostris* (Lönnberg, 1889) Baylis, 1926
Hosts (B): *Cepphus grylle* (as *Uria grylle*) (TH), *Ce. columba*, *Chlidonias* sp., *Chroicocephalus ridibundus*, *Fulmarus glacialis*, *Larus argentatus*, *L. crassirostris*, *L. canus*, *L. canus kamtschatschensis*, *L. fuscus*, *L. hyperboreus*, *L. marinus*, *L. schistisagus*, *Leucophaeus atricilla*, *Pagophila eburnea*, *Rissa tridactyla*, *Stercorarius parasiticus*, *Sterc. pomarinus*, *Sterna dougallii*, *Stern. hirundo*, *Stern. paradisaea*, *Uria aalge*
Distribution: North America; Greenland; Europe (Scandinavia); Russia (Barents Sea; Bering Island; Moneron Island; Tuljen Island; Anivský Bay); Japan; Sri Lanka
Tetrabothrius (*Oriana*) *filiformis* Nybelin, 1916
Hosts (B): *Ardenna gravis*, *Oceanites oceanicus*, *Procellaria aequinoctialis* (as *Majaqueus aequinoctialis*) (TH)
Distribution: north Atlantic Ocean; south Atlantic Ocean (Gough Island); southern Africa (Saint Sebastian Bay); Antarctic
Tetrabothrius (*Oriana*) *fuhrmanni* Nybelin, 1916
Hosts (B): *Procellaria aequinoctialis*, *Thalassogeron chlororhynchos* (TH)
Distribution: Angola (Port Alexander); Antarctic (South Georgia Island; South Shetland Islands; South Orkney Islands); south Atlantic Ocean (Kerguelen Islands)
Tetrabothrius (*Oriana*) *heteroclitus* Diesing, 1850
Hosts (B): *Ardenna grisea*, *Daption capense* (*Procellaria capensis*) (TH), *Diomedea exulans*, *Fulmarus glacialoides*, *Macronectes giganteus*, *Pachyptila desolata*, *Pagodroma nivea*, *Pelecanoides urinatrix*, *Phoebetria palpebrata*, *Procellaria aequinoctialis*, *Pro. cinerea*, *Procellaria* sp., *Thalassarche chlororhynchos*, *Thalassoica antarctica*
Distribution: Brazil ("Sebastopoli"); southern Africa (Cape of Good Hope); Peru; Antarctic (Balleny Island; Crozet Island)
Tetrabothrius (*Oriana*) *hoyeri* Szpotanska, 1929
Host (B): *Sula* sp.
Distribution: Antarctic
Tetrabothrius (*Oriana*) *innominatus* Baer, 1954
Host (B): *Steno bredanensis*
Distribution: Tropical Pacific Ocean
Tetrabothrius (*Oriana*) *jaegerskioeldi* Nybelin, 1916
Hosts (B): *Alca torda*, *Cepphus grylle* (TH), *C. carbo*, *Fratercula arctica*, *F. cirrhata*, *Stercorarius parasiticus*, *Synthliboramphus antiquus*, *Uria aalge*
Distribution: Sweden; Greenland; Russia (Barents Sea; Chukotka; Kuril Islands)

Tetrabothrius (*Oriana*) *mawsoni* Johnston, 1937
Hosts (B): *Stercorarius skua*, *S. maccormicki* (as *Catharacta maccormicki*) (TH)
Distribution: Antarctic (Ross Sea)
Tetrabothrius (*Oriana*) *morschtini* Murav'eva, 1968
Host (B): *Larus hyperboreus*
Distribution: Russia (Kanin Peninsula)
Tetrabothrius (*Oriana*) *nelsoni* Leiper & Atkinson, 1914
Hosts (B): *Phoebetria palpebrata* (TH), *Thalassarche melanophrys*
Distribution: Antarctic
Tetrabothrius (*Oriana*) *pelecaniaquilae* (Rudolphi, 1819) Fuhrmann, 1908
Hosts (B): *Fregata aquila* (as *Pelecani aquilae*), *F. magnificens rotschildi*, *F. minor*, *Sula leucogaster*
Distribution: Europe; West Indies (Jamaica); Brazil
Tetrabothrius (*Oriana*) *polyorchis* Nybelin, 1916
Host (B): *Fregata ariel*
Distribution: North Australia; New Caledonia
Tetrabothrius (*Oriana*) *ruudi* Nybelin, 1928
Hosts (C): *Balaenoptera physalus* (TH), *Eubalaena glacialis*
Distribution: Norway; France; Pacific Ocean; Antarctic
Tetrabothrius (*Oriana*) *schaeferi* Markowski, 1955
Host (C): *Balaenoptera musculus*
Distribution: Antarctic (South Georgia)
Tetrabothrius (*Oriana*) *skoogi* Nybelin, 1916
Host (B): *Ardenna grisea* (as *Puffinus griseus*) (TH), *Puffinus tenuirostris*
Distribution: Angola (Port Alexander); Indian Ocean; Japan
Tetrabothrius (*Oriana*) *sulae* Szpotanska, 1929
Hosts (B): *Pelecanus occidentalis*, *Sula* sp. (TH), *Sula leucogaster*, *S. sula*
Distribution: Mexico; West Indies
Subgenus *Tetrabothrius* Rudolphi, 1819
Tetrabothrius (*Tetrabothrius*) *macrocephalus* **(**Rudolphi, 1808) Rudolphi, 1819 (type of genus and subgenus)
Hosts (B): *Brachyrhamphus marmoratus*, *Gavia stellata*, *G. adamsii*, *G. arctica viridigularis*, *G. arctica*, *G. immer*, *Podiceps auritus*, *P. cristatus*, *Phalacrocorax aristotelis*, *Rissa tridactyla*, *Rostratula bengalensis*, *Somateria mollissima*
Distribution: Arctic (Barents Sea); Russian Far East (Moneron Island, Kamchatka); **Norway** (Bear Island); Scotland; Black Sea; France; Madagascar
Tetrabothrius (*Tetrabothrius*) *curilensis* Gubanov, 1952 in Delyamure, 1955
Hosts (C): *Balaenoptera acutorostrata*, *Physeter catodon* (TH)
Distribution: Sea of Okhotsk (Kuril Islands); Antarctic
Tetrabothrius (*Tetrabothrius*) *diomedea* Fuhrmann in Shipley, 1900
Hosts (B): *Ardenna gravis*, *Diomedea exulans* (TH), *Thalassarche chlororhynchos*
Distribution: south Atlantic Ocean (Gough Island); Antarctic
Tetrabothrius (*Tetrabothrius*) *forsteri* (Krefft, 1871) Fuhrmann, 1904
Hosts (C): *Delphinus capensis*, *D. delphis* (as *D. fosteri*) (TH), *Globicephalus melas*, *Hyperoodon ampullatus*, *Lagenorhynchus acutus*, *Mesoplodon bidens*, *M. hectori*, *M. stejnegeri*, *Phocoenoides dalli*, *Stenella attenuate graffmari*, *Stene. clymene*, *Stene. coeruleoalba*, *Steno bredanensis*, *Tursiops truncatus*
Distribution: north Atlantic Ocean (USA); south Atlantic Ocean (Brazil); Mediterranean Sea (Sardinia; Spain), Pacific Ocean (Australia; New Zealand); Bering Sea (Alaska)
Tetrabothrius (*Tetrabothrius*) *heterosoma* (Baird, 1853) Fuhrmann, 1913
Hosts (B): *Fregata aquila* (TH), *Morus bassanus*
Distribution: Jamaica; Europe
***Tetrabothrius* (*Tetrabothrius*) *hobergi* Nikolov, Cappozzo, Berón-Verat, Crespo, Raga & Fernándezi, 2010**
Host (C): *Mesoplodon hectori*
Distribution: Argentina
Tetrabothrius (*Tetrabothrius*) *kowalewskii* Szpotanska, 1917
Hosts (B): *Daption capense*, *Diomedea exulans* (TH), *Procellaria aequinoctialis*, *Thalassarche chlororhynchos*
Distribution: Antarctic
Tetrabothrius (*Tetrabothrius*) *minor* (Lönnberg, 1893) Fuhrmann, 1899
Hosts (B): *Calonectris diomedea*, *Fulmarus glacialis*, *Hydrobastes furcatus*, *Phoebastria irrorata*, *Thalassoica antarctica*
Distribution: Greenland; Finland; North-West Shetland Islands; North Pacific Ocean (Commander Islands); South Pacific Ocean (Galapagos Islands)

Incertae sedis (with respect to subgeneric assignment)
  Tetrabothrius argentinum Szidat, 1964
    Hosts (B): *Chroicocephalus maculipennis*, *Larus dominicanus*, *L. maculipennis* (TH)
    Distribution: Argentina
  Tetrabothrius baeri Burt, 1976
    Host (B): *Sula leucogastra plotus*
    Distribution: Sri Lanka
  Tetrabothrius bairdi Burt, 1978
    Host (B): *Fregata magnificens rothschildi*
    Distribution: Jamaica
  Tetrabothrius bassani Burt, 1978
    Host (B): *Morus bassanus*
    Distribution: Jamaica
  Tetrabothrius mozambiquus Deblock, 1966
    Host (B): *Phaethon rubricauda*
    Distribution: Mozambique
  Tetrabothrius peregrinatoris Burt, 1976
    Host (B): *Sula leucogastra*
    Distribution: Sri Lanka
  Tetrabothrius phalacrocoracis Burt, 1977
    Host (B): *Phalacrocorax aristotelis aristotelis*
    Distribution: Scotland
  Tetrabothrius reditus Burt, 1978
    Host (B): *Fregata ariel iredalei*
    Distribution: Sri Lanka
  Tetrabothrius shinni Hoberg, 1987
    Host (B): *Phalacrocorax atriceps bransfieldensis*
    Distribution: Antarctic (Cormorant Island; Arthur Harbor; Anvers Island)
Trigonocotyle Baer, 1932
  Trigonocotyle monticellii (Linton, 1923) Baer, 1932
    Host (C) *Globicephala melas* (TH)
    Distribution: North Atlantic Ocean (Massachussetts)
  Trigonocotyle globicephalae Baer, 1954
    Hosts (C): *Globicephala macrorhynchus*, *G. melas* (as *Globicephala melaena*) (TH), *G. melas edwardii*, *Stenella coeruleoalba*
    Distribution: Mediterranean Sea; Atlantic Ocean; Pacific Ocean (off Japan); South Africa (Cape Town)
  Trigonocotyle prudhoei Markowski, 1955
    Hosts (C): *Lagenorhynchus australis*, *L. cruciger*, *L. obscurus*, *Steno bredanensis* (TH)
    Distribution: Falkland Islands; Antarctic
  Trigonocotyle sexitesticulae Hoberg, 1990
    Host (C): *Feresa attenuata*
    Distribution: Florida coast
  Trigonocotyle spasskyi Gubanov 1952 in Delamure, 1955
    Host (C): *Orcinus orca* (as *Orca orca*)
    Distribution: Sea of Okhotsk (Kuril Islands)

20

"Tetraphyllidea" van Beneden, 1850 relics

By
Janine N. Caira[1], Kirsten Jensen, and Timothy R. Ruhnke

TETRAPHYLLIDEA AS THEY WERE KNOWN PRIOR TO THE PBI PROJECT

Diversity and Classification. This group had its origin with van Beneden (1850a; pg. 277), who established the family "Tétraphyllidés" for cestodes with "quatre lobes mobiles et à forms trés-variables, pédiculés ou sessiles armés de crochets ou inermes" (i.e., four mobile lobes of very variable form, pedunculate or sessile, armed with hooks or without hooks) that parasitize elasmobranchs (i.e., sharks and batoids). Van Beneden (1850a) recognized three sections within the family: the non-hooked Phyllobothriens (with the genera *Echeneibothrium* van Beneden, 1850, *Phyllobothrium* van Beneden, 1850, *Anthobothrium* van Beneden, 1850, and *Bothriocephalus* Rudolphi, 1808 as members), the hooked Phyllacanthiens (with the genus *Acanthobothrium* Blanchard, 1848 as the only member), and the Phyllorynchiens [sic] (with the genus *Rhynchobothrius* van Beneden, 1850 as the only member). In 1850, treating the Tétraphyllés as a section, van Beneden (1850b) recognized the following three tribes: (1) the Phyllobotriens [sic] van Beneden, 1850, which he no longer considered to include *Bothriocephalus*, (2) the Phyllacanthiens van Beneden, 1850, which he expanded to include *Onchobothrium* de Blainville, 1828 and *Calliobothrium* van Beneden, 1850, and (3) the Phyllorhynchiens, which he expanded to include a number of additional trypanorhynch taxa. Although Carus (1863; pg. 481) was the first to use the name "Tetraphyllidea," he too recognized this group at the family-level, acknowledging van Beneden as the authority. Thus, although subsequent key authors (e.g., Braun, 1894–1900; Euzet, 1994) credited Carus for the order, van Beneden (1850a) is the proper authority.

In what went on to serve as the foundation of modern classification schemes for many major cestode groups, Braun (1894–1900; pg. 1698) treated the Tetraphyllidea as an order consisting of four families. Among these families, he formally established the Onchobothriidae Braun, 1900 and the Phyllobothriidae Braun, 1900 (pg. 1701) for the Phyllacanthiens (hooked members) and Phyllobothriens (non-hooked members), respectively. (His other two families [i.e., Lecanicephalidae Braun, 1890 and Ichthyotaeniidae Ariola, 1899] went on to be treated as, or in, other cestode orders and will not be discussed further here.) Braun (1894–1900) also recognized the order Trypanorhyncha for the Phyllorhynchiens of van Beneden (1850a). Braun's concepts of both the Phyllobothriidae and Onchobothriidae were much more expansive than those of previous authors. In the Phyllobothriidae, in addition to van Beneden's (1850b) *Anthobothrium*, *Phyllobothrium*, and *Echeneibothrium*, Braun included the nine genera *Calyptrobothrium* Monticelli, 1893, *Crossobothrium* Linton, 1889, *Dinobothrium* van Beneden, 1889, *Diplobothrium* van Beneden, 1889, *Monorygma* Diesing, 1863, *Orygmatobothrium* Diesing, 1863, *Spongiobothrium* Linton, 1889 (with *Pelichnibothrium* Monticelli, 1889 as a possible

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[1] Corresponding author (janine.caira@uconn.edu)

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synonym), *Trilocularia* Olsson, 1867, and *Tritaphros* Lönnberg, 1889. Braun (1894–1900) further considered *Discobothrium* van Beneden, 1871 and *Rhinebothrium* Linton, 1890 as possible synonyms of *Echeneibothrium*. Similarly, in the Onchobothriidae, beyond van Beneden's (1850b) inclusion of *Acanthobothrium*, *Calliobothrium*, and *Onchobothrium*, Braun (1894–1900) included the six additional genera *Ceratobothrium* Monticelli, 1892, *Cylindrophorus* Diesing, 1863, *Phoreibothrium* Linton, 1889, *Platybothrium* Linton, 1890, *Prosthecobothrium* Diesing, 1863, and *Thysanocephalum* Linton, 1890.

It is beyond the scope of this chapter to provide a detailed account of the membership of the order since then. Suffice it to say that over the next almost century, the membership of the Tetraphyllidea continued to expand, in fact, so much so that the order ultimately became notable for the astounding variety of scolex forms it included. However, much of this growth was because the order was often treated as a dumping ground for elasmobranch-hosted genera that lacked the distinctive diagnostic features of the other elasmobranch-hosted cestode orders, rather than the possession of distinctive uniting features of their own. For example, beyond a series of nine *genera inquirendae,* Wardle and McLeod (1952) assigned all elasmobranch-hosted genera that they did not otherwise assign to the Trypanorhyncha, Lecanicephala [sic], or Disculicepitidea, to the Tetraphyllidea. Within this order, Wardle and McLeod (1952) considered Phyllobothriidae to house 11 genera. These included four genera beyond those of Braun (1894–1900) but excluded six of Braun's genera. Only four of the eight genera Wardle and McLeod (1952) considered to belong to the Onchobothriidae were from Braun's original members. Yamaguti (1959) had a similar concept of the order, treating all elasmobranch-hosted genera that he did not consider to belong to the Diphyllidea, Trypanorhyncha, or Lecanicephalidea, as members of the Tetraphyllidea. In total he recognized 33 genera—18 in the Phyllobothriidae and 13 in the Onchobothriidae. He also established the new families Triloculariidae Yamaguti, 1959 for the monotypic *Trilocularia* and Maccallumiellidae Yamaguti, 1959 for the monotypic new genus *Maccallumiella* Yamaguti, 1959.

The two most recent comprehensive treatments of the Tetraphyllidea prior to 2008 increased the membership and thus morphological variation seen across members of the order even further. Schmidt (1986) added the family Cathetocephalidae Dailey & Overstreet 1973 for the enigmatic *Cathetocephalus* Dailey & Overstreet, 1973—a genus he and Beveridge (Schmidt and Beveridge, 1990) later transferred to the new order Cathetocephalidea. He treated 27 genera in the Phyllobothriidae, 16 genera in the Onchobothriidae, and three (*Pentaloculum* Alexander, 1963, *Trilocularia*, and *Zyxibothrium* Hayden & Campbell, 1981) in the Triloculariidae. Schmidt (1986) made no mention of the Maccallumiellidae. Thus, by 1986, the order had come to house a total of 46 genera.

However, the most expansive concept of the order formulated up to 2008 was that of Euzet (1994) in which the number of genera and families reached historical highs, at 53 and eight, respectively. Specifically, Euzet (1994) recognized 15 hooked genera in the Onchobothriidae and 32 non-hooked genera in the Phyllobothriidae; in the latter family he recognized five subfamilies: the Echeneibothriinae de Beauchamp, 1905, the Phyllobothriinae, the Rhinebothriinae Euzet, 1953, the Thysanocephalinae Euzet, 1953, and the Triloculariinae. He treated genera previously assigned to the orders Cathetocephalidea (see Schmidt and Beveridge, 1990), Dioecotaeniidea (see Schmidt, 1986), Disculicepitidea (see Wardle and McLeod, 1952), and Litobothriidea (see Dailey, 1969) as families within the Tetraphyllidea. He also included the unusual ratfish-parasitizing *Chimaerocestos* Williams & Bray, 1984, which was unknown to Schmidt (1986), in the order, in the monotypic family Chimaerocestidae Williams & Bray, 1984. Thus, beyond the Onchobothriidae and Phyllobothriidae, Euzet

(1994) considered the Tetraphyllidea to include the following six monogeneric families: the Cathetocephalidae Dailey & Overstreet, 1973, Chimaerocestidae, Dioecotaeniidae Schmidt, 1969, Disculicepitidae Joyeux & Baer, 1936, Litobothriidae Dailey, 1969, and Prosobothriidae Baer & Euzet, 1955.

Species-level diversity of the Tetraphyllidea has varied with opinions on its generic membership. Most relevant here, perhaps is that at the inception of the PBI project, the most recent assessment of tetraphyllidean species diversity was that of Schmidt (1986) who listed a total of 185 species in the 46 genera he considered to belong to the order. We note that, if, for comparative purposes, Schmidt's (1986) list of 46 genera is culled to include only the 20 genera known at that time that remain in the Tetraphyllidea subsequent to PBI project efforts, the total number of recognized species at that time was 59.

MORPHOLOGY. Regardless of which subset of genera has been treated as belonging to the Tetraphyllidea, the members of the order have collectively exhibited remarkably disparate variation in scolex morphologies. From its inception in 1850, the order has included both hooked and non-hooked forms. Over time, these forms have included species bearing bothridia that were stalked or sessile, with or without suckers, with or without muscular pads, with or without facial loculi, and with or without a myzorhynchus. In contrast, the proglottid anatomy of taxa assigned to the order over time has been much more conserved—this is likely one of the factors that led many genera to be originally assigned to this order. For example, the genital pores are typically lateral and irregularly alternate; in many taxa the vagina crosses the vas deferens and opens anterior to the cirrus-sac; the testes are numerous; the ovary is posterior and bi- or tetralobed in cross-section; the vitellarium is follicular and the vitelline follicles are usually arranged in two lateral bands; and the uterus is medioventral. A detailed treatment of the morphology of genera once considered to belong to the order is of limited use given the current much more restricted membership in the order. Readers are instead referred to the section below treating the morphology of genera considered to belong in the order as its membership is understood at the end of the PBI project.

PHYLOGENETIC RELATIONSHIPS. Despite the tumultuous history of generic assignments to the order, the concepts of individual genera have generally been relatively stable. As a consequence, genera have been transferred among higher taxa much more frequently than species have been transferred among genera. Nonetheless, the results of all morphological (e.g., Euzet et al., 1981; Brooks et al., 1991; Hoberg, et al. 1997; Caira et al., 1999, 2001) and molecular (e.g., Mariaux, 1998; Olson and Caira, 1999; Olson et al., 1999, 2001; Kodedová et al., 2000; Healy, 2006; Waeschenbach et al., 2007) phylogenetic analyses conducted prior to 2008 that included exemplars of more than one genus of tetraphyllidean have attested to the non-monophyly of the order as it was defined prior to 2008. Because taxon sampling among these studies differed substantially, it is difficult to make meaningful comparisons across studies. However, in the molecular works with the greatest taxon sampling across the order (i.e., Olson et al., 2001; Waeschenbach et al., 2007), a subset of the tetraphyllideans with hooks (e.g., *Acanthobothrium* and *Platybothrium*) grouped as a series of early diverging lineages to a clade comprising what was then recognized as the Proteocephalidea; that combination of taxa also generally grouped as sister to the cyclophyllideans and their kin; and certain non-hooked tetraphyllidean genera (e.g., *Clistobothrium*, *Rhinebothrium*, and their kin) grouped as the sister group to the former larger clade.

The morphological and molecular results of the analyses of Caira et al. (2005), together with the discovery and description of the new genus *Sanguilevator* Caira, Mega & Ruhnke, 2005, provided convincing support for Schmidt and Beveridge's (1990) earlier recognition of the Cathetocephalidea as an order independent of the Tetraphyllidea rather than as a family within the Tetraphyllidea as suggested by Euzet (1994). Caira et al. (2005) formally resurrected the Cathetocephalidea to house the two genera *Cathetocephalus* and *Sanguilevator*.

The unpublished dissertation work of Healy (2006), which focused on members of the phyllobothriid subfamily Rhinebothriinae, played a key role in furthering the formal dismantling of the order Tetraphyllidea as circumscribed by Euzet (1994). The results of Healy's (2006) molecular phylogenetic analyses consistently yielded a highly cohesive clade of some (i.e., *Rhinebothrium, Rhinebothroides* Mayes, Brooks & Thorson, 1981, *Rhabdotobothrium* Euzet, 1953, *Scalithrium* Ball, Neifar & Euzet, 2003, and specimens of 4 putatively new genera), but not all (i.e., not *Caulobothrium* Baer, 1948 and *Duplicibothrium* Williams & Campbell, 1978) rhinebothriine genera. Given that the latter two genera grouped with the onchobothriids included in her analyses, this work prompted a larger scale investigation of tetraphyllidean, and specifically rhinebothriine, relationships overall. Although initiated prior to 2008, that study did not appear in the literature until after 2008 (i.e., Healy et al., 2009) and thus is treated in the section below describing the phylogenetic relationships of the order as its membership is understood at the end of the PBI project. By 2008, it was clear that substantial taxonomic rearrangement of the genera then assigned to the Tetraphyllidea was required if the monophyly of all cestode orders was to be achieved.

HOST ASSOCIATIONS. Based on the inclusive nature of the concept of tetraphyllidean membership in 2008, elasmobranchs of essentially all eight orders of sharks and all four orders of batoids had been reported to host one or more members of the order. The addition of *Chimaerocestos* to the Tetraphyllidea by Williams and Bray (1984) extended the host associations of the order beyond elasmobranchs to the Holocephali (i.e., ratfish). As noted in the discussion of morphology above, the substantial change in composition of the Tetraphyllidea between 2008 and the end of the PBI project makes further discussion of their host associations prior to 2008 unproductive here. Instead, once again readers are referred to the section below discussing the host associations of the order as its membership is understood at the end of the PBI project.

GEOGRAPHIC DISTRIBUTION. Prior to 2008, species attributed to the Tetraphyllidea had been reported from elasmobranchs and holocephalans in 11 of Spalding et al.'s (2007) 12 marine realms of the world. The exception was Temperate Southern Africa, which had received little attention from those working on marine cestodes prior to 2008. Once again, however, it is unfruitful to discuss the geographic distribution of the order prior to 2008 given the substantial changes in its membership that have occurred since then. Here too readers are directed to the section below describing the geographic distribution of the order as its membership is understood at the end of the PBI project.

CURRENT STATUS OF THE "TETRAPHYLLIDEA" RELICS

Although erection of the new orders Rhinebothriidea by Healy et al. (2009), and Onchoproteocephalidea and Phyllobothriidea by Caira et al. (2014), to house subsets of genera traditionally assigned to the "Tetraphyllidea" substantially reduced the extent of the polyphyly of this order, the use of quotation marks around its name serves as a reminder that the order remains polyphyletic even in its revised form. The 27 genera (2 of which are undescribed but have been included in molecular work) currently assigned to the "Tetraphyllidea" (Table 3) are an eclectic assortment of elasmobranch-hosted taxa most of which lack clear affiliations with any other named tapeworm order. The complexity of the situation is illustrated in the schematic phylogenetic framework provided in Figure 1. This figure is modified from figure

2 of Caira et al. (2014) based on additional morphological and molecular work to include several genera beyond those analyzed by Caira et al. (2014). In this figure the two gray clades (depicted as gray triangles) represent cestode orders recognized prior to PBI work and the three black clades (depicted as black triangles) represent taxa previously assigned to the "Tetraphyllidea" but recognized as their own orders since 2008. All of the remaining genera, which are indicated in font colors other than black and gray, are members of the "Tetraphyllidea" as it currently stands. As is evident from this illustration, these 27 genera represent ten morphologically, and also molecularly divergent groups albeit with varying degrees of nodal support. Family names are available for five of the six groups that are both morphologically cohesive and relatively highly supported in molecular phylogenetic analyses: Balanobothriidae Pintner, 1928, Calliobothriidae Perrier, 1897, Dioecotaeniidae, Gastrolecithidae Euzet, 1955, and Serendipidae Brooks & Barriga, 1995. We propose the new family name Rhoptrobothriidae n. fam. for a sixth, highly supported group. The affinities of constituent genera of the other four groups both relative to one another and relative to these six families remain to be assessed in more detail. As a consequence, they have not been formally named and are instead referred to here as Clades 1 through 4. The six families and four clades are treated separately in each section that follows below.

DIVERSITY AND CLASSIFICATION. The classification and valid taxa recognized here in the six families and four clades of "Tetraphyllidea" relics are given in Table 3. Also listed are three genera and 14 species that may also be valid members of one of these groups, but that are treated as *incertae sedis* until their affinities to these ten assemblages can be examined in more detail. We have refrained from treating the over 70 nominal taxa, tens of which were described from India, that are considered *nomina dubia*, *nomina nuda*, and *species inquirendae* owing to the superficial nature of their descriptions. Readers are directed to the Global Cestode Database (www.tapewormdb.uconn.edu) for these invalid or unavailable names.

Balanobothriidae: This family was established by Pintner (1928) for *Balanobothrium* Hornell, 1912. Subsequent authors have treated this taxon within the order Lecaniceaphalidea (e.g., Yamaguti, 1959; Schmidt, 1986), but it has been treated as a member of the family Onchobothriidae (as a tetraphyllidean) by others (e.g., Caira and Pritchard, 1986; Butler, 1987; Euzet, 1994). Here we resurrect and expand the concept of the family to include four related genera: *Pedibothrium* Linton, 1908, *Pachybothrium* Baer & Euzet, 1962, *Spiniloculus* Southwell, 1925, and *Yorkeria* Southwell, 1927. A total of 38 valid species are currently recognized in the family. In order of increasing diversity these are: *Pachybothrium* (1 sp.), *Balanobothrium* (3 spp.), *Spiniloculus* (5 spp.), *Yorkeria* (14 spp.), and *Pedibothrium* (15 spp.). In total, three new species in this family, all members of *Spiniloculus*, were described over the course of the PBI project (see Desjardins and Caira, 2011). One additional species was transferred to this genus when its original genus, *Spinibiloculus* Deshmukh & Shinde, 1980, was determined by Desjardins and Caira (2011) to be a junior synonym of *Spiniloculus*.

Calliobothriidae: This taxon was originally established as a tribe (i.e., Calliobothriinae Perrier, 1897) by Perrier (1897), with *Calliobothrium* van Beneden, 1850 as its type genus. Although Perrier considered this tribe to also include multiple genera now assigned to other orders (e.g., the onchoproteocephalideans *Acanthobothrium*, *Phoreiobothrium*, *Platybothrium*, and *Onchobothrium*; and the phyllobothriidean *Thysanocephalum*), the name Calliobothriidae is appropriate for the clade that houses *Calliobothrium* and its kin (i.e., at present *Biloculuncus* Nasin, Caira & Euzet, 1997, *Erudituncus* Healy, Scholz & Caira, 2001, and *Symcallio* Bernot, Caira & Pickering, 2015); it is herein elevated to family level. The family currently comprises 26 species, which, in order of increasing diversity by genus, are: two species of *Erudituncus*,

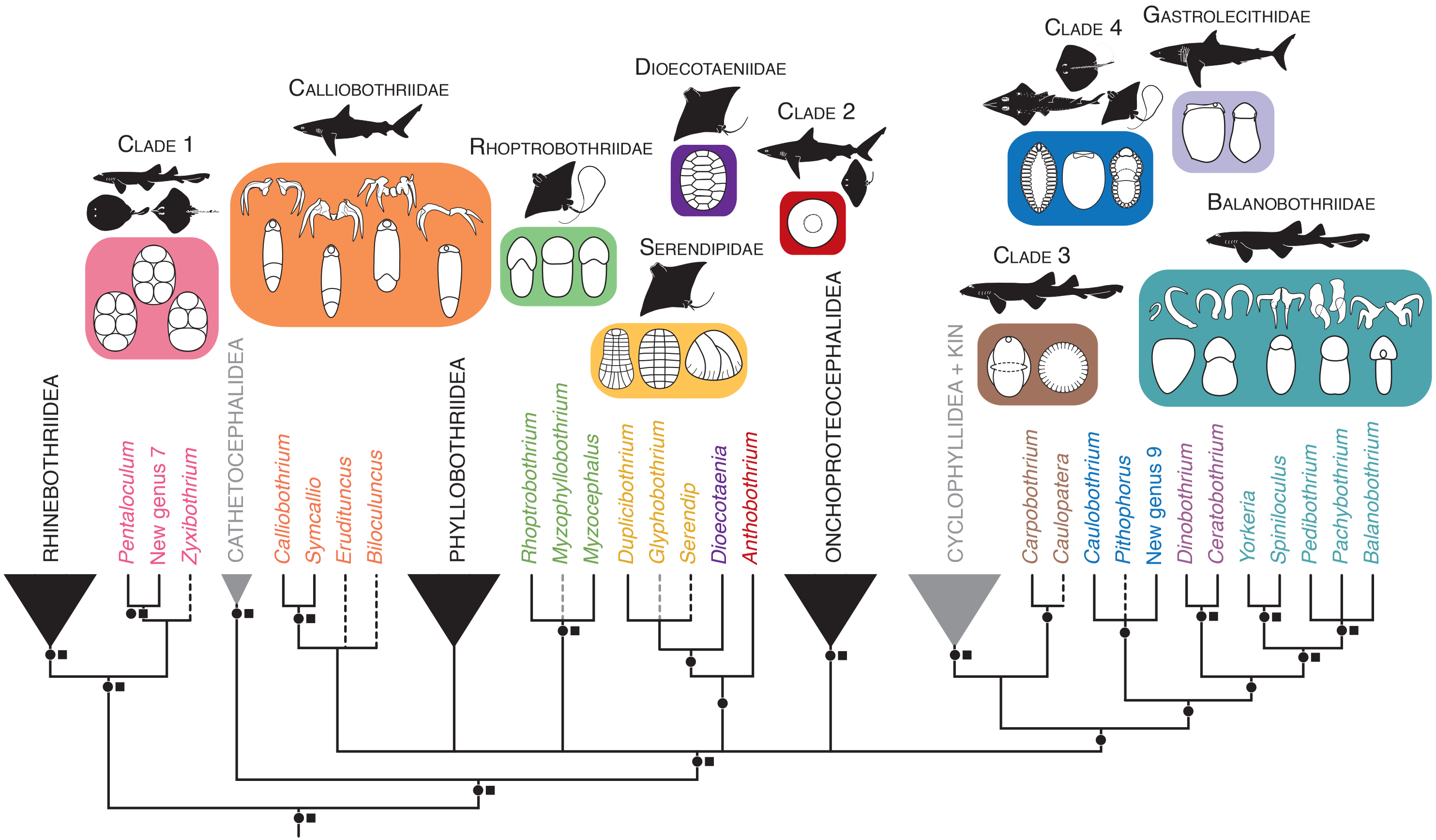


Figure 1. Schematic phylogenetic framework for the ten independent groups that remain as "tetraphyllidean" relics (modified from figure 2 of Caira et al. [2014]). Black triangles represent lineages assigned to the "Tetraphyllidea" prior to 2008; gray triangles represent other orders. Dashed lines indicate genera not included in Caira et al. (2014); their placement is based on close morphological resemblance to other members of their respective families (gray dashed lines) and/or the results of unpublished molecular phylogenetic analyses (black dashed lines). Nodal support is indicated with solid circles for posterior probabilities of 0.95 or greater from Bayesian inference and solid squares for bootstrap values 75% or greater from maximum likelihood analysis. For each of the ten independent groups, bothridial and, if applicable, hook morphologies are illustrated. General host associations are indicated with black host icons.

three species of *Biloculuncus*, nine species of *Calliobothrium*, and 12 species of *Symcallio*. It is common for members of two of these genera to parasitize the same species of host—a fact that accounts for the relatively high diversity in the family given its limited host associations (see below). In total, four new species were described in this family over the course of the PBI project. Three of these are members of *Calliobothrium* (see Bernot et al., 2015, 2016). The fourth is a member of *Symcallio*. The latter genus was established by Bernot et al. (2015) for a subset of smaller, non-laciniate species, 11 of which they transferred from *Calliobothrium* to their new genus and one of which they also redescribed.

