The lecanicephalidean fauna of three species of eagle rays of the genus *Aetomylaeus* (Myliobatiformes: Myliobatidae).

by

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AUTHOR'S DISCLAIMER

All taxonomic actions in this work are hereby disclaimed for nomenclatural purposes, as recommended in Article 8 of the International Code of Zoological Nomenclature. (Ride *et al.*, 1999)

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ABSTRACT

The eagle ray genus *Aetomylaeus* comprises four species: *A. vespertilio*, *A. maculatus*, *A. niehofii,* and *A. milvus*. Five specimens of *A. vespertilio* (from Northern Australia), five of *A. maculatus* (from Borneo), and 17 of *A. niehofii* (ten from Borneo and seven from Northern Australia) were collected. While cestodes have been reported from *A. niehofii* and *A. maculatus*, no cestode data exist for *A. vespertilio*. Each ray species hosted an assemblage of species representing up to five of the seven orders of elasmobranch cestodes, with the lecanicephalideans being most diverse. The lecanicephalideans encountered were identified as belonging to the genera *Aberrapex*, *Tylocephalum*, *Polypocephalus*, and *Lecanicephalum,* and four genera new to science. *Aetomylaeus vespertilio*, *A. maculatus*, and *A. niehofii* hosted 13, ten, and seven lecanicephalidean species, respectively, with all unique and new to science. This represents the most comprehensive investigation of the cestode fauna of a genus of rays to date.

INTRODUCTION

Cestodes represent a monophyletic group of parasitic flatworms in the class Cestoda of the phylum Platyhelminthes. Commonly known as tapeworms, these mainly intestinal helminths parasitize members of all classes of vertebrates, i.e., fishes, "reptiles," amphibians, mammals, birds, and chondrichthyans (Wardle and McLeod, 1952). The greatest diversity of tapeworms is found in the latter three classes; over 900 species of tapeworms are currently known from chondrichthyans (sharks, rays, and ratfishes). Within this group, by far the greatest diversity is encountered in the elasmobranchs (sharks and rays) (Caira and Healy, 2004); collectively, ratfishes are host to only a handful of tapeworm species. In elasmobranchs, tapeworms reside in an organ called the spiral intestine (Caira and Healy, 2004).

The cestode body plan consists of an anteriorly located scolex, which is a structure used in attaching to the intestinal wall of its definitive host, and a posterior strobila, made up of individual segments, or proglottids, each containing a set of both male and female reproductive systems. Cestodes are characterized by their complete lack of a digestive system. Consequently, they absorb nutrients through their tegument (i.e., outer body covering) from the surrounding environment of their host's intestine (Caira and Littlewood, 2001). In addition, specialized microscopic surface elaborations, known as microtriches, presumably aid in nutrient absorption (Caira and Littlewood, 2001).

The approximately 900 species of elasmobranch tapeworms are distributed among seven orders, the Trypanorhyncha, Tetraphyllidea, Diphyllidea, Lecanicephalidea, Litobothriidea, Cathetocephalidea, and Rhinebothriidea. As adults, members of these orders exclusively parasitize elasmobranchs. It has been repeatedly suggested that the diversity of cestodes in these groups is highly underestimated (Caira and Healy, 2004; Jensen, 2005). Moreover, with the exception of members of the Trypanorhyncha, these tapeworms appear to

demonstrate oioxenous specificity (*sensu* Caira *et al*., 2003), with each species of tapeworm parasitizing a single elasmobranch species (Caira *et al*., 2001; Jensen, 2005). This suggests that each elasmobranch species hosts, in general, a unique assemblage of cestode species.

Of the seven orders of elasmobranch cestodes, the Lecanicephalidea are a monophyletic group of tapeworms (Caira *et al*., 1999; Caira *et al*., 2001; Jensen, 2005), mainly parasitizing rays (Jensen, 2005). Compared to the Tetraphyllidea and Trypanorhyncha, with approximately 500 and 277 species, respectively (Palm *et al*., 2009), the Lecanicephalidea is a relatively small order. Based on the most recent revision of the group by Jensen (2005), 72 species are considered valid in 14 genera, in addition to seven species that have been described since 2005 (Pramanik and Manna, 2007; Jensen, 2006). The diversity in this group appears centered in rays of the Indo-Pacific and Australian region (Jensen, 2005). Lecanicephalideans are characterized by a scolex possessing four acetabula (*sensu* Caira *et al*., 1999) that may be sucker-like or bothridiate in form, an apical organ, and a vagina that opens into the genital atrium posterior to the cirrus sac (Jensen, 2005). While not unique to this order, these features collectively distinguish lecanicephalideans from other elasmobranch tapeworms. Most interesting about this group is the vast diversity its members exhibit in the shape, size, and complexity of the apical organ. Apical organs can be small and nipple-like as in *Hornellobothrium* Shipley and Hornell, 1906, and *Healyum* Jensen, 2001, large and bulbose as in *Tylocephalum* Linton, 1890, and *Tetragonocephalum* Shipley and Hornell, 1905, or divided into tentacles as in *Polypocephalus* Braun, 1878, just to name a few. In addition, apical organs can be glandular and/or muscular combined with the ability to be retractable and/or invaginable.

Aetomylaeus Garman is a genus of eagle rays in the family Myliobatidae Bonaparte. Myliobatids are a relatively small group of elasmobranchs, inhabiting mainly inshore habitats of temperate and tropical waters (Last and Stevens, 2009). Among the four genera within this

ray family, *Aetomylaeus, Myliobatis* Cuvier*, Pteromylaeus* Garman*,* and *Aetobatus* Blainville, there are 21 recognized species (Compagno, 2005). The interrelationships of these genera remain unresolved. Studies that have included three of the four genera (i.e., *Pteromylaeus* has not been included in studies of phylogenetic relationships), however, suggest *Aetomylaeus* and *Aetobatus* to be sister taxa (Nishida, 1990; Gonzalez-Isais and Dominguez, 2004).

The genus *Aetomylaeus* is comprised of four species, but only tapeworms of three were investigated in this study: *A. vespertilio* (Bleeker), the ornate eagle ray, *A. maculatus* (Gray), the mottled eagle ray, and *A. niehofii* (Schneider), the banded eagle ray. An additional species, *A. milvus* (Valenciennes, in Müller and Henle) is often listed, however, the status of *A. milvus* as a valid species has been questioned and the possibility that this species is actually the juvenile form of either *A. maculatus* or *A. vespertilio* has been suggested (Compagno, 1999a). Molecular analysis carried out by Gavin P. Naylor at Florida State University revealed that species identified as *A. milvus* from the Persian Gulf, close to its type locality, the Red Sea, grouped apart from the other three species (personal communication).

While all three species are relatively similar in general morphology, they differ in distribution, life history, and maximum size. However, overall, relatively little is known about their biology (Last and Stevens, 2009). *Aetomylaeus vespertilio* is distributed throughout the Indo-West Pacific, ranging from Southern Mozambique, Indonesia (both Java and Borneo), and Malaysia, and from Thailand and Taiwan, in the South China Sea, to off of Northern Australia (see Fig. 1A) (Compagno, 1999b; Last and Stevens, 2009). This little-known ray is exclusively marine and benthopelagic, ranging from inshore to an offshore depth of 110 m (Compagno, 1999b). *Aetomylaeus vespertilio* is the largest of the three species, attaining a disc width of up to 350 cm and is a strong swimmer (White *et al*., 2006). The habitat may include coral reefs as well as muddy bays and banks (Compagno, 1999b; Last and Stevens, 2009).

The range of *Aetomylaeus maculatus* is more restricted from India and Sri Lanka to

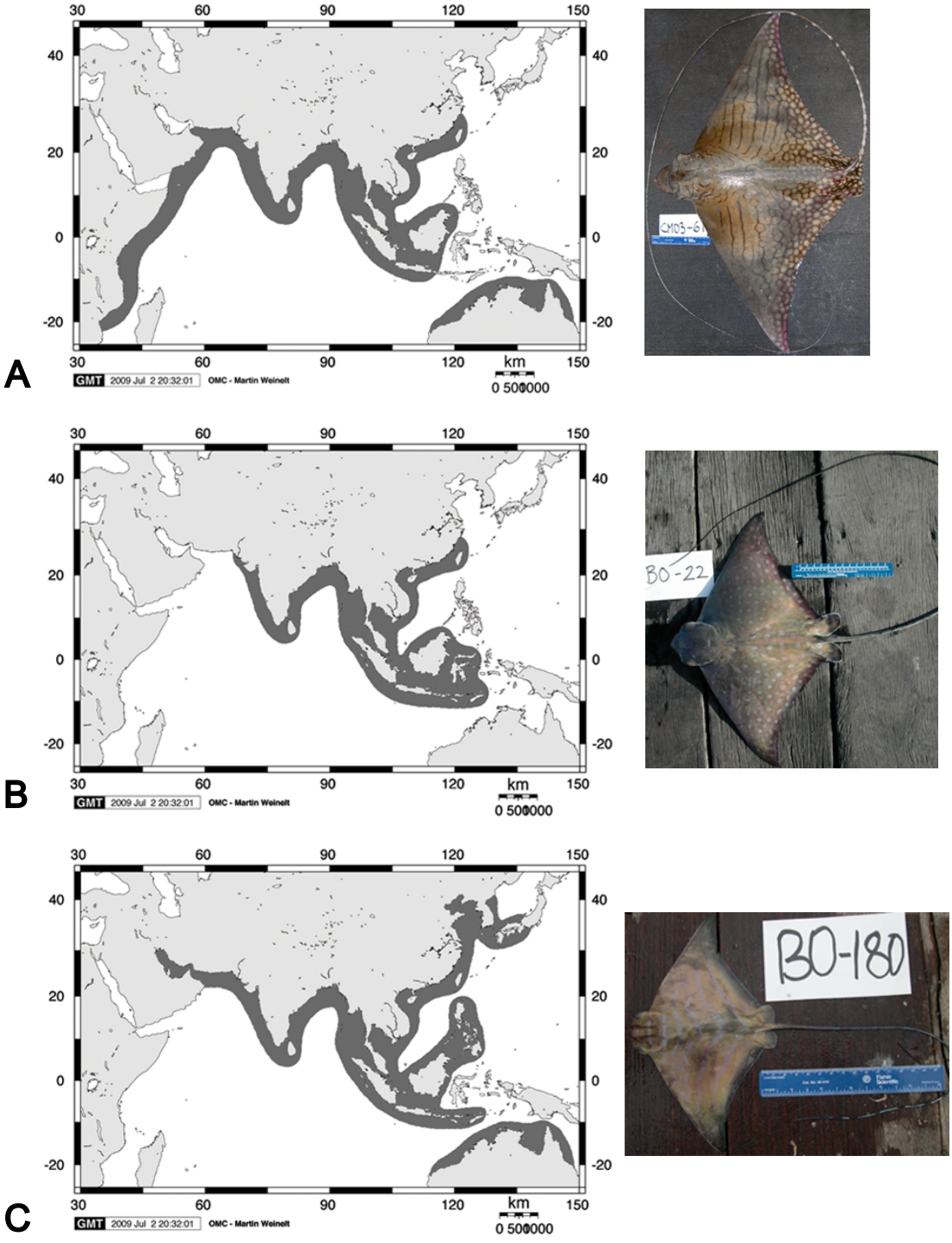

Figure 1. Distribution of *Aetomylaeus*. (A) Distribution of *A. vespertilio* and image of host specimen. (B) Distribution of *A. maculatus* and image of host specimen. (C) Distribution of *A. niehofii* and image of host specimen.

Indonesia (Java and Borneo) and Malaysia, and from Singapore to Thailand, southern China, and Taiwan (see Fig. 1B) (Compagno, 1999b; Last and Stevens, 2009). *Aetomylaeus maculatus* is found inshore in brackish and marine waters up to a depth of only 18 m (Myers, 1999). This ray is mainly associated with coral reefs, but may also inhabit mangrove creeks and protected sandy channels (Myers, 1999). *Aetomylaeus maculatus* is a smaller ray that attains a disc width of at least 78 cm (White *et al*., 2006) to possibly 200 cm (Sommer *et al*., 1996).

Aetomylaeus niehofii ranges more broadly in the Indo-West Pacific from Korea to Australia and from the Persian Gulf to the Philippines (see Fig. 1C) (Compagno, 1999b; Last and Stevens, 2009). *Aetomylaeus niehofii* occurs inshore and offshore to a depth of at least 70 m (Compagno, 1999b). This ray may enter brackish water (Michael, 1993). The smallest species in this genus, *A. niehofii* has a maximum disc width of only 72 cm (Last and Stevens, 2009).

Recently, a number of parasites in groups other than tapeworms have been described from species of *Aetomylaeus*. For example, Benz *et al*. (2007) described a new genus and species of eudactylinid copepod and Chisholm and Whittington (2009) a new genus and species of monocotylid monogenean from the gill lamellae of *Aetomylaeus vespertilio* from Australia. In addition, two new species of monogenes of the genus *Myliocotyle* each have been described from *Aetomylaeus maculatus* and *A. niehofii* from Sarawak, Malaysian Borneo (Chisholm and Whittington, 2004).

However, the cestode fauna of *Aetomylaeus* has received relatively little attention and remains poorly known. Prior to this study, no tapeworm species have been reported from *A. vespertilio*, while a few records exist for members of the orders Tetraphyllidea, Diphyllidea, and Lecanicephalidea from *A. maculatus* and *A. niehofii* (see Tab. 1): three species of tetraphyllideans (Shipley and Hornell, 1906; Shipley, 1909; Srivastav *et al*., 1995), and one species each of lecanicephalideans and diphyllideans (Shipley and Hornell, 1906) from *A.*

Table 1. Cestode species described from *Aetomylaeus* prior to this study.

Host species	Cestode species	Type locality
Aetomylaeus vespertilio	None	
Aetomylaeus maculatus		
Order Tetraphyllidea	*Acanthobothrium myliomaculata* Srivastav, Lohia & Mathur, 1995	Madras coast, India
	Rhoptrobothrium myliobatidis Shipley & Hornell, 1906	Gulf of Manaar, Sri Lanka
	Anthobothrium panjadi Shipley, 1909 [1]	Ceylon
Order Lecanicephalidea	*Tylocephalum dierama* Shipley & Hornell, 1906 [1]	Gulf of Manaar, Ceylon
Order Diphyllidea	*Diagonobothrium asymmetrum* Shipley & Hornell, 1906 [1]	Dutch Bay, Ceylon
Aetomylaeus niehofii		
Order Tetraphyllidea	*Rhoptrobothrium chongi* Jensen & Caira, 2006	Mukah, Sarawak, Malaysia
	Rhoptrobothrium gambangi Jensen & Caira, 2006	Mukah, Sarawak, Malaysia
	Rhoptrobothrium limae Jensen & Caira, 2006	Sematan, Sarawak, Malaysia
	Acanthobothrium hanumantharaoi Rao, 1977 [2]	Waltair Coast, Bay of Bengal
	Acanthobothrium rhynchobatidis Subhapradha, 1955 [3]	Madras coast, India
	Myliobatibothrium alii Shinde & Mohekar, 1983 [2]	Arabian Sea, Ratnagiri, India
	Myliobatibothrium singhi Sarwade, Shinde, Pawar & Mahajan, 1995 [4]	Aurangabad, India

[1] The type host was given as *Myliobatis maculata.*

[2] The type host was given as *Myliobatus nieuhofii* [sic].

[3] This species was reported from *Aetomylaues nicofii* [sic] from Queensland, Australia by Campbell & Beveridge (2002). The type host is *Rhynchobatus djiddensis*.

[4] The type host was given as *Myliobatus nieullofii* [sic].

maculatus, and seven species of tetraphyllideans from *A. niehofii* (Subhapradha, 1955; Rao, 1977; Shinde and Mohekar, 1983; Sarwade *et al*., 1995; Campbell and Beveridge, 2002; Jensen and Caira, 2006). The most recent work on the tapeworms of this group of rays was conducted by Jensen and Caira (2006) who described three new species of the tetraphyllidean genus *Rhoptrobothrium* Shipley and Hornell, 1906 from *Aetomylaes maculatus* and *A. niehofii*.

Surprisingly, only a single lecanicephalidean species has been described from any of the *Aetomylaeus* species. However, 12 species of lecanicephalideans have been reported from *Aetobatus narinari* (see Jensen, 2005; Pramanik and Manna, 2007; Caira *et al.,* 2009), one of three species in the genus considered sister to *Aetomylaeus*. This suggested that, potentially, a similarly diverse lecanicephalidean fauna could be expected from species of *Aetomylaeus*.

Extensive collections of elasmobranchs over the last ten years from both Malaysian and Indonesian Borneo and Northern Australia resulted in a number of specimens of three species of *Aetomylaeus*. While specimens of *A. vespertilio* and *A. maculatus* were only collected from Australia and Borneo, respectively, specimens of *A. niehofii* were collected from both Malaysian and Indonesian Borneo as well as off of Northern Australia. These two localities are divided geographically by a deepwater trench running southwest from the southern tip of the Philippines and between Borneo and Sulawesi and between Bali and New Guinea, otherwise known as Wallace's Line (Lomolino *et al*., 2006). This geographic feature is well known in regard to the distinct differences in the terrestrial biotas of the Oriental and Australiasian zoogeographic regions. This distinction is due to the exposure and separation during the Pleistocene (1.8 million to 10,000 years ago) of the Sunda Shelf, which is part of the Southeast Asian continental shelf, and Sahul Shelf, which connects Australia and New Guinea (Voris, 2000; Lomolino *et al*., 2006). Thus, while the existence of Wallace's Line for terresterial organisms is well documented, it has also been suggested as a barrier

for some marine species (Barber *et al*., 2000; Lourie *et al*., 2004). Because this substantial geographic feature segregates the waters of Borneo and Northern Australia, any patterns in the lecanicephalidean fauna of *A. niehofii* specimens collected from both of these localities would be in support of this idea.

This study sought to examine the lecanicephalidean fauna of three species of *Aetomylaeus* for which little to no information was available prior to this study. The main goals were to (1) characterize and identify all lecanicephalidean species found to parasitize *A. vespertilio, A. maculatus*, and *A. niehofii*, (2) describe at least a subset of the new lecanicephalidean genera and species encountered, (3) compare the lecanicephalidean species, their composition and diversity at the genus and species levels among *A. vespertilio*, *A. maculatus*, and *A. niehofii*, and (4) document patterns in the lecanicephalidean fauna of *A. niehofii* specimens collected from the disparate localities of Borneo and Northern Australia.

MATERIALS AND METHODS

Collections

A total of five specimens of *Aetomylaeus vespertilio* from Northern Australia were examined. These rays were collected either with gill nets or by a commercial trawling vessel. The five specimens consisted of one immature female (disk width [DW] 95 cm) collected off Weipa (12°40'S, 141°52'E), Queensland, Gulf of Carpenteria on May 15, 2004; two females (DW 148 and 150 cm) collected off Buffalo Creek (12°20'S, 130°54'39"E), Darwin, Northern Territory, Timor Sea on August 6, 1997; one female (DW 86 cm) collected east of the Wessel Islands (11°17'S, 136°59'E) off the Northern Territory, Arafura Sea between November 11 and 22, 1999; and one specimen (sex and DW unknown) collected off Cairns (16°52'S, 145°16'E), Queensland, Pacific Ocean on July 8, 2002.

A total of five specimens of *Aetomylaeus maculatus* from both Malaysian and Indonesian Borneo were examined. Rays were collected mainly by trawling. Specimens from Malaysian Borneo consisted of one immature female (DW 43 cm) collected off Sematan (01°48'N, 109°46'E), Sarawak, South China Sea on June 3, 2002; one immature male and one female (DW 29 and 36 cm, respectively) collected off Sematan (01°48'N, 109°46'E), Sarawak, South China Sea on May 15, 2003. Specimens from Indonesian Borneo consisted of one immature male (DW 38 cm) collected off Kota Baru (03°14'S, 116°13'E), South Kalimantan, Makassar Strait on November 28, 2006; and one female (DW 35 cm) collected off Kalepseban (03°14'S, 112°54'E), Central Kalimantan, Java Sea on December 4, 2006.

A total of seventeen specimens of *Aetomylaeus niehofii* from Malaysian and Indonesian Borneo, as well as Northern Australia were examined. All rays were collected by trawling. Specimens from Malaysian Borneo consisted of three females (DW 42, 50, and 35 cm, respectively) collected off Mukah (02°53'N, 112°05'E), Sarawak, South China Sea on June 8, 9, and 11, 2002, respectively; and one immature male and one female (DW 20 and

22 cm, respectively) collected off Sematan (02°53'N, 112°05'E), Sarawak, South China Sea on May 13 and 15, 2003, respectively. Specimens from Indonesian Borneo consisted of one female (DW 45 cm) and one male (DW 45 cm) collected off Manggar (01°12'S, 116°58'E), East Kalimantan, Makassar Strait on November 22, 2006 and August 3, 2008, respectively; one immature male (DW 29 cm) collected off Muara Kintap (03°54'S, 115°15'E), South Kalimantan, Makassar Strait on November 30, 2006; one female (DW 35 cm) collected off Takisung (03°54'N, 114°36'E), South Kalimantan, Java Sea on December 2, 2006; and one female (DW 31 cm) collected off Sepuk Laut (00°12'S, 109°05'E), West Kalimantan, South China Sea on July 13, 2008. Specimens from Northern Australia consisted of five males (DW 49, 44, 53, 43, and 33 cm) and two females (DW 58 and 44 cm) collected east of the Wessel Islands (11°17'S, 136°59'E), Northern Territory, Arafura Sea on November, 1999.

In the field, the body cavity of each host specimen was opened via a ventral longitudinal incision from the anus to the pericardial chamber and the spiral intestine was removed. Each spiral intestine was opened by a longitudinal incision. Cestodes encountered were immediately removed and fixed in vials in 10% formalin buffered with seawater and later transferred to 70% ethanol for storage. The spiral intestines and their contents were fixed in 10% formalin buffered with seawater and later transferred to 70% ethanol for storage. A piece of liver tissue from each individual was preserved in 95% ethanol for later confirmation of host species identification.

Specimen preparation

At the University of Kansas, the spiral intestines were examined for cestodes using a dissecting microscope in the laboratory. All cestode specimens were sorted to order and lecanicephalideans further sorted to genus. Lecanicephalidean specimens prepared as whole mounts for examination with light microscopy were hydrated in distilled water, stained

with Delafield's hematoxylin, differentiated in tap water, destained in 70% acid ethanol, alkalinized in 70% basic ethanol, dehydrated in a graded ethanol series, then cleared in methyl salicylate, and mounted in Canada balsam on glass slides.

Lecanicephalidean whole worms and scoleces prepared for scanning electron microscopy (SEM) were hydrated in a graded ethanol series, post-fixed in 1% osmium tetroxide overnight, washed in distilled water, dehydrated in a graded ethanol series, transferred to hexamethyldisilizane (HMDS) for 20 minutes, air-dried, and mounted on aluminum stubs on double-sided adhesive carbon tape. Specimens were sputter coated with *c*.300Å of gold and examined with a Zeiss LEO 1550 field emission scanning electron microscope at the Microscopy and Analytical Imaging Laboratory, University of Kansas, Lawrence, Kansas, USA.

Selected lecanicephalidean whole worms, scoleces, and proglottids prepared as histological sections were dehydrated in a graded ethanol series, cleared in xylene, and embedded in paraffin wax according to conventional techniques. Serial sections were cut at 7 µm intervals using a TBS OLYMPUS CUT 4060 microtome, attached to glass slides by floating sections on 3% sodium silicate solution and air-drying. Sections were subsequently stained with Delafield's haematoxylin, counterstained with eosin, differentiated in Scott's solution, dehydrated in a graded ethanol series, cleared in xylene, and mounted in Canada balsam.

Selected lecanicephalidean scoleces and proglottids were prepared as histological sections and stained using an adaptation of McManus' periodic acid-Shiff (PAS) reaction (Sheehan and Hrapchak, 1987) in order to visualize glandular tissues. Sections were placed in xylene to remove the paraffin, hydrated in a graded ethanol series followed by distilled water, immersed in periodic acid, rinsed in distilled water, immersed in Shiff"s reagent, rinsed in very warm distilled water (~55°C), washed in running tap water, counterstained in Harris's

hematoxylin, washed again in running tap water, dehydrated in a graded ethanol series, cleared in xylene, and mounted in Canada balsam.

Line drawings were made using a drawing tube attached to a Zeiss Axioskop 2 Plus. Light microscopy images of whole mounts and histological sections were taken using a Leica FireCam DFC 320 of DFC 480 and a scale bar was added in ImageJ 1.36b. Measurements were taken using a computer video imaging system using a Leica Firecam DFC 320 digital camera mounted on a Zeiss Axioscop 2 Plus and the image analysis program Openlab Demo Version 4.0.4. Reproductive organs were measured in mature proglottids only. Measurements are given in micrometers (μm) unless otherwise indicated, and are provided as the range followed in parentheses by the mean, standard deviation, number of worms examined, and the total number of measurements if more than one measurement was taken per worm.

Ecological terms are defined as follows (*sensu* Bush *et al*., 1997): 1) Prevalence is defined as the number of hosts infected by a parasite species divided by the number of hosts examined (expressed as a percentage) 2) Intensity is defined as the number of parasites of a species infecting a host individual 3) Infracommunity is defined as all parasites of different species in a host individual). Host taxonomy follows Last and Stevens (2009), and Compagno (1999a). Microtriche terminology follows Faliex *et al*. (2000).

Museum abbreviations are used as follows: IPCAS, Institute of Parasitology, ASCR, Ceské Budejovice, Czech Republic; LRP, Lawrence R. Penner Parasitology Collection, Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut, U.S.A.; MZUM, Muzium Zoologi, Universiti Malaya, Kuala Lumpur, Malaysia; MZB, Museum Zoologicum Bogoriense, Center for Biology, Indonesian Institute of Science, Cibinong, Jakarta-Bogor, Java, Indonesia; QM, Queensland Museum, Queensland, Australia; SBC, Sarawak Biodiversity Center, Kuching, Sarawak, Malaysia; USNPC, United States National Parasite Collection, Beltsville, Maryland, U.S.A.

Maps of host distributions and lecanicephalidean faunal comparisons were generated using Online Map Creation (version 4.1) (http://www.aquarius.ifm-geomar.de), using GMT (The Generic Mapping Tools) (Wessel and Smith, 1998).

RESULTS

Of the 27 *Aetomylaeus* host specimens examined, only one specimen of *A. vespertilio* was not infected with tapeworms; the other 26 specimens were parasitized by tapeworms. A total of approximately 550 lecanicephalidean whole mounts were prepared and examined for this study. Collectively, members of five of the seven orders of elasmobranch cestodes were found to parasitize specimens of the three species of *Aetomylaeus*. They were the Lecanicephalidea, Tetraphyllidea, Rhinebothriidea, Diphyllidea, and Trypanorhyncha. Members of the Cathetocephalidea and Litobothriidea were not encountered in this system. Members of the Lecanicephalidea were represented by the greatest diversity both in terms of number of genera and species in each of the three ray species. A total of 30 distinct lecanicephalidean species across ten genera were found to parasitize the members of the genus *Aetomylaeus* (see Tab. 2). While it is apparent that elasmobranch cestodes seem to demonstrate oioxenous specificity, this is not assumed and does not guide species identification. The lecanicephalidean species within and among the three *Aetomylaeus* species were determined to be distinct from one another. In contrast, relatively fewer genera and species of members of the other four cestode orders were present in these rays. While the lecanicephalidean fauna of each host species will be addressed in detail in separate sections, more general observations regarding the presence of members of the other four orders are given here.

Aetomylaeus vespertilio hosted members of the orders Tetraphyllidea,

Table 2. Number of lecanicephalidean species in each genus reported from *Aetomylaeus* at the conclusion of this study.

	A. vespertilio	***A. maculatus***	***A. niehofii***
Lecanicephalidean genus			
Rexapex n. gen.	1 sp.		
Collicocephalus n. gen.	1 sp.		
Aberrapex Jensen, 2001	1 sp.		
Elicilacunosus n. gen.		1 sp.	3 spp.
Tylocephalum Linton, 1890	6 spp.	6 spp.	
Polypocephalus Braun, 1878	2 spp.	2 spp.	1 sp.
Lecanicephalum Linton, 1890		1 sp.	
New genus			3 spp.
Unidentified genus 1	1 sp.		
Unidentified genus 2	1 sp.		
Total	13 spp.	10 spp.	7 spp.

Rhinebothriidea, and Trypanorhyncha. All three orders were present in three of the five host specimens, while only tetraphyllideans and/or rhinebothriideans were present in the fourth host specimen, albeit in low numbers and poor condition. Trypanorhynchs were found in three of the five host specimens. Diphyllideans were not encountered. No tapeworms were found in the fifth host specimen possibly due to its poor condition (i.e., lack of freshness).

Aetomylaeus maculatus was parasitized by members of the Tetraphyllidea, Rhinebothriidea, and Diphyllidea. The tetraphyllidean genus *Rhoptrobothrium* was found in three of the five rays. One of these three *A. maculatus* specimens was parasitized by additional tetraphyllideans and/or rhinebothriideans. Diphyllideans were recovered from two of the five specimens. Trypanorhynchs were conspicuously absent from specimens of *A. maculatus*.

Aetomylaeus niehofii revealed members of the Tetraphyllidea, Rhinebothriidea, Trypanorhyncha, and Diphyllidea. The tetraphyllidean genus *Rhoptrobothrium* was

represented in seven of the 17 host specimens. Tetraphyllideans and/or rhinebothriideans were found in two of these seven as well as an additional *A. niehofii* specimen. Diphyllideans were present in 12 of the 17 host individuals. Trypanorhynchs infected the seven specimens collected in the Arafura Sea off Northern Australia, but only one additional specimen from Kalimantan, Borneo.

Lecanicephalidean Fauna of *Aetomylaeus vespertilio*

A total of 13 lecanicephalidean species in seven different genera were identified as parasitizing specimens of *Aetomylaeus vespertilio* (Tab. 3). Two of these species exhibited scolex morphologies that did not allow placement into any of the currently recognized lecanicephalidean genera. Consequently, two new genera, *Rexapex* and *Collicocephalus*

Table 3. Lecanicephalidean infracommunities in specimens of *Aetomylaeus vespertilio*.