Dioecotaeniidae: The family was established by Schmidt (1969) for the highly unusual *Dioecotaenia cancellata* (Linton, 1890) Schmidt, 1969. A second species was described by Mayes and Brooks (1981). Due to its dioecious nature (see morphology below), this taxon is highly unique among the "Tetraphyllidea" and thus we have retained it as a distinct family, independent of the Serendipidae (see below).

Gastrolecithidae: In addition to providing a detailed summary of the history of *Dinobothrium* van Beneden, 1889 and *Gastrolecithus* Yamaguti, 1952, and erecting *Reesium* Euzet, 1955 for the species previously known as *Dinobothrium paciferum* Sproston, 1948, Euzet (1955) erected the family Gastrolecithidae for *G. planus* (Linton, 1922) Yamaguti, 1952. Although this family has essentially passed into obscurity since then, such that even Euzet (1994) did not recognize it as valid, it is resurrected here for *Ceratobothrium* and *Dinobothrium*. *Gastrolecithus* and *Reesium* are consider at this point to be junior synonyms of *Dinobothrium*. However, we stress that the latter two genera remain poorly known and their status as synonyms remains to be confirmed. Thus, at present, the family houses two genera and four species.

Rhoptrobothriidae n. fam.: This family is established here for three genera, all of which were erected by Shipley and Hornell (1906): *Myzocephalus* Shipley & Hornell, 1906, *Myzophyllobothrium* Shipley & Hornell, 1906, and *Rhoptrobothrium* Shipley & Hornell, 1906. We have selected *Rhoptrobothium* as the nominotypical genus for the family because, beyond inclusion of two specimens of *Myzocephalus* in the analyses of Caira et al. (2001), the former two monotypic genera have not been reported since they were originally described. In contrast, *Rhoptrobothrium* was revised relatively recently by Jensen and Caira (2006) and now includes four species all of which are reasonably well known. The diagnosis is as follows: Scolex with four bothridia, simple or divided by a septum, without accessory suckers; cephalic peduncle with four, stalked, remi; remi simple or highly folded, with our without areolae. Proglottids acraspedote, euapolytic. Testes numerous; post-vaginal testes present on poral side. Ovary posterior, tetralobed in cross section. Vagina opening anterior to cirrus-sac, crossing vas deferens. Vitellarium follicular; vitelline follicles in two lateral columns, interrupted by ovary. Uterus saccate, extending to midlevel of proglottid. Adults in spiral intestine of Myliobatidae. Type genus *Rhoptrobothrium* Shipley & Hornell, 1906.

Serendipidae: This family has housed *Serendip* Brooks & Barriga, 1995, *Duplicibothrium* Williams & Campell, 1978, and *Glyphobothrium* Williams & Campbell, 1977 since it was erected by Brooks and Barriga in 1995. With the addition of *Serendip danbrooksi* Monks, Zaragoza-Tapia, Pulido-Flores & Violante-González, 2015 by Monks et al. (2015), its species now number six in total. We consider the Glyphobothriidae Monks, Zaragoza-Tapia, Pulido-Flores & Violante-González, 2015 to be a junior synonym of the Serendipidae.

The four clades recognized, but not assigned to families, are moderately diverse.

Clade 1: This clade consists of three monotypic genera that are hosted by an eclectic selection of elasmobranchs: *Pentaloculum* was established by Alexander (1963) for specimens from the blind electric ray, *Typhlonarke aysoni* (Hamilton) (Torpediniformes). *Zyxibothrium* was established by Hayden and Campbell (1981) for cestodes from the smooth skate, *Malacoraja senta* (Garman) (Rajiformes). The undescribed genus, introduced in the molecular analyses of Caira et al. (2014) as New genus 7, parasitizes the collared carpetshark, *Parascyllium collare* Ramsay & Ogilby (Orectolobiformes).

Clade 2: At present this group consists solely of the eight species assigned to the genus *Anthobothrium* by Ruhnke and Caira (2009) (Table 3). However, preliminary examination of cestodes from species of carcharhinid (and triakid) sharks not previously examined for cestodes has revealed additional as-of-yet undescribed diversity in this genus (Table 2).

Clade 3: This clade consists of *Caulopatera* Cutmore, Bennett & Cribb, 2010 and *Carpobothrium* Shipley & Hornell, 1906. The former was established by Cutmore et al. (2010); the latter was revised by Koontz and Caira (2016). In addition to resolving the substantial confusion surrounding the identity of *Carpobothrium*, the PBI efforts of Koontz and Caira (2016) led to a redescription of the genus and description of a new species.

Clade 4: This final clade is beginning to emerge from obscurity. In addition to the monotypic *Pithophorus* Southwell, 1925 and a selection of new species assigned to an undescribed genus referred to by Caira et al. (2014) as New genus 9, it houses seven described species of *Caulobothrium* (Table 3). In addition, numerous undescribed species of *Caulobothrium* were discovered over the course of the PBI project. Subsets of up to five species of *Caulobothrium* have been included in the phylogenetic analyses of Healy et al. (2009) and Caira et al. (2014).

MORPHOLOGY. The non-monophyly of the "Tetraphyllidea" renders a combined discussion of the morphology of its current members essentially uninformative. That said, all members possess a scolex with four muscular bothridia and, with the exception of the Dioecotaeniidae, hermaphroditic proglottids with numerous testes, an ovary that is posterior in position, and a follicular vitellarium with follicles arranged in two lateral bands. The distinctive scolex and proglottid features of each of the six families and four clades are treated below.

Balanobothriidae: Members of all five genera bear bothridia with one pair of anterior hooks and one (Fig. 2A–C, E), or in the case of *Spiniloculus* (Fig. 2D) two, post-hook loculi. In the cases of *Balanobothrium* (Fig. 2A) and *Pedibothrium* (Fig. 2C), each hook in a pair is bipronged; in the cases of *Pachybothrium* (Fig. 2B), *Spiniloculus*, and *Yorkeria* (Fig. 2E), each hook in a pair is unipronged. The bothridia of *Spiniloculus* (Fig. 2D) and *Yorkeria* (Fig. 2E) are unusual in that the left and right bothridia are each fused in back-to-back pairs and each pair is borne on a pedicel. These genera also possess a region anterior to the hooks, but this region is highly variable in form across genera. In *Balanobothrium* and *Pedibothrium,* it is a muscular pad with an apical sucker that is either small (Fig. 2A) or large (Fig. 2C); in *Pachybothrium* it is a muscular pad (Fig. 2B) but that is deeply embedded in the anterior region of the bothridium (see the sections in figs. 62 and 63 of Caira et al. [1999]); in *Spiniloculus* it is interpreted as a loculus (Fig. 2D); the interpretation of this structure in *Yorkeria* is problematic because its large, anteriorly directed hooks take up much of this region of the bothridium. All five genera also possess a uterus that extends anteriorly only to the level of the genital pore (Fig. 8A). Many members of the family exhibit fields of testes that do not extend posterior to the cirrus-sac (Fig. 8A). Exceptions include the monotypic *Pachybothrium* and some species of *Pedibothrium* in which the field of testes extends to the anterior margin of the ovary on the aporal side of the proglottid, as well as *Spiniloculus calhouni* Desjardins & Caira, 2011 in which a post-poral field of testes is also present (Desjardins and Caira, 2011).

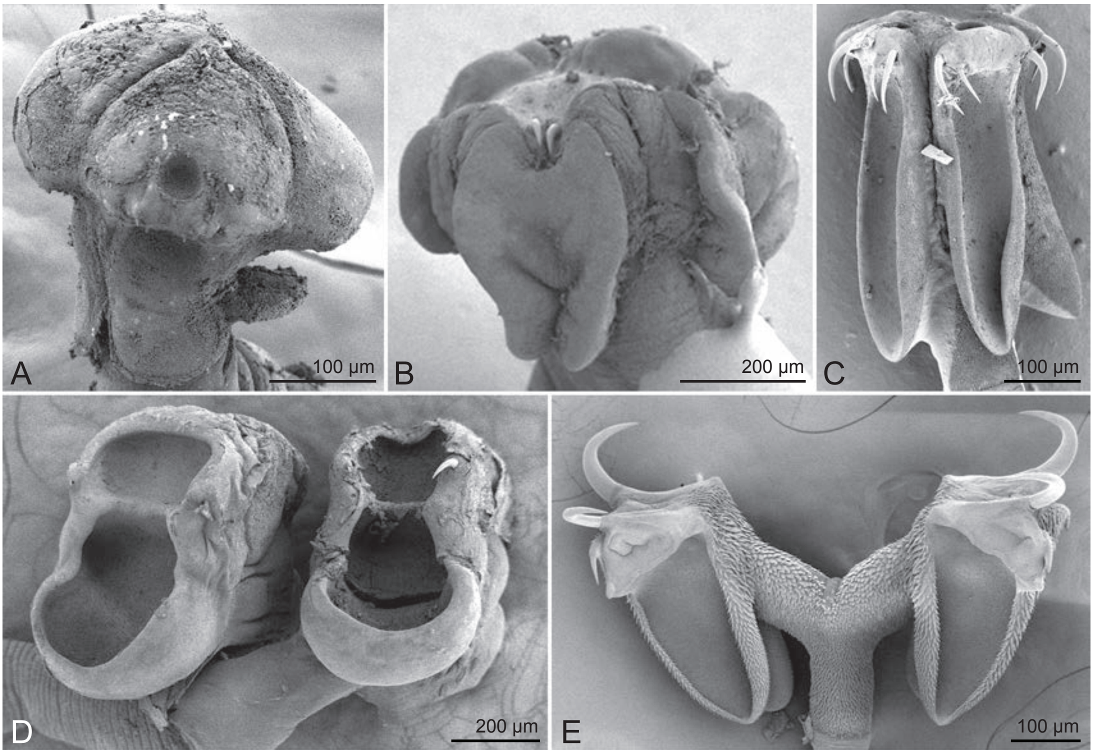


Figure 2. Scanning electron micrographs of scoleces of balanobothriid "tetraphyllidean" relics. BALANOBOTHRIIDAE: **(A)** *Balanobothrium* sp. ex *Stegostoma fasciatum* from Tanzania. **(B)** *Pachybothrium hutsoni* ex *Nebrius ferrugineus* from Australia. **(C)** *Pedibothrium longispine* ex *Ginglymostoma cirratum* from Florida, USA. **(D)** *Spiniloculus calhouni* ex *Chiloscyllium punctatum* from Malaysian Borneo. **(E)** *Yorkeria izardi* ex *Chiloscyllium* cf. *puncatum sensu* Naylor et al. (2012a) from northern Australia.

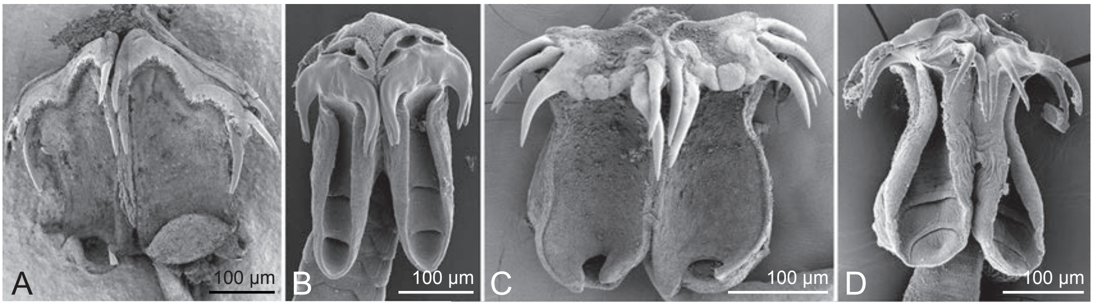


Figure 3. Scanning electron micrographs of scoleces of calliobothriid "tetraphyllidean" relics. CALLIOBOTHRIIDAE: **(A)** *Biloculuncus pritchardae* ex *Furgaleus macki* from Australia. **(B)** *Calliobothrium cisloi* ex *Mustelus canis* from Long Island Sound, USA. **(C)** *Eruditu ncus musteli* ex *Hemitriakis japanica* from Taiwan. **(D)** *Symcallio peteri* ex *Mustelus palumbes* from South Africa.

Calliobothriidae: The four genera in this family (Fig. 1) share the unique possession of at least two pairs of hooks, with or without accessory pieces. They also all bear bothridia with an apical pad that in all genera except *Calliobothrium* is interpreted to bear a single sucker (Fig. 3C, D); in *Calliobothrium* the pad bears three suckers (Fig. 3B). The bothridia also bear either two (i.e., *Biloculuncus* [Fig. 3A] and *Erudituncus* [Fig. 3C]) or three (i.e., *Calliobothrium* [Fig. 3B] and *Symcallio* [Fig. 3D]) post-hook loculi. The majority of species bear proglottids with extensive fields of testes and laciniate posterior margins (Fig. 8B).

Dioecotaeniidae: Both species in this family bear bothridia with three columns of facial loculi (Fig. 4A). However, the remarkable nature of this species was not fully comprehended by Linton (1890) who placed it in *Rhinebothrium* largely because of its possession of facial loculi. Based on newly collected material, Schmidt (1969) recognized that this species is at least functionally dioecious for among the 11 worms he examined, each specimen bore proglottids that were either entirely male or entirely female. Both species in the family are unusual among all eucestodes in possessing a convoluted vagina that lacks a vaginal pore, vitelline follicles and a seminal vesicle that are essentially incorporated into the tissue of the bilobed ovary, and a horizontally bilobed uterus. A thick-walled cirrus-sac (Fig. 8C) and prominent genital pore with protruding papilla are additional distinctive features. These worms undergo hypodermic insemination and the long cirrus of the male proglottid remains in a longitudinal sheath within the female proglottid following release of sperm.

Gastrolecithidae: The two genera in this family are united by their possession of bothridia with an apical pad alone (i.e., *Ceratobothrium* [Fig. 5B]) or apical pad with an accessory sucker (i.e., *Dinobothrium* [Fig. 5C]). The pad bears muscular extensions on its posterolateral margins. In both genera, there is a single loculus posterior to this region (Fig. 5B, C). Following Euzet's (1959) redescription, beyond the general "tetraphyllidean" features listed above, the elongate proglottids of *Ceratobothrium* (Fig. 8D) are somewhat unusual in that they bear a vagina that extends well anterior in the proglottid before recurving posteriorly to the ovarian bridge. The proglottid anatomy of species of *Dinobothrium* is much less well known. Descriptions vary from proglottids that are longer than wide (e.g., Linton, 1922) to those that are wider than long (e.g., Euzet, 1952).

Rhoptrobothriidae n. fam.: The scolex of members of this family is like that of several other families in bearing four muscular bothridia each consisting of an anterior loculus and a main loculus (Fig. 5D, E). However, it differs conspicuously from those of members of all other families of "Tetraphyllidea" (and all other orders of elasmobranch-hosted cestodes) in that the cephalic peduncle bears four stalked extensions, referred to as remi by Jensen and Caira (2006), which may (Fig. 5E), or may not, bear muscular areoli. As is typical of other "tetraphyllideans," the proglottids of rhoptrobothriids bear testes arranged in two regular columns and lateral bands of vitelline follicles that are interrupted by the ovary (Fig. 8E). Unlike most other "tetraphyllideans" other than the Balanobothriidae and Clade 3, rhoptrobothriids bear a uterus that extends anteriorly only to the level of the genital pore.

Serendipidae: The bothridia of all three genera bear numerous facial loculi. In *Duplicibothrium* (Fig. 4B), these loculi are arranged in one to three regular columns, and in some species there is also a single posterior row of loculi each of which is longer than wide. In *Glyphobothrium* (Fig. 4C), the loculi are arranged in three regular columns. In contrast, the loculi of *Serendip* are irregular in both shape and arrangement (Fig. 4D). The bothridia of *Duplicibothrium* share the unique condition of back-to-back fusion of pairs of left and right bothridia, similar to that seen in the balanobothriids *Yorkeria* and *Spiniloculus*. The proglottids of serendipid genera share vitelline follicles that are at least partially confluent dorsally, a highly digitiform ovary, and a cirrus-sac that is positioned near the anterior end of the proglottid (Fig. 8F).

Key morphological features of the four "tetraphyllidean" clades that are not currently assigned to families are as follows.

Clade 1: The three genera in this clade share the possession of bothridia that bear four or five conspicuous facial loculi, a subset of which are arranged in pairs. In New genus 7 *sensu* Caira et al. (2014) (Fig. 6A), these are arranged, from anterior to posterior, as a single loculus followed by two consecutive pairs of loculi. In *Pentaloculum*, these are arranged as two consecutive pairs of loculi followed by a single loculus. In *Zyxibothrium* (Fig. 6B), these are arranged as a single anterior loculus, followed by a pair of loculi and then a single loculus. While *Zyxibothrium* and New genus 7 (Fig. 8G) share genital pores that are extremely anterior in position in the proglottid, *Pentaloculum* exhibits genital pores that are posterior in position.

Clade 2: As described by Ruhnke and Caira (2009), the scolex of *Anthobothrium* (Fig. 5A) is highly unusual in that it entirely lacks any sort of facial sucker or loculi; instead its bothridia bear one or two facial circular bands of musculature. All eight valid species also bear laciniations on the posterior margins of their proglottids (Fig. 8H)—a feature seen only in *Calliobothrium* among the other "tetraphyllidean" groups.

Clade 3: Members of this clade possess bothridia that are unarmed. The bothridia of *Caulopatera* are circular and lack an apical sucker (Fig. 7B) and bear marginal striations or loculi (Cutmore et al., 2010). In contrast, the bothridia of *Carpobothrium* (Fig. 7A) are pouch-like with a slit-like opening surrounded by anterior and posterior retractable flaps and an apical sucker on the anterior flap (see Koontz and Caira, 2016). The proglottid anatomy of species of *Carpobothrium* and *Caulopatera* closely resembles those seen in the Balanobothriidae; most conspicuously the uterus extends only to the level of the cirrus-sac and the testes are restricted to the region of the proglottid anterior to the cirrus-sac (Fig. 8I).

Clade 4: Scolex morphology varies across genera in this clade. The bothridia of New genus 9 (*sensu* Caira et al. [2014]) bear an apical sucker, a central pouch, and marginal loculi (Fig. 7D). The bothridia of *Pithophorus* are superficially pouch-like, but in fact bear a proximal pore such that they are essentially tube-like in configuration (Fig. 7E). They lack marginal loculi and the presence of an apical sucker remains to be confirmed. In contrast, the bothridia of *Caulobothrium* (Fig. 7C) are essentially flat—a pouch is entirely lacking. In addition to marginal loculi, it is now clear that the bothridia of *Caulobothrium* bear an apical sucker, but this feature is very tiny in some species (e.g., Fig. 7C). Proglottid anatomy across the three genera is more consistent. All three bear proglottids in which the testes extend from the ovary

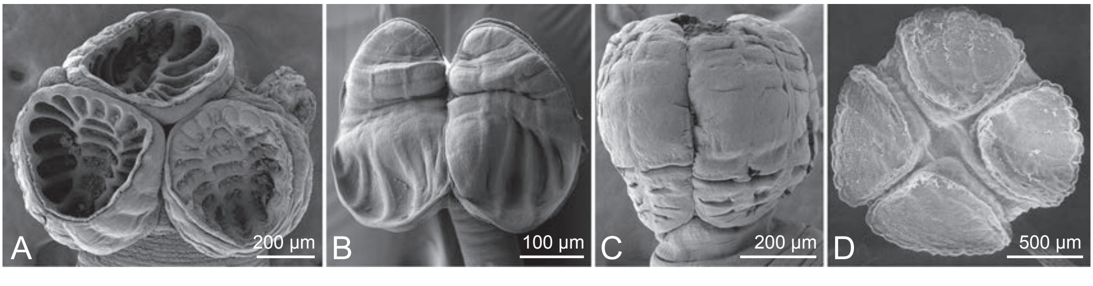


Figure 4. Scanning electron micrographs of scoleces of dioecotaeniid and serendipid "tetraphyllidean" relics. **(A)** DIOECOTAENIIDAE: *Dioecotaenia* sp. ex *Rhinoptera bonasus* from the western Atlantic Ocean. **(B–D)** SERENDIPIDAE: **(B)** *Duplicibothrium* sp. ex *Rhinoptera* cf. *steindachneri sensu* Naylor et al. (2012a) from the Gulf of Mexico, USA. **(C)** *Glyphobothrium zwerneri* ex *Rhinoptera bonasus* from Virginia, USA. **(D)** *Serendip deborahae* ex *Rhinoptera steindachneri* from Ecuador (modified from Brooks and Barriga [1995]).

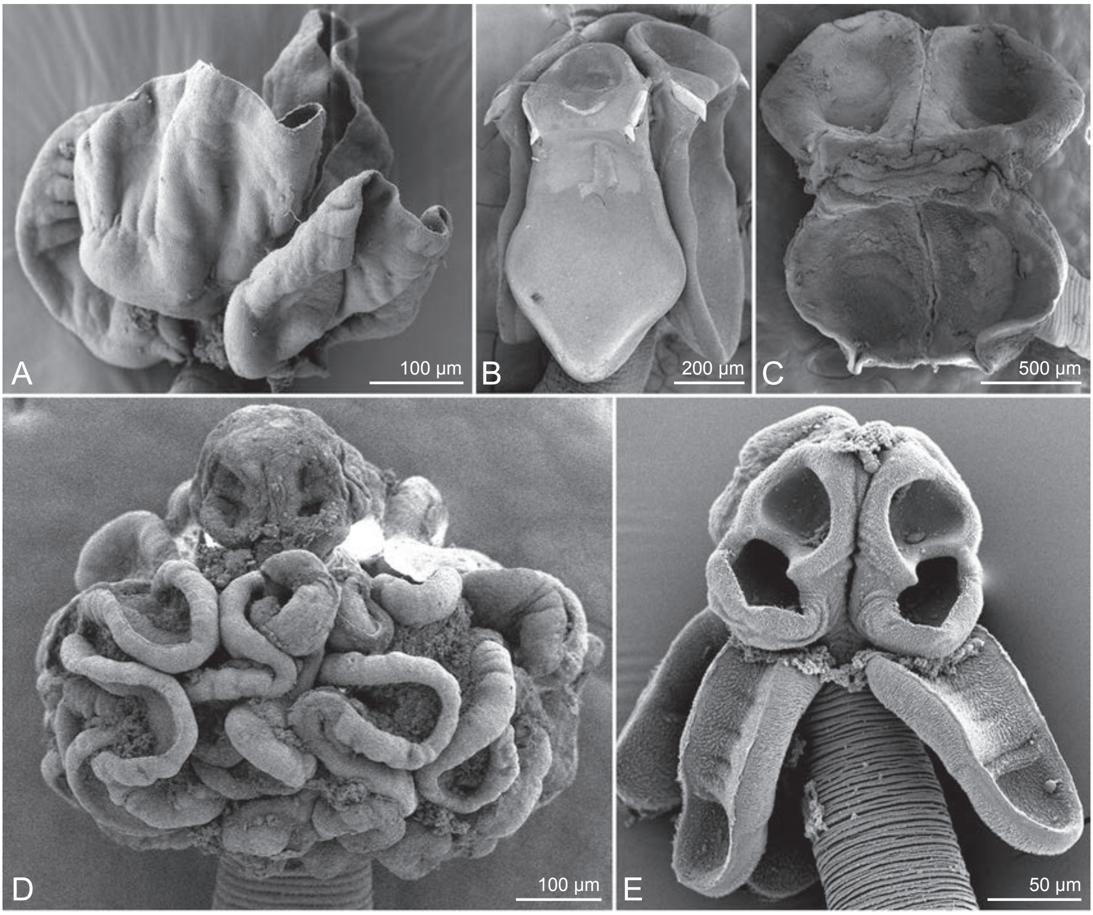


Figure 5. Scanning electron micrographs of scoleces of members of Clade 2, gastrolecithiid, and rhoptrobothriid n. fam. "tetraphyllidean" relics. **(A)** CLADE 2: *Anthobothrium* sp. ex *Carcharhinus limbatus* from the Gulf of Mexico, USA. **(B, C)** GASTROLECITHIDAE: **(B)** *Ceratobothrium xanthocephalum* ex *Isurus oxyrinchus* from New York, USA. **(C)** *Dinobothrium* sp. ex *Lamna nasus* from Georges Bank, northwestern Atlantic Ocean. **(D, E)** RHOPTROBOTHRIIDAE N. FAM.: **(D)** *Myzocephalus* sp. ex *Aetobatus ocellatus* from Australia. **(E)** *Rhoptrobothrium myliobatidis* ex *Aetomylaeus maculatus* from Malaysian Borneo.

to near the anterior margin of the proglottid, an ovary that is posterior in position (that can be bilobed or tetralobed), two lateral bands of vitelline follicles, and a uterus that extends to near the anterior margin of the proglottid (Fig. 8J).

Phylogenetic Relationships. The polyphyletic nature of the "Tetraphyllidea"—a fact supported by essentially all morphological and molecular phylogenetic analyses conducted prior to the inception of the PBI project—was confirmed by molecular phylogenetic work conducted as a result of PBI efforts (i.e., Waeschenbach et al., 2012; Caira et al., 2014). As noted above, several steps were taken over the course of the PBI project to help resolve the polyphyly, at least in part. Healy et al. (2009) established the new order Rhinebothriidea for genera bearing stalked bothridia and facial loculi that had previously been assigned to the "Tetraphyllidea" (see Chapter 17 this volume, Ruhnke et al., 2017a). As a result of their more taxonomically comprehensive phylogenetic work, Caira et al. (2014) established the

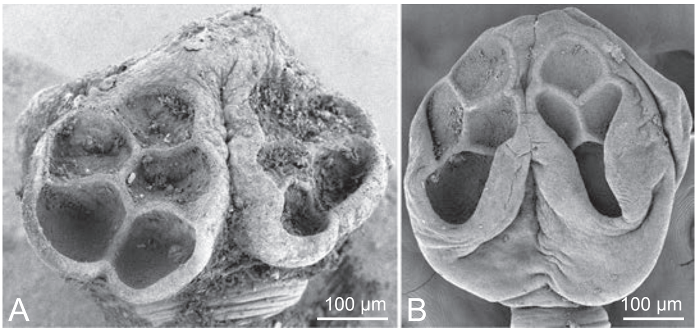


FIGURE 6. Scanning electron micrographs of scoleces of members of "tetraphyllidean" relics CLADE 1. **(A)** New genus 7 (*sensu* Caira et al. [2014]) n. sp. ex *Parascyllium collare* from Australia. **(B)** *Zyxibothrium kamienae* ex *Malacoraja senta* from the Gulf of Maine, USA.

two additional new orders Onchoproteocephalidea (see Chapters 14 and 15 this volume, de Chambrier et al., 2017 and Caira et al., 2017, respectively) and Phyllobothriidea (see Chapter 16 this volume, Ruhnke et al., 2017b). The former order houses a subset of hooked genera that were once considered to belong to the "Tetraphyllidea," most of which bear spinitriches that extend throughout the length of the strobila, and most species of which parasitize batoids. The latter order now houses a series of genera that were previously assigned to the "Tetraphyllidea" relics, which bear non-hooked, uniloculated bothridia, essentially all of which parasitize sharks.

Nonetheless, as noted above, even in their more restricted configuration, the "Tetraphyllidea" remain polyphyletic (Fig. 1). With the exception of the eight genera indicated in Figure 1 with dashed lines, the topology of the tree in Figure 1 is based on that of figure 2 of Caira et al. (2014). The phylogenetic positions of genera indicated with black dashed lines come from unpublished molecular phylogenetic analyses of 28S rDNA data conducted over the course of the PBI project (J. N. Caira, T. R. Ruhnke, M. Pickering, unpubl. data). The positions of *Myzophyllobothrium* and *Glyphobothrium* are indicated with gray dashed lines to reflect their close morphological resemblance to the other members of their respective families, the Rhoptrobothriidae and Serendipidae, respectively, but both genera have yet to be included in molecular phylogenetic work. This tree serves to illustrate: (1) the extent of the molecular support for each of the ten clades consisting of more than a single genus, (2) the typical scolex features of members of each clade, (3) the highly unresolved nature of the interrelationships among the ten clades, and (4) the highly polyphyletic nature of the order.

The following observations can be made with respect to interrelationships among the ten clades. Similarities in scolex morphology support close affinities between the single genus of the Dioecotaeniidae and the Serendipidae; this sister-group relationship was recovered in the trees resulting from the molecular phylogenetic work of Caira et al. (2014). Although Caira et al. (2014) found *Pentaloculum* and New genus 7 to group with the Rhinebothriidea, these affinities were not supported by the subsequent molecular phylogenetic work of Ruhnke et al. (2015) or Marques and Caira (2016). However, it should be noted that both of the latter studies included a much more restricted sampling of "tetraphyllidean" genera than that of Caira et al. (2014). The presence of stalked, facially loculated bothridia in *Pentaloculum* and New genus 7 supports the hypothesis that these taxa, together with *Zyxibothrium* may ultimately be determined to have rhinebothriidean affinities. The phylogenetic affinities of each of Clades 2, 3, 4, and the Gastrolecithidae are least well understood; these groups were by far the most labile in position across the analyses and data partitions employed by Caira et al. (2014) and also in preliminary analyses we conducted over the course of the PBI project (J. N. Caira, T. R. Ruhnke, M. Pickering, unpubl. data). These results, in combination with substantial morphological differences between families and clades, lead us to suspect that the

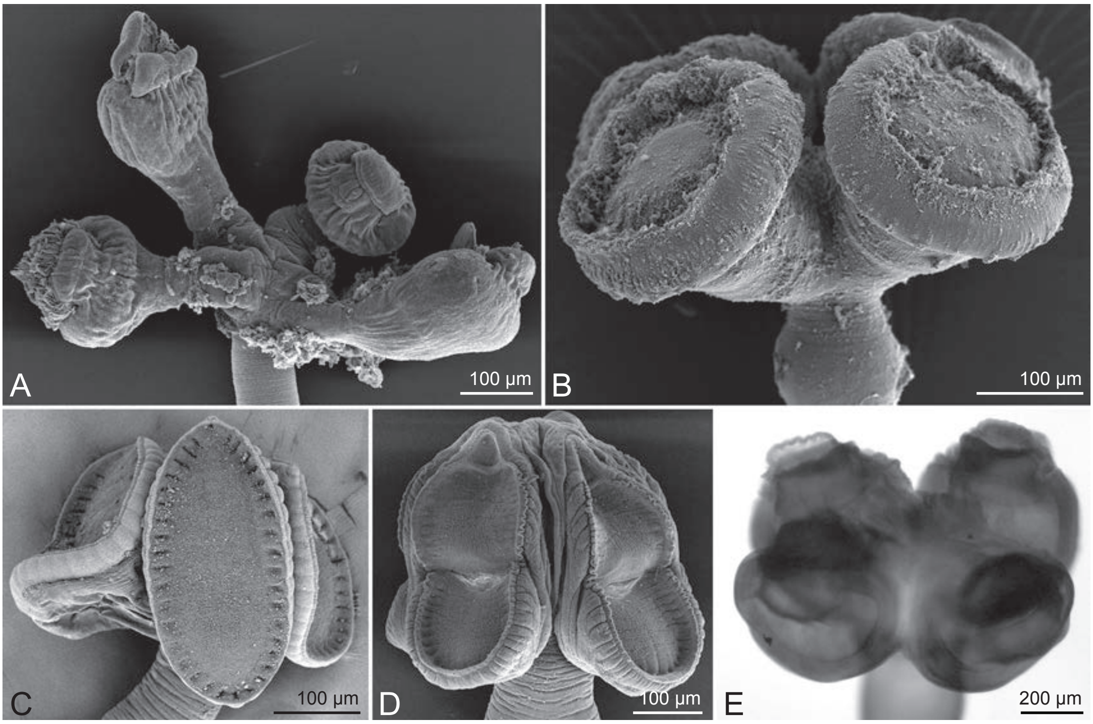


FIGURE 7. Scanning electron micrographs (and light micrograph [E]) of scoleces of selected "tetraphyllidean" relics in CLADE 3 and CLADE 4. **(A–B)** CLADE 3: **(A)** *Carpobothrium eleanorae* ex *Chiloscyllium hasseltii* from Malaysian Borneo. **(B)** *Caulopatera pagei* ex *Chiloscyllium* cf. *puncatum* (*sensu* Naylor et al. [2012a]) from northern Australia. **(C–E)** CLADE 4: **(C)** *Caulobothrium* n. sp. ex *Pastinachus solocirostris* from Malaysian Borneo. **(D)** New genus 9 (*sensu* Caira et al. [2014]) n. sp. ex *Rhina ancylostoma* from northern Australia. **(E)** *Pithophorus* cf. *tetraglobus* ex *Rhynchobatus australiae* from northern Australia.

following four elements of the tree presented in Figure 1 are highly suspect: (1) the sister-group relationship between *Anthobothrium*, and the Serendipidae and Dioecotaeniidae, (2) the sister-group relationship between Clade 3 and the mammal and bird parasitizing Cyclophyllidea, (3) the sister group relationship between the Gastrolecithidae and the Balanobothriidae, and (4) the sister group relationship between Clade 4, and the Gastrolecithidae and Balanobothriidae.

What is, however, undeniable is that these ten clades do not collectively comprise a monophyletic group for they are distributed across a tree that also includes five other orders of cestodes. It seems likely that future phylogenetic work will result in the "Tetraphyllidea" being abandoned altogether in favor of the establishment of a series of smaller orders containing monophyletic subsets of these genera, at least some of which may correspond to the clades identified here.

HOST ASSOCIATIONS. Each of the ten families and clades of "tetraphyllideans" generally parasitizes a relatively small subset of elasmobranch groups.