Specimen No.	**CMO3-61**	**AU-42**	**AU-43**	**NT-56**	**CMJ-7**
Species					
Rexapex nanus n. gen., n. sp.	X				
Collicocephalus baggioi n. gen., n. sp.	X				
Aberrapex weipaensis n. sp.	X	X			
Tylocephalum n. sp. 1	X	X		uninfected	uninfected
Tylocephalum n. sp. 2	X				
Tylocephalum n. sp. 3	X				
Tylocephalum n. sp. 4	X	X	X		
Tylocephalum n. sp. 5	X	X	X		
Tylocephalum n. sp. 6		X			
Polypocephalus n. sp. 1	X	X			
Polypocephalus n. sp. 2		X			
Unidentified genus 1 n. sp. 1		X			
Unidentified genus 2 n. sp. 1		X			

are diagnosed below. A total of nine species were identified as representing three currently recognized genera: *Aberrapex*, *Tylocephalum*, and *Polypocephalus*. Finally, three to six specimens each of two additional, morphologically distinct species were identified. These specimens could not be easily attributed to currently recognized lecanicephalidean genera given the low number of specimens at hand. Preliminary identification suggests these two species to be distinct from all other species discovered in this study, and to possibly represent an additional two new genera. At this time, however, these two species are referred to as "Unidentified genus 1 sp. 1" and "Unidentified genus 2 sp. 1."

With respect to the number of species in each genus, only one species each of the two new genera, *Aberrapex,* and the two unidentified genera were found in *A. vespertilio*. In contrast, a considerable six congeners of *Tylocephalum* were identified. The genus *Polypocephalus* was represented by two congeners in this host. All 13 lecanicephalidean species were identified as being new to science.

Descriptions of New Taxa

Rexapex **n. gen.**

Generic Diagnosis

Worms euapolytic. Scolex with 4 acetabula, apical modification of the scolex proper, and apical organ. Acetabula bothridiate in form, free anteriorly and posteriorly. Apical modification of scolex proper in form of shallow dome with pore-like aperture at center, housing apical organ. Apical organ retractable, muscular, non-glandular, in form of inverted cone with 18 short, finger-like projections surrounding circular anterior-most pad when everted.

Scolex covered with elongate to long filitriches; anterior margin of rims of acetabula

and anterior margin of apical modification of scolex proper also covered with blade-like spinitriches. Strobila covered with long filitriches, becoming shorter and more conical toward posterior margins of each proglottid.

Cephalic peduncle absent. Proglottids craspedote, non-laciniate. Immature proglottids at anterior of strobila conspicuously laterally expanded. Testes in single column, anterior to ovary. Vas deferens expanded to form conspicuous external seminal vesicle. External seminal vesicle saccate, extending from ootype region anteriorly to posterior margin of cirrus sac. Internal seminal vesicle absent. Cirrus sac pyriform. Cirrus unarmed. Ovary H-shaped in frontal view, bilobed in cross-section. Vagina extending laterally in mature proglottids with testes (medially in mature proglottids in which testes are degenerated) from ootype region to gential atrium, opening posterior to cirrus sac into genital atrium. Genital pores lateral. Uterus medial, saccate. Vitellaria follicular, in 4 columns, 2 columns on each lateral margin of proglottid, extending from anterior margin of proglottid to anterior margin of ovary, slightly overlapping ovary. Single pair of excretory ducts. Eggs unknown. In spiral intestine of *Aetomylaeus* Bloch and Schneider, 1801 (Myliobatidae). Northern Australia.

Taxonomic Summary

Type and only species: *Rexapex nanus* n. gen., n. sp.

Etymology: *Rex*, L. king. This genus was named for its apical organ, which when everted resembles a crown.

Remarks

Its possession of a scolex with four acetabula and an apical organ, a vagina opening into the genital atrium posterior to the cirrus sac, and the presence of an extensive external seminal clearly places *Rexapex* n. gen. in the order Lecanicephalidea.

Rexapex n. gen. can be distinguished from *Paraberrapex* Jensen, 2001, and *Aberrapex* based on its possession of an apical organ, rather than the lack thereof. Moreover, *Rexapex* n. gen. can be distinguished from the remaining ten lecanicephalidean genera currently recognized by its unusual shape of the apical organ in the form of a crown (i.e., an apical muscular pad with 18 finger-like projections on the periphery). It can be further distinguished from *Eniochobothrium* Shipley and Hornell, 1906, *Healyum, Hornellobothrium, Lecanicephalum, Paraberrapex, Tetragonocephalum*, and *Tylocephalum* by its possession of testes in a single column rather than in several columns. Despite the superficial resemblence of the finger-like projections on the apical organ of *Rexapex* n. gen. to the apical organ divided into tentacles of *Polypocephalus*, the two genera are otherwise very different morphologically. *Rexapex* n. gen. can be easily distinguished from *Polypocephalus* in its possession of immature proglottids that are laterally expanded and the presence of one pair of excretory ducts rather than two pairs. A bilobed ovary in cross-section is characteristic of *Rexapex* n. gen. while the ovary of *Corrugatocephalum* Caira, Jensen, and Yamane, 1997, and *Quadcuspibothrium* Jensen, 2001, are trilobed and that of *Aberrapex* is tetralobed in cross-section. *Rexapex* n. gen. is superficially most similar to *Hornellobothrium* in its possession of laterally expanded immature proglottids. However, unlike the non-eversible glandular apical organ of *Hornellobothrium*, *Rexapex* n. gen. possesses an eversible, highly muscular apical organ.

***Rexapex nanus* n. gen., n. sp.**

(Figs. 2-4)

Description

Based on 18 specimens: 14 whole mounts of mature worms, cross-sections of 2 mature

proglottids, and 2 whole worms prepared for SEM.

Worms 910-2,017 (1,414 ± 363; 14) long; maximum width at terminal proglottid, euapolytic; proglottids 22-30 (25 ± 2; 14) in number. Scolex 43-58 (51 ± 5; 14) long by 39-70 (55 ± 10; 14) wide, consisting of 4 acetabula, apical modificaton of scolex proper, and apical organ. Acetabula bothridiate in from, cup-shaped, free anteriorly and posteriorly, 23-30 (27 ± 2; 11; 20) long by 20-29 (25 ± 3; 11; 20) wide. Apical modification of scolex proper with pore-like aperture at center, housing apical organ. Apical organ muscular, retractable, non-glandular, when everted in form of inverted cone with 18 short, finger-like projections surrounding circular anterior-most pad, 36-50 (44 ± 4; 14) long by 32-59 (47 ± 9; 14) wide when retracted.

Rims of acetabula covered with blade-like spinitriches and long filitriches (Fig. 3D, E); blade-like spinitriches absent from posterior margin of rim. Distal acetabular surface and surface of scolex proper covered with elongate filitriches (Fig. 3G); anterior margin of apical modification of scolex proper also covered with blade-like spinitriches forming band around base of everted apical organ (Fig. 3B, F). Strobila covered with long filitriches becoming shorter and more conical toward posterior margins of each proglottid (Fig. 3H, I); microtriches on more mature proglottids longer than those on immature proglottids.

Cephalic peduncle absent. Proglottids craspedote, non-laciniate. Immature proglottids at anterior of strobila conspicuously expanded laterally. Immature proglottids 21-29 (24 ± 2; 14) in number, initially wider than long, becoming longer than wide with maturity; posterior-most immature proglottid 149-485 (264 ± 91; 14) long by 85-162 (111 ± 26; 14) wide. Mature proglottids 1 or 2 in number; mature proglottids with testes 394-822 (579 ± 124; 8) long by 100-173 (137 ± 21; 8) wide; mature proglottids in which most testes are degenerated 439-844 (602 ± 148; 6) long by 128-193 (158 ± 26; 6) wide. Testes 9-14 (12 ± 1; 14) in number, 17-66 (31 ± 13; 14; 42) long by 32-92 (63 ± 16; 14; 42) wide, in single field, extending from

just posterior to anterior margin of proglottid to ovary, slightly overlapping anterior margin of ovary, 1 column in frontal view, 1 row deep in cross-section (Fig. 6A), post-ovarian testes absent. Vas efferens not observed. Vas deferens in fully mature proglottids in which testes are degenerated enlarged to form conspicuous external seminal vesicle; external seminal vesicle extensive, saccate, extending more or less along mid-line of proglottid from ootype region anteriorly to cirrus sac. Internal seminal vesicle not observed. Cirrus sac pyriform, slightly angled anteriorly, 58-86 (71 ± 9; 8) long by 43-84 (65 ± 13; 8) wide in maturing proglottids with testes, 84-106 (93 ± 8; 6) long by 48-88 (75 ± 16; 6) wide in fully mature proglottids in which testes are degenerated, containing coiled cirrus. Cirrus microtriches not observed. Ovary H-shaped in frontal view, bilobed in cross-sections (Fig. 4C), 91-233 (159 ± 43; 8) long by 68-111 (88 ± 17; 8) wide in maturing proglottids with testes, 56-301 (183 ± 79; 6) long by 93-155 (116 ± 22; 6) wide in fully mature proglottids in which testes are degenerated, lobulated, symmetrical; ovarian bridge at center of ovary. Mehlis' gland present posterior to ovarian bridge. Vagina extending laterally in mature proglottids with testes (medially in mature proglottids in which testes are degenerated) from ootype region to genital atrium, opening posterior to cirrus sac into genital atrium. Genital pores lateral, irregularly alternating, 48-63% (56 ± 4; 14) of proglottid length from posterior end. Uterus saccate, extending along mid-line of proglottid from ovarian bridge to anterior margin of proglottid. Vitellaria follicular, medullary, lateral, in 4 columns, 2 follicles on each lateral margin of proglottid in cross-section (Fig. 4B), extending from posterior to anterior margin of proglottid to anterior margin of ovary, slightly overlapping ovary in few specimens; vitelline follicles 10-35 (19 ± 8; 8; 24) long by 13-42 (24 ± 8; 8; 24) wide in maturing proglottids with testes, 13-41 (23 ± 8; 6; 18) long by 25-75 (50 ± 13; 6; 18) wide in fully mature proglottids in which testes are degenerated. Single pair of excretory ducts (Fig. 4B). Eggs not observed.

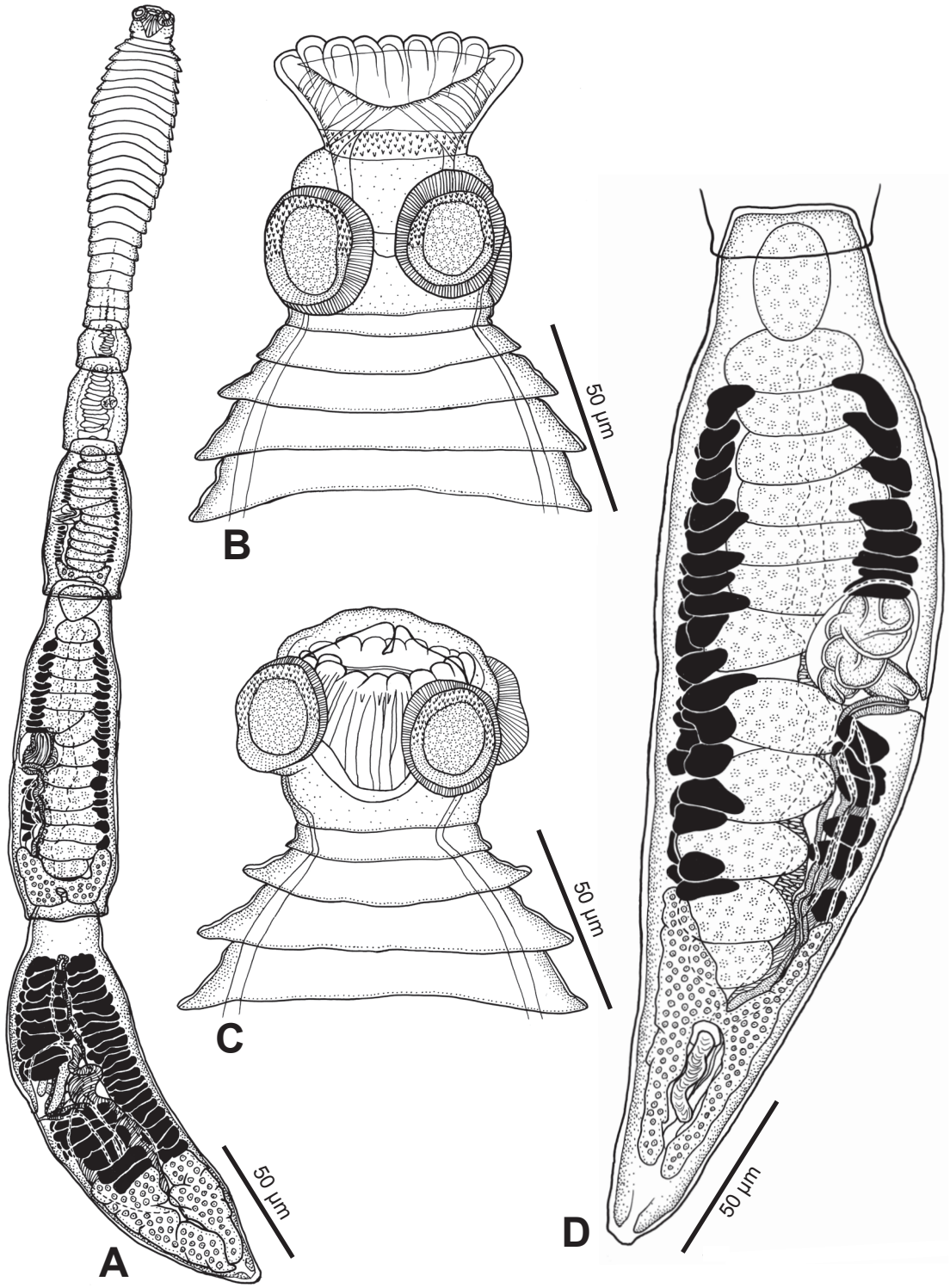

Figure 2. Line drawings of *Rexapex nanus* n. gen., n. sp. (A) Whole worm. (B) Scolex with apical organ everted. (C) Scolex with apical organ retracted. (D) Mature terminal proglottid.