Balanobothriidae: All 38 species in this family parasitize sharks of the order Orectolobiformes. Species of *Pedibothrium* have been reported from all three genera of the Ginglymostomatidae Gill (nurse sharks) (e.g., see Caira, 1992), although one species has been reported from a bamboo shark in the hemiscylliid genus *Chiloscyllium* Müller & Henle; *Pachybothrium* has been reported from a subset of ginglymostomatids—specifically the monotypic *Nebrius* Rüppell (see Caira et al., 1999). All three valid species of *Balanobothrium* are known only from the monotypic *Stegostoma fasciatum* Müller & Henle (see Butler, 1987). *Spiniloculus* and *Yorkeria* are most commonly found in species of *Chiloscyllium* (Hemiscylliidae) (see Caira et al., 2007a; Desjardins and Caira, 2011), although if the host identity of Deshmukh (1979) is accurate, one species of *Yorkeria* parasitizes the tawny nurse shark, *Nebrius ferrugineus* Rüppell. The relatively high diversity seen in *Pedibothrium* and *Yorkeria* is largely a result of the fact that their host associations extend across several shark genera and in both cases multiple species are known to parasitize the same host species (see Caira, 1992; Caira et al., 2004, 2007a).

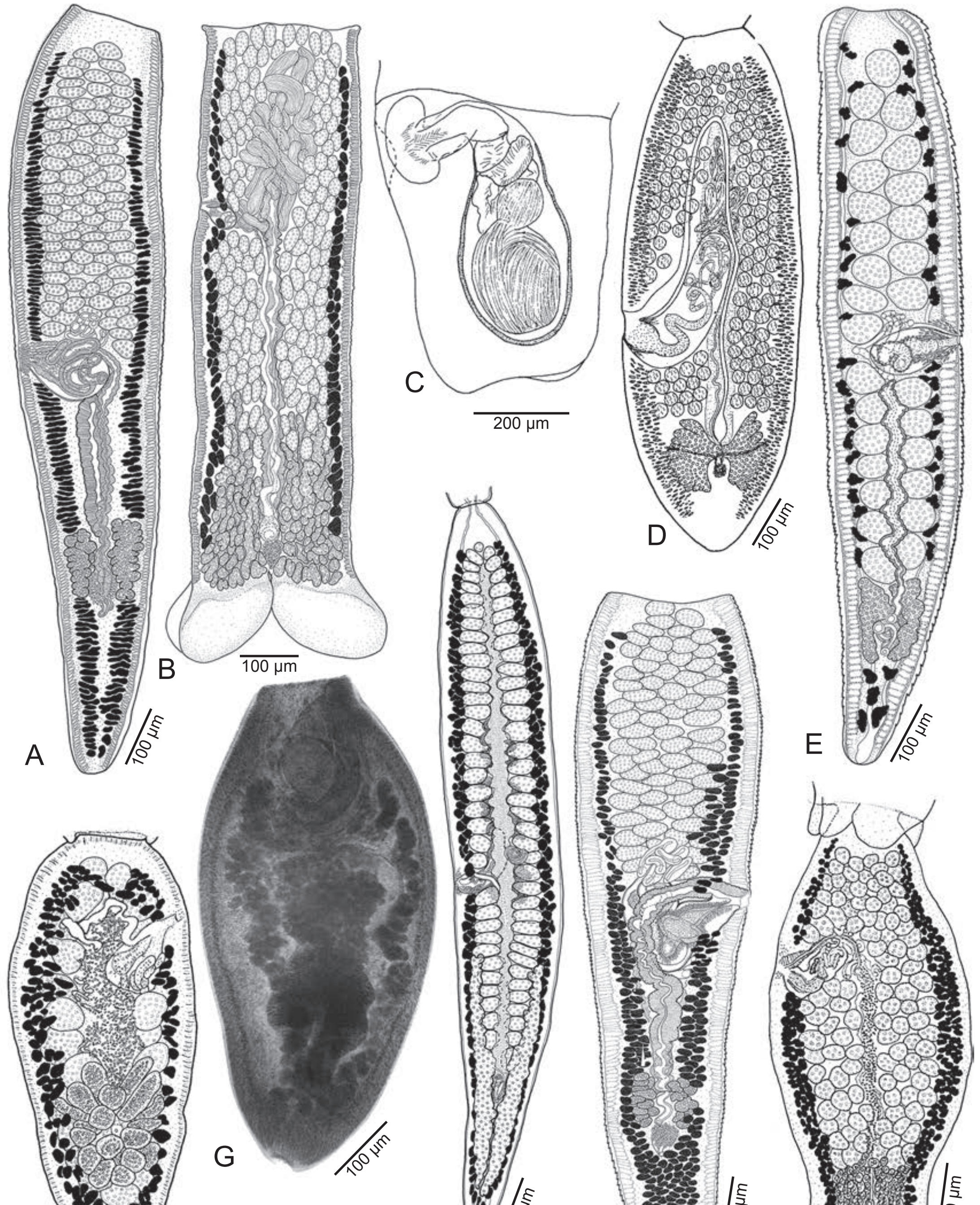
Calliobothriidae: This family parasitizes only carcharhiniform sharks of the family Triakidae Gray. Within this family, *Calliobothrium* and *Symcallio* both typically parasitize species of *Mustelus* Link (smooth-hound sharks; see Bernot et al., 2015, 2016); Butler (1987) reported a species of *Calliobothrium* from *Galeorhinus galeus* (L.) (the school shark) in Moreton Bay, Australia. However, in his survey of the fish fauna of Moreton Bay, Johnson (2010) indicated that records of *G. galeus* from that body of water are likely misidentifications. Given that the only triakid shark reported by Johnston to occur in Moreton Bay is *Mustelus walkeri* White & Last (a species not described until 2008 by White and Last), this is the likely host of Butler's 1987 record. Both described species of *Erudituncus* were reported from a species of *Hemitriakis* Herre (topesharks) (see Healy et al., 2001; Kurashima et al., 2014). The elusive *Biloculuncus* was originally described from the monotypic *Furgaleus macki* (Whitley) (whiskery shark), but Caira et al. (2007b) expanded the host associations of that genus to include *Mustelus* with the transfer of two species to the genus; as a result of PBI collections, we have expanded the host associations of this genus to also include *Hemitriakis*.

Dioecotaeniidae: Both described members of this family parasitize the cownose ray *Rhinoptera bonasus* (Mitchell) in the myliobatiform family Rhinopteridae Jordan & Evermann (see Mayes and Brooks, 1981); over the course of the PBI project work, Jensen and Bullard (2010) documented the presence of this group also in *Rhinoptera* cf. *steindachneri* (*sensu* Naylor et al. [2012a]; as *R. bonasus*).

Gastrolecithidae: To date, records of this family are restricted to two families of Lamniformes: the Lamnidae Müller & Henle (mackerel sharks) and the Cetorhinidae Gill (basking sharks). Within the former family, *Ceratobothrium* has been reported from the porbeagle shark (*Lamna nasus* [Bonnaterre]) and the shortfin mako shark (*Isurus oxyrinchus*) (see Euzet, 1959). New collections from Taiwan conducted as a result of PBI efforts included specimens of this genus from the longfin mako shark (*Isurus paucus* Guitart). A species each of *Dinobothrium* has been reported from the porbeagle shark (*Lamna nasus*) (see Euzet, 1959) and the great white shark (*Carcharodon carcharias* [L.]) (both Lamnidae), as well as from the basking shark *Cetorhinus maximus* Blainville (Cetorhinidae) (see Linton, 1922).

Rhoptrobothriidae n. fam.: Species of all three genera are restricted to myliobatiform stingrays. *Myzocephalus* and *Myzophyllobothrium* are known only from a single species of *Aetobatus* Blainville (spotted eagleray; Aetobatidae Agassiz); species of *Rhoptrobothrium* parasitize species of *Aetomylaeus* Garman (Myliobatidae Bonaparte) (see Jensen and Caira, 2006).

Serendipidae: Members of this family also exhibit extremely restricted host associations. All six described species have been reported from only two species of *Rhinoptera* (cownose rays; Rhinopteridae). Our PBI work has expanded these host associations to include *Rhinoptera peli* Bleeker from Senegal and *R.* cf. *steindachneri* (*sensu* Naylor et al. [2012a]) in the Gulf of Mexico.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With the exception of Clade 3, the host associations of most of the "tetraphyllidean" clades not assigned to families are somewhat less restricted than those of the six families. It is possible that this reflects the non-monophyly of at least some of these assemblages.

Clade 1: The host associations of this clade are by far the most puzzling among all of the "tetraphyllidean" groups. New genus 7 (*sensu* Caira et al. [2014]) parasitizes the collared carpetshark *Parascyllium collare* (Orectolobiformes) (see Caira et al., 2014). *Zyxibothrium* parasitizes species of the skate genus *Malacoraja* Stehman (see Hayden and Campbell, 1981) (Rajiformes). The single described species of *Pentaloculum* was reported from the blind electric ray *Typhlonarke aysoni* (Torpediniformes) (see Alexander, 1963). Preliminary examination of specimens of a species of the second parascyliid genus, *Cirrhoscyllium* Smith, in Taiwan yielded material of what appears to be yet another member of this clade. As these records stand, members of this group parasitize subsets of taxa belonging to three different orders that span both major clades of elasmobranchs (i.e., Selachoidea and Batoidea; see Naylor et al., 2012b). Given the relatively high support for the monophyly of this clade, these associations would be interesting to explore further. Of particular interest would be the faunas of the other four species of *Parascyllium* and two species of *Cirrhoscyllium*, the other three species of *Malacoraja*, none of which, to our knowledge has been examined for cestodes.

Clade 2: The revision of the concept of *Anthobothrium* (see Williams et al., 2004; Ruhnke and Caira, 2009), and thus also of species appropriately assigned to this genus, has done much to focus the known host associations of the members of this clade. With the exception of the somewhat puzzling report by Neifar et al. (2002) of a species from the spiny butterfly ray (*Gymnura altavela* [L.]), the genus appears to be restricted to carcharhiniform sharks, mostly of the family Carcharhinidae Jordan & Evermann. However, two species have been described from the triakid shark *Galeorhinus galeus* (see Suriano, 2002). Among carcharhinid sharks, species of *Anthobothrium* have been described from members of the genera *Carcharhinus* Blainville and *Prionace* Cantor (see Ruhnke and Caira, 2009), and *Rhizoprionodon* Whitley (see Subhapradha, 1955). New collections and examination of previously collected specimens over the course of the PBI project from a diversity of carcharhiniform sharks has revealed the presence of additional species of *Anthobothrium* in five species of *Carcharhinus* not previously known to host members of the genus, in a second species of *Rhizoprionodon* (see Jensen and Bullard, 2010), in the carcharhinid *Lamiopsis*, and in a second genus of triakid shark (i.e., *Hemitriakis*).

Clade 3: All four species in this group parasitize orectolobiform sharks. To date, species of *Carpobothrium* and the monotypic *Caulopatera* are known only from species of bamboo sharks of the genus *Chiloscyllium* (Hemiscylliidae) (see Cutmore et al., 2010; Koontz and Caira, 2016).

◄—Figure 8. Line drawings and light micrograph of proglottid anatomy of the ten independent clades considered as "tetraphyllidean" relics. **(A)** BALANOBOTHRIIDAE: *Spiniloculus fylerae* ex *Chiloscyllium punctatum* from Malaysian Borneo (modified from Desjardin and Caira [2011]). **(B)** CALLIOBOTHRIIDAE: *Calliobothrium wightmanorum* ex *Mustelus asterias* from the North Sea, UK (modified from Bernot et al. [2016]). **(C)** DIOECOTAENIIDAE: *Dioecotaenia* sp., male proglottid, ex *Rhinoptera bonasus* from the western Atlantic Ocean (modified from Caira et al. [1999]). **(D)** GASTROLECITHIDAE: *Ceratobothrium xanthocephalum* ex *Isurus oxyrinchus* from the Mediterranean Sea (modified from Euzet [1959]). **(E)** RHOPTROBOTHRIIDAE N. FAM.: *Rhoptrobothrium gambangi* ex *Aetomylaeus nichofii* from Malaysian Borneo (modified from Jensen and Caira [2006]). **(F)** SERENDIPIDAE: *Duplicibothrium paulum* ex *Rhinoptera steindachneri* from the Gulf of California (modified from Ruhnke et al. [2000]). **(G)** CLADE 1: *Zyxibothrium kamienae* ex *Malacoraja senta* from the Gulf of Maine, USA. **(H)** CLADE 2: *Anthobothrium caseyi* ex *Prionace glauca* from Massachusetts, USA (modified from Ruhnke and Caira [2009]). **(I)** CLADE 3: *Carpobothrium eleanorae* ex *Chiloscyllium hasseltii* from Malaysian Borneo (modified from Koontz and Caira [2016]). **(J)** CLADE 4: *Caulobothrium* n. sp. ex *Pastinachus ater* from Australia (modified from Healy [2006]).

However, PBI collections yielded an undescribed species of this clade in *Brachaelurus* Ogilby (Brachaeluridae Ogilby) and also one from *Orectolobus japonicus* Regan (Orectolobidae Gill).

Clade 4: The host associations of the two described genera in this clade are relatively straightforward. The monotypic *Pithophorus* was originally reported from a species of the wedgefish in the genus *Rhynchobatus* Müller & Henle (see Southwell, 1912) (Rhinidae Müller & Henle). The specimen included in our PBI project molecular phylogenetic work was collected from a second member of this host genus. New collections and examination of specimens conducted over the course of the PBI project have helped to clarify and expand the host associations of species of *Caulobothrium*. The seven species we recognize as valid all came from bat rays of the genus *Myliobatis* Cuvier (Myliobatidae Bonaparte); the known associations of *Caulobothrium* were expanded to include a diversity of species of the stingray genera *Pastinachus* Rüppell and *Urogymnus* Müller & Henle. The hosts from which material of New genus 9 (*sensu* Caira et al. [2014]) has been collected include a wide array of myliobatiform and rhinopristiform batoids. As this genus has not yet been formally established, we will refrain from providing details here except to note that new hosts of members of this genus include additional species of *Himantura* Müller & Henle, *Maculabatis* Last, Naylor & Manjaji-Matsumoto, *Pateobatis* Last, Naylor & Manjaji-Matsumoto, *Rhina* Bloch & Schneider, and *Rhynchobatus*.

The existing known number of species (including both described and undescribed taxa) for each of the six families and four clades currently assigned to the "Tetraphyllidea" relics is given in Tables 1 and 2. The total known diversity summed across all ten groups is 154 species. The estimated total global diversity for each group, based on the known diversity and host associations for each group, is also provided in Tables 1 and 2. The predicted total number across all ten groups is more than 450 species, suggesting that only 33% of the total global diversity of the "Tetraphyllidea" relics is currently known. The limited nature of the host associations of the Dioecotaeniidae and Gastrolecithidae, both of which are restricted to one or three families of myliobatiform or lamniform elasmobranchs, respectively, leads us to believe that these two groups are likely to remain the least speciose of the ten groups, at eight species each. The Calliobothriidae, Clade 2, and Clade 4 are predicted to be the most speciose of these with 72, 75, and 118 species, respectively. In the case of the Calliobothriidae, this is largely a result of their association with the relatively speciose triakid shark genus *Mustelus* and the fact that each species of *Mustelus* that has been examined for cestodes has been found to host two to three members of this family (e.g, Bernot et al., 2015, 2016). Similarly, in the case of Clade 2, the relatively high predicted number of species is largely a result of the association of species of *Anthobothrium* with members of the highly speciose carcharhinid shark genus *Carcharhinus*. Assuming that the monophyly of Clade 4 is confirmed, the relatively high predicted diversity in this group is largely a result of the fact that *Caulobothrium* and New genus 9 are both associated with different, relatively diverse, families of batoids.

GEOGRAPHIC DISTRIBUTION. The distribution of each of the ten groups of "tetraphyllidean" relics are obviously determined by those of the elasmobranch groups they parasitize. However, overall, to our knowledge, all ten groups occur between 60° N and S latitudes.

Balanobothriidae: As a consequence of their exclusive association with orectolobiform sharks, members of this family are predominantly found in the waters of the Indo-Pacific. The association of six species of *Pedibothrium* with the nurse shark genus *Ginglymostoma* Müller & Henle, extends the distribution of the Balanobothriidae to include, at a minimum, the western Atlantic Ocean and Gulf of California (see Caira and Euzet, 2001).

Calliobothriidae: PBI project collections extended the known distribution of this family to include South Africa (Bernot et al., 2015). As a consequence this family, like its triakid shark hosts, has now been reported from the coastal waters of all continents except Antarctica.

Dioecotaeniidae: This family remains known only from Venezuela (Mayes and Brooks, 1981), the western Atlantic Ocean off of Maryland (Schmidt, 1969), and the Gulf of Mexico (Jensen and Bullard, 2010).

Gastrolecithidae: Records to date of this family come from the western Atlantic seaboard, and off the coasts of Italy, Spain, and Japan (see Yamaguti, 1959). Specimens examined over the course of the PBI project extend this distribution to include the Gulf of California, Taiwan, and New Zealand. However, the highly migratory behavior and thus the cosmopolitan distributions of the members of its two lamniform host families lead us to believe the gastrolecithids are likely cosmopolitan in distribution.

Rhoptrobothriidae n. fam.: This family appears to be restricted to members of *Aetobatus* and *Aetomylaeus* that occur in the waters of the Indo-Pacific. However, our collections indicate that the two species of *Aetobatus* that do occur outside of that region (see White et al., 2010) do not host this family.

Serendipidae: Although species of *Rhinoptera* parasitized by members of this cestode group occur throughout the warmer waters of the world's oceans, the serendipids have been reported only from cownose ray species in the western Atlantic Ocean (Williams and Campbell, 1978), including the Gulf of Mexico (Jensen and Bullard, 2010) and the eastern Pacific Ocean, more specifically in the Gulf of California (Ruhnke et al., 2000), off the coast of Ecuador (Brooks and Barriga, 1995), and off the eastern coast of mainland México (Pulido-Flores and Monks, 2014). Our PBI project collections have extended the Atlantic distribution to include Belize as well as the eastern Atlantic Ocean off Senegal.

The distributions of the groups not assigned to families are as follows.

Clade 1: At present this clade is known from the waters off New Zealand (*Pentaloculum* and an additional undescribed genus from *Brochiraja* Last & McEachran, 2006), the western North Atlantic Ocean (*Zyxibothrium*), and off southeastern Australia (New genus 7 *sensu* Caira et al. [2014]). If species of *Pentaloculum* and New genus 7 are truly only associated with *Typhlonarke*, *Brochiraja*, and *Parascyllium*, their distributions are unlikely to be expanded much beyond their known distribution because *Typhlonarke* and most species of *Brochiraja* are endemic to New Zealand and *Parascyllium* and the remaining species of *Brochiraja* are endemic to southern and southeastern Australia. The three species of *Malacoraja* that remain to be examined for cestodes occur throughout the eastern and western Atlantic Ocean, and thus the Atlantic distribution of the group could be expanded further.

Clade 2: *Anthobothrium* has been reported from both sides of the northern Atlantic Ocean as well as in the Mediterranean Sea, Argentina, India, and Australia (see Williams et al., 2004; Ruhnke and Caira, 2009). Examination of material over the course of the PBI extends the known distribution to include Borneo and Taiwan. We anticipate, however that the genus will be found to occur throughout all warm and temperate seas, as do its carcharhinid shark hosts.

Clade 3: Members of this clade have been described from India, Sri Lanka, and Australia. Results of PBI work extend the distribution to include Borneo. As a consequence of their association with orectolobiform sharks of the genus *Chiloscyllium*, they are likely to be found to be restricted to waters of Indo-Pacific (e.g., Cutmore et al., 2010; Koontz and Caira, 2016). The new undescribed material from *Brachaelurus* and *Orectolobus* came from Australia and Japan, respectively, and thus is also Indo-Pacfic.

Clade 4: The species of *Myliobatis* from which the majority of species of *Caulobothrium* have been described occur in the waters on either the eastern or western (e.g., Riser, 1955) seaboards of the United States or South America (e.g., Brooks et al., 1981). The report of *C.*

tobijei (Yamaguti, 1934) Baer, 1948 from Japan by Yamaguti (1934) (as *Echeneibothrium tobijei* Yamaguti, 1934) indicates the distribution of the genus extends to Pacific waters. Indeed, PBI work also yielded specimens of this genus in waters off Australia, Borneo, Senegal, Solomon Islands, and Taiwan. Given *Pithophorus* was described from Sri Lanka by Southwell (1912) and our undescribed material of New genus 9 (*sensu* Caira et al. [2014]) comes from numerous localities throughout Australia and Borneo, we anticipate these genera will ultimately be found to occur in all warm and temperate seas that are home to their hosts.

CONCLUSIONS

The polyphyletic assemblage of taxa that remains in the Tetraphyllidea, as the "tetraphyllidean" relics, includes six relatively well defined clades that can be assigned to morphologically diagnosable families, each of which is also supported by molecular data: the Balanobothriidae (with 5 genera and 38 species), Calliobothriidae (with 4 genera and 26 species), Dioecotaeniidae (with 1 genus and 2 species), Gastrolecithidae (with 2 genera and 6 species), Rhoptrobothriidae n. fam. (newly erected here with 3 genera and 6 species), and Serendipidae (with 3 genera and 6 species). The host associations of each of these families are relatively restricted; none parasitize species in more than one order of elasmobranchs and most parasitize only a subset of families or even genera in these orders. Their distributions vary in breadth with those of their respective host groups. Based on their host associations, the Calliobothriidae are likely to include the greatest amount of undiscovered diversity because the number of potential hosts is high, and many of these have not been examined for cestodes. The situation with the remaining four clades is less clear. This is exacerbated by the fact that none of these groups include more than ten species and thus they are generally poorly known. Clade 1 (*Pentaloculum, Zyxibothrium*, and New genus 7 *sensu* Caira et al. [2014]) is relatively well supported by molecular data and scolex morphological features, but its three genera parasitize hosts belonging to different orders of elasmobranchs. Clade 2 comprises a single genus (*Anthobothrium*), the phylogenetic affinities of which are unresolved. Members of Clade 3 (*Carpobothrium* and *Caulopatera*) parasite orectolobiform sharks; although they lack scolex armature, they bear proglottids that resemble those of the Balanobothriidae, which also parasitize this order of sharks. However, close affinities between these two groups is not supported by existing molecular data. Different pairs of the three genera in Clade 4 (i.e., *Caulobothrium*, *Pithophorus*, and New genus 9 *sensu* Caira et al. [2014]) share morphological similarities and host associations, but the group overall is not very cohesive. Support for its monophyly from molecular data is weak. Given their host associations, Clade 2 (i.e., *Anthobothrium*) and *Caulobothrium* from Clade 4 are likely to include the greatest amount of undiscovered diversity. Progress in understanding the classification and phylogenetic relationships of the elasmobranch-hosted eucestodes, and in fact eucestodes overall, hinges on a more thorough understanding of these ten groups of genera. It seems likely that future work will result in the "Tetraphyllidea" being abandoned in favor of a series of smaller, monophyletic groups, at least a subset of which will likely correspond to the ten groups recognized here.

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TABLE 1. Expected global elasmobranch associations of "tetraphyllidean" relic species (in yellow), by family and clade. Number of elasmobranch species per genus given in parentheses (includes known undescribed elasmobranch species). First column: number of species parasitizing each elasmobranch taxon as of 2017 (includes known undescribed cestode species); second column: predicted total number of "tetraphyllidean" species parasitizing each elasmobranch taxon globally. Quotes indicate non-monophyletic taxa (Naylor et al., 2012b; Last et al., 2016a, b). Question marks indicate genera not yet examined for cestodes. Estimated total number of "tetraphyllidean" species parasitizing elasmobranchs globally given at bottom of each Table.

Balanobothriidae spp.	2017	ESTIM.
SELACHOIDEA		
ORECTOLOBIFORMES	**38**	**60**
Brachaeluridae	**0**	**0**
Ginglymostomatidae	**15**	**19**
Ginglymostoma (2 spp.)	6	8
Nebrius (1 sp.)	8	8
Pseudoginglymostoma (1 sp.)	1	3
Hemiscylliidae	**18**	**36**
Chiloscyllium (9 spp.)	18	36
Hemiscyllium (9 spp.)	0	0
Orectolobidae	**0**	**0**
Parascylliidae	**0**	**0**
Rhincodontidae	**0**	**0**
Stegostomatidae	**5**	**5**
Stegostoma (1 sp.)	5	5
SHARK TOTAL	**38**	**60**
BATOID TOTAL	**0**	**0**
ELASMOBRANCH TOTAL	**38**	**60**

Calliobothriidae spp.	2017	ESTIM.
SELACHOIDEA		
CARCHARHINIFORMES	**27**	**77**
Carcharhinidae	**0**	**0**
Hemigaleidae	**0**	**0**
Leptochariidae	**0**	**0**
Pentanchidae	**0**	**0**
Proscylliidae	**0**	**0**
Pseudotriakidae	**0**	**0**
"Scyliorhinidae"	**0**	**0**
Sphyrnidae	**0**	**0**
Triakidae	**27**	**77**
Furgaleus (1 sp.)	1	1
Galeorhinus (1 sp.)	0	0
Gogolia (1 sp.)	?	2
Hemitriakis (8 spp.)	3	8
Hypoglaeus (1 sp.)	?	1
Iago (5 spp.)	0	0
Mustelus (30 spp.)	23	60
Scylliogaleus (1 sp.)	?	1
Triakis (5 spp.)	0	4
SHARK TOTAL	**27**	**77**
BATOID TOTAL	**0**	**0**
ELASMOBRANCH TOTAL	**27**	**77**

Dioecotaeniidae spp.	2017	ESTIM.
BATOIDEA		
MYLIOBATIFORMES	**2**	**8**
Aetobatidae	**0**	**0**
Dasyatidae	**0**	**0**
Gymnuridae	**0**	**0**
Hexatrygonidae	**0**	**0**
Mobulidae	**0**	**0**
Myliobatidae	**0**	**0**
Plesiobatidae	**0**	**0**
Potamotrygonidae	**0**	**0**
Rhinopteridae	**2**	**8**
Rhinoptera (8 spp.)	2	8
Urolophidae	**0**	**0**
Urotrygonidae	**0**	**0**
BATOID TOTAL	**2**	**8**
SHARK TOTAL	**0**	**0**
ELASMOBRANCH TOTAL	**2**	**8**

Gastrolecithidae spp.	2017	ESTIM.
SELACHOIDEA		
LAMNIFORMES	**6**	**8**
Alopiidae	**0**	**0**
Cetorhinidae	**1**	**2**
Cetorhinus (1 sp.)	1	2
Lamnidae	**5**	**6**
Carcharodon (1 sp.)	1	2
Isurus (2 spp.)	2	2
Lamna (2 spp.)	2	2
Megachasmidae	**0**	**0**
Mitsukurinidae	**0**	**0**
Odontaspididae	**0**	**0**
Pseudocarcharhiidae	**0**	**0**
SHARK TOTAL	**6**	**8**
BATOID TOTAL	**0**	**0**
ELASMOBRANCH TOTAL	**6**	**8**

Rhoptrobothriidae spp.	2017	ESTIM.
BATOIDEA		
MYLIOBATIFORMES	**6**	**19**
Aetobatidae	**2**	**4**
Aetobatus (7 spp.)	2	4
Dasyatidae	**0**	**0**
Gymnuridae	**0**	**0**
Hexatrygonidae	**0**	**0**
Mobulidae	**0**	**0**
Myliobatidae	**4**	**15**
Aetomylaeus (9 spp.)	4	15
Myliobatis (11 spp.)	0	0
Plesiobatidae	**0**	**0**
Potamotrygonidae	**0**	**0**
Rhinopteridae	**0**	**0**
Urolophidae	**0**	**0**
Urotrygonidae	**0**	**0**
BATOID TOTAL	**6**	**19**
SHARK TOTAL	**0**	**0**
ELASMOBRANCH TOTAL	**6**	**19**

Serendipidae spp.	2017	ESTIM.
BATOIDEA		
MYLIOBATIFORMES	**9**	**24**
Aetobatidae	**0**	**0**
Dasyatidae	**0**	**0**
Gymnuridae	**0**	**0**
Hexatrygonidae	**0**	**0**
Mobulidae	**0**	**0**
Myliobatidae	**0**	**0**
Plesiobatidae	**0**	**0**
Potamotrygonidae	**0**	**0**
Rhinopteridae	**9**	**24**
Rhinoptera (8 spp.)	9	24
Urolophidae	**0**	**0**
Urotrygonidae	**0**	**0**
BATOID TOTAL	**9**	**24**
SHARK TOTAL	**0**	**0**
ELASMOBRANCH TOTAL	**9**	**24**

TABLE 2. Continued.

“Tetraphyllidean” spp.—Clade 1	2017	ESTIM.
SELACHOIDEA		
ORECTOLOBIFORMES	**2**	**8**
Brachaeluridae	**0**	**0**
Ginglymostomatidae	**0**	**0**
Hemiscylliidae	**0**	**0**
Orectolobidae	**0**	**0**
Parascylliidae	**2**	**8**
Cirrhoscyllium (3 spp.)	1	3
Parascyllium (5 spp.)	1	5
Rhincodontidae	**0**	**0**
Stegostomatidae	**0**	**0**
SHARK TOTAL	**2**	**8**

“Tetraphyllidean” spp.—Clade 1	2017	ESTIM.
BATOIDEA		
TORPEDINIFORMES	**1**	**6**
Hypnidae	**0**	**0**
Narcinidae	**0**	**0**
Narkidae	**1**	**6**
Crassinarke (1 sp.)	?	1
Electrolux (1 sp.)	?	1
Heteronarce (4 spp.)	?	1
Narke (3 spp.)	0	1
Temera (1 sp.)	?	1
Typhlonarke (1 sp.)	1	1
Torpedinidae	**0**	**0**
RAJIFORMES	**2**	**38**
Anacanthobatidae	**0**	**0**
Arhynchobatidae	**1**	**29**
Arhynchobatis (1 sp.)	?	0
Atlantoraja (3 spp.)	0	0
Bathyraja (57 spp.)	0	0
Brochiraja (9 spp.)	1	9
Insentiraja (2 spp.)	?	2
Irolita (2 spp.)	?	0
Notoraja (12 spp.)	?	12
Pavoraja (6 spp.)	?	6
Psammobatis (8 spp.)	0	0
Pseudoraja (1 sp.)	?	0
Rhinoraja (3 spp.)	?	0
Rioraja (1 sp.)	0	0
Sympterygia (4 spp.)	0	0

“Tetraphyllidean” spp.—Clade 1	2017	ESTIM.
Gurgesiellidae	**0**	**0**
Rajidae	**1**	**9**
Amblyraja (9 spp.)	0	0
Beringraja (6 spp.)	0	0
Breviraja (5 spp.)	?	0
Dactylobatus (2 spp.)	?	0
Dentiraja (11 spp.)	?	0
Dipturus (52 spp.)	0	0
Hongeo (1 sp.)	?	0
Leucoraja (13 spp.)	0	0
Malacoraja (4 spp.)	1	4
Neoraja (5 spp.)	?	5
Okamejei (12 spp.)	0	0
Orbiraja (3 spp.)	0	0
Raja (17 spp.)	0	0
Rajella (20 spp.)	0	0
Rostroraja (10 spp.)	0	0
Spiniraja (1 sp.)	0	0
BATOID TOTAL	**3**	**44**
ELASMOBRANCH TOTAL	**5**	**52**

“Tetraphyllidean” spp.—Clade 2	2017	ESTIM.
SELACHOIDEA		
CARCHARHINIFORMES	**16**	**74**
Carcharhinidae	**13**	**68**
Carcharhinus (44 spp.)	8	44
Galeocerdo (2 spp.)	0	0
Glyphis (6 spp.)	1	6
Isogomophodon (1 sp.)	?	1
Lamiopsis (2 spp.)	1	2
Loxodon (2 spp.)	0	0
Nasolamia (1 sp.)	?	0
Negaprion (2 spp.)	0	0
Prionace (1 sp.)	1	1
Rhizoprionodon (10 spp.)	2	10
Scoliodon (3 spp.)	0	3
Triaenodon (1 sp.)	0	1
Hemigaleidae	**0**	**0**
Leptochariidae	**0**	**0**

“Tetraphyllidean” spp.—Clade 2	2017	ESTIM.
Pentanchidae	**0**	**0**
Proscylliidae	**0**	**0**
Pseudotriakidae	**0**	**0**
"Scyliorhinidae"	**0**	**0**
Sphyrnidae	**0**	**0**
Triakidae	**3**	**6**
Furgaleus (1 sp.)	0	0
Galeorhinus (1 sp.)	2	2
Gogolia (1 sp.)	?	0
Hemitriakis (8 spp.)	1	4
Hypoglaeus (1 sp.)	?	0
Iago (5 spp.)	0	0
Mustelus (30 spp.)	0	0
Scylliogaleus (1 sp.)	?	0
Triakis (5 spp.)	0	0
SHARK TOTAL	**16**	**74**

“Tetraphyllidean” spp.—Clade 2	2017	ESTIM.
BATOIDEA		
MYLIOBATIFORMES	1	1
Aetobatidae	**0**	**0**
Dasyatidae	**0**	**0**
Gymnuridae	**1**	**1**
Gymnura (15 spp.)	1	1
Hexatrygonidae	**0**	**0**
Mobulidae	**0**	**0**
Myliobatidae	**0**	**0**
Plesiobatidae	**0**	**0**
Potamotrygonidae	**0**	**0**
Rhinopteridae	**0**	**0**
Urolophidae	**0**	**0**
Urotrygonidae	**0**	**0**
BATOID TOTAL	**1**	**1**
ELASMOBRANCH TOTAL	**17**	**75**

Table 2. Continued.