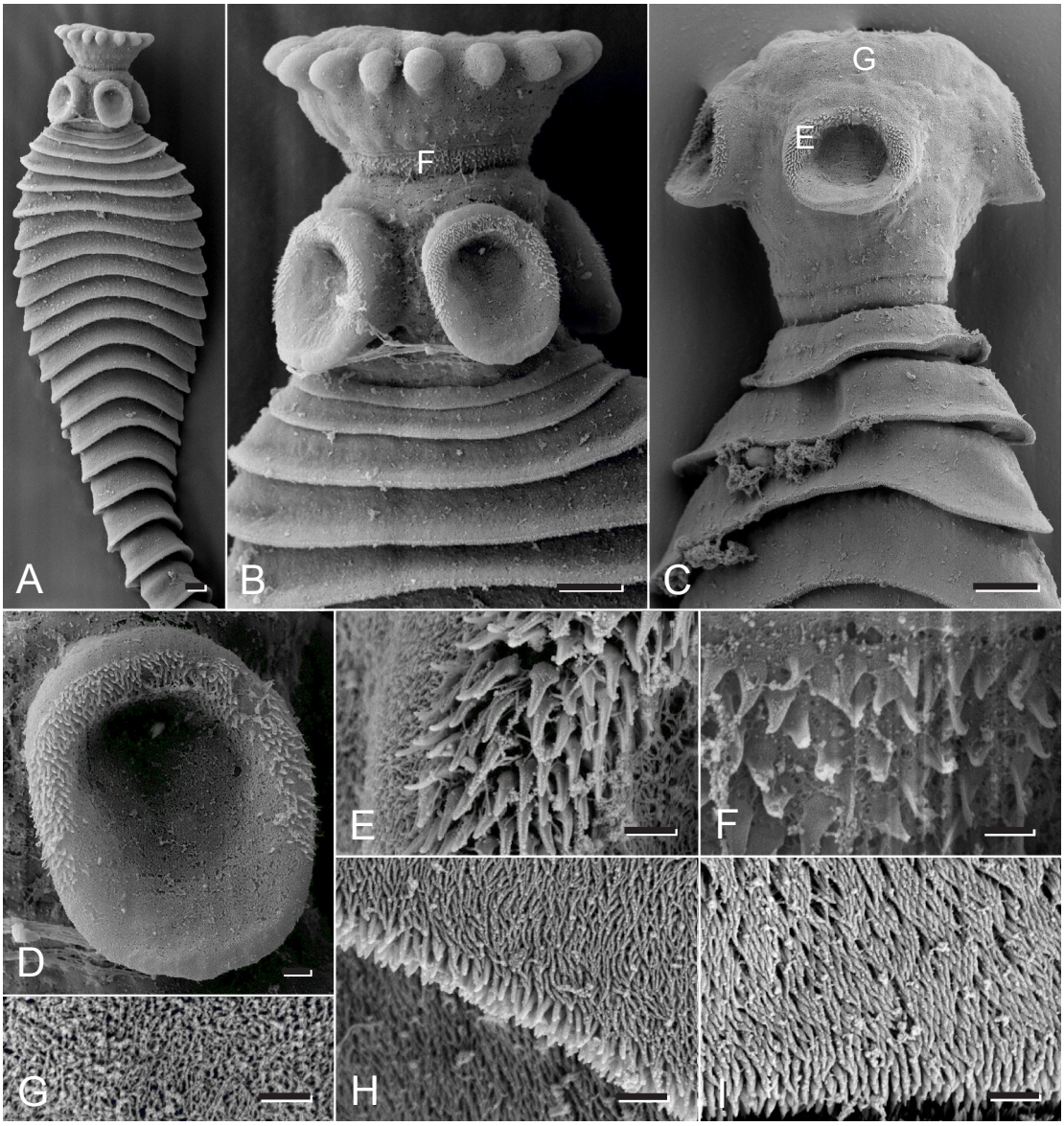

Figure 3. Scanning electron micrographs of *Rexapex nanus* n. gen., n. sp. (A) Scolex and anterior strobila. (B) Scolex with apical organ everted. Small letter indicates location of details shown in Fig. F. (C) Scolex with apical organ retracted. Small letters indicate location of details shown in Figs. E and G. (D) Enlarged view of sucker. (E) Microtriches on sucker rim. (F) Microtriches on apical modification of scolex proper. (G) Microtriches on scolex proper. (H) Microtriches on posterior margin of anterior proglottid. (I) Microtriches on posterior margin of posterior proglottid. Scale bars: A-C = 10 μm; D = 2 μm; E-I = 1 μm.

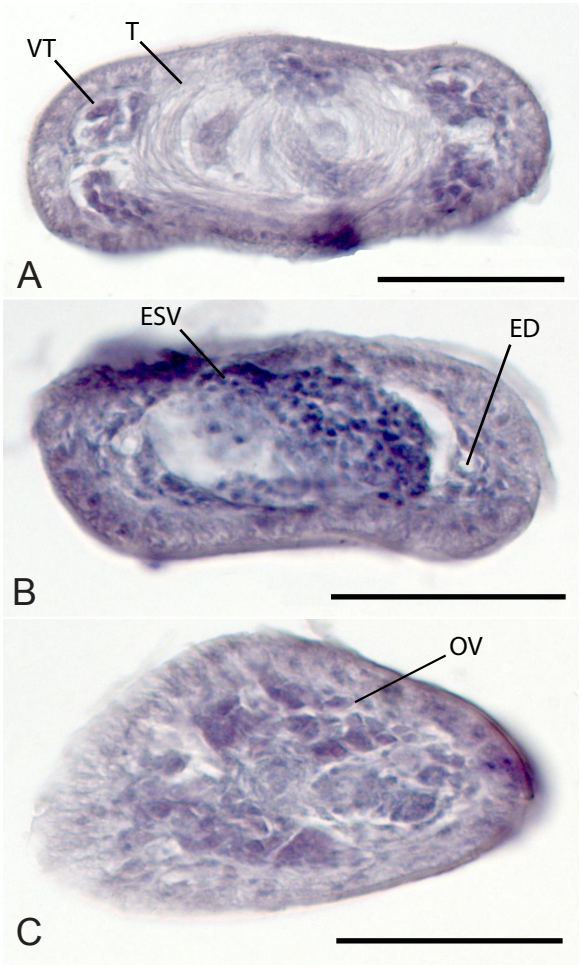

Figure 4. *Rexapex nanus* n. gen., n. sp. (A) Cross-section through mature proglottid at level of testes, showing one testis, and 4 vitelline follicles. (B) Cross-section through mature proglottid at level of external seminal vesicle, showing 2 excretory ducts. (C) Cross-section through mature proglottid at level of bilobed ovary. Abbreviations: ED, excretory duct; ESV, external seminal vesicle; OV, ovary; T, testis; VT, vitelline follicle. Scale bars: A-C = 50 μm.

Taxonomic Summary

Type host: *Aetomylaeus vespertilio* (Bleeker, 1852), the ornate eagle ray (Myliobatiformes: Myliobatidae).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Off Weipa (12°40’S, 141°52’E), Queensland, Australia, Gulf of Carpenteria.

Type specimens: Holotype (QM No. G000000), five paratypes (four whole mounts and one proglottid cross-section) (QM Nos. G000000); five paratypes (USNPC Nos. 00000); six paratypes (five whole mounts and one proglottid cross-section) (LRP Nos. 0000 – 0000). Two whole worms prepared for SEM retained in the personal collection of Dr. Kirsten Jensen at the University of Kansas.

Prevalence: 20% (i.e., 1 of 5 host individuals examined).

Etymology: *Nanus*, L. dwarf. This species was named for its small size.

Collicocephalus **n. gen.**

Generic Diagnosis

Worms euapolytic. Scolex with 4 acetabula, apical modification of scolex proper, and apical organ. Acetabula in form of suckers. Apical modification of scolex proper with large aperture at center, housing apical organ. Apical organ retractable, large, muscular, with glandular surface, in form of oval pad when everted.

Rims of acetabula covered with blade-like spinitriches and long filitriches. Distal surfaces of acetabula and scolex proper covered with long filitriches. Apical organ covered with short filitriches. Strobila covered with elongate to long filitriches.

Cephalic peduncle absent. Proglottids craspedote, laciniate. Testes in 2 columns, anterior to ovary. Vas deferens expanded to form conspicuous external seminal vesicle. External seminal vesicle saccate, extending from ootype region anteriorly to anterior margin of cirrus sac. Internal seminal vesicle absent. Cirrus sac pyriform. Cirrus unarmed. Ovary H-shaped in frontal view, tetralobed in cross-section. Vagina extending laterally in mature proglottids with testes (medially in mature proglottids in which testes are degenerated) from

ootype region to to gential atrium, opening posterior to cirrus sac into genital atrium. Genital pores lateral. Uterus medial, saccate. Vitellaria follicular, in 4 columns, 2 columns on each lateral margin of proglottid, extending from just posterior to anterior margin of proglottid to anterior margin of ovary, slightly overlapping ovary. Single pair of excretory ducts. Eggs unknown. In spiral intestine of *Aetomylaeus* Bloch and Schneider, 1801 (Myliobatidae). Northern Australia.

Taxonomic summary

Type and only species: *Collicocephalus baggioi* n. sp.

Etymology: *Kollix, -ikos*, Gr., roll or loaf of bread. This genus was named for the shape of its apical organ which, when everted, due to its oblong and puffy appearance, resembles a loaf of bread.

Remarks

Its possession of a scolex consisting of four acetabula in the form of suckers and an apical organ, a vagina opening into the genital atrium posterior to the cirrus sac, and the presence of an extensive external seminal vesicle clearly place *Collicocephalus* n. gen. in the order Lecanicephalidea.

Collicocephalus n. gen. can be distinguished from *Paraberrapex* and *Aberrapex* based on its possession of an apical organ, rather than the lack thereof. Moreover, its possession of a large, muscular, retractable apical organ clearly distinguishes it from *Eniochobothrium*, *Hornellobothrium*, *Healyum*, and *Quadcuspibothrium*, which possess small, conical, glandular apical organs, and *Polypocephalus*, which possesses an apical organ divided into tentacles. The testes are arranged in two columns in *Collicocephalus* n. gen., while they are in a single column in *Anteropora*. Unlike the craspedote and laciniate proglottids of *Collicocephalus* n.

gen., the proglottids of *Tetragonocephalum* are neither craspedote nor laciniate. This genus differs from *Tylocephalum* in its possession of a retractable apical organ. A tetralobed ovary in cross-section is characteristic of *Collicocephalus* n. gen., while that of *Corrugatocephalum* is trilobed in cross-section. *Collicocephalus* n. gen. is distinct from *Rexapex* in its possession of acetabula that are sucker-like rather than bothridiate in form, and lack of laterally expanded anterior proglottids. *Collicocephalus* n. gen. is most similar to *Lecanicephalum*. It can, however, be distinguished from the latter genus in that its proglottids are craspedote and laciniate, rather than only weakly craspedote, as well as its lack of post-ovarian vitellaria. Moreover, the distinctive circular muscle bundles of the apical organ described in *Lecanicephaum* are absent in *Collicocephalus* n. gen.

Collicocephalus baggioi **n. gen., n. sp.**

(Figs. 5-7)

Description

Based on 28 specimens: 16 whole mounts of mature worms, frontal sections of 2 scoleces with apical organ everted, frontal sections of 2 scoleces with apical organ retracted, cross-sections of 1 mature proglottid, and 6 scoleces and 1 whole worm prepared for SEM.

Worms 2,088-5,140 (3,142 ± 915; 16) long; maximum width at scolex, euapolytic; proglottids 20-71 (39 ± 16; 16) in number. Scolex 129-203 (161 ± 24; 11) long by 218-350 (291 ± 34; 14) wide, consisting of 4 acetabula, apical modificaton of scolex proper, and apical organ. Acetabula in the form of suckers, 54-82 (64 ± 7; 13; 26) long by 56-74 (65 ± 5; 13; 26) wide. Apical modification of scolex proper with large aperture at center, housing apical organ. Apical organ retractable, large, muscular, with glandular surface, in form of oval pad when everted (Fig. 7A).

Rims of acetabula covered with blade-like spinitriches and long filitriches (Fig. 6F, G). Distal surfaces of acetabula and scolex proper covered with long filitriches (Fig. 6I). Apical organ covered with short filitriches (Fig. 6J). Strobila covered with elongate to long filitriches (Fig. 6E).

Cephalic peduncle absent. Proglottids craspedote, laciniate. Immature proglottids 18-69 (37 ± 16; 16) in number, initially wider than long, becoming longer than wide with maturity; posterior-most immature proglottid 236-554 (375 ± 77; 16) long by 122-312 (216 ± 53; 16) wide. Mature proglottids 1-3 in number 770-1,103 (945 ± 85; 16) long by 146-282 (216 ± 53; 16) wide. Testes 19-29 (23 ± 3; 14) in number, 18-74 (42 ± 14; 16; 45) long by 27-109 (67 ± 18; 16; 45) wide, in single field, extending from anterior margin of proglottid to ovary, slightly overlapping anterior margin of ovary, 2 columns in frontal view, 1 column deep in cross-sections (Fig. 7C), post-ovarian testes absent. Vas efferens not observed. Vas deferens in mature proglottids in which testes are degenerated enlarged to form conspicuous external seminal vesicle. External seminal vesicle extensive, saccate, extending medially along proglottid from ootype region to just anterior of cirrus sac. Internal seminal vesicle not observed. Cirrus sac pyriform, slightly angled anteriorly, 87-170 (130 ± 23; 16) long by 67-146 (103 ± 19; 16) wide, containing coiled cirrus. Cirrus microtriches not observed. Ovary H-shaped in frontal view, tetralobed in cross-section (Fig. 7E), 223-351 (299 ± 40; 15) long by 108-434 (169 ± 76; 15) wide, lobulated, symmetrical; ovarian bridge at center of ovary. Mehlis' gland near posterior margin of ovary. Vagina extending laterally in mature proglottids from ootype region to genital atrium, opening posterior to cirrus sac into genital atrium. Genital pores lateral, irregularly alternating, 56-70% (61 ± 4; 16) of proglottid length from posterior end. Uterus saccate, extending medially, ending just posterior to anterior margin of proglottid. Vitellaria follicular, medullary, lateral, in 4 columns, 2 follicles on each lateral margin of proglottid in cross-section (Fig. 7C), extending from anterior margin of ovary to

just posterior of anterior margin of proglottid, may overlap ovary; vitelline follicles 10-38 (23 ± 7; 16; 48) long by 14-68 (40 ± 14; 16; 48) wide. Single pair of excretory ducts. Eggs not observed.

Taxonomic Summary

Type host: *Aetomylaeus vespertilio* (Bleeker, 1852), the ornate eagle ray (Myliobatiformes: Myliobatidae).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Off Weipa (12°40'S, 141°52'E), Queensland, Australia, Gulf of Carpenteria.

Type specimens: Holotype (QM No. G000000), 7 paratypes (5 whole mounts and frontal sections of 1 scolex with apical organ everted and 1 with apical organ retracted) (QM Nos. G000000); 5 paratypes (USNPC Nos. 00000); 8 paratypes (5 whole mounts, frontal sections of 1 scolex with apical organ everted and 1 with apical organ retracted, and cross-sections of 1 proglottid) (LRP Nos. 0000 – 0000). Whole worm and scoleces prepared for SEM retained in the personal collection of Dr. Kirsten Jensen at the University of Kansas.

Prevalence: 20% (i.e., in 1 of 5 host individuals examined).

Etymology: This species is named for Julian Baggio, of Cairns Marine, Australia, for his assistance with collections of host specimens from Weipa.

Remarks

This species has an unusually wide range in total length as compared to the other lecanicephalidean species described in this study. Of the 16 whole worm paratypes included in this description, ten were of a larger type and six were of a smaller type. These differences

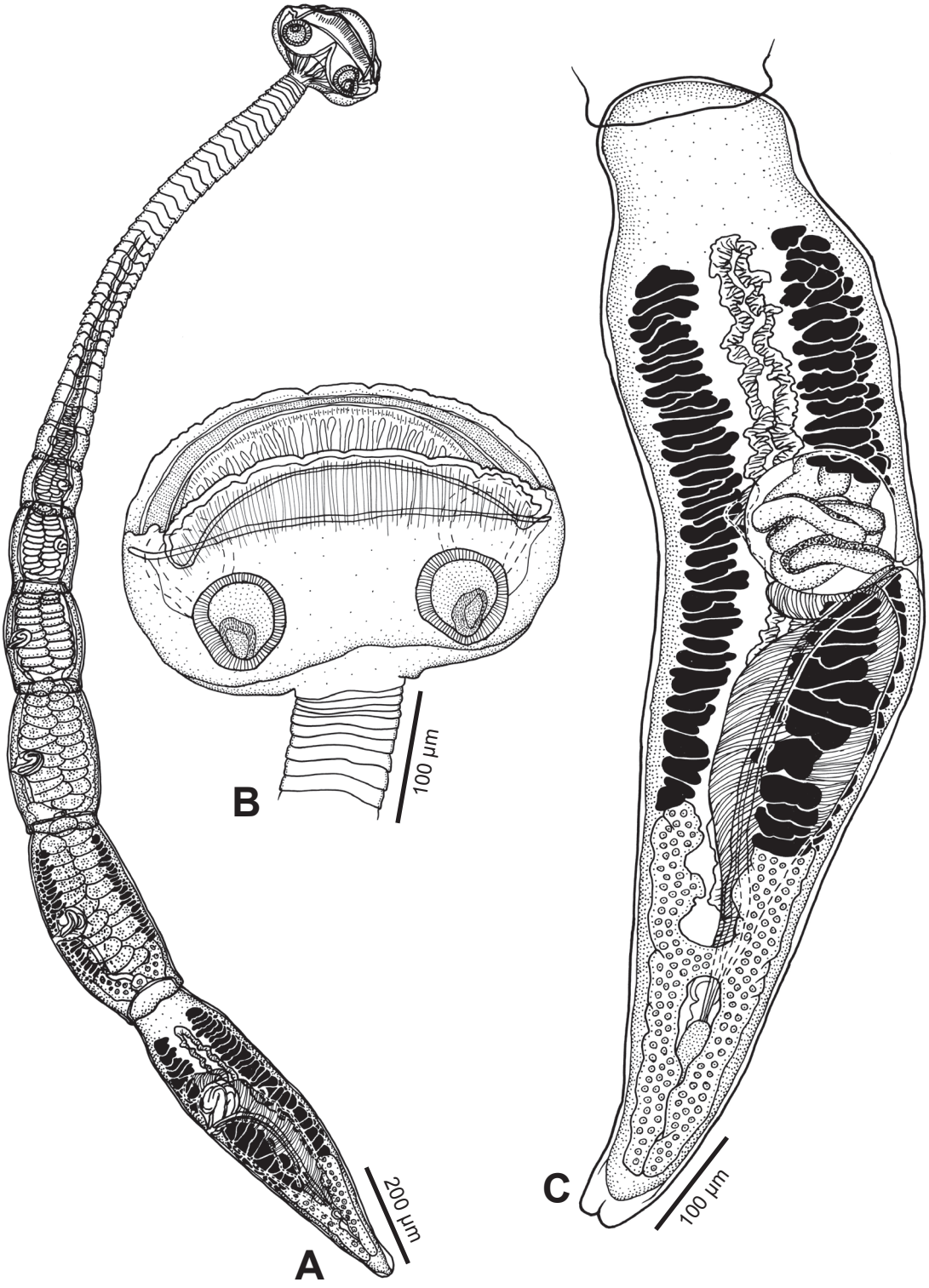

Figure 5. Line drawings of *Collicocephalus baggioi* n. gen., n. sp. (A) Whole worm. (B) Scolex. (C) Mature terminal proglottid.

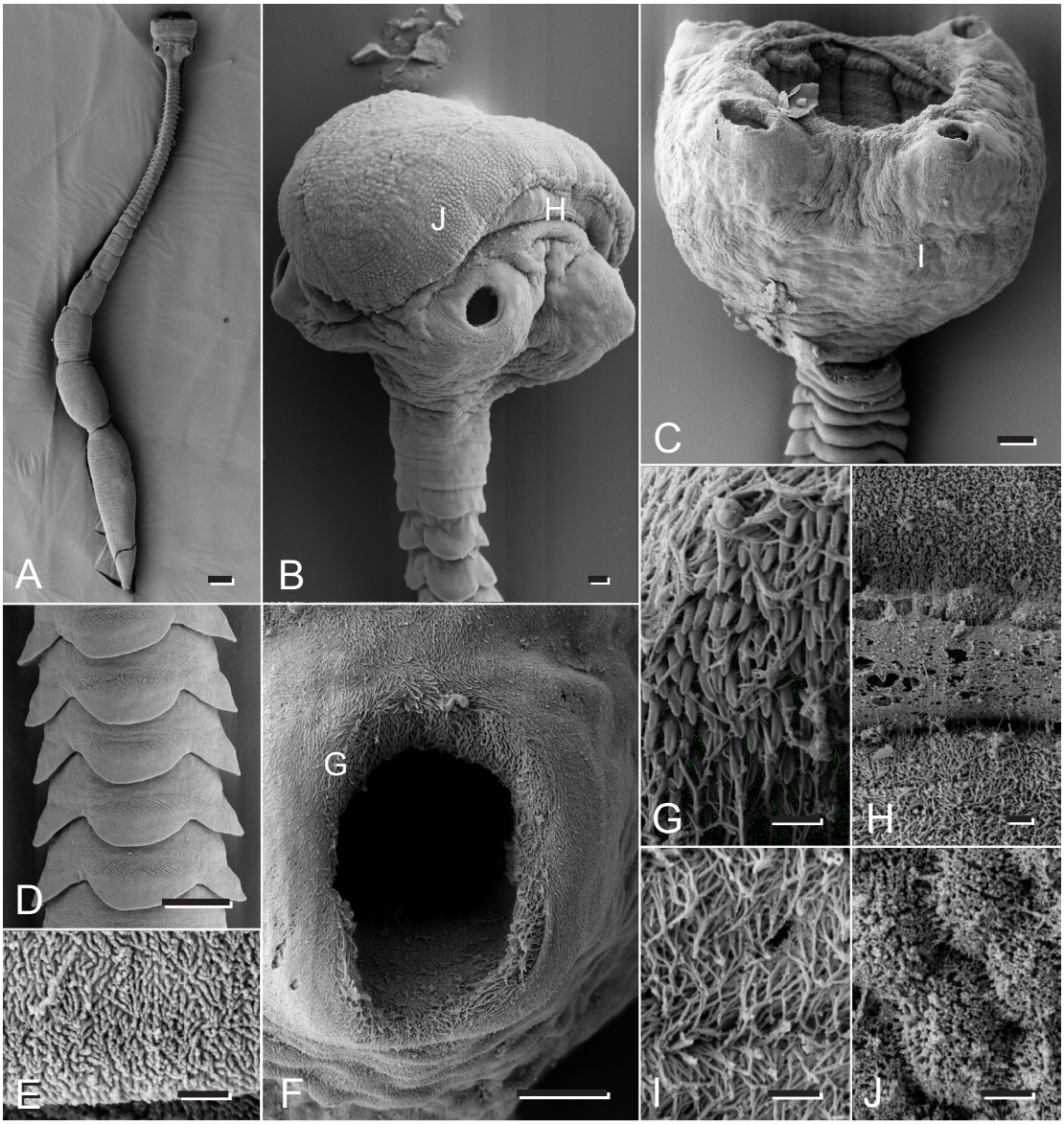

Figure 6. Scanning electron micrographs of *Collicocephalus baggioi* n. gen., n. sp. (A) Whole worm with apical organ fully everted. (B) Scolex with apical organ partially everted. Small letters indicate location of details shown in Figs. H and J. (C) Scolex with apical organ retracted. Small letters indicate location of details shown in Fig. I. (D) Enlarged view of laciniate proglottids. (E) Microtriches on posterior margin of anterior proglottid. (F) Enlarged view of sucker. Small letters indicate location of details shown in Fig. G. (G) Microtriches on sucker rim. (H) Enlarged view of apical modification of scolex proper. (I) Microtriches on scolex proper. (J) Microtriches on apical organ. Scale bars: A = 100 μm; B, F = 10 μm; C-D = 20 μm; E, G-J = 1 μm.

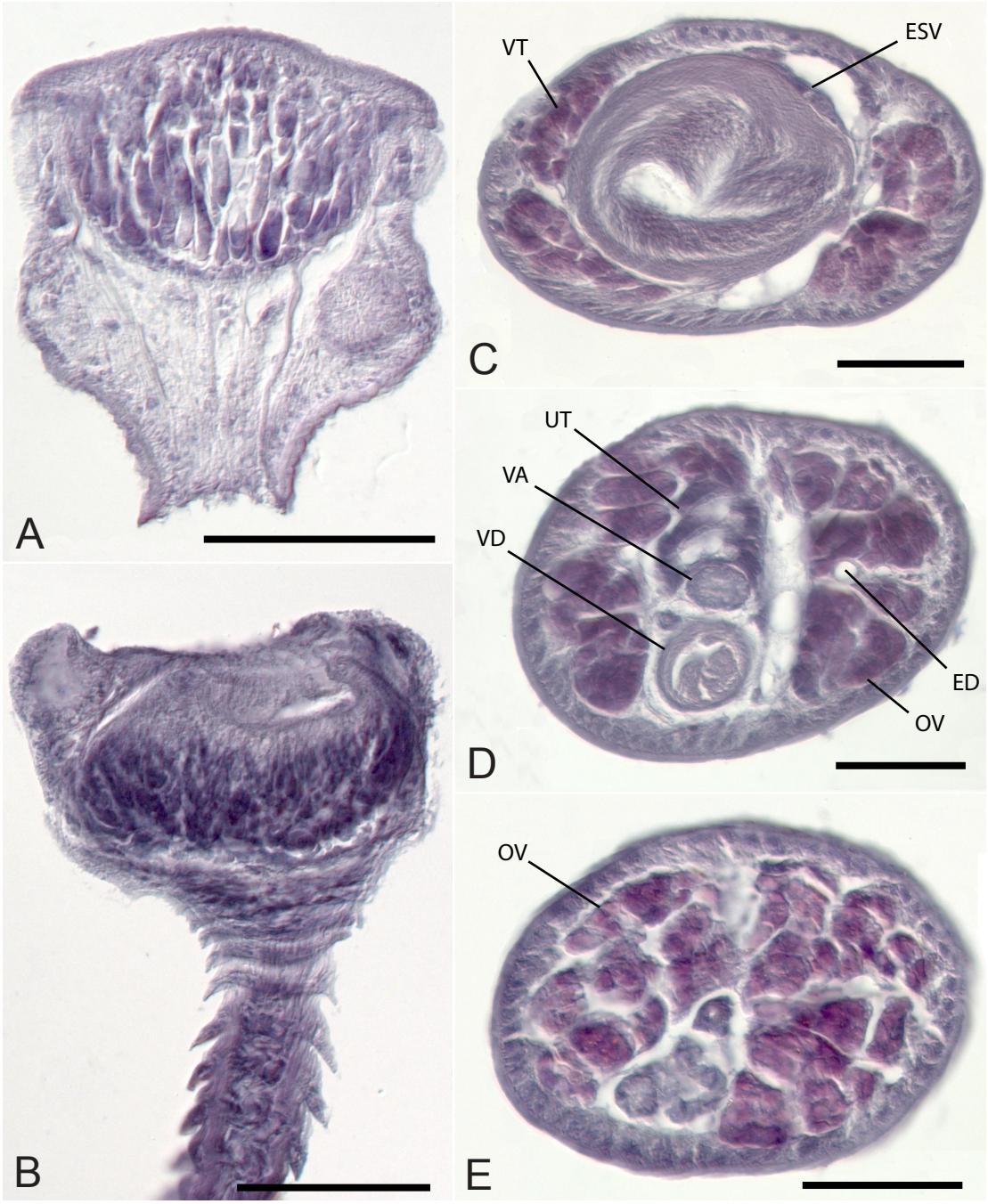

Figure 7. *Collicocephalus baggioi* n. gen., n. sp. (A) Frontal section through scolex with apical organ partially everted. (B) Frontal section through scolex with apical organ retracted. (C) Cross-section through mature proglottid at level of external seminal vesicle. (D) Cross-section through mature proglottid at level of ovary anterior to ovarian bridge. (E) Cross-section through mature proglottid at level of ovary, showing ovarian bridge. Abbreviations: ED, excretory duct; ESV, external seminal vesicle; OV, ovary; UT, uterus; VA, vagina; VD, vas deferens; VT, vitellarium. Scale bars: A, B = 100 μm; C-E = 50 μm.

were considered well within the range of intraspecific variation. The relatively large difference in total length appears to be mainly caused by variation in the length of the neck (i.e., the chain of immature proglottids), with smaller worms having shorter necks consisting of fewer proglottids than those of larger worms, as well as the number of mature proglottids, with smaller worms having only one or two mature proglottids, while larger worms have up to three mature proglottids.

Aberrapex weipaensis n. sp.

(Figs. 8-10)

Description

Based on 14 specimens: 12 whole mounts of mature worms, cross-sections of 1 mature proglottid, and 1 whole worm prepared for SEM.

Worms 475-1,902 (1,174 ± 410; 12) long, maximum width at terminal proglottid, euapolytic; proglottids 21-28 (24 ± 3; 12) in number. Scolex 40-63 (52 ± 7; 11) long by 62-79 (70 ± 5; 6) wide, consisting of 4 acetabula. Acetabula bothridiate in form, cup-shaped, 46-56 (51 ± 3; 9) long by 33-43 (37 ± 3; 9) wide. Apical modification of scolex proper and apical organ absent.

Proximal acetabular surface covered with large blade-like spinitriches and long filitriches (Fig. 9F). Distal acetabular surface and apex of scolex proper covered with short filitriches only (Fig. 9C, E). Strobila covered with long filitriches that become shorter toward posterior margins of proglottid (Fig. 9D).

Cephalic peduncle absent. Proglottids craspedote, non-laciniate. Immature proglottids 20-27 (23 ± 3; 12) in number, initially wider than long, becoming longer than wide with maturity; posterior-most immature proglottid 76-393 (156 ± 85; 11) long by 83-129 (103 ±

14; 11) wide. Mature proglottids 1 or 2 in number; terminal mature proglottids with testes 288-462 (405 ± 71; 5) long by 117-159 (137 ± 15; 5) wide; terminal mature proglottids in which most testes are degenerated 409-774 (562 ± 120; 7) long by 135-173 (150 ± 13; 7) wide. Testes 10-17 (14 ± 3; 10) in number, 12-33 (24 ± 6; 8) long by 31-69 (49 ± 11; 8) wide, in single field extending from ovar to just posterior to the anterior margin of proglottid, slightly overlapping anterior margin of ovary, 1-2 irregular columns in frontal view, 1 row deep in cross-section (Fig. 10A), post-ovarian testes absent. Vas efferens not observed. Vas deferens in terminal mature proglottids in which testes are degenerated enlarged to form conspicuous external seminal vesicle; external seminal vesicle extensive, saccate, extending medially along proglottid from ootype region to approximately half-way between anterior margin of cirrus sac and anterior margin of vitellaria. Internal seminal vesicle not observed. Cirrus sac pyriform, slightly angled anteriorly, 29-42 (38 ± 6; 4) long by 55-65 (59 ± 4; 4) wide in maturing proglottids with testes, 62-105 (84 ± 15; 7) long by 25-73 (52 ± 17; 7) wide in terminal mature proglottids in which testes are degenerated, containing coiled cirrus. Cirrus microtriches not observed. Ovary H-shaped in frontal view, tetralobed in cross-section (Fig. 12B), 93-106 (98 ± 6; 4) long by 72-114 (95 ± 17; 4) wide in maturing proglottids with testes, 118-272 (202 ± 46; 7) long by 89-122 (100 ± 11; 7) wide in mature proglottids in which testes are degenerated, lobulated, symmetrical; ovarian bridge at center of ovary. Mehlis' gland near posterior margin of ovary. Vagina extending laterally in mature proglottids with testes (more medially in mature proglottids in which testes are degenerated) from ootype region to genital atrium, opening posterior to cirrus sac into genital atrium. Genital pores lateral, irregularly alternating, 58-65% (62 ± 3; 4) of proglottid length from posterior end in maturing proglottids with testes, 58-63% (61 ± 2; 7) in terminal mature proglottids in which testes are degenerated. Uterus saccate, extending along mid-line of proglottid from ovarian bridge to anterior margin of vitellaria. Vitellaria follicular, medullary, lateral, in 4 columns, 2 follicles on each lateral

margin of proglottid in cross-section (Fig. 10A), extending from anterior margin of ovary to just posterior to anterior margin of proglottid, slightly overlapping ovary; vitelline follicles 9-21 (13 ± 4; 3; 9) long by 9-29 (21 ± 6; 3; 9) wide in maturing proglottids with testes, 11-29 (19 ± 5; 7; 21) long by 26-52 (39 ± 8; 7; 21) wide in mature proglottids in which testes are degenerated. Single pair of excretory ducts. Eggs not observed.