"Tetraphyllidean" spp.—Clade 3	2017	ESTIM.
SELACHOIDEA		
Orectolobiformes	**6**	**21**
Brachaeluridae	**1**	**2**
Brachaelurus (2 spp.)	1	2
Ginglymostomatidae	**0**	**0**
Hemiscylliidae	**4**	**9**
Chiloscyllium (9 spp.)	4	9
Hemiscyllium (9 spp.)	0	0
Orectolobidae	**1**	**10**
Eucrossorhinus (1 sp.)	0	0
Orectolobus (10 spp.)	1	10
Sutorectus (1 sp.)	0	0
Parascylliidae	**0**	**0**
Rhincodontidae	**0**	**0**
Stegostomatidae	**0**	**0**
SHARK TOTAL	**6**	**21**
BATOID TOTAL	**0**	**0**
ELASMOBRANCH TOTAL	**6**	**21**

"Tetraphyllidean" spp.—Clade 4	2017	ESTIM.
BATOIDEA		
Myliobatiformes	**24**	**94**
Aetobatidae	**0**	**0**
Dasyatidae	**17**	**66**
"*Bathytoshia*" (3 spp.)	0	0
Brevitrygon (5 spp.)	0	0
Dasyatis (5 spp.)	0	0
Fluvitrygon (3 spp.)	0	0
Fontitrygon (4 spp.)	0	0
Hemitrygon (10 spp.)	0	0
Himantura (8 spp.)	2	8
Hypanus (12 spp.)	0	0
Maculabatis (13 spp.)	2	26
Makararaja (1 sp.)	?	0
Megatrygon (1 sp.)	0	0
Neotrygon (13 spp.)	0	0
Pastinachus (6 spp.)	11	18
Pateobatis (7 spp.)	1	7
Pteroplatytrygon (1 sp.)	0	0
Taeniura (5 spp.)	0	0
Taeniurops (2 spp.)	0	0
"*Telatrygon*" (4 spp.)	0	0
Urogymnus (7 spp.)	1	7
Gymnuridae	**0**	**0**
Hexatrygonidae	**0**	**0**
Mobulidae	**0**	**0**
Myliobatidae	**7**	**28**
Aetomylaeus (9 spp.)	3	14
Myliobatis (11 spp.)	4	14
Plesiobatidae	**0**	**0**
Potamotrygonidae	**0**	**0**
Rhinopteridae	**0**	**0**
Urolophidae	**0**	**0**
Urotrygonidae	**0**	**0**
Rhinopristiformes	**3**	**18**
Glaucostegidae	**0**	**0**
Platyrhinidae	**0**	**0**
"Pristidae"	**0**	**0**
Rhinidae	**3**	**18**
Rhina (1 sp.)	1	1
Rhynchobatus (8 spp.)	2	16
Rhynchorhina (1 sp.)	?	1
"Rhinobatidae"	**0**	**0**
Trygonorrhinidae	**0**	**0**
Zanobatidae	**0**	**0**
BATOID TOTAL	**27**	**112**
SHARK TOTAL	**0**	**0**
ELASMOBRANCH TOTAL	**27**	**112**

TABLE 3. List of "tetraphyllidean" taxa. New taxa and taxonomic actions resulting from PBI project activities indicated in bold. * Host identification requiring confirmation.

VALID TAXA

- FAMILY BALANOBOTHRIIDAE PINTNER, 1928
  - *Balanobothrium* Hornell, 1912
    - *Balanobothrium tenax* Hornell, 1912 (type) ex *Stegostoma fasciatum* (as *Stegostoma tigrinum*)
    - *Balanobothrium astomum* Khambata & Bal, 1954 ex *Stegostoma fasciatum* (as *Stegostoma tigrinum*)
    - *Balanobothrium stegostomatis* Yamaguti, 1954 ex *Stegostoma fasciatum* (as *Stegostoma tigrinum*)
  - *Pachybothrium* Baer & Euzet, 1962
    - *Pachybothrium hutsoni* (Southwell, 1911) Baer & Euzet, 1962 (type) ex *Nebrius ferrugineus* (as *Ginglymostoma concolor*)
  - *Pedibothrium* Linton, 1908 (syn. *Phyllobothroides* Southwell, 1911)
    - *Pedibothrium globicephalum* Linton, 1908 (type) ex *Ginglymostoma cirratum*
    - *Pedibothrium brevispine* Linton, 1908 ex *Ginglymostoma cirratum*
    - *Pedibothrium cabrali* Caira, Tracy & Euzet, 2004 ex *Nebrius ferrugineus*
    - *Pedibothrium kerkhami* (Southwell, 1911) Southwell, 1925 ex *Chiloscyllium indicum*
    - *Pedibothrium kistnerae* Caira, Tracy & Euzet, 2004 ex *Nebrius ferrugineus*
    - *Pedibothrium lintoni* Shinde, Jadhav & Deshmukh, 1980 ex *Stegostoma fasciatum* (as *Stegostoma tigrinum*)
    - *Pedibothrium lloydae* Caira, Tracy & Euzet, 2004 ex *Nebrius ferrugineus*
    - *Pedibothrium longispine* Linton, 1908 ex *Ginglymostoma cirratum*
    - *Pedibothrium maccallumi* Caira & Pritchard, 1986 ex *Ginglymostoma cirratum*
    - *Pedibothrium manteri* Caira, 1992 ex *Ginglymostoma cirratum*
    - *Pedibothrium mounseyi* Caira, Tracy & Euzet, 2004 ex *Nebrius ferrugineus*
    - *Pedibothrium puerobesus* Caira, Tracy & Euzet, 2004 ex *Nebrius ferrugineus*
    - *Pedibothrium servattorum* Caira, 1992 ex *Ginglymostoma cirratum*
    - *Pedibothrium toliarensis* Caira & Rasolofonirina, 1998 ex *Pseudoginglymostoma brevicaudatum*
    - *Pedibothrium veravalensis* Shinde, Jadhav & Deshmukh, 1980 ex *Stegostoma fasciatum* (as *Stegostoma tigrinum*)
  - *Spiniloculus* Southwell, 1925 (syn. *Spinibiloculus* Deshmukh & Shinde, 1980)
    - *Spiniloculus mavensis* Southwell, 1925 (type) ex *Chiloscyllium* cf. *punctatum sensu* Naylor et al. (2012a) (as *Mustelus* sp.)
    - ***Spiniloculus calhouni* Desjardins & Caira, 2011** ex *Chiloscyllium punctatum*
    - ***Spiniloculus fylerae* Desjardins & Caira, 2011** ex *Chiloscyllium punctatum*
    - ***Spiniloculus paigeae* Desjardins & Caira, 2011** ex *Chiloscyllium punctatum*
    - *Spiniloculus ratnagiriensis* (Deshmukh & Shinde, 1980) **Desjardins & Caira, 2011** ex *Nebrius ferrugineus* (as *Ginglymostoma concolor*)
  - *Yorkeria* Southwell, 1927
    - *Yorkeria parva* Southwell, 1927 (type) ex *Chiloscyllium indicum*
    - *Yorkeria chiloscyllii* Shinde, Mohekar & Jadhav, 1986 ex *Chiloscyllium griseum*
    - *Yorkeria chonburiensis* Purivirojkul & Boonsoong, 2012 ex *Chiloscyllium punctatum*
    - *Yorkeria garneri* Caira, Jensen & Rajan, 2007 ex *Chiloscyllium hasseltii* (as *Chiloscyllium hasselti* [sic])
    - *Yorkeria hilli* Caira & Tracey, 2002 ex *Chiloscyllium punctatum*
    - *Yorkeria izardi* Caira, Jensen & Rajan, 2007 ex *Chiloscyllium* cf. *punctatum sensu* Naylor et al. (2012a)
    - *Yorkeria kelleyae* Caira & Tracey, 2002 ex *Chiloscyllium punctatum*
    - *Yorkeria longstaffae* Caira, Jensen & Rajan, 2007 ex *Chiloscyllium* cf. *punctatum sensu* Naylor et al. (2012a)
    - *Yorkeria pusillulus* Caira, Jensen & Rajan, 2007 ex *Chiloscyllium punctatum*
    - *Yorkeria saliputium* Caira, Jensen & Rajan, 2007 ex *Chiloscyllium punctatum*
    - *Yorkeria southwelli* Deshmukh, 1979 ex *Nebrius ferrugineus* (as *Ginglymostoma concolor*)
    - *Yorkeria teeveeyi* Caira, Jensen & Rajan, 2007 ex *Chiloscyllium indicum*
    - *Yorkeria xiamenensis* Li & Wang, 2006 ex *Chiloscyllium plagiosum*
    - *Yorkeria yubodohensis* Caira, Jensen & Rajan, 2007 ex *Chiloscyllium punctatum*
- FAMILY CALLIOBOTHRIIDAE PERRIER, 1897
  - *Biloculuncus* Nasin, Caira & Euzet, 1997
    - *Biloculuncus pritchardae* (Caira & Ruhnke, 1990) Nasin, Caira & Euzet, 1997 (type) ex *Furgaleus macki*
    - *Biloculuncus dubius* (Prudhoe, 1969) Caira, Reyda & Mega, 2007 ex *Mustelus antarcticus**
    - *Biloculuncus musteli* (Prudhoe, 1969) Caira, Reyda & Mega, 2007 ex *Mustelus antarcticus**
  - *Calliobothrium* van Beneden, 1850
    - *Calliobothrium verticillatum* (Rudolphi, 1819) van Beneden, 1850 (type) ex *Mustelus* sp.* (as "Squali Galei")
    - *Calliobothrium australis* Ostrowski de Nunez, 1973 ex *Mustelus schmitti*

***Calliobothrium cisloi* Bernot & Caira, 2017** ex *Mustelus canis*
Calliobothrium creeveyae Butler, 1987 ex *Galeorhinus galeus* (as *Galeorhinus australis*)
***Calliobothrium euzeti* Bernot, Caira & Pickering, 2015** ex *Mustelus palumbes*
Calliobothrium nodosum Yoshida, 1917 ex *Mustelus manazo* (as *Cynias manazo*)
Calliobothrium shirozame Kurashima, Shimizu, Mano, Ogawa, & Fujita, 2014 ex *Mustelus griseus*
Calliobothrium tylotocephalum Alexander, 1963 ex *Mustelus lenticulatus*
***Calliobothrium wightmanorum* Bernot & Caira, 2017** ex *Mustelus asterias*

Erudituncus Healy, Scholz & Caira, 2001
Erudituncus musteli (Yamaguti, 1952) Healy, Scholz & Caira, 2001 (type) ex *Hemitriakis japanica* (as *Mustelus manazo*)
Erudituncus xiamenensis (Wang & Yang, 2001) Kurashima, Shimizu, Mano, Ogawa & Fujita, 2014 ex *Hemitriakis japanica* (as *Mustelus griseus*)

***Symcallio* Bernot, Caira & Pickering, 2015**
***Symcallio peteri* Bernot, Caira & Pickering, 2015** (type) ex *Mustelus palumbes*
Symcallio barbarae (Ivanov & Brooks, 2002) **Bernot, Caira & Pickering, 2015** ex *Mustelus schmitti*
Symcallio eschrichti (van Beneden, 1850) **Bernot, Caira & Pickering, 2015** ex *Mustelus* sp.* (as *Mustelus vulgaris*)
Symcallio evani (Caira, 1985) **Bernot, Caira & Pickering, 2015** ex *Mustelus lunulatus* (as unidentified shark)
Symcallio hayhowi (Nasin, Caira & Euzet, 1997) **Bernot, Caira & Pickering, 2015** ex *Mustelus antarcticus*
Symcallio leuckarti (van Beneden, 1850) **Bernot, Caira & Pickering, 2015** ex *Mustelus asterias* (as *Mustelus vulgaris*) **(redescription Bernot, Caira and Pickering, 2017)**
Symcallio lintoni (Euzet, 1954) **Bernot, Caira & Pickering, 2015** ex *Mustelus mustelus* (as *Mustelus laevis*)
Symcallio lunae (Ivanov & Brooks, 2002) **Bernot, Caira & Pickering, 2015** ex *Mustelus schmitti*
Symcallio pellucidum (Riser, 1955) **Bernot, Caira & Pickering, 2015** ex *Mustelus californicus* (as *Mustellus* [sic] *californicus*)
Symcallio riseri (Nasin, Caira & Euzet, 1997) **Bernot, Caira & Pickering, 2015** ex *Mustelus henlei*
Symcallio schneiderae (Pickering & Caira, 2008) **Bernot, Caira & Pickering, 2015** ex *Mustelus lenticulatus*
Symcallio violae (Nasin, Caira & Euzet, 1997) **Bernot, Caira & Pickering, 2015** ex *Mustelus canis*

FAMILY DIOECOTAENIIDAE SCHMIDT, 1969

Dioecotaenia Schmidt, 1969
Dioecotaenia cancellata (Linton, 1890) Schmidt, 1969 (type) ex *Rhinoptera bonasus** (as *Rhinoptera quadriloba*)
Dioecotaenia campbelli Mayes & Brooks, 1981 ex *Rhinoptera bonasus*

FAMILY GASTROLECITHIDAE EUZET, 1955 (SYN. FAMILY REESIIDAE EUZET, 1959)

Ceratobothrium Monticelli, 1892
Ceratobothrium xanthocephalum Monticelli, 1892 (type) ex *Lamna nasus* (as *Lamna cornubica*)

Dinobothrium van Beneden, 1889 (syn. *Diplobothrium* van Beneden, 1889; *Gastrolecithus* Yamaguti, 1952)
Dinobothrium septaria van Beneden, 1889 (type) ex *Lamna nasus* (as *Lamna cornubica*)
Dinobothrium planum Linton, 1922 ex *Cetorhinus maximus*
Dinobothrium plicitum Linton, 1922 ex *Carcharodon carcharias*

FAMILY RHOPTROBOTHRIIDAE NEW FAMILY (THIS STUDY)

Myzocephalus Shipley & Hornell, 1906
Myzocephalus narinari Shipley & Hornell, 1906 (type) ex *Aetobatus ocellatus** (as *Aetobatis narinari*)

Myzophyllobothrium Shipley & Hornell, 1906
Myzophyllobothrium rubrum Shipley & Hornell, 1906 (type) ex *Aetobatus ocellatus** (as *Aetobatis narinari*)

Rhoptrobothrium Shipley & Hornell, 1906
Rhoptrobothrium myliobatidis Shipley & Hornell, 1906 (type) ex *Aetomylaeus maculatus* (as *Myliobatis maculata*)
Rhoptrobothrium chongi Jensen & Caira, 2006 ex *Aetomylaeus nichofii* (as *Aetomylaeus niehofii*)
Rhoptrobothrium gambangi Jensen & Caira, 2006 ex *Aetomylaeus nichofii* (as *Aetomylaeus niehofii*)
Rhoptrobothrium limae Jensen & Caira, 2006 ex *Aetomylaeus nichofii* (as *Aetomylaeus niehofii*)

FAMILY SERENDIPIDAE BROOKS & BARRIGA, 1995 (SYN. GLYPHOBOTHRIIDAE MONKS, PULIDO-FLORES & GARDNER, 2015)

Duplicibothrium Williams & Campbell, 1978
Duplicibothrium minutum Williams & Campbell, 1978 (type) ex *Rhinoptera bonasus**
Duplicibothrium cairae Ruhnke, Curran & Holbert, 2000 ex *Rhinoptera steindachneri*
Duplicibothrium paulum Ruhnke, Curran & Holbert, 2000 ex *Rhinoptera steindachneri*

Glyphobothrium Williams & Campbell, 1977
Glyphobothrium zwerneri Williams & Campbell, 1977 (type) ex *Rhinoptera bonasus**

Serendip Brooks & Barriga, 1995
Serendip deborahae Brooks & Barriga, 1995 (type) ex *Rhinoptera steindachneri*
Serendip danbrooksi Monks, Zaragoza-Tapia, Pulido-Flores & Violante-González, 2015 ex *Rhinoptera steindachneri*

CLADE 1
  New genus 7 *sensu* Caira et al. (2014)
    New genus 7 n. sp. 1 *sensu* Caira et al. (2014) ex *Parascyllium collare*
  Pentaloculum Alexander, 1963
    Pentaloculum macrocephalum Alexander, 1963 (type) ex *Typhlonarke aysoni*
  Zyxibothrium Hayden & Campbell, 1981
    Zyxibothrium kamienae Hayden & Campbell, 1981 (type) ex *Malacoraja senta* (as *Raja senta*)

CLADE 2
  Anthobothrium van Beneden, 1850
    Anthobothrium cornucopia van Beneden, 1850 (type) ex *Galeorhinus galeus* (as *Galeus canis*)
    Anthobothrium altavelae Neifar, Euzet & Ben Hassine, 2002 ex *Gymnura altavela*
    ***Anthobothrium caseyi* Ruhnke & Caira, 2009** ex *Prionace glauca*
    Anthobothrium galeorhini Suriano, 2002 ex *Galeorhinus galeus*
    Anthobothrium laciniatum Linton, 1890 ex *Carcharhinus obscurus* (as *Carcharias obscurus*)
    Anthobothrium lesteri Williams, Burt & Caira, 2004 ex *Carcharhinus melanopterus*
    ***Anthobothrium lyndoni* Ruhnke & Caira, 2009** ex *Carcharhinus plumbeus*
    Anthobothrium spinosum Subhapradha, 1955 ex *Rhizoprionodon acutus** (as *Carcharias acutus*)

CLADE 3
  Carpobothrium Shipley & Hornell, 1906
    Carpobothrium chiloscyllii Shipley & Hornell, 1906 (type) ex *Chiloscyllium indicum*
    ***Carpobothrium eleanorae* Koontz & Caira, 2016** ex *Chiloscyllium hasseltii*
    Carpobothrium megaphallum Subhapradha, 1955 ex *Chiloscyllium griseum*
  Caulopatera Cutmore, Bennett & Cribb, 2010
    Caulopatera pagei Cutmore, Bennett & Cribb, 2010 (type) ex *Chiloscyllium punctatum*

CLADE 4
  Caulobothrium Baer, 1948
    Caulobothrium longicolle (Linton, 1890) Baer, 1948 (type) ex *Myliobatis freminvillei*
    Caulobothrium myliobatidis Carvajal, 1977 ex *Myliobatis chilensis*
    Caulobothrium opisthorchis Riser, 1955 ex *Myliobatis californica* (as *Aetobatus californicus*)
    Caulobothrium ostrowskiae Brooks, Mayes & Thorson, 1981 ex *Myliobatis goodei*
    Caulobothrium tetrascaphium Riser, 1955 ex *Myliobatis californica* (as *Aetobatus californicus*)
    Caulobothrium tobijei (Yamaguti, 1934) Baer, 1948 ex *Myliobatis tobijei*
    Caulobothrium uruguayense Brooks, Mayes & Thorson, 1981 ex *Myliobatis uruguayensis*
  New genus 9 *sensu* Caira et al. (2014)
    New genus 9 n. sp. 1 *sensu* Caira et al. (2014) ex *Himantura uarnak* (as *Himantura uarnak* 3 *sensu* Naylor et al. [2012a])
  Pithophorus Southwell, 1925
    Pithophorus tetraglobus (Southwell, 1912) Southwell, 1925 (type) ex *Rhynchobatus djiddensis** (as *Rhynchobatus djeddensis*)

TAXA *INCERTAE SEDIS*

Dinobothrium keilini Sproston, 1948
Echeneibothrium javanicum Shipley & Hornell, 1906
Marsupiobothrium karbharii Deshmukh & Shinde, 1975
Marsupiobothrium rhinobati Shinde & Deshmukh, 1980
Marsupiobothrium rhynchobati Shinde & Deshmukh, 1980
Mixophyllobothrium Shinde & Chincholikar, 1980
Mixophyllobothrium okamuri Shinde & Chincholikar, 1980 (type)
Phyllobothrium dagnallium Southwell, 1927
Phyllobothrium flami Pramanik & Manna, 2009
Phyllobothrium minutum Shipley & Hornell, 1906
Pithophorus pakistanensis Zaidi & Khan, 1976
Reesium Euzet, 1955
Reesium paciferum (Sproston, 1948) Euzet, 1955 (type)
Spongiobothrium lintoni Southwell, 1912
Tiarabothrium Shipley & Hornell, 1906
Tiarabothrium javanicum Shipley & Hornell, 1906 (type)
Yorkeria indica Sanaka, Vijaya Lakshmi, & Hanumantha Rao, 1984

21

Trypanorhyncha Diesing, 1863

By

Ian Beveridge[1], Mohammed Haseli, Verónica A. Ivanov, Adriana Menoret, and
Bjoern C. Schaeffner*

TRYPANORHYNCHA AS THEY WERE KNOWN PRIOR TO THE PBI PROJECT

Diversity and Classification. The order Trypanorhyncha was established by Diesing (1863) to accommodate genera of cestodes with four eversible armed tentacles. Although its validity has never been seriously questioned, it has been described in the past as the most "chaotic" of all the cestode orders (Wardle and McLeod, 1952; pg. 287) due in part to the very large numbers of *genera inquirendae* and *species inquirendae*, and the complex synonymies for some of the more commonly encountered species, incomplete descriptions, lost or non-existent types, and incorrect interpretations of the tentacular armature (Campbell and Beveridge, 1994; pg. 51). An important treatise on the order is that of Dollfus (1942), who established a classification based on the larval stage (with or without a surrounding blastocyst), the patterns of the tentacular armature (homeoacanthous, heteroacanthous, or poeciloacanthous), and the number of bothria (i.e., 2 or 4 muscular attachment organs) (Fig. 1A–H). Subsequent treatments of the order by Wardle and McLeod (1952), Yamaguti (1959), and Schmidt (1986) have generally followed Dollfus (1942), allowing for the addition of new families and genera. Campbell and Beveridge (1994) provided a key to the genera of the order based primarily on the system of Dollfus (1942) but extending and modifying the features of the tentacular armature utilized. They abandoned Dollfus' (1942) suborder, the Atheca Diesing, 1854 (without blastocysts) and Thecaphora Diesing, 1854 (with blastocysts), and instead used four superfamilies based on the patterns of tentacular armature: Homeacanthoidea Dollfus, 1942 (hooks arranged in quincunxes), Heteracanthoidea Dollfus, 1942 (hooks arranged in ascending rows, the "typical" heteroacanths), Otobothrioidea Dollfus, 1942 ("atypical" heteroacanths with intercalary hook rows and a band of hooks on the external surface of the tentacle), and Poecilacanthoidea Dollfus, 1942 (with a longitudinal file of hooks, i.e., a "chainette" on the external surface of the tentacle) (Fig. 1A–F).

Palm (1997, 2004) by contrast argued for the use of additional characters such as the presence or absence of prebulbar organs and bothrial pits (see below) in higher-level classifications. In Palm's (2004) classification, the order was divided into five superfamilies: the Tentacularioidea Poche, 1926 characterized primarily by an homeoacanthous tentacular armature, the Gymnorhynchoidea Dollfus, 1935 characterized by a typical heteroacanthous armature, the Lacistorhynchoidea Guiart, 1927 characterized by an atypical heteroacanthous armature, the Otobothrioidea Dollfus, 1942 characterized by the possession of bothrial pits, and the Eutetrarhynchoidea Guiart, 1927 characterized by the presence of prebulbar organs and gland cells within the tentacular bulbs.

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[1] Corresponding author (ibeve@unimelb.edu.au); * Authors in alphabetical order.

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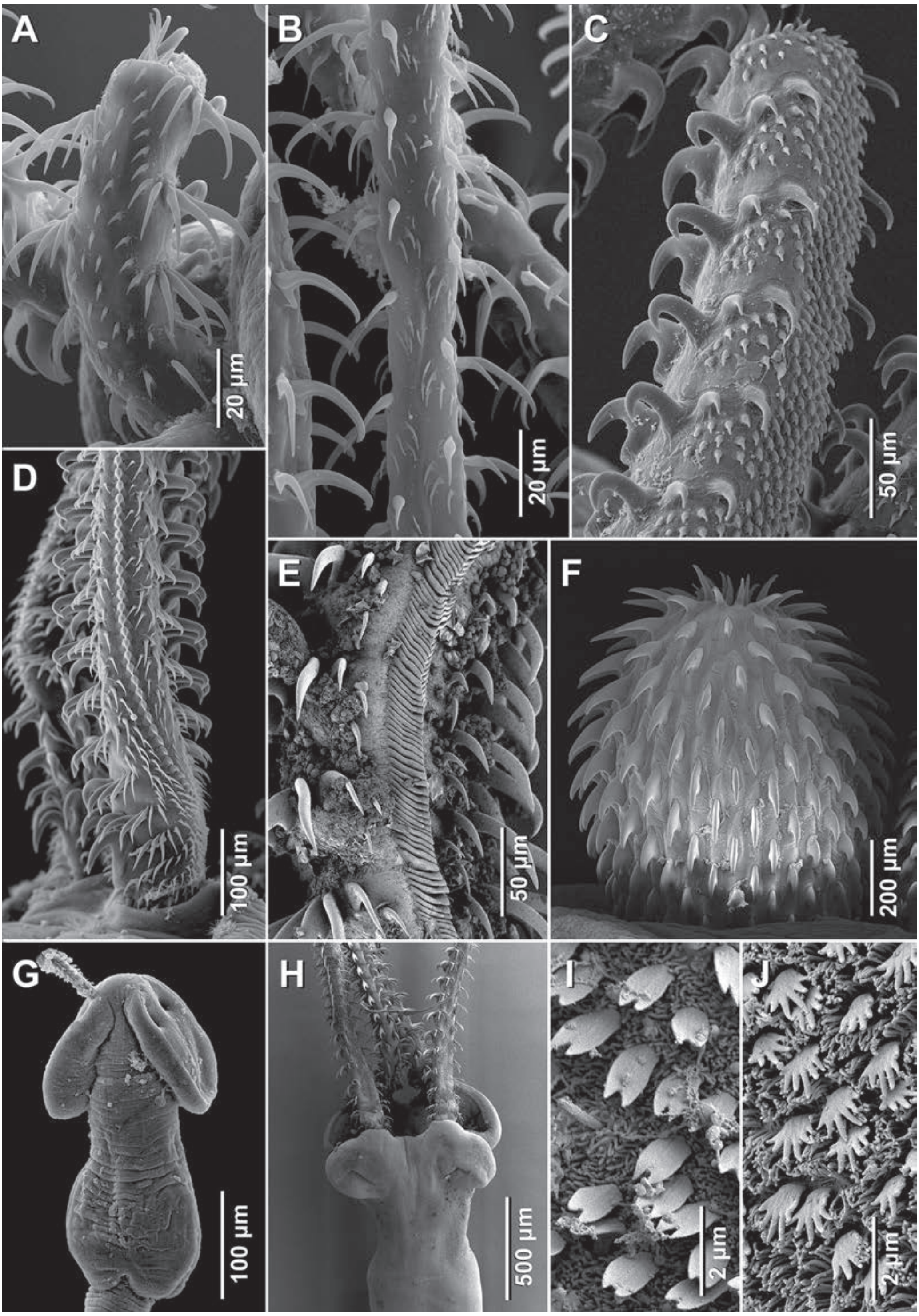
A
20 µm
B
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50 µm
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100 µm
E
50 µm
F
200 µm
G
100 µm
H
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I
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J
2 µm

Since the publication of Palm's (2004) monograph, in which 66 genera and 254 species were recognized, the number of known species and genera has continued to increase such that prior to the commencement of the PBI project, 73 genera and 280 species were considered valid.

HOST ASSOCIATIONS. Trypanorhynch cestodes are currently known from virtually all major groups of elasmobranchs globally. Adult trypanorhynch cestodes have been described from all eight orders of sharks (24 of 35 families) and all four orders of batoids (24 of 26 families) (Palm, 2004) (host classification follows Naylor et al. [2012]). Among the sharks, the carcharhiniform families Carcharhinidae Jordan & Evermann and Triakidae Gray are hosts to the widest range of trypanorhynch cestodes, while in the case of the rays, it is the family Dasyatidae Jordan (Myliobatiformes), in this case parasitized by species belonging mainly to the Eutetrarhynchoidea (Palm, 2004). This observation may reflect the level of diversity within each of the host families, but could equally reflect ease of sampling. Relatively few species of trypanorhynch cestodes have been described from deep-sea elasmobranchs (Palm, 2004), due undoubtedly to sampling difficulties. Many species of deep-sea elasmobranchs belong to the Dalatiidae Gray and Rajidae Bonaparte and this may account for the relative paucity of records for these host families.

GEOGRAPHIC DISTRIBUTION. The best-studied areas are European waters, the Gulf of Mexico, the Gulf of California, Indonesia, and the waters surrounding Australia. Most species occur in the spiral intestine of their host, with a smaller number found in the stomach, and even a few described from the nephridial (= excretory) system and gall bladder of devil rays (species of *Mobula* Rafinesque) (see Campbell and Beveridge, 2006). Host specificity is variable, ranging from species that are highly host-specific (oioxenous) to species with a broad spectrum of hosts (euryxenous). For example, Menoret and Ivanov (2012), in a review of specificity in the genus *Grillotia* Guiart, 1927, identified species such as *Grillotia australis* Beveridge & Campbell, 2001, which is known from a single host species, and *Squatina australis* Regan, and *Grillotia erinaceus* (van Beneden, 1858) Guiart, 1927 reported from 23 definitive host species, most of them belonging to the Rajiformes. Specificity is generally lower in teleost intermediate hosts than in elasmobranch definitive hosts (Palm and Caira, 2008). The specificity of larval stages in species using crustaceans as intermediate hosts has not been assessed.

MORPHOLOGY. The most comprehensive account of the morphology of trypanorhynch cestodes observable under the light microscope is that of Dollfus (1942) who summarized all information known at that time. The trypanorhynch scolex is unique among cestodes in exhibiting a rhyncheal apparatus (in adults and larvae) comprising four armed, invaginable tentacles, tentacle sheaths, and retractor muscles including muscular bulbs (Figs. 1G–H, 2A, B, D) (see Campbell and Beveridge [1994] and Palm [2004] for additional terminology); although a few taxa lack this feature altogether (e.g., *Aporhynchus* Nybelin, 1918). Also present on the scolex are two or four bothria of various shapes and sizes that may be completely

◄—FIGURE 1. Scanning electron micrographs of trypanorhynch cestodes. **(A)** Typical heteroacanthous tentacular armature of *Parachristianella damiani* ex *Myliobatis goodei* (Argentina). **(B)** Atypical heteroacanthous tentacular armature of *Grillotia carvajalregorum* ex *Squatina guggenheim* (Argentina). **(C)** Multiatypical heteroacanthous armature of *Grillotia patagonica* ex *Psammobatis rudis* (Argentina). **(D)** Poeciloacanthous tentacular armature with single-winged chainette elements of *Dasyrhynchus pacificus* ex *Cynoscion guatucupa* (Argentina). **(E)** Poeciloacanthous tentacular armature with double-winged chainette elements of *Halysiorhynchus macrocephalus* ex *Himantura leoparda* (Australia). **(F)** Homeoacanthous tentacular armature of *Hepatoxylon trichiuri* ex *Cynoscion guatucupa* (Argentina). **(G)** Scolex with two bothria of *Otobothrium carcharidis* ex *Eusphyra blochii* (Australia). **(H)** Scolex with four bothria of *Pterobothrium crassicolle* ex *Potamotrygon scobina* (Brazil). **(I)** Bifid spinitriches and acicular filitriches on distal bothrial surface of *Pseudolacistorhynchus shipleyi* ex *Nebrius ferrugineus* (Australia). **(J)** Palmate spinitriches and capilliform filitriches on mid-region of pars vaginalis of *Pseudogilquinia thomasi* ex *Sphyrna mokarran* 2 (*sensu* Naylor et al. [2012]) (Australia).

sessile or pedicellate (Figs. 1G, H, 2A, D). Proglottid anatomy is similar in many respects to that of other elasmobranch-hosted tapeworm groups (Fig. 2C) (e.g., Onchoproteocephalidea and "Tetraphyllidea"). The testes generally occupy the entire length of the proglottid. The ovary is composed of four ovarian lobes and positioned posteriorly in the proglottid. The vitellarium is follicular with vitelline follicles generally circumcortical, but forming lateral bands in some species. Genital pores are lateral or sub-lateral, usually irregularly alternating. The uterus is saccate in fully gravid proglottids. The vagina usually opens posteriorly to the cirrus-sac, and is positioned ventral, rather than dorsal, to the uterus. In addition, the Trypanorhyncha as a whole exhibit remarkable variation in the arrangement of their terminal genitalia, which may include accessory, internal, and external seminal vesicles, a hermaphroditic duct or vesicle.

Because many species have been described from larval forms, the morphology of adults of some species remains unknown, although this is gradually being addressed through redescriptions. Transmission electron microscopic studies of morphology are relatively few and have concentrated on the rhyncheal system (Beveridge and Smith, 1988; Jones, 2000), features of the scolex (Jones and Beveridge, 1998), bothrial pits (Jones, 2000), and sensory receptors (Palm et al., 2000). Additional studies have focused on spermiogenesis and the ultrastructure of spermatozoa (Świderski, 1976; Miquel and Świderski, 2006; Miquel et al., 2007; Marigo et al., 2011). Scanning electron microscopy (SEM) has been used increasingly to examine features of the tentacular armature and the tegumental microthrix patterns (Fig. 1A–J) reviewed by Palm (2004). Historically, Dollfus (1942) and other authors used the term "bothridia" for purely practical reasons. While recognizing the difference between "bothria" and "bothridia," the former lacking a delimiting membrane, histological sections are needed to establish the presence or absence of this structure. To avoid the necessity of histological sections of the scolex in the description of every species, Dollfus (1942) chose to continue to use the term "bothridium" (Jones et al., 2004). There is, however, sufficient evidence now to suggest that a delimiting membrane, the feature of the "bothridium," is lacking in the attachment organs of trypanorhynchs and that therefore they should be referred to as bothria (see Caira et al., 1999; Jones et al., 2004).

PHYLOGENETIC RELATIONSHIPS. A preliminary morphological phylogenetic analysis of the Trypanorhyncha by Beveridge et al. (1999), based on trypanorhynch genera as terminal taxa, encountered difficulties in deciding upon an appropriate outgroup taxon and therefore in determining the polarity of characters associated with the rhyncheal system of trypanorhynchs, which is not found in any other group of cestodes. Consequently, Beveridge et al. (1999) considered simple hook patterns, as exemplified by species of *Nybelinia* Poche, 1926, to be plesiomorphic in their cladistic analysis. The resulting cladogram, which yielded eight major clades, differed substantially from the then most recent classification of Campbell and Beveridge (1994) who recognized four superfamilies.