Taxonomic Summary

Type host: *Aetomylaeus vespertilio* (Bleeker, 1852), the ornate eagle ray (Myliobatiformes: Myliobatidae).

Additional hosts: None.

Site of infection: Spiral intestine.

Type locality: Off Weipa (12°40'S, 141°52'E), Queensland, Gulf of Carpenteria, Australia.

Type specimens: Holotype (QM No. G000000), 3 paratypes (QM Nos. G000000); 4 paratypes (USNPC Nos. 00000); 5 paratypes (4 whole mounts and cross-section of 1 proglottid (LRP Nos. 0000 – 0000). Whole worm prepared for SEM retained in the personal collection of Dr. Kirsten Jensen at the University of Kansas.

Prevalence: 40% (i.e., in 2 of 5 host individuals examined).

Etymology: This species is named for its type locality off Weipa, Queensland, Australia.

Remarks

This species is consistent with the generic diagnosis of *Aberrapex* due to its lack of an apical modification of the scolex proper and an apical organ, its possession of an unarmed cirrus, a large vas deferens serving as an external seminal vesicle which originates at the level of the ovary, and a vagina opening into the genital atrium posterior to the cirrus sac. Moreover, much like in other species of *Aberrapex*, the vagina extends along the lateral

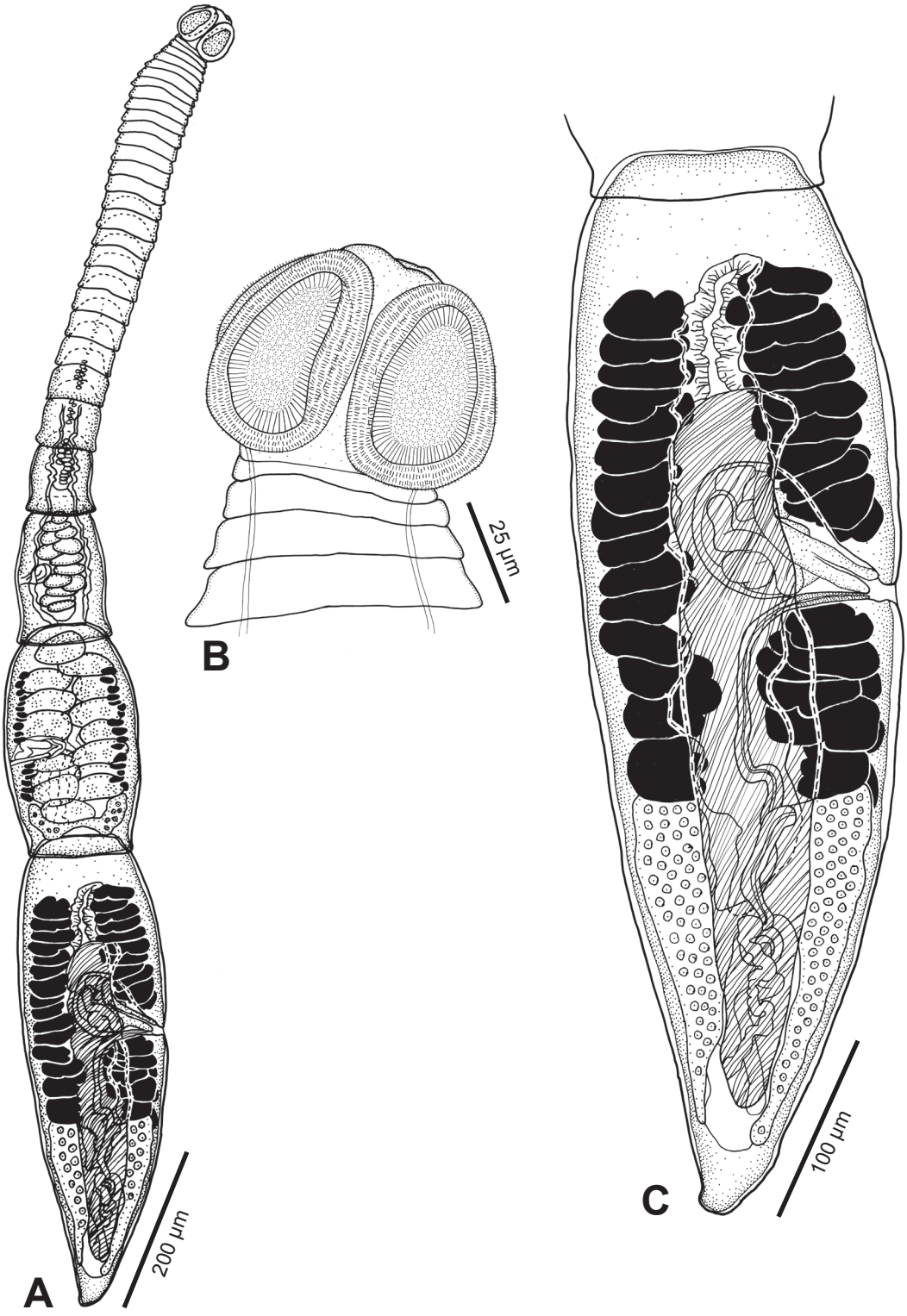

Figure 8. Line drawings of *Aberrapex weipaensis* n. sp. (A) Whole worm. (B) Scolex. (C) Mature terminal proglottid.

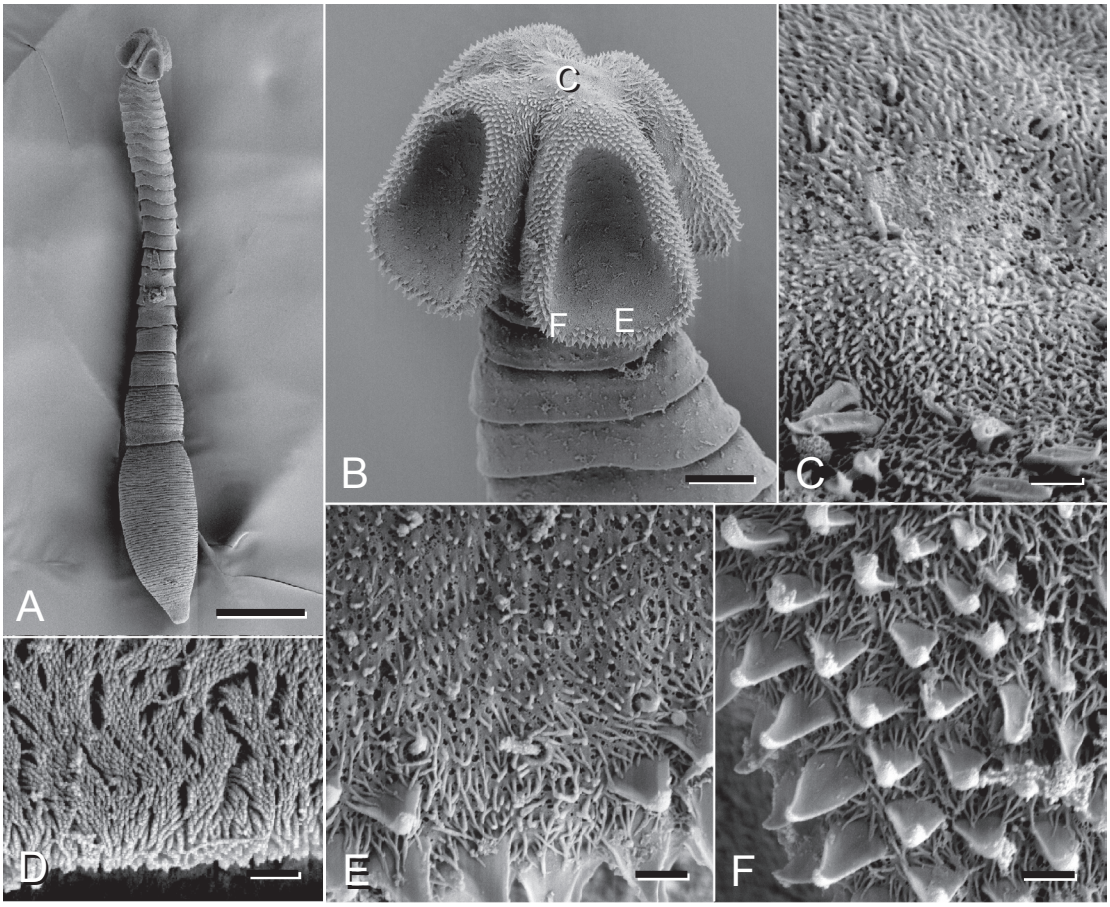

Figure 9. Scanning electron micrographs of *Aberrapex weipaensis* n. sp. (A) Whole worm. (B) Scolex. Small letters indicate details shown in Figs. C, E, and F. (C) Microtriches on apex of scolex apex. (D) Microtriches on posterior margin of subterminal proglottid. (E) Microtriches on acetabular surface. (F) Microtriches on proximal acetabular surface. Scale bars: A = 100 μm; B = 10 μm; C-F = 1 μm..

margin of the proglottid in mature proglottids with testes, while in mature proglottids in which testes are degenerated the vagina extends more medially in the proglottid.

Jensen (2005) recognized three species of the genus *Aberrapex*: *A. senticosus* Jensen, 2001, *A. arrhynchum* (Brooks, Mayes, and Thorson, 1981) Jensen, 2005, and *A. manjajiae* Jensen, 2006. *Aberrapex weipaensis* n. sp. differs from all three species in its smaller scolex (40-63 long by 62-79 wide *vs* 100-130 long by 125-170 wide, 177-186 long by 233-326 wide and 82-101 long by 119-164 wide, respectively) and its lack of vitellaria posterior to

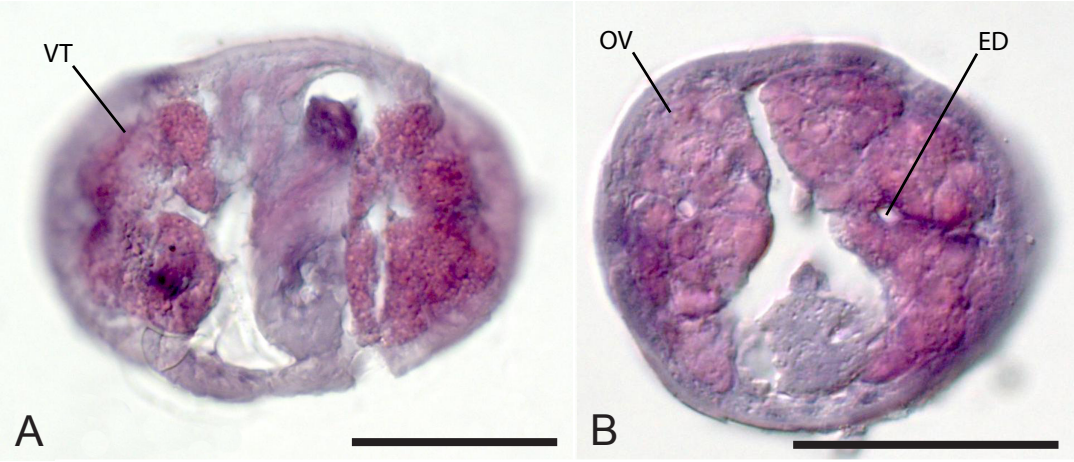

Figure 10. *Aberrapex weipaensis* n. sp. (A) Cross-section through mature proglottid at level of external seminal vesicle. (B) Cross-section through mature proglottid at level of ovary. Abbreviations: ED, excretory duct; OV, ovary; VT, vitellarium. Scale bars: A, B = 50 μm.

ovary, whereas the other three species have vitellaria that are anterior and posterior to the ovary. *Aberrapex weipaensis* n. sp. can further be distinguished from *A. senticosus* by having a smaller number of testes (10-17 *vs* 20-40), smaller cirrus sac in those proglottids in which testes have degenerated (37-105 long by 25-88 wide *vs* 127-182 long by 130-150 wide), and a shorter ovary in proglottids in which testes have degenerated (118-272 *vs* 335-444). *Aberrapex weipaensis* n. sp. further differs from *A. arrhynchum* in having fewer proglottids (21-28 *vs* 43-48), and differs from both *A. arrhynchum* and *A. manjajiae* in having a genital pore located much more anteriorly or more posteriorly, respectively (58-65% *vs* 25-32 and 76-85%).

Other Lecanicephalidean Species of *Aetomylaeus vespertilio*

Lecanicephalideans were only present in three of five host specimens of *Aetomylaeus vespertilio*; two specimens each hosted nine lecanicephalidean species, while one only hosted two species (Tab. 3). Of the thirteen new species in seven genera recovered from *Aetomylaeus vespertilio*, ten were not formally described in this study. These include six species of

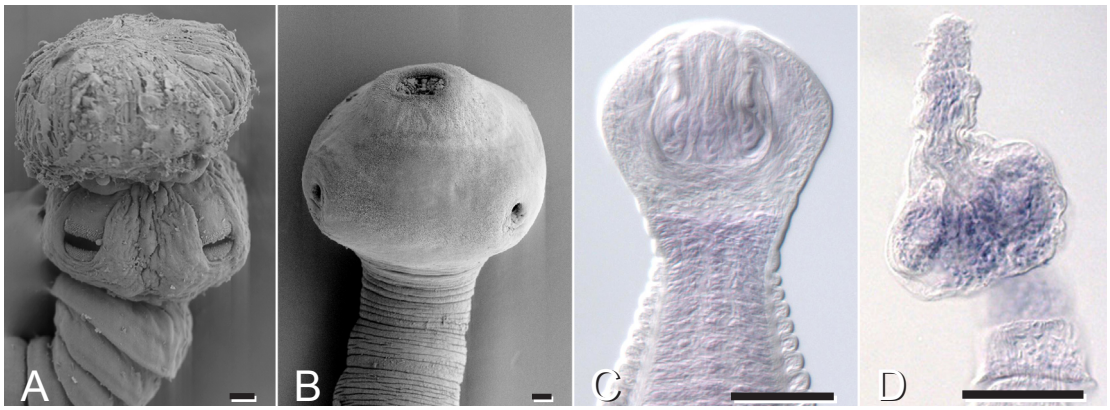

Figure 11. Scanning electron micrographs and light micrographs of scoleces of representatives of other lecanicephalidean taxa from *Aetomylaeus vespertilio*. (A) *Tylocephalum* new species 3. (B) *Polypocephalus* new species 2. (C) Unidentified genus 1 new species 1. (D) Unidentified genus 1 new species 2. Scale bars: A = 10 μm; B = 20 μm; C-D = 50 μm.

Tylocephalum, two species of *Polypocephalus*, and one species each in the two unidentified genera. Regardless, observations that distinguish these species and may facilitate their description in the future are presented here.

The six congeners of *Tylocephalum* were identified as members of this genus due to their scoleces consisting of four sucker-like acetabula and a large, globular, muscular, and non-retractable nor invaginable apical organ, as well as the internal anatomy of their proglottids (based on diagnosis in the most recent treatment of the Lecanicephalidea from Jensen [2005]). The six species identified in this study are distinct from one another, but can be divided into three groups based on overall morphology. *Tylocephalum* new species 1, 4, and 5 are large and bulky worms of considerable length (~ 1.5-3 cm). Their scoleces are large and robust, and strobilae are comprised of a long thick neck and many immature and mature proglottids. In contrast, *Tylocephalum* new species 2 and 6 very long and thin (~ 1-1.5 cm). They possess a small scolex, followed by a long, thin neck, consisting of many proglottids. Finally, *Tylocephalum* new species 3 (Fig. 11A) is very small in comparison to its five congeners (~ 2 mm). These specimens possess a minute scolex and a short neck followed by

only a few proglottids. The terminal segment is the only mature proglottid in this species.

Based on the presence of an apical organ divided into tentacles, the two congeners of *Polypocephalus* could be easily attributed to this genus (Braun, 1878; Jensen, 2005; Subhapradha, 1951). Both species have 6 testes, but differ in a number of other respects. *Polypocephalus* new species 1 is an extremely long and thin worm with a large scolex relative to its strobila. The scolex possesses an apical organ divided into a great number of tentacles – many more than exhibited by other species of *Polypocephalus*. This species can be characterized by an extremely elongate cirrus sac, running anteriorly, parallel to the wall of the proglottid. *Polypocephalus* new species 2 (Fig. 11B) is a much shorter but thicker worm. The apical organ possesses fewer tentacles than the first species. The strobila consists of far fewer proglottids than new species 1, which are much less elongate as well.

The new species of Unidentified genus 1 (Fig. 11C) possesses a scolex consisting of four sucker-like acetabula and a globular, retractable apical organ. This species is most similar in its morphology to the members of the lecanicephalidean genus *Cephalobothrium*, a genus currently considered a *genus inquirendum* (Jensen, 2005), in that it has a scolex with four small sucker-like acetabula and proglottids that are wider than broad with the exception of the last few (see Shipley and Hornell, 1906). However, this new species does not belong in *Cephalobothrium* because instead of possessing an apical organ in form of a large anterior sucker, it has a globular, retractable apical organ.

The new species of Unidentified genus 2 (Fig. 11D) is characterized by a scolex consisting of four sucker-like acetabula and a tiered, trunk-like apical organ that appears to be retractable. The strobila consists of a short, thin neck and is made up of few proglottids, with the terminal segment being the only mature proglottid. It is most similar to the *Tylocephalum*. This species does not coincide very closely with the diagnosis of this genus, but the worm it most closely resembles is *Tylocephalum* new species 3 from this study due to its sucker-

like acetabula and single mature proglottid containing lateral bands of vitellaria. However, Unidentified genus 2 species 1 differs from *Tylocephalum* in that its apical organ is divided into separate tiers and is retractable.

Lecanicephalidean Fauna of *Aetomylaeus maculatus*

Examination of the lecanicephalidean fauna of *Aetomylaeus maculatus* revealed a total of ten additional species new to science (Tab. 4). These ten species were determined to be distinct from the 13 species identified as parasites of *A. vespertilio*. Lecanicephalideans were present in only four of five host specimens; two host specimens were parasitized by five and six species, respectively, while the two remaining host specimens were parasitized by two species each. These ten species represented four different genera. One of these ten species exhibited a scolex and proglottid morphology that did not allow placement into any of the currently recognized lecanicephalidean genera. Consequently, a new genus is diagnosed

Table 4. Lecanicephalidean infracommunities in specimens of *Aetomylaeus maculatus*. Note: BO indicates specimens from Malaysia; KA indicates specimens from Indonesia.

Specimen No.	**BO-22**	**BO-178**	**BO-179**	**KA-53**	**KA-104**
Species					
Elicilacunosus lasti n. gen., n. sp			X		
Tylocephalum n. sp. 7					X
Tylocephalum n. sp. 8		X	X		
Tylocephalum n. sp. 9	X	X	X		
Tylocephalum n. sp. 10	X				
Tylocephalum n. sp. 11		X			X
Tylocephalum n. sp. 12			X		
Polypocephalus n. sp. 3		X	X		
Polypocephalus n. sp. 4		X			
Lecanicephalum n. sp. 1			X		

uninfected

below to accommodate this species. The remaining nine species could be attributed to the genera *Tylocephalum*, *Polypocephalus*, and *Lecanicephalum.*

Only a single lecanicephalidean species, *Tylocephalum* new species 11, parasitized *Aetomylaeus maculatus* specimens collected from both Malaysian and Indonesian Borneo (Fig. 12). Eight of the remaining 9 species hosted by *A. maculatus* were present only in rays collected from Malaysian Borneo, while a single species was present only in Indonesian Borneo.

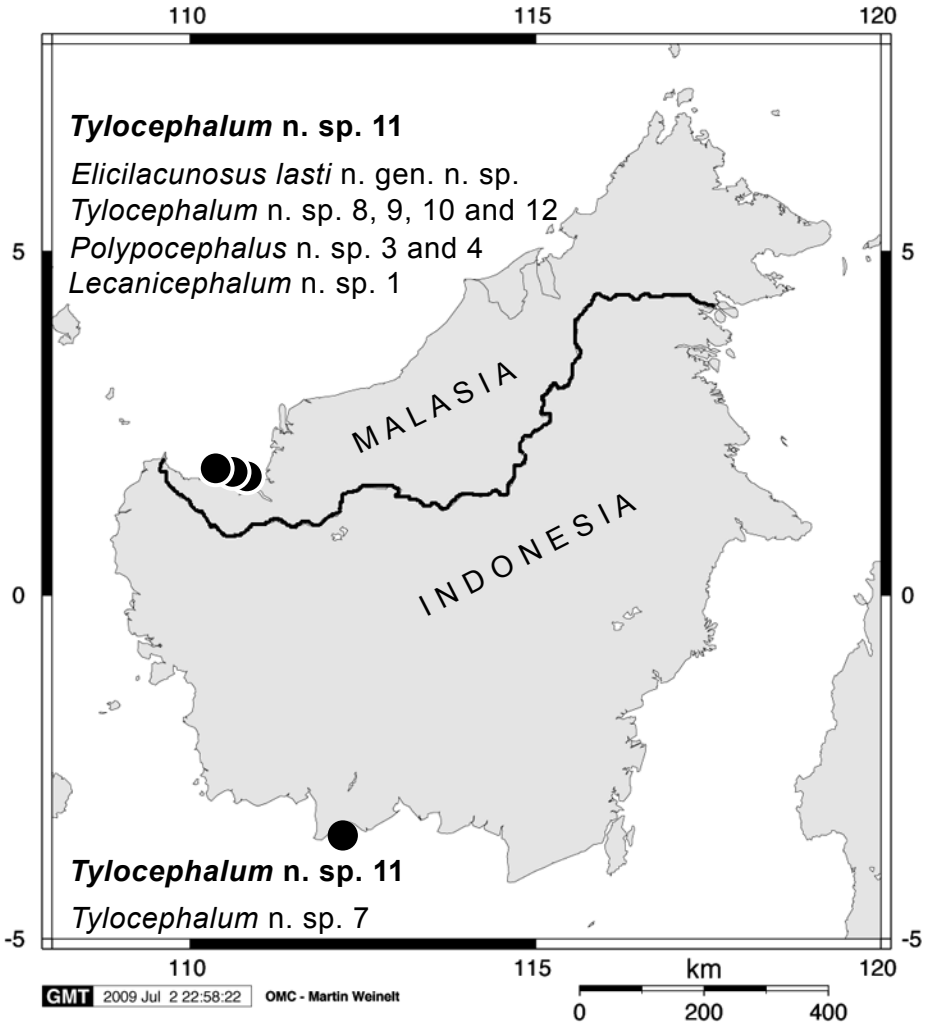

Figure 12. Map indicating specific localities of the 4 *Aetomylaeus maculatus* specimens infected with lecanicephalideans and a list of lecanicephalidean species found in either Malaysia or Indonesia; species found in both localities are indicated in bold.

The new genus and *Lecanicephalum* are each represented by a single species. Just as in *Aetomylaeus vespertilio*, the genus *Tylocephalum* is represented by six congeners in this host. Two new species of *Polypocephalus* were also identified from *A. maculatus*. All of these ten new species are non-overlapping with those of *A. vespertilio*, including the congeners of *Tylocephalum* and *Polypocephalus*, and are new to science.

Descriptions of New Taxa

Elicilacunosus n. gen.

Generic Diagnosis

Worms euapolytic. Scolex with 4 acetabula, apical modification of the scolex proper, and apical organ. Acetabula in the form of suckers. Apical modification of scolex proper elongate, cylindrical, retractable into scolex proper, with pore-like aperture at center, housing apical organ. Apical organ elongate, primarily glandular, retractable.

Scolex proper covered with short filitriches. Anterior margin of rim of acetabula covered with blade-like spinitriches and long filitriches. Strobila covered with triangular microtriches, becoming shorter toward posterior margins of each proglottid.

Cephalic peduncle absent. Proglottids craspedote, non-laciniate, with region of muscular and glandular tissue along dorsal and ventral midline of proglottids, represented externally by column of numerous depressions. Testes in 2 columns anterior to ovary. Vas deferens extending laterally from ootype region to cirrus sac. Internal and external seminal vesicles not observed. Cirrus sac pyriform. Cirrus unarmed. Ovary H-shaped in frontal view, bilobed in cross-section. Vagina extending laterally from ootype region to genital atrium, opening posterior to cirrus sac into genital atrium. Genital pores lateral, irregularly alternating. Uterus submedial, saccate. Vitellaria follicular, in 4 columns, 2 columns on each

lateral margin dorsal and ventral to testes, extending from anterior margin of proglottid to anterior margin of ovary, slightly overlapping ovary. Single pair of excretory ducts. Eggs unknown. In spiral intestine of *Aetomylaeus* Bloch and Schneider, 1801 (Myliobatidae). South China Sea.

Taxonomic Summary

Type species: *Elicilacunosus lasti* n. sp.

Etymology*: Elix, -icis,* L., trench; *lacuna*, L., cavity, hollow. This genus name indicates the unique feature of these worms, i.e., the column of numerous depressions visible externally along the dorsal and ventral midline of the proglottids.

Remarks

Its possession of a scolex with four acetabula and an apical organ, and a vagina opening into the genital atrium posterior to the cirrus sac clearly places *Elicilacunosus* n. gen. in the order Lecanicephalidea.

Elicilacunosus n. gen. can be easily distinguished from the 14 lecanicephalidean genera recognized as valid by its unique dorsal and ventral regions of muscular and glandular tissue along the midline of the proglottids, externally represented by a column of numerous depressions. Furthermore, *Elicilacunosus* n. gen. possesses acetabula in the form of suckers whereas *Aberrapex, Anteropora, Hornellobothrium, Paraberrapex,* and *Quadcuspibothrium* possess bothridiate acetabula. *Elicilacunosus* n. gen. can be further distinguished from *Lecanicephalum, Polypocephalus, Tetragonocephalum,* and *Tylocephalum* by its possession of a single pair of excretory ducts while these other genera possess two pairs. *Corrugatocephalum* and *Healyum* each possess only three testes while *Elicilacunosus* n. gen. possesses many testes arranged in two distinct lateral columns. The anterior immature

proglottids are not laterally expanded in *Elicilacunosus* n. gen. in contrast to the laterally expanded region in *Eniochobothrium, Hornellobothrium*, and *Rexapex*. *Elicilacunosus* n. gen. can be further distinguished from *Collicocephalus* based on the presence of a long, retractable apical organ, rather than an oval pad.

The presence of regions of muscular and glandular tissue along dorsal and ventral midline of the proglottids that are represented externally by a column of numerous depressions is a feature unique to this genus; this feature has not been observed in any of the other over 72 species of lecanicephalideans. The function of this structure is unknown. This region appears to be associated with the worm's tegument and parenchyma, and shows no apparent connection to the reproductive or excretory system. However, given its glandular and muscular nature, it can be speculated that this region might aid in attachment of these small worms to the intestinal mucosa. To my knowledge, a structure of this kind has not been described from any other tapeworm outside of the Lecanicephalidea either.

***Elicilacunosus lasti* n. gen., n. sp.**

(Figs. 13 and 14)

Description

Based on 10 specimens: 8 whole mounts of mature worms and 2 whole worms prepared for SEM.

Worms 890-1,830 (1,175 ± 354; 7) long; maximum width at terminal proglottid, euapolytic; proglottids18-24 (22 ± 2; 8) in number. Scolex 43-74 (53 ± 11; 7) long by 50-63 (55 ± 4; 7) wide, consisting of 4 acetabula, apical modificaton of scolex proper, and apical organ. Acetabula in form of suckers, 26-33 (30 ± 2; 7; 14) long by 22-31 (27 ± 3; 7; 12) wide. Apical modification of scolex proper slightly elongate, cylindrical, retractable into scolex proper, with pore-like aperture at center, housing apical organ. Apical organ primarily

glandular, retractable; apical modification of scolex proper and apical organ combined 17-38 (23 ± 7; 6) long by 30-38 (35 ± 3; 7) wide (includes retracted and everted specimens).

Rims of acetabula covered with blade-like spinitriches and long filitriches; blade-like spinitriches absent from posterior margin of rim (Fig. 16C, D). Scolex proper covered with short filiform microtriches (Fig. 16E). Strobila covered with triangular microtriches, becoming shorter and more conical toward posterior margins of each proglottid (Fig. 16H); anterior region of proglottids with larger, spiniform mircotriches (Fig. 16H).

Cephalic peduncle absent. Proglottids craspedote, non-laciniate. Immature proglottids 17-23 (21 ± 2; 8) in number, initially wider than long, becoming longer than wide with maturity; posterior-most immature proglottid 138-390 (210 ± 89; 8) long by 80-190 (116 ± 44; 8) wide. Mature proglottids 1 in number, 336-600 (441 ± 79; 8) long by 110-188 (143 ± 29; 8) wide. Testes 16-19 (17 ± 1; 8) in number, 26-55 (38 ± 7; 7; 21) long by 21-71 (45 ± 13; 7; 21) wide, in single field, extending from anterior margin of proglottid to ovary, slightly overlapping anterior margin of ovary, 2 columns in frontal view, 1 row deep, post-ovarian testes absent. Vas efferens not observed. Vas deferens in form of thick tube, extending from ootype region to cirrus sac along lateral margin of proglottid; external and internal seminal vesicles not observed. Cirrus sac pyriform, slightly angled anteriorly, 33-52 (41 ± 8; 7) long by 32-66 (46 ± 14; 7) wide, containing coiled cirrus. Cirrus microtriches not observed. Ovary H-shaped in frontal view, bilobed in cross-section, 60-146 (94 ± 27; 7) long by 73-144 (92 ± 25; 7) wide, lobulated, symmetrical; ovarian bridge at center of ovary. Mehlis' gland near posterior margin of ovary. Vagina extending laterally from ootype to genital atrium, opening posterior to cirrus sac into genital atrium. Genital pores lateral, irregularly alternating, 44-49% (47 ± 2; 7) of proglottid length from posterior end. Uterus saccate, submedial, extending from just posterior of testes to anterior margin of vitellaria. Vitellaria follicular, medullary, lateral, in 4 columns, 2 follicles on each side with 1 follicle dorsal and 1 ventral to testes

(never lateral to testes), extending from just posterior to anterior margin of proglottid to anterior margin of ovary, may overlap ovary; vitelline follicles 7-24 (15 ± 5; 8; 24) long by 16-46 (28 ± 7; 8; 24) wide in mature proglottids. Single pair of excretory ducts. Eggs not observed.

Taxonomic Summary

Type host: *Aetomylaeus maculatus* (Gray, 1834), the mottled eagle ray (Myliobatiformes: Myliobatidae).

Type locality: Sematan (01°48'N, 109°46'E), Sarawak, Malaysia, South China Sea.

Site of infection: Spiral intestine.

Specimens deposited: Holotype (MZUM No. 00000), 1 paratype (SBC No. 00000); 3 paratypes (USNPC Nos. 00000); 3 paratypes (LRP Nos. 0000 – 0000). Whole worms prepared for SEM retained in the personal collection of Dr. Kirsten Jensen at the University of Kansas.