In order to overcome some of the difficulties associated with polarization of rhyncheal system characters, Palm (2004) considered the most common character to be plesiomorphic in a parsimony analysis also undertaken at the generic level but based on an expanded data set including microthrix characteristics and recoding some of the characters used by Beveridge et al. (1999). This analysis resulted in a slightly different tree topology than that recovered by Beveridge et al. (1999). Palm (2004) erected a new classification for the order based on the results of his parsimony analysis. However, discrepancies remain between the classification of Palm (2004) and the more recent molecular phylogeny (Palm et al., 2009), in particular the observation that the homeoacanthous armature pattern of tentacular hooks, the "most

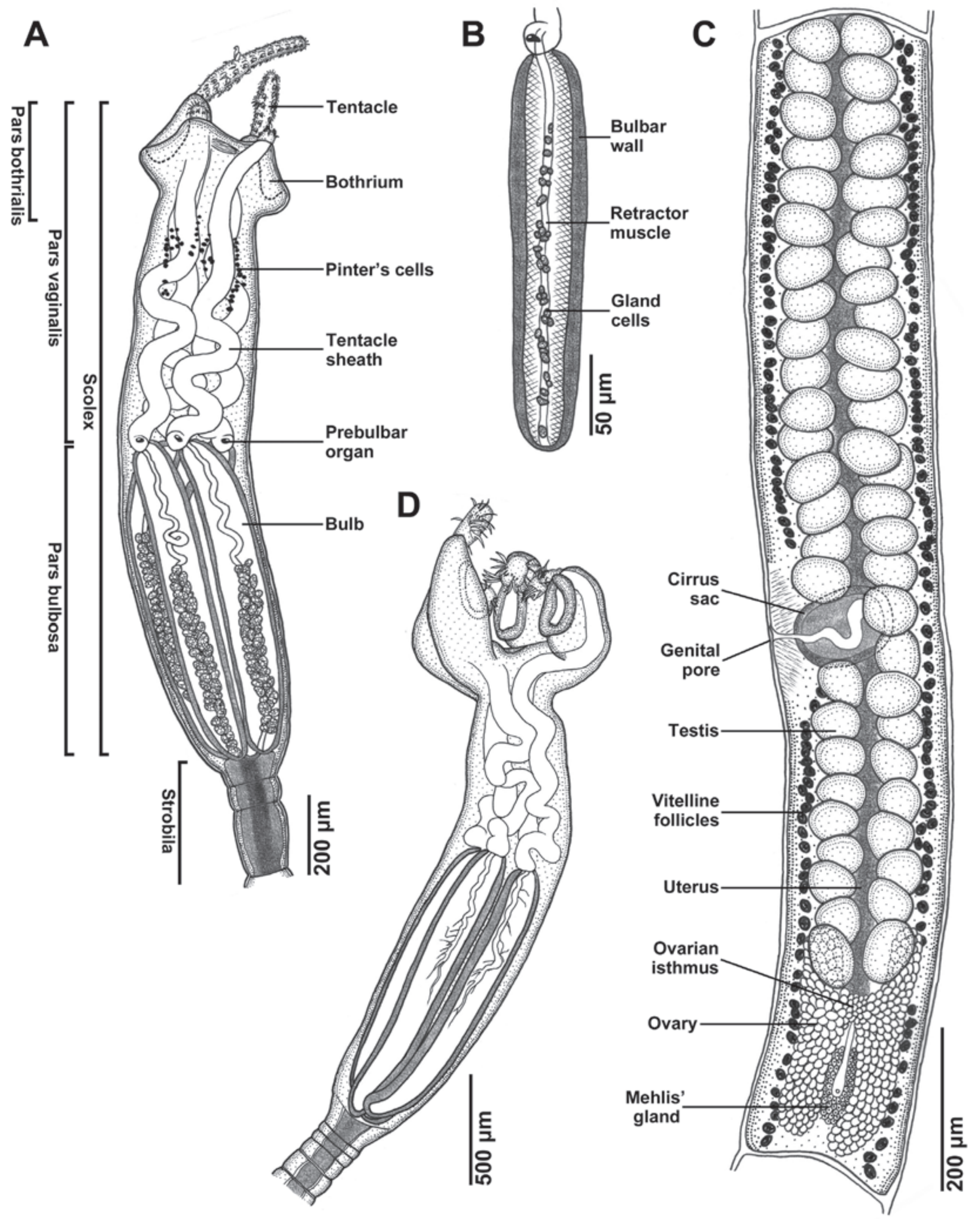

FIGURE 2. Line drawings of general body morphology of trypanorhynch cestodes. **(A)** Scolex of *Trimacracanthus* ex *Hypanus guttata* (Panama). **(B)** Bulb of *Parachristianella* ex *Hypanus longus* (Panama). **(C)** Mature proglottid of *Oncomegas wageneri* ex *Hypanus guttata* (Brazil). **(D)** Scolex of *Pterobothrium* sp. ex *Styracura schmardae* (Belize).

simple" and therefore presumed plesiomorphic feature, and used as a basis for classification since 1942 (Dollfus, 1942), was both apomorphic and homoplasious.

CURRENT STATUS OF THE TRYPANORHYNCHA

Diversity and Classification. Over the course of the PBI project, taxonomic work was undertaken in several different geographical regions contributing to the current knowledge on trypanorhynch diversity and systematics. In total, as a result of the PBI project, 31 new species were described, including eight new genera. Additionally, six new combinations and seven synonymies were proposed (see below) together with redescriptions of 24 named species (Table 1). An additional five species were described as a result of non-PBI efforts (i.e., Haseli [2013], Palm and Bray (2014), Haseli and Palm (2015), Schaeffner (2016), and Dallarés et al. [2017]) as well as the resurrection of a species of *Shirleyrhynchus* Beveridge & Campbell, 1988 by Schaeffner (2016). The results of the taxonomic efforts in the Trypanorhyncha are presented by country and/or region below.

(A) Borneo and northern Australia: A large collection of trypanorhynch cestodes from elasmobranchs from Borneo was examined. In total, trypanorhynchs from 163 elasmobranchs belonging to 43 species (17 species of sharks and 26 species of rays) were examined (Schaeffner and Beveridge, 2014). In addition, a collection of cestodes from northern Australia, also made by Janine Caira and Kirsten Jensen prior to the start of the PBI, was examined.

Two new monotypic genera, *Ancipirhynchus* Schaeffner, Gasser & Beveridge, 2011 and *Cavearhynchus* Schaeffner & Beveridge, 2012, were described from Borneo (Schaeffner et al., 2011; Schaeffner and Beveridge, 2012a), one new monotypic genus, *Pristiorhynchus* Schaeffner & Beveridge, 2013, was described from northern Australia (Schaeffner and Beveridge, 2013a), and an additional new genus, *Hispidorhynchus* Schaeffner & Beveridge, 2012, was found parasitizing elasmobranchs in both Borneo and northern Australia (Schaeffner and Beveridge, 2012b). In addition, a new species of *Oncomegas* Dollfus, 1929, *O. trimegacanthus* Schaeffner & Beveridge, 2012, was described from Borneo and three new combinations were proposed (see Schaeffner and Beveridge, 2012b), including the transfer of a species described over the course of the PBI project (*Oncomegas aetobatidis* Campbell & Beveridge, 2009, now *Hispidorhynchus aetobatidis* [Campbell & Beveridge, 2009] Schaeffner & Beveridge, 2012) (see Campbell and Beveridge, 2009; Schaeffner and Beveridge, 2012b). In addition, *Oncomegoides* Beveridge & Campbell, 2005 was synonymized with *Oncomegas*. Five new species of *Prochristianella* Dollfus, 1946 were described from Borneo and one from Australia (Schaeffner and Beveridge, 2012c, 2013b): *Proc. cairae* Schaeffner & Beveridge, 2012, *Proc. jensenae* Schaeffner & Beveridge, 2012, *Proc. kostadinovae* Schaeffner & Beveridge, 2012, *Proc. mattisi* Schaeffner & Beveridge, 2013, and *Proc. scholzi* Schaeffner & Beveridge, 2012. Numerous additional new host and locality records were established for members of *Prochristianella*, and *Proc. macracantha* Palm, 2004 was considered to be a synonym of *Proc. butlerae* Beveridge, 1990 (see Schaeffner and Beveridge, 2012c, 2013b). Schaeffner and Beveridge (2013c) described five new species of *Dollfusiella* Campbell & Beveridge, 1994, namely *D. angustiformis* Schaeffner & Beveridge, 2013, *D. hemispinosa* Schaeffner & Beveridge, 2013, *D. imparispinis* Schaeffner & Beveridge, 2013, *D. parva* Schaeffner & Beveridge, 2013, and *D. spinosa* Schaeffner & Beveridge, 2013, and Schaeffner (2014) described one new species of *Eutetrarhynchus* Pintner, 1913, *E. beveridgei* Schaeffner, 2014, all from batoids from Borneo. Three previously described species of *Parachristianella* Dollfus, 1946 were encountered among the cestodes from Borneo, as well as numerous new host and locality records for these species (Schaeffner and Beveridge, 2014). Schaeffner and Beveridge

(2013a, d) also presented the first descriptions of the adults of a number of otobothrioid species and presented descriptions and new host and locality records for various species of pterobothriids (Schaeffner and Beveridge, 2012a).

(B) Indonesia: A new rhinoptericolid genus and species, *Nataliella marcelli* Palm, 2010, was described from fishes from Indonesia (Palm, 2010).

(C) New Caledonia: New collections in New Caledonia resulted in the description of two new species of *Prochristianella*, *Proc. aciculata* Beveridge & Justine, 2010 and *Proc. omunae* Beveridge & Justine, 2010 (see Beveridge and Justine, 2010).

(D) Argentina: A survey of 1,675 teleost (85 species) and 449 elasmobranch (38 species) specimens collected off Argentina, resulted in the discovery of six new species of trypanorhynchs as well as additional new host and locality records (Menoret and Ivanov, 2009, 2012, 2013, 2014, 2015). Plerocerci of *Progrillotia dollfusi* Carvajal & Rego, 1983 were redescribed from a diverse array of teleosts, and the adults were described from the angelshark, *Squatina guggenheim* Marini. Based on this work, *Prog. dollfusi* was transferred to *Grillotia*, necessitating the creation of a new name, *G. carvajalregorum* Menoret & Ivanov, 2009, because of homonymy with *G. dollfusi* Carvajal, 1971 (see Menoret and Ivanov, 2009). Plerocerci and adults of *G. patagonica* Menoret & Ivanov, 2012 were found in five species of teleosts in the families Bovichtidae Gill, Cheilodactylidae Bonaparte, Moridae Moreau, and Nototheniidae Günther, and the arhynchobatid *Psammobatis rudis* Günther, respectively (Menoret and Ivanov, 2012). The description of *Heteronybelinia mattisi* Menoret & Ivanov, 2012 was based on plerocercoids found in two species of teleosts and adults from *Sympterygia bonapartii* Müller & Henle (Arhynchobatidae Fowler). Adults of *Dollfusiella taminii* Menoret & Ivanov, 2014 and *D. acuta* Menoret & Ivanov, 2015 were described from arhynchobatids, and adults of *Parachristianella damiani* Menoret & Ivanov, 2014 and *Mecistobothrium oblongum* Menoret & Ivanov, 2015 were described from myliobatids. An amended description was provided for *D. vooremi* (São Clemente & Gomes, 1989) Beveridge, Neifar & Euzet, 2004 (see Menoret and Ivanov, 2014, 2015).

(E) Persian Gulf and Gulf of Oman, Iran: Prior to the start of the PBI project, few records of trypanorhynch cestodes from the Persian Gulf and the Gulf of Oman existed (see Palm, 2004). Collections of cestodes from elasmobranchs of the Persian Gulf undertaken during the period of the current project have yielded numerous new host and locality records. A total of 14 trypanorhynch species was reported and seven additional taxa were identified to genus only (Haseli et al., 2010). In addition, Haseli et al. (2011) examined teleost fishes from the Persian Gulf and identified four trypanorhynch species. As a result, four new teleost host records were established. The Gulf of Oman was also reported to possess a previously unrecognized diverse fauna of trypanorhynch species. Haseli (2013) reported six trypanorhynch species from elasmobranchs from the Gulf of Oman, and described a new species, *Proc. garshaspi* Haseli, 2013.

(F) Deep-sea sharks (Portugal and Taiwan): The trypanorhynch fauna of deep-sea sharks, mainly of the order Squaliformes and the carcharhiniform family Scyliorhinidae Gill is very poorly known, but appears to be dominated by members of the families Gilquiniidae Dollfus, 1942 and Aporhynchidae Poche, 1926 (see Beveridge, 1990; Beveridge and Justine, 2006). Collections of deep-sea sharks off the Azores (Portugal) and Taiwan, made over the course of the PBI project, resulted in the description of one new genus *Nakayacestus* Caira, Kuchta & Desjardins, 2010 and four new species of aporhynchid cestodes, *Aporhynchus menezesi* Noever, Caira, Kuchta & Desjardins, 2010, *A. pickeringae* Noever, Caira, Kuchta & Desjardins, 2010, *N. takahashii* Caira, Kuchta & Desjardins, 2010 and *N. tanyderus* Caira, Kuchta & Desjardins, 2010 (see Caira et al., 2010; Noever et al., 2010).

(G) Cosmopolitan: The genus *Grillotia* was revised. Following the preliminary phylogenetic analysis of the order based on morphological data (Beveridge et al., 1999), it was evident that this speciose, cosmopolitan genus was polyphyletic. Revisions of subsets of species of *Grillotia* were undertaken prior to the start of, or outside of the PBI project (Palm, 2004; Beveridge and Campbell, 2007, 2010). Additional taxonomic work on members of the genus were completed during and as a result of the PBI project leading to the erection of one new genus (*Bathygrillotia* Beveridge & Campbell, 2012), the description of two new species (*G. gastrica* Beveridge & Campbell, 2013 and *G. patagonica*), as well as the establishment of two new synonymies (see Beveridge and Campbell, 2012, 2013; Menoret and Ivanov, 2012). Moreover, partial life-cycles were proposed for *G. carvajalregorum* and *G. patagonica*, for which plerocerci and adults could be described from the same geographic region (Menoret and Ivanov, 2009, 2012).

MORPHOLOGY. While no major morphological novelties were encountered during the PBI project, a few unexpected morphological conditions are worth some mention. A new lacistorhynchoid genus described as part of the PBI project, *Cavearhynchus*, was found to possess pit-like structures, superficially resembling bothrial pits found in the Otobothrioidea (see Schaeffner and Beveridge, 2012a). Observations on these pit-like structures using SEM indicated significant structural differences to the bothrial pits of otobothrioids (see Palm, 2004) (i.e., they were completely devoid of microtriches rather than bearing spinitriches) suggesting that the structures are not homologous between the two taxa (Schaeffner and Beveridge, 2012a).

An additional new genus described during the project, *Ancipirhynchus*, possessed tentacular armature very similar to that seen in some of the otobothriid genera, but lacked bothrial pits. Initial molecular data supported its inclusion within the Otobothrioidea (Schaeffner et al., 2011), while in the molecular phylogeny generated as part of this chapter (Fig. 3) its phylogenetic affinities within the Otobothriidae Dollfus, 1942 remain uncertain, and the superfamily is not recognized. However, it may potentially be an additional species in the family lacking the key morphological character of the clade.

Also, within the Otobothriidae, the adult stages of several species and genera were described for the first time (Schaeffner and Beveridge, 2013a, d), confirming the presence of a hermaphroditic duct and a hermaphroditic sac (rather than a cirrus-sac) in virtually every species examined. This is also characteristic for the species within the Lacistorhynchidae Guiart, 1927.

HOST ASSOCIATIONS. As trypanorhynch cestodes were already known from many groups of elasmobranchs (see above) from most regions of the world, it was not expected that the host associations would be significantly expanded by additional collections which concentrated on host families that had already been examined. However, even following PBI project efforts, no records of trypanorhynch cestodes exist for eleven shark families and two families of rays, indicating the provisional nature of the current data.

GEOGRAPHIC DISTRIBUTION. Our knowledge of the trypanorhynch fauna in several specific regions of the world was increased. Prior to the commencement of the PBI project, very few trypanorhynchs were known from the waters surrounding Borneo (Schaeffner and Beveridge, 2014). Over the course of the current project, this number was increased to 50 species, of which 28% appear to be endemic (Schaeffner et al., 2011; Schaeffner and Beveridge, 2012a–c, 2013a, c, d, 2014; Schaeffner, 2014). Several species were described or redescribed from Australia and new host and locality records were provided for several trypanorhynch taxa (Schaeffner and Beveridge, 2012c, 2013a, b, d, e). Likewise, the known trypanorhynch fauna of the Persian Gulf and the Gulf of Oman has been expanded during this project (Haseli, 2013; Haseli et al., 2010, 2011). In the case of deep-sea sharks, the new descriptions published over the course the project (Caira et al., 2010; Noever et al., 2010) have increased the number of aporhynchid cestodes from two to six species. As deep-sea sharks have been examined in detail in only a few localities worldwide (northern Europe and Tasmania), the current collections from the Azores and Taiwan (Caira et al., 2010; Noever et al., 2010) suggest that numbers of additional species remain to be discovered. It is possible that their low prevalence (see Caira and Pickering, 2013) has been a factor in the description of the limited number of species known to date. Recent discoveries of novel trypanorhynch taxa from Argentina increased the number of known species from South America as well as the host spectrum for several already known species (Menoret and Ivanov, 2012, 2013, 2014, 2015). However, the diversity of trypanorhynchs from waters surrounding the South American continent still remains largely unknown and new discoveries are likely.

PHYLOGENETIC RELATIONSHIPS. Over the course of the PBI project, two molecular phylogenies of the Trypanorhyncha have been published (Palm et al., 2009; Olson et al., 2010) based on molecular sequence data for the 18S and 28S rDNA genes. The topology of both phylogenetic trees was similar but differed significantly from the topology recovered as part of the morphological analysis of Palm (2004). In particular, the molecular studies revealed two major clades within the order that were not evident in the earlier studies based on morphological characters alone. These two clades were recognized as the suborders Trypanoselachoida and Trypanobatoida by Olson et al. (2010), the former primarily infecting sharks and the latter batoids. In addition, these molecular studies revealed that the homeoacanthous armature pattern of tentacular hooks, the "most simple" and therefore presumed to be a plesiomorphic feature in previous phylogenies (see Beveridge et al., 1999), and which had been used as a basis for classification since 1942 (Dollfus, 1942), was both apomorphic and homoplasious. The mapping of morphological characters onto the topology resulting from Bayesian inference of molecular sequence data by Olson et al. (2010) indicated that only 17 of the 45 characters used were phylogenetically informative and of these, only three (bothrial pits, origin of retractor muscle, and presence of a rhyncheal system) were not homoplasious. The analysis suggested that most of the important characters used in current classifications (metacestode type, number of bothria, prebulbar organs, uterine pores, and characters of the tentacular armature) were homoplasious.

The molecular tree presented here (Fig. 3) is a diagrammatic representation of a phylogeny, based on published large and small nuclear ribosomal RNA gene data (28S rDNA and 18S rDNA) and novel mitochondrial gene data (16S rDNA and COI) generated over the course of the PBI project. This tree is based on a Bayesian inference analysis, constructed using the program MrBayes version 3.2.1 (Ronquist et al., 2012), but is meant purely as a graphic representation to guide the narrative of this chapter, rather than as a detailed phylogenetic tree for further interpretation. For this reason no details are given for the alignment construction and phylogenetic analysis. This tree was generated based on a subset of taxa used in previous studies based on 18S and 28S rDNA sequence data (Palm et al., 2009; Olson et al., 2010). Additional details are provided by Waeschenbach and Littlewood (Chapter 22 this volume, Waeschenbach and Littlewood, 2017). To that end, as many voucher specimens as possible of those specimens used by Palm et al. (2009) and Olson et al. (2010) were examined. A small number of specimens for which there were no vouchers available for examination or for which vouchers are held in a personal collection (HP: Harry Palm) but for which there was little doubt concerning the validity of the identification, were retained. These

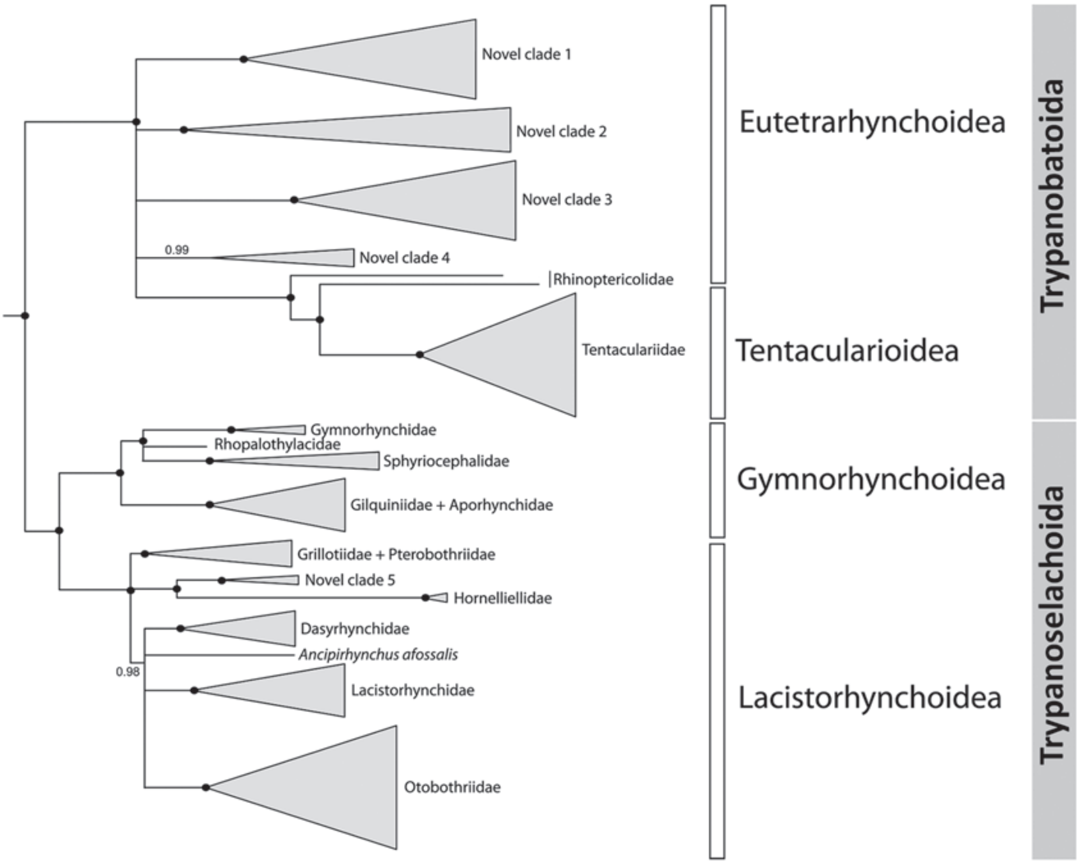

Figure 3. Schematic molecular phylogeny of the Trypanorhyncha showing the major clades with the currently recognized suborders and superfamilies. Existing and available family names are shown for each clade. The family names Grillotiidae and Dasyrhynchidae are available names that were suppressed in the classification of Palm (2004). Clades 1–5 are novel clades for which no existing family name is available or for which major redefinitions would be required before an available name could be applied.

were: *Gilquinia squali* (Fabricius, 1794) Dollfus, 1930 (HP 39: code for specimen in Palm et al. [2009]), *Hepatoxylon trichiuri* (Holten, 1802) Bosc, 1811 (HP 17), *Lacistorhynchus tenuis* (van Beneden, 1858) Pintner, 1913 (HP 39), *Poecilancistrium caryophyllum* (Diesing, 1850) Dollfus, 1929, *Pseudotobothrium dipsacum* (Linton, 1897) Dollfus, 1942, *Otobothrium cysticum* (Mayer, 1842) Dollfus, 1942 (HP 37) (although this species was not considered valid by Beveridge and Justine [2007]), *Progrillotia* sp., *Nybelinia surmenicola* Okada in Dollfus, 1929 (HP 49), and *Nybelinia* cf. *africana* Dollfus, 1960 (HP 23). A total of 47 species was included in the analysis.

The topology of the molecular phylogenetic tree presented here (Fig. 3) is similar to that of previously published trees (Palm et al., 2009; Olson et al., 2010) with respect to higher categories, supporting the division into two major clades, the Trypanobatoida and the Trypanoselachoida. Many of the more terminal nodes established by these earlier works were also supported by the present phylogeny. Olson et al. (2010) evaluated the classification of Palm (2004) against the results of their phylogenetic analysis. Here, we take the opportunity to (1) present an updated hypothesis of trypanorhynch interrelationships based on phylogenetic analysis of molecular sequence data, (2) evaluate the resulting topology against groups traditionally defined by morphological features, and (3) attempt to identify potential morphological features shared by taxa in each clade.

As indicated by Olson et al. (2010), additional investigations into morphological diagnostic features defining the Trypanoselachoida and the Trypanobatoida are needed, beyond the strong support from molecular sequence data and overall differences in host preference. Various armature types (homeoacanthous, heteroacanthous, and poeciloacathous) occur in both clades. There do appear to be differences in the terminal genitalia, particularly associated with the cirrus-sac, with modifications to the external seminal vesicle (i.e., members of the Gymnorhynchoidea) or the presence of a hermaphroditic duct (i.e., members of the Lacistorhynchoidea and the taxa they assigned to the Otobothrioidea) in the Trypanoselachoida (Olson et al., 2010). In contrast, the terminal genitalia of the Trypanobatoida lack any specialized modifications. Olson et al. (2010) identified the presence of a prebulbar organ, gland cells within the bulbs, and retractor muscles that originate at the base of the tentacular bulb as potential synapomorphies for the Trypanobatoida. However, there are exceptions: the first two features are absent in the Tentaculariidae Poche, 1926, while gland cells are absent in the Rhinoptericolidae Carvajal & Campbell, 1975. Trypanoselachoida lack a prebulbar organ and gland cells within the bulbs, and, in all but the Gymnorhynchoidea, the retractor muscles originate near the middle of the tentacular bulb (Olson et al., 2010). Palm et al. (2009) similarly identified the prebulbar organ as a synapomorphy for the Trypanobatoida, but also the presence of solid hooks (a plesiomorphy according to Olson et al. [2010]), overlooking the presence of hollow hooks in a number of genera of eutetrarhynchoids (i.e., all species of *Dollfusiella* and some species of *Prochristianella*). Thus, while a series of morphological features has been identified to diagnose the majority of taxa belonging to each suborder, a global synapomorphy characterizing each suborder has yet to be identified.

One significant difference in the current phylogeny (Fig. 3) as compared to those of Palm et al. (2009) and Olson et al. (2010) that potentially affects the existing nomenclature within the group is the status of the Otobothriidae. With respect to the superfamilies recognized by Palm (2004), the otobothrioids comprised a clade within the larger lacistorhynchoid clade in Palm et al. (2009). In contrast, the otobothrioids formed the sister group to the lacistorhynchoids in the trees resulting from the analyses of Olson et al. (2010). In the tree resulting from the phylogenetic analysis conducted as part of this chapter (Fig. 3), the otobothriids nested within the lacistorhynchoids suggesting recognition of the otobothrioid taxa at the family level (i.e., Otobothriidae) within the Lacistorhynchoidea.

In the following sections, specific comments on each clade in the tree (Fig. 3) are discussed as they pertain to potential membership and diagnostic features. No attempt has been made to establish a novel classification based on the molecular data available to date. Rather, comments are presented on the extent to which morphological characters concord with molecular associations and to suggest alternative morphological characters which might support the clades identified in the molecular studies.

I. SUBORDER TRYPANOBATOIDA

The Trypanobatoida comprise two of the currently recognized superfamilies of Palm (2004), the Eutetrarhynchoidea and the Tentacularioidea. The morphological differences between the two superfamilies are striking and each can be defined by one or more synapomorphies. The Eutetrarhynchoidea possess pre-bulbar organs and gland cells within the bulbs, while the Tentacularioidea possess ventro-submarginal genital pores and a uterus that develops laterally from the distal end of the uterine duct. Palm (2010) argued that the Rhinoptericolidae represent a transition from the Eutetrarhynchoidea to the Tentacularioidea. By contrast, in the current molecular phylogeny, the Eutetrarhynchoidea are not monophyletic, the Tentacularioidea are a highly derived group and the Rhinoptericolidae (included in the Eutetrarhynchoidea by Palm [2004]) are paraphyletic with the Tentacularioidea. In addition, there are four novel clades within the currently accepted Eutetrarhynchoidea. Only terminal clades shown in Figure 3 are considered here and no nomenclatural changes are made. These may be made in the future.

Superfamily Tentacularioidea

The Tentacularioidea are characterized by two synapomorphies: a ventro-submarginal genital pore and a uterus that develops laterally from the end of the uterine duct. The Tentacularioidea currently comprise two families, the Tentaculariidae and the Paranybeliniidae Schmidt, 1970. The latter family was placed with the Tentaculariidae by Campbell and Beveridge (1994) (in their superfamily Homeacanthoidea), but was transferred to the Otobothrioidea by Palm (1997) since it possessed bothrial pits. Subsequently, Palm (2008) re-examined specimens of *Pseudonybelinia odontacantha* Dollfus, 1966 using scanning electron microscopy and renamed the bothrial pits as "tegumental grooves" based on their microthrix pattern. Palm (2008) consequently returned the family to the Tentacularioidea. Members of this family are known only from larval stages in plankton and therefore their true status remains to be determined. A third family included by Palm (2004), the Sphyriocephalidae Pintner, 1913, is treated here as a member of the Gymnorhynchoidea (Fig. 3). The phylogenetic analysis conducted here included species of the following genera: *Heteronybelinia* Palm, 1999, *Kotorella* Euzet & Radujkovic, 1989, *Mixonybelinia* Palm, 1999, *Nybelinia*, and *Tentacularia* Bosc, 1797. Within this family, the armature may be homeoacanthous (in some species of *Nybelinia*) or heteroacanthous in the basal armature transitioning to homeoacanthous in the metabasal armature (in *Tentacularia*) (see Beveridge and Campbell, 1996). Olson et al. (2010) commented on the paraphyletic nature of some genera within this family, but again, more detailed studies based on additional loci and denser taxon representation of the family are needed to resolve this issue. The only tentaculariid genus not included was *Kotorelliella* Palm & Beveridge, 2002. While its morphology is fully consistent with the concept of the Tentaculariidae as defined by Palm (2004), its placement based on molecular sequence data remains to be confirmed.

Superfamily Eutetrarhynchoidea

The Eutetrarhynchoidea, as recognized by Palm (2004), are characterized morphologically by the presence of prebulbar organs and gland cells within the bulbs (absent only in the Rhinoptericolidae and 1 species of *Prochristianella*). Both of these features represent putative synapomorphies for the group. However, the tree resulting from the phylogenetic analysis based on molecular sequence data presented herein did not show the Eutetrarhynchoidea to form a monophyletic clade.

The "eutetrarhynchoids" included in the phylogenetic analysis (i.e., those taxa consistent with the current circumscription of the Eutetrarhynchoidea based on morphology) form four clades, each of which is novel, and the non-monophyletic Rhinoptericolidae composed of two lineages.

Novel clade 1. Included in this clade are two species of *Prochristianella* (*P. aciculata* and *P. scholzi*), *Progrillotia* Dollfus, 1946, *Oncomegas*, and *Mecistobothrium* Heinz & Dailey, 1974. All of these taxa have two bothria, divergent hooks 1(1'), and hollow hooks. However, none of these features is unique to the clade. For example, two bothria are found in selected groups across the Trypanorhyncha, members of Novel clades 2 and 5 also exhibit divergent hooks 1(1′), and hollow hooks are the predominant condition in the Trypanoselachoida. *Prochristianella* and *Mecistobothrium* are typical heteroacanths; *Oncomegas* is a typical heteroacanth with a basal macrohook, and *Progrillotia* is an atypical heteroacanth. Thus, a morphological synapomorphy to define this clade has yet to be identified. Palm (2004) erected the family name Progrillotiidae Palm, 2004 for the single atypical heteroacanth genus *Progrillotia*. This name would be available for Novel clade 1.

Novel clade 2. Included in this large clade are taxa with (i) two bothria (i.e., *Prochristianella hispida* [Linton, 1890] Campbell & Carvajal, 1975 and *Pro. clarkeae* Beveridge, 1990, both species with solid hooks; *Parachristianella baverstocki* Beveridge, 1990, *Par. indonesiensis* Palm, 2004, *Par. monomegacantha* Kruse, 1959, and *Parachristianella* sp. [HP 43]; and *Trimacracanthus* Beveridge & Campbell, 1987) and (ii) four bothria and a chainette (i.e., *Halysiorhynchus* Pintner, 1913 and *Trygonicola* Beveridge & Campbell, 1998). Most genera in this group have a typical heteroacanthous metabasal armature, with the exception of *Halysiorhynchus* and *Trygonicola* which are poeciloacanths. All species have divergent hooks 1(1′). However, as mentioned above, this feature is also shared with members of other clades (e.g., Novel clade 1). Similarly, all taxa in this clade possess solid hooks. This latter feature is treated here as a putative synapomorphic character for the clade, which, within the Trypanobatoida, it also shares with the paraphyletic Rhinoptericolidae. *Halysiorhynchus* and *Trygonicola* are included in the Mixodigmatidae Dailey & Vogelbein, 1982 (as represented by *Mixodigma* Dailey & Vogelbein, 1982) in the classification of Palm (2004), characterized by a poeciloacanthous armature. This family name is potentially available for the clade.

Novel clade 3. This clade contains species of *Dollfusiella* (6 of 28 valid species were included in the phylogenetic analysis; i.e., *D. martini* [Beveridge, 1990] Beveridge & Jones, 2000, *D. michiae* [Southwell, 1929] Beveridge, Neifar & Euzet, 2004, *D. spinulifera* [Beveridge & Jones, 2000] Beveridge, Neifar & Euzet, 2004, *D. angustiformis*, *D. hemispinosa*, and *D. ocallaghani* [Beveridge, 1990] Beveridge & Jones, 2000), *Tetrarhynchobothrium* Diesing, 1850, and *Paroncomegas* Campbell, Marques & Ivanov, 1999. Although the majority of the six species of *Dollfusiella* included in this study formed a subclade, *D. geraschmidti* (Dollfus, 1974) Beveridge & Jones, 2000 grouped with *Hispidorhynchus* in Novel clade 4 (Fig. 3). This clade is characterized by its possession of convergent hooks 1(1′) and hollow hooks; the armature is either homeoacanthous or heteroacanthous. *Dollfusiella* is most similar morphologically to *Eutetrarhynchus* (see Campbell and Beveridge, 1994). However, molecular data are lacking for the latter genus to confirm its placement among the taxa in this group. The genus *Tetrarhynchobothrium* nested within this clade and as such there is no support for the Tetrarhynchobothriidae Dollfus, 1969, a family recognized by Beveridge (2008) but not by Palm (2004). If *Eutetrarhynchus* is ultimately placed in this group, the family name Eutetrarhynchidae Guiard, 1927 would be available for this clade. To date, no morphological synapomorphy has been identified to define Novel clade 3.

Novel clade 4. This clade contains *D. geraschmidti* and the genus *Hispidorhynchus*. Species of *Hispidorhynchus* are characterized by the presence of hollow, convergent hooks, a heteroacanthous metabasal armature, and a basal macrohook. The basal macrohook is the only potential synapomorphy for the clade, although not present in *D. geraschmidti*; the feature also occurs in members of Novel clade 1 (i.e., in species of *Oncomegas*). The presence of a separate field of testes posterior to the ovary in *Hispidorhynchus* is unique within the Eutetrarhynchoidea and represents a potential synapomorphy for the clade, although absent in *D. geraschmidti*. In *Tetrarhynchobothrium* (a member of Novel clade 3) testes may extend on either side of the ovary to the posterior ovarian margin, thus their distribution is continuous rather than comprising a separate post-ovarian field. Given the unusual position of *D. geraschmidti* with respect to its congeners, recollections and new sequences are needed to confirm the affinities of this species. There is no currently available family name for this clade.

"Rhinoptericolidae". The Rhinoptericolidae (represented in the molecular phylogeny by *Rhinoptericola* and *Nataliella* Palm, 2010) appear to be paraphyletic, with a subset of taxa sister to the Tentaculariidae, and the remaining sister to that larger clade (i.e., Tentaculariidae + Rhinoptericolidae [in part]). For simplicity and because a family name exists, it is treated here as a taxonomic entity, referred to as Rhinoptericolidae in quotation marks to reflect its paraphyly. The "Rhinoptericolidae" are characterized by their possession of four bothria, solid hooks, and typical heteroacanthous (e.g., *Rhinoptericola*) or homeoacanthous (e.g., *Nataliella*) armatures, of which only the solid hooks and four bothria provide synapomorphies for the family. The lack of gland cells within the bulbs could further be used to define the family. Palm (2010) noted that the family was paraphyletic but was reluctant to erect another monotypic family. One additional genus, *Cetorhinicola* Beveridge & Campbell, 1988, remains to be added to the phylogenetic analysis to clarify "rhinoptericolid" membership and interrelationships.

In summary, each of the eutetrarhynchoid clades (the "Rhinoptericolidae" and four novel clades) can potentially (apart from Novel clade 3) be defined by a combination of morphological characters; the majority of defining characters are homoplasious and synapomorphies are few. In addition, there is clear evidence for the paraphyly of *Prochristianella*, whose members, as currently defined, exhibit taxa with either solid or hollow hooks. Fifteen genera of the Eutetrarhynchoidea were included in the study. However, an additional ten genera remain to be added. These are *Didymorhynchus* Beveridge & Campbell, 1988, *Fellicocestus* Campbell & Beveridge, 2006, *Hemionchos* Campbell & Beveridge, 2006, *Mobulocestus* Campbell & Beveridge, 2006, *Poecilorhynchus* Schaeffner & Beveridge, 2013, *Pseudochristianella* Campbell & Beveridge, 1990, *Trigonolobium* Dollfus, 1929, *Shirleyrhynchus*, *Zygorhynchus* Beveridge & Campbell, 1988, and *Mixodigma*. Of these, *Didymorhynchus* and *Zygorhynchus* have been placed along with *Tetrarhynchobothrium* in a separate family, Tetrarhynchobothriidae (see Campbell and Beveridge, 1994). Palm (2004) suppressed the Tetrarhynchobothriidae considering it to be part of the Eutetrarhynchidae, including in his definition of the latter family genera with both homeoacanthous and heteroacanthous armatures. Beveridge (2008) suggested the provisional retention of the Tetrarhynchobothriidae based on its homeoacanthous armature, but currently there are insufficient molecular data to test these conflicting hypotheses.

II. SUB-ORDER TRYPANOSELACHOIDA

Within the Trypanoselachoida, there are two well-defined clades which correspond to the Gymnorhynchoidea and Lacistorhynchoidea of Palm (2004).

Superfamily Gymnorhynchoidea

Three clades within the Gymnorhynchoidea correspond with the current families Gymnorhynchidae Dollfus, 1935, Sphyriocephalidae, and Gilquiniidae (incl. the Aporhynchidae), while *Pintneriella* Yamaguti, 1934, the sole representative of the Rhopalothylacidae Guiart, 1935 forms a polytomy with the Gymnorhynchidae and Sphyriocephalidae. All genera of the Gymnorhynchidae (i.e., *Chimaerarhynchus* Beveridge & Campbell, 1989, *Gymnorhynchus* Rudolphi, 1819, *Molicola* Dollfus, 1935, and *Plesiorhynchus*

Beveridge, 1990), Sphyriocephalidae (i.e., *Hepatoxylon* Bosc, 1811, *Heterosphyriocephalus* Palm, 2004, and *Sphyriocephalus* Pintner, 1913), and Rhopalothylacidae (i.e., *Pintneriella*) were included in the phylogenetic analysis conducted for this study. These families share the following features: a modification of the external seminal vesicle either by enlargement and investment in a glandular epithelium (in *Gymnorhynchus*), doubling (in *Pintneriella*), or the formation of an accessory seminal vesicle (in Gilquiniidae, a subset of Gymnorhynchidae such as species of *Chimaerarhynchus* and *Molicola,* and one species of Sphyriocephalidae in the genus *Sphyriocephalus*), and the deviation of the uterus towards the genital pore (in *Heterosphyriocephalus* and *Sphyriocephalus*). All taxa included in this clade also share a number of scolex features. These are the lack of bothrial pits, the presence of hollow hooks, divergent hooks 1(1′) (except in 1 species of *Plesiorhynchus, P. etmopteri* Beveridge, 1990), and heteroacanthous-typical metabasal armature with the following exceptions: a subset of Sphyriocephalidae (i.e., *Hepatoxylon* and some species of *Sphyriocephalus*) possess a homeoacanthous metabasal armature, and both the gymnorhynchid *Gymnorhynchus* and the gilquiniid *Chimaerarhynchus* are poeciloacanthous. It is worth noting that while the presence of chainettes is homoplasious in trypanorhynchs (Olson et al., 2010), the chainette of *Chimaerarhynchus* is so distinctive morphologically, with alternating pairs of hooks and single winged hooks (Beveridge and Campbell, 1989), that it is almost certainly a unique feature for this genus.

Potential characters used to diagnose each of the families are as follows: (i) the presence of two bothria and a typical heteroacanthous armature in the Rhopalothylacidae; (ii) the presence of two bothria with a median internal longitudinal septum, retractor muscles not entering the bulbs, a transverse uterus, and armature in a subset of the genera becoming homeoacanthous in the metabasal region in the Sphyriocephalidae; and (iii) the presence of poeciloacanthous (i.e., a chainette) or heteroacanthous (i.e., a longitudinal band of hooks) armature in the Gymnorhynchidae.

Genera of the Gilquiniidae included in this clade were *Aporhynchus* (currently placed in a separate family Aporhynchidae), *Chimaerarhynchu*s (currently considered to be a member of the Gymnorhynchidae) (see Beveridge and Campbell, 1989; Palm, 1994), *Deanicola* Beveridge, 1990, *Gilquinia* Guiart, 1927, *Sagittirhynchus* Beveridge & Justine, 2006, and *Vittirhynchus* Beveridge & Justine, 2006. Members of these genera are united by their possession of an accessory seminal vesicle and typical heteroacanthous armature (except for *Aporhynchus* which lacks tentacles and *Chimaerarhynchus* which is a poeciloacanth). As indicated above, it is likely that *Nakayacestus*, the only other member of the Aporhynchidae, will also be included in this clade. Its singular autapomorphy is the secondary loss of the rhyncheal system.

With respect to metacestodes, those of the Sphyriocephalidae possess plerocercoids, the Gilquiniidae and Rhopalothylacidae possess plerocerci, while some species of the Gymnorhynchidae possess merocercoids (e.g., *Molicola uncinatus* [Linton, 1924] Palm, 2004). The significance of this latter character is not clear as the metacestode stage of other species (e.g., *Gymnorhynchus isuri* Robinson, 1959) is not known.

Superfamily Lacistorhynchoidea

Virtually all taxa within this clade examined thus far possess a hermaphroditic duct, as noted by both Palm et al. (2009) and Olson et al. (2010), although serial sections may be needed to demonstrate this feature unambiguously in all species. The only taxon in which serial sections have failed to reveal such a structure is *Ancipirhynchus* (see Schaeffner et al., 2011). Within the Lacistorhynchoidea, our analysis revealed six well-supported clades to which existing or recently suppressed family names can be applied and a lineage composed only of *Ancipirhynchus afossalis* Schaeffner, Gasser & Beveridge, 2011 (Fig. 3).

Grillotiidae Dollfus, 1969 and Pterobothriidae Pintner, 1931. Although the two of 17 species of *Grillotia* included in the current phylogenetic analysis (i.e., *G. gastrica* and *G. yuniariae* Palm, 2004) were placed among species of Pterobothriidae, in the results of the phylogenetic analyses of both Palm et al. (2009) and Olson et al. (2010), the three species of *Grillotia* included therein (*G. rowei* Campbell, 1977 [now *Bathygrillotia rowei*], *G. erinaceus*, and *G. pristiophori* Beveridge & Campbell, 2001) formed a clade, albeit poorly supported, to the exclusion of species of the Pterobothriidae. The two families differ conspicuously in the number of bothria as well as the oncotaxy, and for these reasons, both family names have been retained pending further studies.

The family Grillotiidae was erected by Dollfus (1969) and formally defined by Campbell and Beveridge (1993) but was reduced to a subfamily by Palm (2004). The family was characterized by the presence of two bothria, an atypical heteroacanthous armature, one to four intercalary hook rows, and a band of hooks on the external surface of the tentacle (Campbell and Beveridge, 1993). However, within the Lacistorhynchoidea, none of these represent a synapomorphy. *Grillotia* was the only grillotiid genus included in the current study. Based on the classification of Palm (2004), three additional genera (i.e., *Pseudogrillotia* Dollfus, 1969, *Microbothriorhynchus* Yamaguti, 1952, and *Campbelliella* Palm, 2004) are also likely to be members of the Grillotiidae.

As currently recognized, the family Pterobothriidae is characterized by the presence of four pedicellate bothria (a unique feature among trypanorhynchs) and five hooks per principal row (here also considered a feature unique for the family). Two of 14 species of *Pterobothrium* Diesing, 1850 were included in the current study. Not included were species of *Pterobothrioides* Campbell & Beveridge, 1997 and *Stragulorhynchus* Beveridge & Campbell, 1988, the latter of which was originally placed in the Gymnorhynchidae but was transferred to the Pterobothriidae by Palm (2004) for reasons that were not explained.

Novel clade 5. Species of *Paragrillotia* Dollfus, 1969 (i.e., *Par. similis* [Linton, 1908] Dollfus, 1969) and *Pseudolacistorhynchus* Palm, 1995 (i.e., *Pse. heroniensis* [Sakanari, 1989] Palm, 2004) comprise Novel clade 5. These genera are characterized by an atypical heteroacanthous armature with a single intercalary hook row. The terminal hooks of the intercalary row may form a chainette (in *Pse. heroniensis*; see fig. 153 in Palm [2004]) or a tiny chainette is present but not related to the principal hook rows (in *Par. similis*; see fig. 148e in Palm [2004]). In all other genera with a chainette, the chainette is formed by the hooks of the principal row. This could therefore constitute a synapomorphy for the clade. Furthermore, members of both representatives of this clade infect orectolobiform sharks. There is no currently available name for this clade.

Hornelliellidae Yamaguti, 1954. This family contains only the genus *Hornelliella* Yamaguti, 1954, represented by *H. annandalei* Hornell, 1912 in the phylogenetic analysis. It grouped with Novel clade 5 but on a long branch. This monotypic family is currently distinguished by the following autapomorphies: presence of a hermaphroditic vesicle and a unique chainette formed by the terminal pair of hooks of each principal row. *Hornelliella annandalei* is found only in the zebra shark, *Stegostoma fasciatum* (Hermann), the sole member of the Stegostomatidae (Orectolobiformes).

Dasyrhynchidae Dollfus, 1942. This clade consists of *Dasyrhynchus* Pintner, 1928, *Protogrillotia* Palm, 2004, *Pseudogilquinia* Bilqees & Khatoon, 1980, and *Grillotiella* Palm, 2004, represented by a single species each of *Dasyrhynchus*, *Protogrillotia*, and *Grillotiella*, and by two species of *Pseudodogilquinia* in the current phylogenetic analysis. The family Dasyrhynchidae was erected by Dollfus (1942), recognized by Campbell and Beveridge (1994), but later suppressed by Palm (2004). The family is characterized by the presence of two bothria, intercalary hook rows, and a heteroacanthous atypical (i.e., longitudinal band of hooks) or poeciloacanthous (i.e., chainette) armature. A subset of these characters is also present in the Grillotiidae (i.e., possession of a band of hooks) such that a character or a unique combination of characters has yet to be identified for the Dasyrhynchidae. Pending inclusion of *Grillotiella* in a phylogenetic analysis, the two clades can be distinguished by their different types of armature: chainettes in the Dasyrhynchidae and longitudinal bands of hooks in the Grillotiidae.

Lacistorhynchidae. The genera *Lacistorhynchus* Pintner, 1913, *Callitetrarhynchus* Pintner, 1931, *Floriceps* Cuvier, 1817, and *Diesingium* Pintner, 1929 form a homogeneous group with a single, but complex, unifying feature based on hook patterns. Each principal row contains eight hooks with hooks 7(7′) and 8(8′) in the so-called "satellite" position (Dollfus, 1942), although Palm (2004) considered hooks 8(8′) to represent an intercalary row. Hooks 9(9′) form a simple median chainette. Only a single genus, not included in this study, *Bombycirhynchus* Pintner, 1930, has a similar armature and may also belong in this family.

Otobothriidae. As indicated above, based on the present phylogeny and that of Palm et al. (2009), this group of taxa would be considered as a family rather than the superfamily Otobothrioidea as used by Palm (2004). Both Palm et al. (2009) and Olson et al. (2010) defined this clade based on the unique presence of bothrial pits, although they are lacking in a subset of species (Beveridge and Justine, 2007; Schaeffner and Beveridge, 2012b). More recently, bothrial pit-like structures have been described in a pterobothriid (Schaeffner and Beveridge, 2012a). However, ultrastructural features suggest that the structures in the latter taxon are not homologous with the bothrial pits of otobothriids. Likewise, the bothrial pits of *Pseudonybelinia odontacantha* were re-examined by Palm (2008) and shown to differ ultrastructurally from the bothrial pits of the otobothrioids. Palm (2004) recognized three families within the Otobothrioidea (Otobothriidae, Pseudotobothriidae Palm, 1995, and Paranybeliniidae Schmidt, 1970) based on armature types, but Palm (2008) subsequently transferred the Paranybeliniidae to the Tentacularioidea. A subset of species of *Otobothrium* Linton, 1890 grouped with members of the Pseudotobothriidae rather than with their congeners. Pending further studies focused on the interrelationships within this family, these ranks are ignored for the present. The genera included in the present study were as follows: a single species each of *Fossobothrium* Beveridge & Campbell, 2005, *Iobothrium* Beveridge & Campbell, 2005, and *Poecilancistrium* Dollfus, 1929, seven of 12 species of *Otobothrium*, one of two species of *Parotobothrium* Palm, 2004, one of three members of *Proemotobothrium* Beveridge & Campbell, 2001, both species of *Pseudotobothrium* Dollfus, 1942, and one of two species of *Symbothriorhynchus* Yamaguti, 1952. Representatives of three genera (*Diplootobothrium* Chandler, 1942, *Poecilacanthum* Palm, 1995, and *Pristiorhynchus*) remain to be included in a phylogenetic analysis, but are herein considered putative members of the Otobothriidae.

In summary, the current molecular phylogeny, in accord with the previous molecular phylogenies of Palm et al. (2009) and Olson et al. (2010), defines a number of clades that are reconcilable with current morphologically-defined families and superfamilies. At the same time, the phylogeny identifies a number of novel clades, not all of which can readily be defined by unique morphological characters, although most can be defined by a combination of non-unique features. However, when comparing molecular and morphological evidence in this instance, it needs to be noted that the molecular data set represents only about one-third of known taxa, and that a number of taxa exhibiting additional unique morphological forms are not represented in the current dataset. Caution needs to be observed therefore when applying presumed diagnostic features to clades that may in fact be inadequately sampled.

CONCLUSIONS

The PBI project has substantially increased the numbers of species and genera recognized within the order, with eight new genera and 31 new species described over the course of the project. Six additional species have been added by workers outside of PBI project personnel. The order therefore currently includes 81 genera and 315 species (Table 1). In addition, the publications resulting from the PBI also include numerous redescriptions of poorly known species and new taxonomic combinations. Of considerable significance has been the expanded geographical distributions and host associations of numerous cestode species, particularly through the first intensive collection efforts, prior to or as part of the PBI project, off Borneo, Argentina, and from the Persian Gulf. However, patterns to date also point towards remaining gaps in our knowledge of this order. Undoubtedly new genera and significant numbers of new species remain to be described, with only a small proportion of known elasmobranch species having been examined for trypanorhynchs. This is particularly the case for deep-sea sharks in which an apparently low prevalence of cestode infections is making collecting even more difficult. A stable classification of the order based on the recognition of monophyletic groups has yet to be achieved. Athough the order was divided into two monophyletic suborders during the current PBI project, and several previously recognized families were shown to be monophyletic, particularly within the Trypanoselachoida, a significant number of non-monophyletic families remain which require further analysis or investigation. A number of the clades identified in the molecular phylogeny presented here lack diagnostic morphological features and it appears that finding such features will be a major challenge in the future. However, the basic foundations for a phylogenetic classification have now been laid and the immediate challenges for future work have been identified.

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TABLE 1. Valid trypanorhynch taxa listed below are arranged by superfamily based on the classification of Palm (2004). New taxa and taxonomic actions resulting from PBI project activities indicated in bold. * Replacement name.

VALID TAXA

- EUTETRARHYNCHOIDEA GUIART, 1927
  - *Cetorhinicola* Beveridge & Campbell, 1988
    - *Cetorhinicola acanthocapax* Beveridge & Campbell, 1988 (type)
  - *Didymorhynchus* Beveridge & Campbell, 1988
    - *Didymorhynchus southwelli* Beveridge & Campbell, 1988 (type)
  - *Dollfusiella* Campbell & Beveridge, 1994
    - *Dollfusiella australis* (Prudhoe, 1969) Campbell & Beveridge, 1994 (type)
    - *Dollfusiella aculeata* Beveridge, Neifar & Euzet, 2004
    - ***Dollfusiella acuta* Menoret & Ivanov, 2015**
    - *Dollfusiella aetobati* (Beveridge, 1990) Beveridge, Neifar & Euzet, 2004
    - ***Dollfusiella angustiformis* Schaeffner & Beveridge, 2013**
    - *Dollfusiella bareldsi* (Beveridge, 1990) Beveridge, Neifar & Euzet, 2004
    - *Dollfusiella carayoni* (Dollfus, 1942) Campbell & Beveridge, 1994
    - *Dollfusiella cortezensis* (Friggens & Duszyinski, 2005) **Schaeffner, 2014**
    - *Dollfusiella elongata* Beveridge, Neifar & Euzet, 2004
    - *Dollfusiella geraschmidti* (Dollfus, 1974) Beveridge & Jones, 2000
    - ***Dollfusiella hemispinosa* Schaeffner & Beveridge, 2013**
    - ***Dollfusiella imparispinis* Schaeffner & Beveridge, 2013**
    - *Dollfusiella lineata* (Linton, 1908) Beveridge, Neifar & Euzet, 2004
    - *Dollfusiella litocephala* (Heinz & Dailey, 1974) Beveridge, Neifar & Euzet, 2004
    - *Dollfusiella macrotrachela* (Heinz & Dailey, 1974) Beveridge, Neifar & Euzet, 2004
    - *Dollfusiella martini* (Beveridge, 1990) Beveridge & Jones, 2000
    - *Dollfusiella michiae* (Southwell, 1929) Beveridge, Neifar & Euzet, 2004
    - *Dollfusiella micracantha* (Carvajal, Campbell & Cornford, 1976) Beveridge & Jones, 2000
    - *Dollfusiella musteli* (Carvajal, 1974) Beveridge, Neifar & Euzet, 2004
    - *Dollfusiella ocallaghani* (Beveridge, 1990) Beveridge & Jones, 2000
    - *Dollfusiella owensi* (Beveridge, 1990) Beveridge & Jones, 2000
    - ***Dollfusiella parva* Schaeffner & Beveridge, 2013**
    - *Dollfusiella qeshmiensis* Haseli & Palm, 2015
    - *Dollfusiella schmidti* (Heinz & Dailey, 1974) Beveridge, Neifar & Euzet, 2004
    - *Dollfusiella spinifer* (Dollfus, 1969) Beveridge & Jones, 2000
    - ***Dollfusiella spinosa* Schaeffner & Beveridge, 2013**
    - *Dollfusiella spinulifera* (Beveridge & Jones, 2000) Beveridge, Neifar & Euzet, 2004
    - ***Dollfusiella taminii* Menoret & Ivanov, 2014**
    - *Dollfusiella tenuispinis* (Linton, 1890) Beveridge, Neifar & Euzet, 2004
    - *Dollfusiella vooremi* (São Clemente & Gomes, 1989) Beveridge, Neifar & Euzet, 2004 **(redescription: Menoret and Ivanov [2014])**
  - *Eutetrarhynchus* Pintner, 1913
    - *Eutetrarhynchus ruficollis* (Eysenhardt, 1829) Pintner, 1913 (type)
    - ***Eutetrarhynchus beveridgei* Schaeffner, 2014**
    - *Eutetrarhynchus leucomelanus* (Shipley & Hornell, 1906) Pintner, 1913
    - *Eutetrarhynchus platycephali* Palm, 2004
  - *Fellicocestus* Campbell & Beveridge, 2006
    - *Fellicocestus mobulae* Campbell & Beveridge, 2006 (type)
  - *Halysiorhynchus* Pintner, 1913
    - *Halysiorhynchus macrocephalus* (Shipley & Hornell, 1906) Pintner, 1913 (type)
  - *Hemionchos* Campbell & Beveridge, 2006
    - *Hemionchos striatus* Campbell & Beveridge, 2006 (type)
    - *Hemionchos maior* Campbell & Beveridge, 2006
    - *Hemionchos mobulae* Campbell & Beveridge, 2006
  - ***Hispidorhynchus* Schaeffner & Beveridge, 2012**
    - *Hispidorhynchus australiensis* (Toth, Campbell & Schmidt, 1992) **Schaeffner & Beveridge, 2012** (type) **(redescription: Campbell and Beveridge [2009])**

***Hispidorhynchus aetobatidis* (Campbell & Beveridge, 2009) Schaeffner & Beveridge, 2012**
Hispidorhynchus paulinae (Toth, Campbell & Schmidt, 1992) **Schaeffner & Beveridge, 2012**
Mecistobothrium Heinz & Dailey, 1974
Mecistobothrium myliobati Heinz & Dailey, 1974 (type)
Mecistobothrium brevispine (Linton, 1897) Campbell & Carvajal, 1975
Mecistobothrium johnstonei (Southwell, 1929) Beveridge & Campbell, 1998
***Mecistobothrium oblongum* Menoret & Ivanov, 2015**
Mecistobothrium pauciortesticulatum Palm, 2004
Mecistobothrium penaeus (Feigenbaum, 1975) Palm, 2004
Mixodigma Dailey & Vogelbein, 1982
Mixodigma leptaleum Dailey & Vogelbein, 1982 (type)
Mobulocestus Campbell & Beveridge, 2006
Mobulocestus nephritidis Campbell & Beveridge, 2006 (type)
Mobulocestus lepidoscolex Campbell & Beveridge, 2006
Mobulocestus mollis Campbell & Beveridge, 2006
***Nataliella* Palm, 2010**
***Nataliella marcelli* Palm, 2010** (type)
Oncomegas Dollfus, 1929 **(new synonymy: Schaeffner and Beveridge [2012b])**
Oncomegas wageneri (Linton, 1890) Dollfus, 1929 (type)
Oncomegas celatus (Beveridge & Campbell, 2005) Schaeffner & Beveridge, 2012
Oncomegas javensis Palm, 2004
***Oncomegas trimegacanthus* Schaeffner & Beveridge, 2012**
Parachristianella Dollfus, 1946
Parachristianella trygonis Dollfus, 1946 (type)
Parachristianella baverstocki Beveridge, 1990
Parachristianella carribensis (Kovaks & Schmidt, 1980) Beveridge, 1990
***Parachristianella damiani* Menoret & Ivanov, 2014**
Parachristianella dimegacantha Kruse, 1959
Parachristianella duadecacantha Palm, 2004
Parachristianella heteromegacantha Feigenbaum, 1975
Parachristianella indonesiensis Palm, 2004
Parachristianella monomegacantha Kruse, 1959
Parachristianella parva Campbell & Beveridge, 2007
Paroncomegas Campbell, Marques & Ivanov, 1999
Paroncomegas araya (Woodland, 1934) Campbell, Marques & Ivanov, 1999 (type)
Paroncomegas baeri (Lopez-Neyra & Diaz-Ungria, 1958) Campbell, Marques & Ivanov, 1999
Paroncomegas myliobatis Palm, 2004
***Poecilorhynchus* Schaeffner & Beveridge, 2013**
***Poecilorhynchus perplexus* Schaeffner & Beveridge, 2013** (type)
Prochristianella Dollfus, 1946
Prochristianella papillifer (Poyarkoff, 1909) Dollfus, 1957 (type)
***Prochristianella aciculata* Beveridge & Justine, 2010**
Prochristianella butlerae Beveridge, 1990 **(new synonymy: Schaeffner and Beveridge [2012c])**
***Prochristianella cairae* Schaeffner & Beveridge, 2012**
Prochristianella clarkeae Beveridge, 1990
Prochristianella fragilis Heinz & Dailey, 1974
Prochristianella garshaspi Haseli, 2013
Prochristianella glabra (Dollfus, 1969) Palm, 2004
Prochristianella heteracantha Dailey & Carvajal, 1976
Prochristianella hispida (Linton, 1890) Campbell & Carvajal, 1975
***Prochristianella jensenae* Schaeffner & Beveridge, 2012**
***Prochristianella kostadinovae* Schaeffner & Beveridge, 2012**
***Prochristianella mattisi* Schaeffner & Beveridge, 2013**
Prochristianella minima Heinz & Dailey, 1974
Prochristianella mooreae Beveridge, 1990
Prochristianella multidum Friggens & Duszynski, 2005
Prochristianella odonoghuei Beveridge, 1990
***Prochristianella omunae* Beveridge & Justine, 2010**

***Prochristianella scholzi* Schaeffner & Beveridge, 2012**
Prochristianella thalassia (Kovaks & Schmidt, 1980) Beveridge, 1990
Prochristianella tumidula (Linton, 1890) Campbell & Carvajal, 1975
Progrillotia Dollfus, 1946
Progrillotia pastinacae Dollfus, 1946 (type)
Progrillotia dasyatidis Beveridge, Neifar & Euzet, 2004
Progrillotia louiseuzeti Dollfus, 1969
Pseudochristianella Campbell & Beveridge, 1990
Pseudochristianella southwelli Campbell & Beveridge, 1990 (type)
Pseudochristianella elegantissima Campbell & Beveridge, 2006
Pseudochristianella nudiscula Campbell & Beveridge, 2006
Rhinoptericola Carvajal & Campbell, 1975
Rhinoptericola megacantha Carvajal & Campbell, 1975 (type)
Shirleyrhynchus Beveridge & Campbell, 1988
Shirleyrhynchus butlerae Beveridge & Campbell, 1988 (type)
Shirleyrhynchus aetobatidis (Shipley & Hornell, 1906) Beveridge & Campbell, 1998
Shirleyrhynchus panamensis Schaeffner, 2016
Tetrarhynchobothrium Diesing, 1854
Tetrarhynchobothrium tenuicolle Diesing, 1854 (type)
Tetrarhynchobothrium australe Beveridge & Campbell, 1988
Tetrarhynchobothrium rossii (Southwell, 1912) Beveridge & Campbell, 1988
Tetrarhynchobothrium striatum Wagener, 1854
Tetrarhynchobothrium unionifactor (Shipley & Hornell, 1904) Beveridge & Campbell, 1988
Trigonolobium Dollfus, 1929
Trigonolobium spinuliferum (Southwell, 1911) Dollfus, 1929 (type)
Trigonolobium laciniatum (Yoshida, 1917) Dollfus, 1929
Trimacracanthus Beveridge & Campbell, 1987
Trimacracanthus aetobatidis (Robinson, 1959) Beveridge & Campbell, 1987 (type)
Trimacracanthus binuncus (Linton, 1908) Beveridge & Campbell, 1987
Trygonicola Beveridge & Campbell, 1998
Trygonicola macropora (Shipley & Hornell, 1906) Beveridge & Campbell, 1998 (type)
Zygorhynchus Beveridge & Campbell, 1988
Zygorhynchus robertsoni Beveridge & Campbell, 1988 (type)
Zygorhynchus borneensis Beveridge, 2008
Zygorhynchus elongatus Beveridge & Campbell, 1988
Zygorhynchus ginglymostomatis Palm, 2004

GYMNORHYNCHOIDEA DOLLFUS, 1935
Aporhynchus Nybelin, 1918
Aporhynchus norvegicus (Olsson, 1868) Nybelin, 1918 (type)
***Aporhynchus menezesi* Noever, Caira, Kuchta & Desjardins, 2010**
***Aporhynchus pickeringae* Noever, Caira, Kuchta & Desjardins, 2010**
Aporhynchus tasmaniensis Beveridge, 1990
Chimaerarhynchus Beveridge & Campbell, 1989
Chimaerarhynchus rougetae Beveridge & Campbell, 1989 (type)
Deanicola Beveridge, 1990
Deanicola protentus Beveridge, 1990 (type)
Deanicola minor Beveridge, 1990
Gilquinia Guiart, 1927
Gilquinia squali (Fabricius, 1794) Dollfus, 1930 (type)
Gilquinia minor Beveridge & Justine, 2006
Gilquinia robertsoni Beveridge, 1990
Gilquinia stevensi Beveridge, 1990
Gymnorhynchus Rudolphi, 1819
Gymnorhynchus gigas (Cuvier, 1817) Rudolphi, 1819 (type)
Gymnorhynchus isuri Robinson, 1959
Hepatoxylon Bosc, 1811
Hepatoxylon trichiuri (Holten, 1802) Bosc, 1811 (type)
Hepatoxylon megacephalum (Rudolphi, 1819) Dollfus, 1942

- *Heterosphyriocephalus* Palm, 2004
  - *Heterosphyriocephalus oheulumiae* Palm, 2004 (type)
  - *Heterosphyriocephalus encarnae* Dallarés, Carrassón & Schaeffner, 2017
- *Molicola* Dollfus, 1935
  - *Molicola horridus* (Goodsir, 1841) Dollfus, 1935 (type)
  - *Molicola uncinatus* (Linton, 1924) Palm, 2004
  - *Molicola walteri* Palm, 2004
- ***Nakayacestus* Caira, Kuchta & Desjardins, 2010**
  - ***Nakayacestus takahashii* Caira, Kuchta & Desjardins, 2010** (type)
  - ***Nakayacestus tanyderus* Caira, Kuchta & Desjardins, 2010**
- *Pintneriella* Yamaguti, 1934
  - *Pintneriella musculicola* Yamaguti, 1934 (type)
  - *Pintneriella gymnorhynchoides* (Guiart, 1935) Beveridge & Campbell, 2003
  - *Pintneriella maccallumi* (MacCallum, 1921) Palm, 2004
  - *Pintneriella pagelli* Palm, 2004
- *Plesiorhynchus* Beveridge, 1990
  - *Plesiorhynchus etmopteri* Beveridge, 1990 (type)
  - *Plesiorhynchus brayi* Palm, 2004
  - *Plesiorhynchus campbelli* Beveridge, 1990
- *Sagittirhynchus* Beveridge & Justine, 2006
  - *Sagittirhynchus aculeatus* Beveridge & Justine, 2006 (type)
- *Sphyriocephalus* Pintner, 1913
  - *Sphyriocephalus viridis* (Wagener, 1854) Pintner, 1913 (type)
  - *Sphyriocephalus dollfusi* Bussieras & Aldrin, 1968
  - *Sphyriocephalus pelorosoma* Heinz & Dailey, 1974
  - *Sphyriocephalus tergestinus* Pintner, 1913
- *Vittirhynchus* Beveridge & Justine, 2006
  - *Vittirhynchus squali* Beveridge & Justine, 2006 (type)

LACISTORHYNCHOIDEA GUIART, 1927

- ***Ancipirhynchus* Schaeffner, Gasser & Beveridge, 2011**
  - ***Ancipirhynchus afossalis* Schaeffner, Gasser & Beveridge, 2011** (type)
- ***Bathygrillotia* Beveridge & Campbell, 2012**
  - *Bathygrillotia rowei* (Campbell, 1977) **Beveridge & Campbell, 2012** (type)
  - *Bathygrillotia kovalevae* (Palm, 1995) **Beveridge & Campbell, 2012**
- *Bombycirhynchus* Pintner, 1931
  - *Bombycirhynchus sphyraenaicum* (Pintner, 1930) Pintner, 1931 (type)
- *Callitetrarhynchus* Pintner, 1931
  - *Callitetrarhynchus gracilis* (Rudolphi, 1819) Pintner, 1931 (type)
  - *Callitetrarhynchus speciosus* (Linton, 1897) Carvajal & Rego, 1985
- *Campbelliella* Palm, 2004
  - *Campbelliella heteropoeciloacantha* Palm, 2004 (type)
- ***Cavearhynchus* Schaeffner & Beveridge, 2012**
  - ***Cavearhynchus foveatus* Schaeffner & Beveridge, 2012** (type)
- *Dasyrhynchus* Pintner, 1928
  - *Dasyrhynchus variouncinatus* (Pintner, 1913) Pintner, 1929 (type)
  - *Dasyrhynchus basipunctatus* (Carvajal, Campbell & Cornford, 1976) Palm & Bray, 2014
  - *Dasyrhynchus giganteus* (Diesing, 1850) Pintner, 1928
  - *Dasyrhynchus pacificus* Robinson, 1959
  - *Dasyrhynchus talismani* Dollfus, 1935
- *Diesingium* Pintner, 1929
  - *Diesingium lomentaceum* (Diesing, 1850) Pintner, 1929 (type)
  - *Diesingium antarcticum* (Campbell & Beveridge, 1988) Beveridge & Campbell, 1994
  - *Diesingium woodsholei* (Dollfus, 1969) Beveridge & Campbell, 1994
- *Diplootobothrium* Chandler, 1942
  - *Diplootobothrium springeri* Chandler, 1942 (type)
- *Floriceps* Cuvier, 1817
  - *Floriceps saccatus* Cuvier, 1817 (type)
  - *Floriceps minacanthus* Campbell & Beveridge, 1987

Fossobothrium Beveridge & Campbell, 2005
Fossobothrium perplexum Beveridge & Campbell, 2005 (type)
Grillotia Guiart, 1927
Subgenus *Grillotia* Guiart, 1927
Grillotia (*Grillotia*) *erinaceus* (van Beneden, 1858) Guiart, 1927 (type)
Grillotia (*Grillotia*) *borealis* Keeney & Campbell, 2001
Grillotia (*Grillotia*) *brayi* Beveridge & Campbell, 2007
Grillotia (*Grillotia*) *dollfusi* Carvajal, 1971
Grillotia (*Grillotia*) *musculara* (Hart, 1936) Dollfus, 1942
Grillotia (_Grillotia_) _patagonica_ Menoret & Ivanov, 2012
Subgenus *Christianella* Guiart, 1931
Grillotia (*Christianella*) *minuta* (van Beneden, 1850) Campbell & Beveridge 1994 (type)
Grillotia (*Christianella*) *australis* Beveridge & Campbell, 2001
Grillotia (_Christianella_) _carvajalregorum_ Menoret & Ivanov, 2009* (redescription and new synonymy: Menoret and Ivanov [2009])
Grillotia (*Christianella*) *longispinis* (Linton, 1890) Beveridge & Campbell, 2010
Grillotia (*Christianella*) *yuniariae* Palm, 2004
Incertae sedis (with respect to subgeneric assignment)
Grillotia adenoplusia (Pintner, 1903) Palm, 2004 **(redescription: Beveridge and Campbell [2013])**
Grillotia amblyrhynchos Campbell & Beveridge, 1993
Grillotia dolichocephala Guiart, 1935 **(redescription and new synonymies: Beveridge and Campbell [2013])**
Grillotia gastrica Beveridge & Campbell, 2013
Grillotia heptanchi (Vaullegeard, 1899) Dollfus, 1942 **(redescription: Beveridge and Campbell [2013])**
Grillotia pristiophori Beveridge & Campbell, 2001
Grillotiella Palm, 2004
Grillotiella exilis (Linton, 1908) Palm, 2004 (type)
Hornelliella Yamaguti, 1954
Hornelliella annandalei (Hornell, 1912) Yamaguti, 1954 (type)
Iobothrium Beveridge & Campbell, 2005
Iobothrium elegans Beveridge & Campbell, 2005 (type)
Lacistorhynchus Pintner, 1913
Lacistorhynchus tenuis (van Beneden, 1858) Pintner, 1913 (type)
Lacistorhynchus dollfusi Beveridge & Sakanari, 1987
Microbothriorhynchus Yamaguti, 1952
Microbothriorhynchus coelorhynchi Yamaguti, 1952 (type)
Microbothriorhynchus reimeri Palm, 2002
Otobothrium Linton, 1890
Otobothrium crenacolle Linton, 1890 (type)
Otobothrium alexanderi Palm, 2004 **(redescription: Schaeffner and Beveridge [2013d])**
Otobothrium australe Palm, 2004 **(redescription: Schaeffner and Beveridge [2013d])**
Otobothrium carcharidis (Shipley & Hornell, 1906) Pintner, 1913
Otobothrium curtum (Linton, 1908) Dollfus, 1942
Otobothrium dinoi (Mendez, 1944) Palm, 2004
Otobothrium insigne Linton, 1905 **(redescription: Schaeffner and Beveridge [2013d])**
Otobothrium minutum Subhapradha, 1955
Otobothrium mugilis Hiscock, 1954 **(redescription: Schaeffner and Beveridge [2013d])**
Otobothrium parvum Beveridge & Justine, 2007
Otobothrium penetrans Linton, 1907 **(redescription: Schaeffner and Beveridge [2013d])**
Otobothrium propecysticum Dollfus, 1969
Paragrillotia Dollfus, 1969
Paragrillotia similis (Linton, 1908) Dollfus, 1969 (type)
Paragrillotia apecteta Beveridge & Justine, 2007
Paragrillotia spratti (Campbell & Beveridge, 1993) Beveridge & Justine, 2007
Parotobothrium Palm, 2004
Parotobothrium balli (Southwell, 1929) Palm, 2004 (type) **(redescription: Schaeffner and Beveridge [2013a])**
Parotobothrium dollfusi (Chandra & Hanumantha Rao, 1985) Palm, 2004
Poeciloacanthum Palm, 1995
Poeciloacanthum oweni Palm, 1995 (type)

- *Poecilancistrium* Dollfus, 1929
  - *Poecilancistrium caryophyllum* (Diesing, 1850) Dollfus, 1929 (type)
- ***Pristiorhynchus* Schaeffner & Beveridge, 2013**
  - ***Pristiorhynchus palmi* Schaeffner & Beveridge, 2013** (type)
- *Proemotobothrium* Beveridge & Campbell, 2001
  - *Proemotobothrium linstowi* (Southwell, 1912) Beveridge & Campbell, 2001 (type)
  - *Proemotobothrium paradisei* Palm, 2004
  - *Proemotobothrium southwelli* Beveridge & Campbell, 2001
- *Protogrillotia* Palm, 2004
  - *Protogrillotia arabiensis* Palm, 2004 (type)
  - *Protogrillotia zerbiae* (Palm, 1995) Palm, 2004
- *Pseudogilquinia* Bilqees & Khatoon, 1980
  - *Pseudogilquinia karachiensis* Bilqees & Khatoon, 1980 (type)
  - *Pseudogilquinia kardoushi* Palm, 2004
  - *Pseudogilquinia microbothria* (MacCallum, 1917) Palm, 2004
  - *Pseudogilquinia pillersi* (Southwell, 1929) Palm, 2004
  - *Pseudogilquinia thomasi* (Palm, 2000) Palm, 2004
- *Pseudogrillotia* Dollfus, 1969
  - *Pseudogrillotia pleistacantha* Dollfus, 1969 (type)
  - *Pseudogrillotia epinepheli* (Scholz, Garippa & Scala, 1993) Palm, 2004
  - *Pseudogrillotia multiminacantha* Palm, 2004
  - *Pseudogrillotia perelica* (Shuler, 1938) Palm, 2004
  - *Pseudogrillotia peruviana* Escalante & Carvajal, 1984
  - *Pseudogrillotia variabilis* Palm, 2004
- *Pseudolacistorhynchus* Palm, 1995
  - *Pseudolacistorhynchus noodti* Palm, 1995 (type)
  - *Pseudolacistorhynchus heroniensis* (Sakanari, 1989) Palm, 2004
  - *Pseudolacistorhynchus matheri* (Southwell, 1929) Palm, 2004
  - *Pseudolacistorhynchus nanus* Beveridge & Justine, 2007
  - *Pseudolacistorhynchus shipleyi* (Southwell, 1929) Palm, 2004
- *Pseudotobothrium* Dollfus, 1942
  - *Pseudotobothrium dipsacum* (Linton, 1897) Dollfus, 1942 (type)
  - *Pseudotobothrium arii* (Bilqees & Shaukat, 1976) Beveridge, Campbell & Jones, 2000 **(redescription: Schaeffner and Beveridge [2013a])**
- *Pterobothrioides* Campbell & Beveridge, 1997
  - *Pterobothrioides carvajali* Campbell & Beveridge, 1997 (type)
  - *Pterobothrioides petterae* Campbell & Beveridge, 1997
- *Pterobothrium* Diesing, 1850
  - *Pterobothrium macrourum* (Rudolphi, 1819) Diesing, 1850 (type, *species inquirenda*)
  - *Pterobothrium acanthotruncatum* Escalante & Carvajal, 1984
  - *Pterobothrium australiense* Campbell & Beveridge, 1996
  - *Pterobothrium crassicolle* Diesing, 1850
  - *Pterobothrium hawaiiense* Carvajal, Campbell & Cornford, 1976
  - *Pterobothrium heteracanthum* Diesing, 1850
  - *Pterobothrium hira* Yamaguti, 1952
  - *Pterobothrium kingstoni* Campbell & Beveridge, 1996
  - *Pterobothrium lesteri* Campbell & Beveridge, 1996 **(redescription: Schaeffner and Beveridge [2012a])**
  - *Pterobothrium lintoni* (MacCallum, 1916) Dollfus, 1942
  - *Pterobothrium pearsoni* (Southwell, 1929) Beveridge & Campbell, 1989
  - *Pterobothrium platycephalum* (Shipley & Hornell, 1906) Dollfus, 1930 **(redescription: Schaeffner and Beveridge [2012a])**
  - *Pterobothrium senegalense* Campbell & Beveridge, 1996
  - *Pterobothrium southwelli* Campbell & Beveridge, 1996
  - *Pterobothrium tangoli* (MacCallum, 1921) Dollfus, 1942
- *Stragulorhynchus* Beveridge & Campbell, 1988
  - *Stragulorhynchus orectolobi* Beveridge & Campbell, 1988 (type)
- *Symbothriorhynchus* Yamaguti, 1952
  - *Symbothriorhynchus uranoscopi* Yamaguti, 1952 (type)
  - *Symbothriorhynchus tigaminacantha* Palm, 2004 **(redescription: Schaeffner and Beveridge [2013a])**

- TENTACULAROIDEA POCHE, 1926
  - *Heteronybelinia* Palm, 1999
    - *Heteronybelinia estigmena* (Dollfus, 1960) Palm, 1999 (type)
    - *Heteronybelinia annakohnae* Pereira & Boeger, 2005
    - *Heteronybelinia australis* Palm & Beveridge, 2002
    - *Heteronybelinia elongata* (Shah & Bilqees, 1979) Palm, 1999
    - *Heteronybelinia eureia* (Dollfus, 1960) Palm, 1999
    - *Heteronybelinia heteromorphi* Palm, 1999
    - ***Heteronybelinia mattisi* Menoret & Ivanov, 2012**
    - *Heteronybelinia minima* Palm, 1999
    - *Heteronybelinia nipponica* (Yamaguti, 1952) Palm, 1999
    - *Heteronybelinia overstreeti* Palm, 2004
    - *Heteronybelinia palliata* (Linton, 1924) Palm & Overstreet, 2000
    - *Heteronybelinia perideraeus* (Shipley & Hornell, 1906) Palm, 1999
    - *Heteronybelinia pseudorobusta* Palm & Beveridge, 2002
    - *Heteronybelinia robusta* (Linton, 1890) Palm, 1999
    - *Heteronybelinia yamagutii* (Dollfus, 1960) Palm, 1999
  - *Kotorella* Euzet & Radujkovic, 1989
    - *Kotorella pronosoma* (Stossich, 1900) Euzet & Radujkovic, 1989 (type)
  - *Kotorelliella* Palm & Beveridge, 2002
    - *Kotorelliella jonesi* Palm & Beveridge, 2002 (type)
  - *Mixonybelinia* Palm, 1999
    - *Mixonybelinia beveridgei* (Palm, Walter, Schwerdtfeger & Reimer, 1997) Palm, 1999 (type)
    - *Mixonybelinia californica* Palm, 2004
    - *Mixonybelinia cribbi* Palm & Beveridge, 2002
    - *Mixonybelinia edwinlintoni* (Dollfus, 1960) Palm & Walter, 2000
    - *Mixonybelinia lepturi* Palm, 2004
    - *Mixonybelinia southwelli* (Palm & Walter, 1999) Palm, 1999
  - *Nybelinia* Poche, 1926
    - *Nybelinia lingualis* (Cuvier, 1817) Dollfus, 1929 (syn. *Nybelinia infulata* [Molin, 1858] Poche, 1926 [type])
    - *Nybelinia aequidentata* (Shipley & Hornell, 1906) Dollfus, 1930
    - *Nybelinia africana* Dollfus, 1960
    - *Nybelinia anguillicola* Yamaguti, 1952
    - *Nybelinia anthicosum* Heinz & Dailey, 1974
    - *Nybelinia basimegacantha* Carvajal, Campbell & Cornford, 1976
    - *Nybelinia bengalensis* Reimer, 1980
    - *Nybelinia bilobata* Palm, 2004
    - *Nybelinia bisulcata* (Linton, 1889) Dollfus, 1929
    - *Nybelinia erythraea* Dollfus, 1960
    - *Nybelinia gopalai* Chandra & Hanumantha Rao, 1985
    - *Nybelinia goreensis* Dollfus, 1960
    - *Nybelinia hemipristis* Palm & Beveridge, 2002
    - *Nybelinia indica* Chandra, 1986
    - *Nybelinia jayapaulazariahi* Reimer, 1980
    - *Nybelinia kamegaii* Palm & Bray, 2014
    - *Nybelinia manazo* Yamaguti, 1952
    - *Nybelinia mehlhorni* Palm & Beveridge, 2002
    - *Nybelinia pintneri* Yamaguti, 1934
    - *Nybelinia queenslandensis* Jones & Beveridge, 1998
    - *Nybelinia riseri* Dollfus, 1960
    - *Nybelinia sakanariae* Palm, 1999
    - *Nybelinia schmidti* Palm, 1999
    - *Nybelinia sphyrnae* Yamaguti, 1952
    - *Nybelinia strongyla* Dollfus, 1960
    - *Nybelinia surmenicola* Okada in Dollfus, 1929
    - *Nybelinia syngenes* (Pintner, 1928) Dollfus, 1930
    - *Nybelinia thyrsites* Korotaeva, 1971
    - *Nybelinia victoriae* Palm & Beveridge, 2002

Paranybelinia Dollfus, 1966
  Paranybelinia otobothrioides Dollfus, 1966 (type)
Pseudonybelinia Dollfus, 1966
  Pseudonybelinia odontocantha Dollfus, 1966 (type)
Tentacularia Bosc, 1797
  Tentacularia coryphaenae Bosc, 1802 (type)

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A molecular framework for the Cestoda

By

Andrea Waeschenbach[1] and D. Timothy J. Littlewood[2]

INTRODUCTION

Since the advent of molecular phylogenetics, progress in resolving the interrelationships of cestodes at higher and lower taxonomic hierarchies has proceeded in leaps and bounds. The nuclear ribosomal RNA genes 18S rDNA (= *ssrDNA*) and 28S rDNA (= *lsrDNA*) have played a central role in unraveling the ordinal-level backbone of the cestode tree (Mariaux, 1998; Olson and Caira, 1999; Kodedová et al., 2000; Hoberg et al., 2001; Mariaux and Olson, 2001; Olson et al., 2001, 2008; Brabec et al., 2006; Waeschenbach et al., 2007; Caira et al., 2014a). However, it was the addition of large fragments (~4,000 bp) of mitochondrial (mt) DNA to the combined 18S rDNA + 28S rDNA dataset that has provided the most stable and best-resolved backbone phylogeny to date (Waeschenbach et al., 2012).

Molecular data have also facilitated the erection of several new orders (Diphyllobothriidea and Bothriocephalidea resulting from a division of the "Pseudophyllidea" Carus, 1863 [see Brabec et al., 2006; Kuchta et al., 2008]; Onchoproteocephalidea resulting from the amalgamation of the Onchobothriidae Braun, 1900 and the Proteocephalidea Mola, 1928 [see Caira et al., 2014a]; Rhinebothriidea [see Healy et al., 2009] and Phyllobothriidea [see Caira et al., 2014a] resulting from a split off the "Tetraphyllidea") and have provided support for the previously erected (Schmidt and Beveridge, 1990) but widely ignored Cathetocephalidea (see Caira et al., 2005). Although controversy remained concerning the ordinal status of the Litobothriidea following its erection in 1969 by Dailey (see Euzet, 1994), molecular data have consistently shown that it represents a distinct lineage, separate from tetraphyllideans (Olson and Caira, 1999; Kodedová et al., 2000; Hoberg et al., 2001; Olson et al., 2001; Waeschenbach et al., 2007, 2012; Caira et al., 2014b). Thus, with the help of molecular data, the number of currently recognized eucestode orders has increased from 12 in Khalil et al. (1994) to a total of 17 following the work of Caira et al. (2014a).

Although phylogenetic frameworks existed for some orders prior to the Planetary Biodiversity Inventory (PBI) project (i.e., Trypanorhyncha [see Palm et al., 2009] "Tetraphyllidea" [see Olson et al., 1999]), for some there were none (e.g., the Lecanicephalidea and Diphyllidea) or they were constructed from only a very limited taxon sampling (e.g., Cyclophyllidea [see von Nickisch-Rosenegk, 1999]). A principal component of the PBI project was the evaluation of newly collected specimens in a molecular phylogenetic context, thus substantially increasing the taxon sampling across the Cestoda. Building on the success of Waeschenbach et al. (2012) in combining 18S rDNA and 28S rDNA with mtDNA, the chosen markers for the PBI project were almost complete 18S rDNA (~2,000 bp), partial (variable

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[1] Corresponding author (a.waeschenbach@nhm.ac.uk)

[2] Corresponding author (t.littlewood@nhm.ac.uk)

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domains D1–D3) 28S rDNA (~1,500 bp), partial large mt ribosomal RNA subunit 16S rDNA (= *rrnL*) (~885 bp) and partial cytochrome *c* oxidase subunit I (COI = *cox1*) (~607 bp). Here, we provide a summary of the advances made through the PBI project to the molecular phylogenetic framework of the Cestoda. Furthermore, we highlight how those data were used to: (i) discover (cryptic) taxonomic novelty, (ii) evaluate morphological characters used traditionally for taxonomic classification, and (iii) identify radiations within host groups or geographic regions.

MATERIALS AND METHODS

The bulk of the sequencing conducted over the course of the PBI project was done at the Natural History Museum London (NHM). Although molecular PBI studies were also undertaken elsewhere, we will only provide the methodologies used at the NHM; methodologies for other studies can be gleaned from the respective publications.

Total genomic DNA (gDNA) was extracted using either the BioSprint 96 robotic work station in combination with the BioSprint 96 DNA Blood Kit (QIAGEN), or the DNeasy Blood & Tissue kit (QIAGEN) following the manufacturer's instructions. Because of the scale of this project, no taxon-specific optimizations were made for polymerase chain reactions (PCRs). If amplification failed the first time, the reaction was repeated for another two times. If still unsuccessful, no further amplification attempts were made. Although amplification of mt genes tended to be less successful than that of the nuclear ribosomal RNA genes, no patterns in terms of taxon-specific failure or success emerged. PCRs were carried out in 25 µl reaction volumes using Illustra PuRe Taq Ready-To-Go PCR beads (GE Healthcare), 2 µl of template gDNA and 1 µl of 10 µM of each primer. For primer details and PCR cycling conditions see Tables 1 and 2. Partial 28S rDNA was amplified using primers ZX-1 and 1500R, almost complete 18S rDNA was amplified using primers WormA and WormB, 16S rDNA was amplified using primers Cest16SFgen and Cest16SRc, and COI was amplified using primers PBI-cox1F_PCR and PBI-cox1R_PCR. Because of the high sequence variability in COI, degenerate primers were designed to ensure amplification across a range of cestode species (see regions in bold in primers listed in Table 1). These primers were then extended at the 5′ end to provide non-ambiguous sequence tags for sequencing (see Table 1 for details). PCR amplicons were either purified using the QIAquick PCR Purification Kit (QIAGEN) or the GENECLEAN II Kit (MP Biomedicals) following the manufacturer's instructions. Sequencing of both strands was carried out on an Applied Biosystems 3730 DNA Analyzer, using Big Dye version 3.1. 28S rDNA PCR products were sequenced using the two PCR primers and internal primers LSU_300F, LSU_300R, ECD2, 400R, 1090F, and LSU_1200F. 18S rDNA PCR products were sequenced using the two PCR primers and internal primers SSU_300F, SSU_300R, 600R, 1270F, 1270R, SSU_1200F, and SSU_1200R. 16S rDNA PCR products were sequenced using the two PCR primers. COI PCR products were sequenced using PBI-cox1F_seq; and PBI-cox1R_seq. Contigs were assembled using SEQUENCHER 4.8 (GeneCodes Corporation). Sequence identity was checked using the Basic Local Alignment Search Tool (BLAST) (www.ncbi.nih.gov/BLAST/). Already published data were deposited in GenBank.

RESULTS AND DISCUSSION

Figure 1 is a cartoon of a phylogeny, based largely on novel molecular data generated by the NHM over the course of the PBI project. Although this tree is based on a maximum likelihood analysis, constructed using the program Garli 2.01 (Zwickl, 2006), it is meant to be a graphic

Table 1. List of PCR and sequencing primers. Positions refer to annealing positions in *Nucula pernula* (AY45419) for 28S rDNA, *Mytilus edulis* (AY527062) for 18S rDNA, and in the 16S rDNA and COI sequences of the complete mitogenome of *Diphyllobothrium latum* (NC_008945).

Primer name	F, forward; R, reverse; Sequence (5' to 3')		Reference
28S rDNA			
ZX-1[1] (1–21)	F	ACCCGCTGAATTTAAGCATAT	Van der Auwera et al. (1994)
1500R (1130–1150)	R	GCTATCCTGAGGGAAACTTCG	Pawlowski et al. (1994)
LSU_300F (329–350)	F	CAAGTACCGTGAGGGAAAGTTG	Littlewood et al. (2000)
LSU_300R (329–350)	R	CAACTTTCCCTCACGGTACTTG	Littlewood et al. (2000)
ECD2 (790–813)	R	CTTGGTCCGTGTTTCAAGACGGG	Littlewood et al. (2000)
1090F (797–813)	F	TGAAACACGGACCAAGG	Littlewood et al. (2008)
LSU_1200F (983–1004)	F	CCCGAAAGATGGTGAACTATGC	Telford et al. (2003)
18S rDNA			
WormA (120–140)	F	GCGAATGGCTCATTAAATCAG	Littlewood and Olson (2001)
WormB (1805–1825)	R	CTTGTTACGACTTTTACTTCC	Littlewood and Olson (2001)
SSU_300F (411–427)	F	AGGGTTCGATTCCGGAG	Elwood et al. (1985)
SSU_300R (421–438)	R	TCAGGCTCCCTCTCCGGA	Littlewood and Olson (2001)
600R (603–620)	R	ACCGCGGCKGCTGGCACC	Littlewood and Olson (2001)
1270F (1183–1200)	F	ACTTAAAGGAATTGACGG	Littlewood et al. (2000)
1270R (1183–1200)	R	CCGTCAATTCCTTTAAGT	Littlewood et al. (2000)
SSU_1200F (1477–1492)	F	CAGGTCTGTGATGCCC	Littlewood and Olson (2001)
SSU_1200R (1477–1492)	R	GGGCATCACAGACCTG	Littlewood and Olson (2001)
16S rDNA			
Cest16SFgen (39–54)	F	TRCCTTTTGCATCATG	Scholz et al. (2013)
Cest16SRc (905–926)	R	AATAGATAAGAACCGACCTGGC	Scholz et al. (2013)
COI			
PBI-cox1F_PCR (697–717)	F	CATTTTGCTGCCGGTCA**RCAYATGTTYTGRTTTTTTGG**[2]	Scholz et al. (2013)
PBI-cox1R_PCR (1280–1294)	R	CCTTTGTCGATACTGCCAAA**RTAATGCATDGGRAA**[2]	Scholz et al. (2013)
PBI-cox1F_seq (N/A)	F	CATTTTGCTGCCGGTC**A**[3]	Scholz et al. (2013)
PBI–cox1R_seq (1275–1293)	R	TAATGCATDGGRAA**AAAAC**[4]	Scholz et al. (2013)

[1] Original ZX-1 (ACCCGCTGAAYTTAAGCATAT; Van der Auwera et al., 1994); Y was replaced with T.

[2] Bolded 3' ends are complementary to the target sequence. Unambiguous 5' end tails were added for sequencing primer annealing (but see footnote 4).

[3] Complement sequence of M13(-20) forward primer, plus an additional adenine at the 3' end, shown in bold.

[4] A previous sequencing primer designed in the 5' end tail yielded only poor sequence data, whereas the current primer, designed in the ambiguous region, and to which additional nucleotides complementary to the target sequence were added (see portion in bold), gave clean sequence data.

Table 2. PCR cycling conditions.

Gene	Cycling profile				
		40 cycles			
28S rDNA	94°C for 3 min	94°C for 30 s	55°C for 30 s	72°C for 2 min	72°C for 10 min
18S rDNA	94°C for 3 min		54°C for 30 s	72°C for 2 min	
16S rDNA	94°C for 2 min		54°C for 30 s	72°C for 1 min	
COI	94°C for 2 min		60°C for 30 s	72°C for 1 min	

representation of the sequencing effort conducted as part of the PBI project, rather than to serve as a phylogenetic tree for further interpretation. For this reason no details are given for the alignment construction and phylogenetic analysis. Although the four genes sequenced during the project provide good nodal support towards the tips of the tree in many clades, support for the internal nodes was poor, which is why the backbone was edited to reflect figure 4 in Waeschenbach et al. (2012) and figure 3 in Caira et al. (2014a). Terminals consist of the 797 specimens sequenced as part of the PBI project by the NHM, the Rhinebothriidea,

TABLE 3. DNA sequence data generated over the course of the PBI project.

Cestode order	**18S rDNA**	**28S rDNA**	**16S rDNA**	**COI**	**No. of sequenced samples**
Amphilinidea	0[1]	0[1]	0[1]	0[1]	0[1]
Gyrocotylidea	0[2]	0[2]	0[2]	0[2]	0[2]
Caryophyllidea	96[3,4]	98[4,5]	67	85[3,4]	100
Spathebothriidea	0[2]	0[2]	0[2]	0[2]	0[2]
Haplobothriidea	0[2]	0[2]	0[2]	0[2]	0[2]
Diphyllobothriidea	30	31	27	29	32
Diphyllidea	49[6]	51[6]	7	45[6]	51
Trypanorhyncha	68[7]	68[7]	74	85	104
Bothriocephalidea	56	56[8]	56	65	71
Litobothriidea	2[9]	7[10]	0	0	7
Lecanicephalidea	67[9]	67[9]	54	62	67
Rhinebothriidea	51[11]	51[11]	12	10	52
Cathetocephalidea	3[12]	312	1	1	3
Phyllobothriidea	21[9]	21[9]	9	12	21
"Tetraphyllidea"	28[12]	33[13]	9	11	34
Onchoproteocephalidea	119 (10)[9,14]	140 (28)[14,15]	112 (7)[14]	121 (8)[14]	149 (29)[14]
Nippotaeniidea	2	2	2	2	2
Tetrabothriidea	8	8	8	8	8
Mesocestoididae	3	3	2	2	3
Cyclophyllidea	300	296	286	291	314
Total	**903**	**935**	**726**	**829**	**1018**

[1] One molecular PBI specimen of *Austramphilina elongata* was collected from a northern snake-neck turtle (*Macrochelodina rugosa*) in Indonesia, but no PCR products could be obtained.
[2] No molecular PBI specimen was collected.
[3] Includes sequences from Brabec et al. (2012).
[4] Includes sequences from Scholz et al. (2011).
[5] Includes sequences from Brabec et al. (2012) and Schaeffner et al. (2011).
[6] 28S rDNA and 18S rDNA sequences were from Caira et al. (2013).
[7] Includes sequences from Olson et al. (2010).
[8] Includes sequences from Kuchta et al. (2012).
[9] Includes sequences from Caira et al. (2014a).
[10] Includes sequences from Caira et al. (2014a, b).
[11] Includes sequences from Healy et al. (2009), Caira et al. (2014a), and Ruhnke et al. (2015).
[12] Includes sequences from Healy et al. (2009) and Caira et al. (2014a).
[13] Includes sequences from Healy et al. (2009), Caira et al. (2014a), and Bernot et al. (2015).
[14] Numbers in parentheses indicate number of Onchobothriidae.
[15] Includes sequences from Fyler et al. (2009), Fyler and Caira (2010), and Caira et al. (2014a).

Phyllobothriidea, Cathetocephalidea, elasmobranch-hosted Onchoproteocephalidea, and "Tetraphyllidea" relics used to construct figure 2 in Caira et al. (2014a), and the 23 taxa in Waeschenbach et al. (2012) for which the contiguous mt fragment had been analyzed. Below we discuss the advances in taxon coverage in the molecular phylogenetic framework of the Cestoda attributed to the PBI project. No molecular material was collected during the PBI project for some of the most species-poor orders (i.e., Gyrocotylidea, Spathebothriidea, and Haplobothriidea), and no molecular data could be obtained from the only amphilinid specimen (*Austramphilina elongata* Johnson 1931), collected from a northern snake-neck turtle (*Macrochelodina rugosa* Ogilby, 1890) in Indonesia.

Progress made in the generation of molecular frameworks for the eucestode orders over the course of the PBI project is discussed below based on the relationships illustrated in Figure 1 beginning with the earliest diverging lineages.

Caryophyllidea

As part of the PBI project, the genera *Caryophyllaeus* Gmelin, 1790 (see Bazsalovicsová et al., 2014), *Khawia* Hsü, 1935 (see Scholz et al., 2011), and *Wenyonia* Woodland, 1923 (see Schaeffner et al., 2011) were evaluated in a molecular phylogenetic context. However, the first overall phylogenetic framework for this order was produced by Brabec et al. (2012). This study included 19 species and was based on 18S and 28S rDNA and a contiguous fragment of mtDNA (trnK + NADH 3 + trnS + trnW + COI). Three further molecular studies published as part of the PBI project are by Scholz et al. (2014) on the cryptic diversity of *Paracaryophyllaeus* Kulakowskaja, 1961, by Scholz et al. (2015) presenting a revision of *Monobothrium* Diesing, 1863 and *Promonobothrium* Mackiewicz, 1968 in light of molecular data, and by Oros et al. (2016) supporting the monophyly of *Promonobothrium* and the validity of the currently recognized eight species of this genus.

Inclusive of the data by Schaeffner et al. (2011), Scholz et al. (2011), and Brabec et al. (2012), 100 terminals were studied over the course of the PBI project. Unpublished analysis of those data show that caryophyllideans underwent radiations not only within host groups but also within geographic regions: a radiation in Afro-Indian catfishes, a radiation in Palaearctic cyprinids, and a radiation in Nearctic suckers. There are an estimated 121 species of Caryophyllidea (see Chapter 4 this volume, Scholz and Oros, 2017); thus, approximately 80% of species have been put into a molecular phylogenetic context. Importantly, Brabec et al. (2012) discovered putative nuclear mitochondrial pseudogenes (numts) amongst their mt data.

Bothriocephalidea and Diphyllobothriidea

Following the discovery of the non-monophyly of the Pseudophyllidea in a number of molecular phylogenetic studies (e.g., Mariaux, 1998; Kodedová et al., 2000; Olson et al., 2001), Brabec et al. (2006) conducted a thorough study of this group using 18S and 28S rDNA data and recommended the erection of the two orders Diphyllobothriidea and Bothriocephalidea, which was formally implemented by Kuchta et al. (2008). The analysis by Brabec et al. (2006) included eight species of Diphyllobothriidea and 17 species of Bothriocephalidea.

Bothriocephalidea. As part of the PBI project, both of these orders were thoroughly studied. A total of 71 bothriocephalidean terminals was analyzed during the PBI project (Table 3). Of those, 46 18S rDNA, 43 28S rDNA, 46 16S rDNA, and 55 COI sequences were combined with published data to produce an overall phylogeny of 59 species (Brabec et al., 2015). Mapping of 22 morphological characters onto the molecular phylogeny revealed that only one of those characters was of phylogenetic utility, emphasizing the conflict between morphology and molecules in this group. Crucially, the study by Brabec et al. (2015) found two (the Echinophallidae Schumacher, 1914 and the Triaenophoridae Lönnberg, 1889) of the three families currently recognized in the order (see Chapter 3 this volume, Kuchta and Scholz, 2017a) to be non-monophyletic. Due to a current lack of morphological synapomorphies for the molecular clades, the existing family-level classification was retained (except for the synonymization of the Philobythiidae Campbell, 1977 with the Triaenophoridae). The challenge that remains is to discover morphological characters that support these clades. There are currently 132 valid species (see Chapter 3 this volume, Kuchta and Scholz, 2017a); thus, approximately 44% of known species have been put into a phylogenetic context.

Diphyllobothriidea. The most comprehensive phylogenetic framework for the Diphyllobothriidea, to date, was produced by Hernández-Orts et al. (2015). However, the taxon choice was largely limited to those species that are the causative agents of human disease (diphyllobothriosis, sparganosis). Similarly, a published complete genome (*Spirometra*

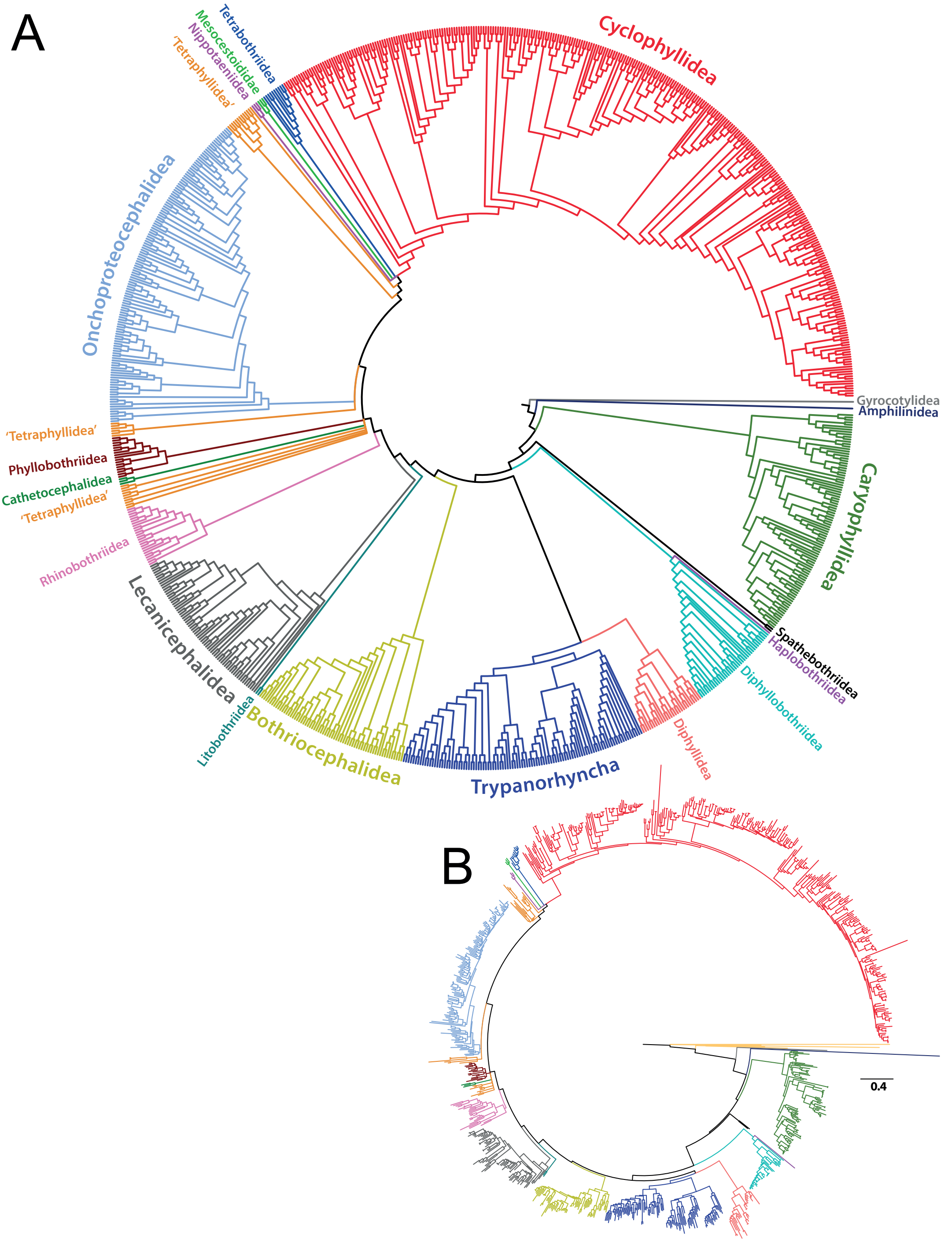

FIGURE 1. Cartoon depicting the majority of the PBI phylogeny in which the backbone had been edited to reflect figure 4 of Waeschenbach et al. (2012) and figure 3 of Caira et al. (2014b). **(A)** Cladogram. **(B)** Phylogram in which the branch length scale bar indicates number of subsitutions per sites.

erinaceieuropaei [Rudolphi, 1891] Faust, Campbell & Kellogg, 1929 by Bennett et al. [2014]) and all published mitochondrial genomes (*Diphyllobothrium nihonkaiense* Yamane, Kamo, Bylund & Wikgren, 1986 by Kim et al. [2007]; *Diphyllobothrium latum* L., 1758 and *D. nihonkaiense* by Nakao et al. [2007]; *Diphyllobothrium latum* by Park et al. [2007]; *Spirometra erinaceieuropaei* by Liu et al. [2012]; *Diplogonoporus balaenopterae* Lönnberg, 1892 and *D. grandis* (Blanchard, 1894) by Yamasaki et al. [2012]; *Spirometra erinaceieuropaei* and *S. decipiens* Diesing, 1850 by Eom et al. [2015]) are exclusively from taxa of medical importance. None of this work was part of the PBI project.

As part of the PBI project, much of the novel sampling of diphyllobothriideans was focused on wildlife parasites. In total, 32 diphyllobothriidean terminals were studied during the PBI project (Table 3). The resulting phylogeny (Waeschenbach et al., accepted) includes 25 species. Several of the internal nodes are unresolved and will require additional data for their resolution. The current assessment of diversity in this order is 70 species (see Chapter 8 this volume, Kuchta and Scholz, 2017b); thus, approximately 36% of known species have been put into a phylogenetic context.

Diphyllidea

Molecular studies of diphyllideans pre-PBI project involved only a handful of species at a time. Bray and Olson (2004) studied the phylogenetic affinities of *Ditrachybothridium macrocephalum* Rees, 1959 from the North East Atlantic Ocean in the context of four *Echinobothrium* van Beneden, 1849 and one *Macrobothridium* Khalil & Abdul-Salam, 1989 species. They generated novel 28S rDNA data for the above and combined it with published data for *Echinobothrium harfordi* McVicar, 1976, *E. chisholmae* Jones & Beveridge, 2001, and *Macrobothridium rhynchobati* Khalil & Abdul-Salam, 1989, which had originally been sequenced for a cestode-wide phylogenetic evaluation (Olson et al., 2001). Dallarés et al. (2015) subsequently sequenced further material of *D. macrocephalum* from the Mediterranean Sea to verify the species identity.

As part of the PBI project, Caira et al. (2013) generated the first comprehensive phylogenetic estimate (based on 18S and 28S rDNA, and COI) of the order. They analyzed 51 specimens from 31 species, of which an astonishing 19 were undescribed. Thus, their study transformed the taxonomic and phylogenetic landscape of diphyllideans. The NHM subsequently sequenced 16S rDNA for seven of those terminals (Table 3). There are a total of 59 valid species (see Chapter 7 this volume, Caira et al., 2017a); thus, approximately 52% of known species have been put into a molecular phylogenetic context.

Trypanorhyncha

Prior to the PBI project, Palm et al. (2009) was the only study to have tackled the molecular phylogeny of Trypanorhyncha. As part of the PBI project, Olson et al. (2010) generated 62 new 18S and 62 new 28S rDNA sequences. Their analysis of 80 species supported the establishment of the two suborders Trypanobatoida and Trypanoselachoida, which primarily parasitize rays and sharks, respectively. Six additional specimens were since analyzed by the NHM, generating six, six, three, and five sequences of 18S, 28S, 16S rDNA, and COI, respectively. Furthermore, complementary 16S rDNA and COI data were generated for 71 and 80 of the existing specimens used in the abovementioned studies, respectively. Palm et al. (2009) estimated the total number of trypanorhynch species as 277. Thirty additional species were described as part of the PBI project. The total number of valid species is 315 (see Chapter 21 this volume, Beveridge et al., 2017). Thus, the 104 species sequenced during the PBI project

(Table 3) amount to approximately 33% of known species diversity. The main challenge that remains is the resolution of the polytomies amongst and within the major lineages of Eutetrarhynchoidea, Tentacularioidea, Gymnorhynchoidea, and Lacistorhynchoidea (see fig. 3 in Chapter 21 this volume, Beveridge et al., 2017).

Litobothriidea

Although included as exemplar taxa in broader phylogenetic analyses (Olson and Caira, 1999; Olson et al., 2001; Waeschenbach et al., 2007, 2012), no dedicated phylogenetic analysis had been conducted on the currently recognized nine species of Litobothriidea prior to the PBI project. As part of the PBI project, Caira et al. (2014a) sequenced 18S and 28S rDNA of two species, using them as exemplar taxa for the order for a broader analysis. The first Litobothriidea-specific phylogenetic analysis was done by Caira et al. (2014b), in which 28S rDNA were generated for six samples, five of which belonged to *Litobothrium aenigmaticum* Caira, Jensen, Waeschenbach & Littlewood, 2014, a worm with an unusual scolex morphology, atypical for litobothriideans. This analysis included four species in total. Sequence data ([D1–D3] 28S rDNA) for a fifth species, *L. daileyi* Kurochkin & Slankis, 1973, were generated and added to the data set of Caira et al. (2014b) as part of a phylogenetic analysis for this volume (see fig. 4 in Chapter 12 this volume, Caira et al., 2017b). Thus, approximately 55% of litobothriidean species have been placed in a molecular phylogenetic context.

Lecanicephalidea

Insights into the interrelationships of the Lecanicephalidea have been revolutionized thanks to the efforts of the PBI project. Lecanicephalideans had previously been included in molecular phylogenetic frameworks only as exemplar representatives (1–3 species) in cestode-wide studies (i.e., 18S rDNA by Olson et al. [1999] and Littlewood and Olson [2001]; 18S rDNA and elongation factor-1α by Olson and Caira [1999]; 18S and 28S rDNA by Olson et al. [2001] and Waeschenbach et al., 2007]; 18S, 28S rDNA, and 4kb mtDNA by Waeschenbach et al. [2012]). Caira et al. (2014a) were the first to have included a significant number of lecanicephalidean species (i.e., 17), in their 18S and 28S rDNA framework. Subsequently, Jensen et al. (2016) generated a further 50, 50, 54, and 62 sequences for 18S, 28S, 16S rDNA, and COI, respectively, providing the final dataset of the main PBI-output publication for this group, which included 61 species (67 specimens) (Table 3), of which 23 are described species. Crucially, this study reaffirmed previous concerns about conflict between scolex and proglottid morphologies as taxonomic characters (Jensen, 2005). The molecular phylogeny of Jensen et al. (2016) demonstrated homoplasy in the evolution of an apical organ divided into tentacles and also revealed extensive variation in scolex morphology among closely related taxa. On the other hand, their results showed that proglottid morphology was relatively conserved, thereby making this a useful feature to characterize the molecular clades. Importantly, Jensen et al. (2016) erected four new families for monophyletic groups obtained using the new molecular data. There are 90 valid species (see Chapter 11 this volume, Jensen et al., 2017), which means that approximately 26% of the currently recognized lecanicephalidean species have been placed in a molecular phylogenetic context.

Rhinebothriidea, Cathetocephalidea, Phyllobothriidea, and “Tetraphyllidea” relics

The group that underwent the most substantial restructuring underpinned by molecular data over the course of the PBI project was the Tetraphyllidea. Although the early beginnings of molecular phylogenetics did not fully recognize the extent to which the Tetraphyllidea would ultimately be dismantled (Olson et al., 1999), the monophyly of the order was challenged by molecular data right from the start (e.g., Mariaux, 1998; Olson and Caira, 1999; Olson et al., 2001).

The first significant step in the disintegration of the Tetraphyllidea was the formal recognition of the previously erected (Schmidt and Beveridge, 1990) but widely ignored Cathetocephalidea using evidence from 18S and 28S rDNA (Caira et al., 2005). There are currently only six valid species of Cathetocephalidea (see Chapter 5 this volume, Caira et al., 2017c), two of which were included in Caira et al. (2005). As part of the PBI project, Caira et al. (2014a) sequenced 18S and 28S rDNA of three species; 16S rDNA and COI data were generated by the NHM for one of them (Table 3). Thus, 75% of known species have been put into a molecular phylogenetic context.

The next step was the erection of the order Rhinebothriidea. Just prior to the start of the PBI project, Healy et al. (2009) generated 18S and 28S rDNA data for 31 species, all of which formed a monophyletic group. Ruhnke et al. (2015) subsequently increased the taxon sampling by another 15 rhinebothriidean species, whilst also erecting two families and Caira et al. (2014a) sequenced a further five species. Marques and Caira (2016) slightly increased the taxon sampling further. 16S rDNA and COI data were generated by the NHM for 12 and ten of these previously collected specimens, respectively (Table 3). At present, 136 species of Rhinebothriidea are recognized (see Chapter 17 this volume, Ruhnke et al., 2017a); thus, approximately 37% have been put into a molecular phylogenetic context.

The subsequent iteration of the dismantling of the Tetraphyllidea, based on 18S and 28S rDNA data, was conducted by Caira et al. (2014a), who, in addition to grouping the tetraphyllidean family Onchobothriidae with the proteocephalideans in the new order Onchoproteocephalidea (see below), also erected the new order Phyllobothriidea. Seventeen of the 19 newly sequenced species formed a monophyletic group and were unambiguously assigned to the Phyllobothriidea, excluding the putative phyllobothriideans *Clistobothrium* Dailey & Vogelbein, 1990 and *Crossobothrium* Linton 1889 (then assigned to the "Tetraphyllidea"). In addition to the data generated by Caira et al. (2014a), 16S rDNA and COI was sequenced for seven and ten of those phyllobothriid specimens by the NHM. Furthermore the full four-gene complement was sequenced for two further species. At present 69 species of Phyllobothriidea are considered valid (see Chapter 16 this volume, Ruhnke et al., 2017b); thus, approximately 29% have been put into a molecular phylogenetic context.

Although this reorganization has assigned much of the previous tetraphyllidean diversity to new taxonomic groups, 104 species remain included in the "Tetraphyllidea" (see Chapter 20 this volume, Caira et al., 2017d). Healy et al. (2009) sequenced 18S and 28S rDNA for eight of those species. This dataset was extended by Caira et al. (2014a) by including a further 20 species. Bernot et al. (2015) subsequently sequenced 28S rDNA for two further species of *Calliobothrium* van Beneden, 1850 and three species of *Symcallio* Bernot, Caira & Pickering, 2015. Furthermore, 16S rDNA and COI data were generated by the NHM for nine and 11 existing specimens, respectively (Table 3). In total, 34 species, equating to 33% of known "tetraphyllidean" relic species have been put into a molecular phylogenetic context.

There remain a considerable number of unresolved nodes amongst the lineages discussed above. The sequencing of mt genomes of representative taxa for key lineages is currently under way in an attempt to remedy this (Waeschenbach et al., in prep).

Onchoproteocephalidea

The Onchoproteocephalidea is a recently erected order that combines a subset of the elasmobranch-hosted Onchobothriidae (previously grouped in the "Tetraphyllidea") and the members of the primarily teleost-hosted former order Proteocephalidea (Caira et al., 2014a). These two groups have been treated separately in all previous literature and are treated as separate chapters (as Onchoproteocephalidea I and II) in this volume (see Chapters 14 and 15 this volume, de Chambrier et al., 2017 and Caira et al., 2017e, respectively).

Onchoproteocephalidea I. Several genus- and subfamily-specific molecular phylogenetic studies had been published for proteocephalideans (Zehnder et al. [2000] generated 28S rDNA, 5.8S rDNA, and ITS2 data for *Nomimoscolex* Woodland, 1934; Zehnder and de Chambrier [2000] generated 28S rDNA, 5.8S rDNA, ITS2, and 16S rDNA data for *Peltidocotyle* Diesing, 1850 and *Othinoscolex* Woodland, 1933; Škeříková et al. [2001] generated 28S rDNA data for *Proteocephalus* Weinland, 1858 and Rosas-Valdez et al. [2004] did so for the Corallobothriinae Freze, 1965; Scholz et al. [2007] generated 18S rDNA, 5.8S rDNA, and ITS2 data for *Proteocephalus*). As part of the PBI project, a phylogeny that included *Macrobothriotaenia ficta* (Meggitt, 1927) Freze, 1965, a proteocephalidean that parasitizes sunbeam snakes and which exhibits an unusual phyllobothriid-like scolex morphology, revealed that this taxon forms a clade together with other snake-infecting proteocephalideans of the genus *Ophiotaenia* La Rue, 1911 (see Scholz et al., 2013).

The earliest overall molecular phylogeny of proteocephalideans, which included 53 species and was based on 16S and 18S rDNA data, was constructed by Zehnder and Mariaux (1999). Their sequence data were supplemented with ITS2 and partial 18S rDNA sequences by Hypša et al. (2005). Both studies recovered trees with a derived polytomous arrangement of mostly Neotropical taxa, which was also found in subsequent iterations based on 28S rDNA by de Chambrier et al. (2004) and also in subsequent PBI work by de Chambrier et al. (2015) (including 30 of the 120 PBI specimens; see Table 3) that included 110 of the currently recognized 319 proteocephalidean species (see Chapter 14 this volume, de Chambrier et al., 2017); thus, with a taxon coverage of approximately 35% it represents the best-sampled phylogeny to date. In addition to the Neotropical radiation, de Chambrier et al. (2015) also revealed a Palaearctic radiation of the *Proteocephalus* aggregate in non-siluriform freshwater fishes, an Afrotropical radiation of genera *Marsypocephalus* Wedl, 1861, *Corallobothrium* Fritsch, 1886, *Barsonella* de Chambrier, Scholz, Beletew & Mariaux, 2009, and *Proteocephalus* Weinland, 1858 in catfishes, and a small Nearctic radiation of genera *Corallotaenia* Freze, 1865, *Essexiella* Scholz, de Chambrier, Mariaux & Kuchta, 2011, and *Megathylacoides* Jones, Kerley & Sneed, 1956 in catfishes. Overall, biogeography and host use seem to be an important determinants of phylogenetic relationships in proteocephalideans. A phylogeny including all PBI project specimens and their full complement of molecular data remains to be published. A crucial outcome of these studies was the discovery of non-monophyly of most subfamilies and genera, highlighting the shortcomings of characters used traditionally for classification (i.e., scolex morphology and position of genital organs in relation to the longitudinal musculature). As alternatives, de Chambrier et al. (2015) advocated the exploration of reproductive traits, such as patterns of uterus development, ovary size, and egg structure, for the classification of proteocephalideans.

Onchoproteocephalidea II. The elasmobranch-hosted Onchoproteocephalidea number 246 species (see Chapter 15 this volume, Caira et al., 2017e). Although representative taxa had been included in several large-scale phylogenies (e.g. Olson et al., 2008; Waeschenbach et al., 2007, 2012), no phylogenetic framework existed for this group prior to the commencement of the PBI project. In addition to the work done by the NHM, Caira et al. (2014a) sequenced 18S and 28S rDNA for ten onchobothriid species, Fyler et al. (2009) and Fyler and Caira (2010) sequenced 28S rDNA for 14 and four onchobothriid taxa, respectively.

As part of the PBI project, 149 onchoproteocephalideans, of which 29 were elasmobranch-hosted species, were sequenced (Table 3). The final sampling covers approximately 38% of known Onchoproteocephalidea I species diversity (see Chapter 14 this volume, de Chambrier et al., 2017) and approximately 12% of Onchoproteocephalidea II species diversity (see Chapter 15 this volume, Caira et al., 2017e). The greatest challenges that remain for this group are the reconciliation of the molecular topology with the definition of proteocephalidean subfamilies and genera, and the resolution of the polytomies amongst the Neotropical taxa and the identification of a solid morphological feature to define the order.

Nippotaeniidea

Apart from exemplar specimens used for cestode-wide molecular phylogenetic scrutiny (Mariaux, 1998; Olson and Caira, 1999; Littlewood and Olson, 2001; Olson et al., 2001; Waeschenbach et al., 2007, 2012) there are currently no molecular studies dedicated to this order. There are six valid species in the order (see Chapter 13 this volume, Scholz et al., 2017). Only two species (*Nippotaenia chaenogobii* Yamaguti, 1939 and *Amurotaenia mogurndae* Gussev, 1955) were analyzed as part of the PBI project (Table 3). Overall, for three species (*Amurotaenia percotti* Akhmerov, 1941, *Nippotaenia contorta* Hine, 1977, and *N. fragilis* Hine, 1977) there exist no sequence data (*Amurotaenia decidua* had previously been sequenced by Mariaux [1998], Olson and Caira [1999], and Olson et al. [2001]); thus, approximately 57% of known species have been put into a phylogenetic context.

Tetrabothriidea

Apart from exemplar specimens used for cestode-wide molecular phylogenetic studies (Mariaux, 1998; Olson and Caira, 1999; Littlewood and Olson, 2001; Olson et al., 2001; Waeschenbach et al., 2007, 2012; Caira et al., 2014a) there are currently no molecular studies dedicated to this order. There are 70 species recognized as valid in the order (see Chapter 19 this volume, Mariaux et al., 2017a). As part of the PBI project, eight specimens were analyzed (Table 3). As the majority of these specimens remain unidentified, no estimate about the sequenced diversity can be given.

Cyclophyllidea (incl. Mesocestoididae)

Although the most species-rich cestode order (with greater than 3,000 species; see Chapter 6 this volume, Mariaux et al., 2017b), the most comprehensive phylogenetic framework published for this group, pre-PBI, was based on only 19 species and was constructed using only a short fragment of small mt ribosomal RNA subunit (von Nickisch-Rosenegk, 1999). Cyclophyllidean clades (or parts thereof) that had been investigated in more detail are the Anoplocephalidae Cholodovsky, 1902 (Hardman et al. [2012] with 28S rDNA; Haukisalmi et al. [2014] with COI and NADH1; Haukisalmi et al. [2016] with COI and 28S rDNA), Hymenolepididae Ariola, 1899 (Haukisalmi et al. [2010a] with 28S rDNA; Jia et al. [2016] with ITS1, ITS2, and NADH1), Taeniidae Ludwig, 1886 (see Lavikainen et al. [2008] with COI and NADH1; Knapp et al. [2011] with RNA polymerase II, phosphoenolpyruvate carboxykinase, and DNA polymerase delta; Nakao et al. [2013a] with 18S rDNA, phosphoenolpyruvate carboxykinase, and DNA polymerase delta), *Catenotaenia* Janicki, 1904 (Haukisalmi et al. [2010b] with 28S rDNA), and Davaineidae Braun, 1900 (Littlewood et al. [2008] with 18S rDNA, 28S rDNA, COI, NADH 1, and 16S rDNA). In addition, there have been a multitude of mt genome studies with a focus on taxa of medical, economical, and veterinary importance (*Taenia crassiceps* Zeder, 1800 by Le et al. [2000]; *Taenia solium* Linnaeus, 1758 by Nakao et al. [2003]; *Taenia asiatica* Eom & Rim, 1993 by Jeon et al. [2005]; *Taenia asiatica* and *T. saginata* Goeze, 1782 by Jeon and Eom [2006]; *Taenia* spp. by Jeon et al. [2007], Jia et al. [2010], Liu et al. [2011], and Terefe et al. [2014]; Taeniidae by Nakao et al. [2013a]; *Hymenolepis diminuta* Rudolphi, 1819 by von Nickisch-Rosenegk et al. [2001]; *Hymenolepis nana* (von Siebold, 1842) by Cheng et al. [2016]; *Echinococcus multilocularis* Leuckart, 1863 by Nakao et al. [2002]; *Echinococcus* spp. by Le et al. [2002], Yang et al. [2005], Nakao et al. [2007, 2013b]; *Echinococcus granulosus* (Batsch, 1786) by Wang et al. [2016]; *Anoplocephala perfoliata* (Goeze, 1782) by Guo [2015]; *Pseudanoplocephala crawfordi* Baylis, 1927 by Zhao et al. [2016]). Similarly, recently sequenced cyclophyllidean genomes were of either medical importance (*Echinococcus multilocularis*, *E. granulosus*, and *T. solium*) or were a laboratory model organism (*Hymenolepis microstoma* [Dujardin, 1845]) (Tsai et al., 2013).

During collecting trips as part of the PBI project, 318 cyclophyllidean samples were sourced for molecular phylogenetic analysis from across the globe from localities in Australia, Brazil, Chile, China, Czech Republic, Ethiopia, France, Gabon, Guyana, Iran, Jordan, Malawi, Malaysia, Philippines, Russia, Slovakia, Sudan, Taiwan, Ukraine, Vietnam, as well as numerous localities throughout the USA (for more detail, see Chapter 6 this volume, Mariaux et al., 2017b). Thus, in terms of taxon sampling, the PBI project has provided a massive leap forward for sampling and sequencing cyclophyllideans infecting wildlife. As in the caryophyllideans, cryptic diversity was also found in cyclophyllideans: cryptic species of the paruterinid *Anonchotaenia* Cohn, 1900 were found to parasitize specific families of hosts (Phillips et al., 2014). The number of currently valid species is estimated at 3,034 (see Chapter 20 this volume, Mariaux et al., 2017b); thus, approximately 10% of species are now represented in a molecular phylogenetic context. Apart from sampling the residual 90%, what remains to be resolved are the interrelationships of the families. Apart from the sister-group relationship of the Amabilidae Braun, 1900 and Dioicocestidae Southwell, 1930 and a clade formed of Progynotaeniidae Fuhrmann, 1936, Acoleidae Fuhrmann, 1899, and Gyrocoeliinae Yamaguti, 1959, the backbone of the cyclophyllidean phylogeny continues to have low support (see fig. 5 in Chapter 6 this volume, Mariaux et al., 2017b). Work is currently underway to sequence ~30 mt genomes, representing the majority of these lineages, which it is hoped will add resolution to the deep nodes of the phylogeny.

FUTURE PERSPECTIVES

Progress in the resolution of a molecular phylogeny for a species-rich taxon, such as the Cestoda, requires an iterative swing between more species and more sequences (or better, loci) in order to provide a tree with robustly supported nodes across all levels of divergence. Prior to the PBI, this was being approached and achieved at a moderate to low rate, driven primarily by the interests of the few who were focused on component groups of species that make up the diversity of the tapeworms. The very nature of working on parasites means that systematic parasitologists are as focused on their hosts as they are on the parasites those hosts yield. This compartmentalization of activity is so granular that it hampers progress in understanding the wider diversity and diversification of the Cestoda as a whole.

The PBI project approach has provided a considerable boost to species sampling, along with modest additions to the number of molecular loci being sequenced (2 partial mitochondrial genes) and provides a much-needed platform from which to ask “what next?” The PBI project's comprehensive effort in addressing the systematics, diversity, and interrelationships of the Cestoda has provided the following: new specimens for morphological study, a wealth of tissue samples for subsequent molecular interrogation, a number of unresolved phylogenies and new hypotheses worthy of attention, and an indication of what is missing in terms of species sampling. One of the most important results is a phylogenetic framework, with vouchered specimens, that provides a strong backbone for evolutionary inferences, trait mapping, host mapping and explorations into the major evolutionary transitions that underpin the radiation of the tapeworms. Some outstanding goals remain.

Dense sampling of taxa, particularly the taxa formerly recognized as tetraphyllideans, has highlighted the need to resolve further the backbone of the Cestoda. The "tetraphyllidean" relics remain as orphaned clades among those new orders gleaned from the traditional Tetraphyllidea. At this stage, more taxa are not as important as new sequence data (loci), and to this end we are investigating whether complete mt genomes of selected exemplar taxa provide stronger support for the remaining unstable nodes of the cestode backbone. If this approach fails to make substantive progress in our quest for stability, a phylogenomic approach would seem to be most appropriate. Various methods are available, but given the scarcity of material and the cost in recovering fresh material any methods dependent upon RNA (e.g., for transcriptomic approaches) would likely not be readily fundable, although future collecting should certainly include sampling fresh, frozen, or RNAlater-fixed material (Giribet, 2016). Approaches that can provide multi-locus data from DNA or ethanol-fixed material would allow existing material to be revisited; for example, by means of genome skimming (Straub et al., 2012; Ripma et al., 2014; Dodsworth, 2015; Richter et al., 2015) and target-enrichment of ultraconserved elements (Faircloth et al., 2015) and single-copy nuclear coding genes (Yuan et al., 2016), and exon capture (Bragg et al., 2016).

Untangling the known from the unknown. Undoubtedly a singular strength of the overall molecular data set that emanated from the PBI project has been the emphasis placed on sequences being attributed to vouchered morphological material. This combination, particularly through the provision of hologenophores, establishes a dataset that can be repeatedly interrogated with associated specimens ready for review and if necessary, revision. However, the use of the molecular markers within the PBI project (particularly 18S and 28S rDNA) has been popular since the outset, and continues to be pursued by many researchers wishing to take advantage of the enormous database of sequences available in GenBank, such that many more "eligible" sequences are available for wider estimates of molecular phylogeny across many taxonomic levels within the Cestoda.

Littlewood et al. (2015) amassed available data from GenBank including many PBI sequences available at that time, but only the overall (backbone) structure of the cestode phylogeny was published. The dataset was restricted to GenBank entries providing 500 bp or more of the 18S and 28S rDNA markers (without duplicating species). Importantly, the larger reference data set and associated phylogeny provided an opportunity to detect errors in GenBank that may have arisen from misidentifications, miscalled nucleotides, or sequence curation. It is unlikely that such errors or inconsistencies will be readily followed up but it is worth bearing in mind that many users of PBI molecular data will come to it via an interrogation of GenBank. There is little provision within GenBank to know what is trustworthy and what is not, and many users will err on the side of a statistical or probabilistic interpretation of results; errors are more readily spotted when an overwhelming amount of data contradict an expected outcome.

Notwithstanding errors in GenBank, the sheer volume of PBI data that span the diversity of Cestoda that has already been deposited in or will ultimately find its way into that database, provides considerable support for the user community. Where PBI specimens influence phylogenetic, systematic, or diagnostic interpretation of novel sequences, the user will likely make better judgments with these data than in their absence. This provides a satisfying next step for the use of these data beyond building a phylogeny.

Sanger versus next generation sequencing. All of the sequencing for the PBI project, barring some mitogenomic work (unpublished) was achieved by means of Sanger sequencing. The method, although not fail safe, did ensure we were targeting homologous genes across the Cestoda and it was cost-effective and relatively efficient at the time of the study. We aspired to make the project high throughput, utilizing available robotic devices for high throughput sequencing, when available, but rapidly discovered variable gDNA quality and the vagaries of PCR conspired to make PCR amplifications and many sequencing reactions a bespoke labor of love.

We are now in an era of relatively inexpensive next-generation sequencing (NGS), and on the cusp of high-throughput field-based genome sequencing. Certainly, where sufficient high quality DNA are available, an NGS approach to sequencing full mt genomes and full ribosomal operons, as well as providing other nuclear markers (e.g., Brabec et al., 2016; Briscoe et al., 2016), would be an enticing, albeit bioinformatically intensive proposition; the added benefit being that a genomic library would be produced and available alongside a tissue collection for future interrogation or study.

Future markers for species diagnosis. In an era in which DNA barcoding remains a goal for rapid and accurate molecular diagnosis, provision of such a marker for the Cestoda has been highly problematic. Trematode researchers have long-established the use of ITS1 and ITS2 as markers of choice, although their use in phylogenetics can be problematic (Blasco-Costa et al., 2016). The prospect of sequencing the barcoding fraction of COI *sensu* Hebert et al. (2003) has long been out of reach for parasitic flatworm workers because of the variability of the regions to which the conserved primers are needed to anneal (Vanhove et al., 2013). Even in our own study, we needed specially adapted primers to successfully amplify and sequence COI fragments, and these are not regions homologous with the recognized barcode region. Meanwhile, during the last year or so, researchers have made some considerable effort in establishing suitable PCR primers to capture the barcode region of cestodes and trematodes (Van Steenkiste et al., 2015) but one wonders whether this will be an advantage given the wealth of COI data now available for another section of the gene. Perhaps a remedial exercise in "COI barcoding" the PBI tapeworms may be desirable or required at some point, as long as it can be demonstrated that they work. In any case, the PBI tissue and DNA collection provides an excellent starting place for testing and developing new species markers.

New uses for new phylogenies. Taking any one or combinations of the four molecular markers and using these to characterize unknown species of cestode adults, eggs or larval forms, or even when examining environmental DNA (eDNA) samples, means that the PBI/GenBank data set can be interrogated for a quick diagnosis of what has been sequenced, whether by similarity search (e.g., BLAST) or phylogenetic methods. In particular, as we enter an era of broad-scale sampling of eDNA and bulk samples of hosts (fecal, gut contents, whole animal), the opportunity to recognize cestodes and provide a broad-scale diagnosis of major order, family association or even species means cestodology enters the world of molecular ecology. Bass et al. (2015) provided a useful review of applications for environmental DNA methods as applied to parasitology. Screening small invertebrate intermediate hosts using high throughput molecular approaches is also now viable and worth pursuing in order to look for infections of known, unknown, or as yet unsequenced tapeworm taxa. Screening available large eDNA data sets in which cestodes may also be present is also possible, as long as the appropriate reference datasets and markers are employed. Additionally, we are aware of large collections of larval cestodes collected from intermediate fish hosts and held in ethanol which can now be screened, perhaps identified to species or characterized as new molecular operational taxonomic units (MOTUs) in the context of the PBI / GenBank database. In turn they can be placed phylogenetically with some taxonomic, as well as perhaps some parasitological, inference. Inferring patterns of trophic transmission from one host to another, via parasitism or paratenesis, is amenable to a molecular approach and is a precursor to actually elucidating life-cycles.

Last thoughts. Finally, over recent years the community has come around to using and perhaps relying on molecular phylogenies for sense-checking comparative morphological and parasitological data, or utilizing molecular data even before assessing tapeworms morphologically. This is not to say molecular estimates of phylogeny are correct—they are certainly labile—but they are inordinately useful. We recognize that a robust phylogeny provokes a focused look at the implications for accepting certain relationships, a search for morphological synapomorphies and a vigorous discussion between all concerned as to whether we have even approached the truth when considering species circumscription and interrelationships.

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Appendix. Publications (organized by year) citing the National Science Foundation Planetary Biodiversity Inventory program grants DEB 0818696 and 0818823. * Postdoctoral fellow; † graduate student; ‡ undergraduate student (at time of the work).

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