Prevalence: 20% (i.e. in 1 of 5 host individuals examined).

Etymology: This species is named for Dr. Peter R. Last, CSIRO Division of Marine Research, Australia, for his assistance with host collections.

Remarks

The apical organ was only everted in one of ten specimens. A more detailed description of the apical organ of this species based on additional specimens would be beneficial to support the observations described here.

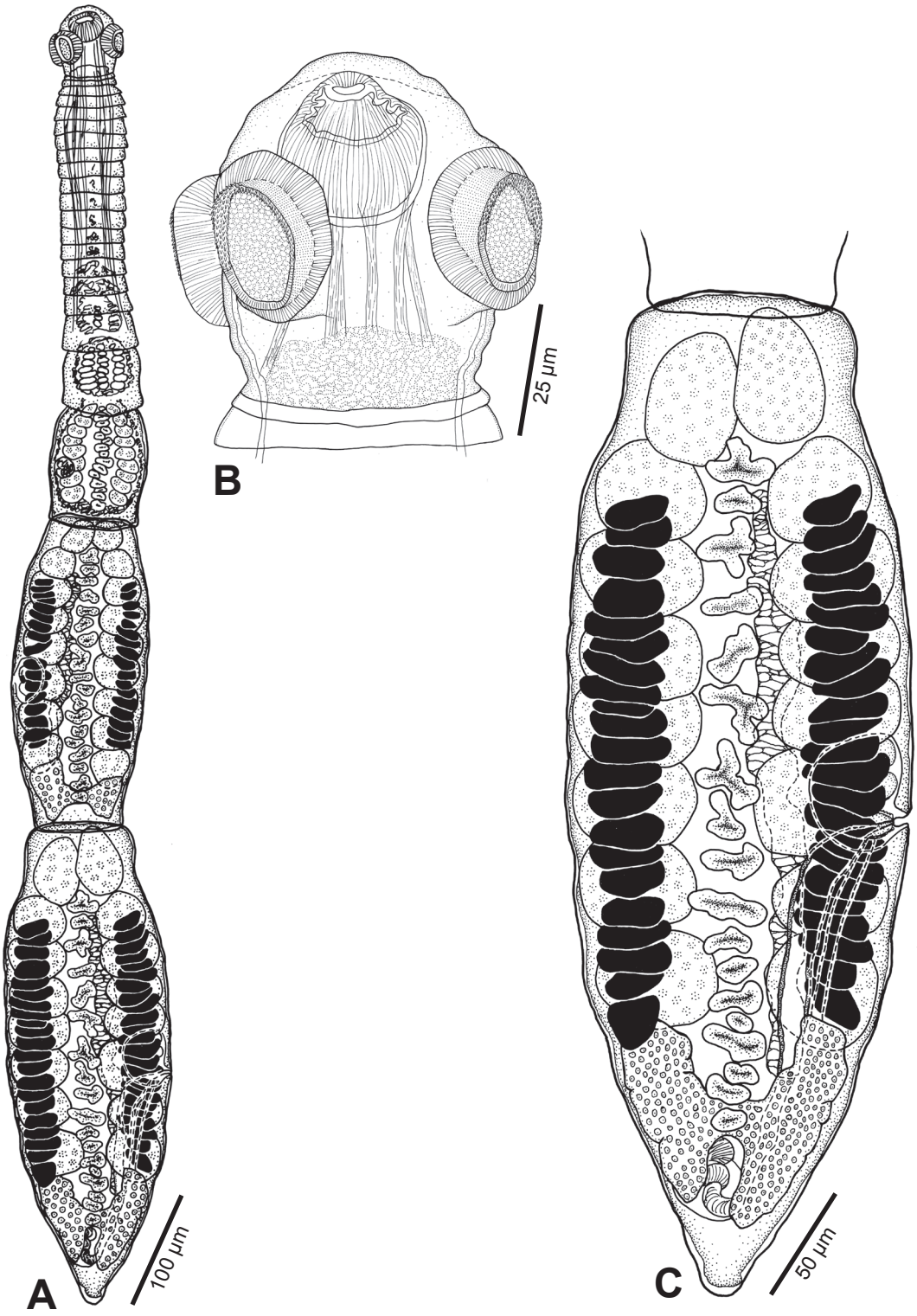

Figure 13. Line drawings of *Elicilacunosus lasti* n. gen., n. sp. (A) Whole worm. (B) Scolex. (C) Mature terminal proglottid.

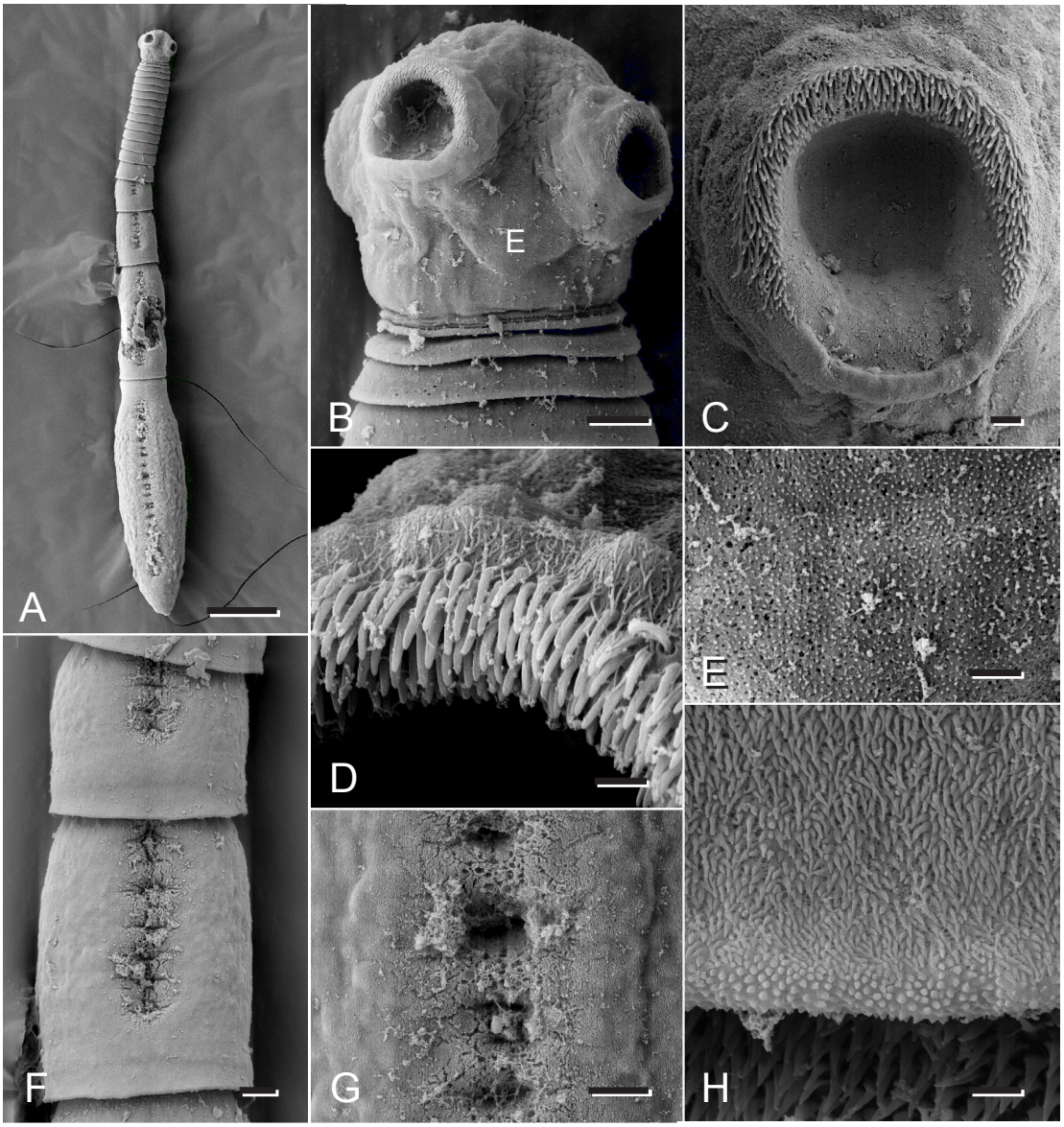

Figure 14. Scanning electron micrographs of *Elicilacunosus lasti* n. gen., n. sp. (A) Whole worm. (B) Scolex. Small letter indicates location of details shown in Fig. E. (C) Enlarged view of sucker. (D) Microtriches on sucker rim. (E) Microtriches on scolex proper. (F) Immature proglottids. (G) Enlarged view of exterior representation of glandular structures. (H) Microtriches on posterior margin of a proglottid. Scale bars: A = 100 μm; B, F-G = 10 μm; C = 2 μm; D-E, H = 1 μm.

Other Lecanicephalidean Species of *Aetomylaeus maculatus*

In addition to the type species of *Elicilacunosus,* nine new lecanicephalidean species representing three genera were found to parasitize *Aetomylaeus maculatu*s. These were six species of *Tylocephalum*, two species of *Polypocephalus*, and one species of *Lecanicephalum*.

The six congeners of *Tylocephalum* were identified. These congeners are clearly distinct species and, much like the six species of *Tylocephalum* from *Aetomylaeus vespertilio*, can be attributed to one of three groups based on general morphology. However, the three groups are defined differently for these six *Tylocephalum* species. *Tylocephalum* new species 7 (Fig. 15A), 8, and 9 are fairly small worms (~ 3-4 mm). Their scoleces are small and their strobilae widen toward the middle. Their proglottids are laciniate and extremely craspedote, a condition unusual among species of *Tylocephalum*. Generally, only the last 1 or 2 proglottids are mature and elongate in form. *Tylocephalum* new species 10 is a larger, bulkier worm with a thick neck and greater number of proglottids. Finally, *Tylocephalum* new species 11 and 12

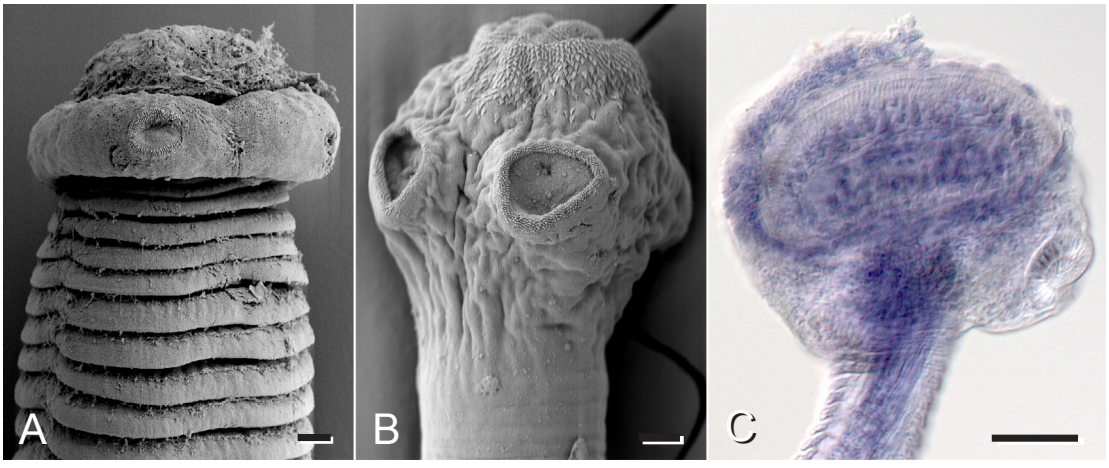

Figure 15. Scanning electron micrographs and light micrograph of scoleces from representatives of other lecanicephalidean taxa from *Aetomylaeus maculatus*. (A) *Tylocephalum* new species 6. (B) *Polypocephalus* new species 4. (C) *Lecanicephalum* new species 1. Scale bars: A-B = 10 μm; C = 50 μm.

are extremely long (~ 1.5-3.5 cm) and large in comparison to the other four congeners found in this host. They possess a large, robust scolex and a strobila consisting of many proglottids. None of the six species of *Tylocephalum* found parasitizing *A. maculatus* were found to match the original description of *T. dierama*.

The two species of *Polypocephalus* could be easily distinguished based on the fact that *Polypocephalus* new species 3 has six testes while *Polypocephalus* n. sp. 4 possesses only four. Moreover, *Polypocephalus* new species 3 possesses a thick strobila, with the terminal proglottids usually being gravid. *Polypocephalus* new species 4 (Fig. 15B) is a very small worm (~ 1 mm) in comparison to any of its other congeners from *Aetomylaeus*.

A single species consistent with the generic diagnosis of *Lecanicephalum* (*sensu* Jensen, 2005) was found in *Aetomylaeus maculatus* (Fig. 15C). This was the only species of *Lecanicephalum* found in any of the *Aetomylaeus* species during this study. It appears to differ from the two currently recognized species, *Lecanicephalum peltatum* Linton, 1890, and *L. coangustatum* Jensen, 2005, in that it is a small worm (~ 2 mm) in comparison to *L. peltatum*, which can reach 12 mm. *Lecanicephalum* n. sp. 1 possesses few proglottids with only one proglottid being mature, whereas the two current species possess many proglottids with up to four mature proglottids.

Lecanicephalidean Fauna of *Aetomylaeus niehofii*

The lecanicephalidean fauna of *Aetomylaeus niehofii* was comprised of a total of seven species new to science, representing three genera (Tab. 5). Not all 17 specimens examined were infected with lecanicephalideans, while they did host cestodes of other orders. Eight specimens did not host lecanicephalideans; of the nine specimens that did, one hosted four species, five hosted three species, two hosted one and two species, respectively (Tab. 5).

Table 5. Lecanicephalidean infracommunities in specimens of *Aetomylaeus niehofii*. Note: eight of seventeen specimens examined were not infected with lecanicephalideans and are not included in this table. BO indicates specimens from Malaysia, KA indicates those from Indonesia, and NT indicates those from Northern Australia.

Specimen No.	**BO-34**	**BO-180**	**KA-96**	**KA-362**	**KA-434**	**NT-52**	**NT-59**	**NT-60**	**NT-79**
Species									
Elicilacunosus dharmadii n. sp.	X			X					
Elicilacunosus fahmii n. sp.				X					
Elicilacunosus n. sp. 1		X							
Polypocephalus n. sp. 5	X	X	X		X				
New genus n. sp. 1	X			X	X	X	X	X	X
New genus n. sp. 2					X		X	X	X
New genus n. sp. 3	X						X	X	X

Specifically, three additional species of *Elicilacunosus* were found. Of these three species, only two species are described below. A mere four specimens of the third congener were available for study. A full description was not possible based on this limited material. Also collected from this host species were three species that could not be attributed to currently recognized lecanicephalidean genera and represent yet another new genus, which, however, will not be formally erected as part of this study. Members of these three species (referred to as New genus species 1-3) are similar to those of species of *Tylocephalum*, but are distinct in their possession of an apical organ that is completely retractable into the scolex proper, unlike the apical organ of *Tylocephalum*, which cannot be retracted (see Euzet, 1994; Ivanov *et al*., 2000; Jensen, 2005). A single species of *Polypocephalus* was also found to parasitize specimens of *A. niehofii*.

Three lecanicephalidean species, *Elicilacunosus dharmadii* n. sp., *Polypocephalus* n. sp. 5, and New genus n. sp. 1 parasitized *Aetomylaeus niehofii* specimens collected from both Malaysian and Indonesian Borneo (Fig. 16). Two each of the remaining 4 species hosted by *A. niehofii* were present only in rays collected from Malaysian Borneo or Indonesian

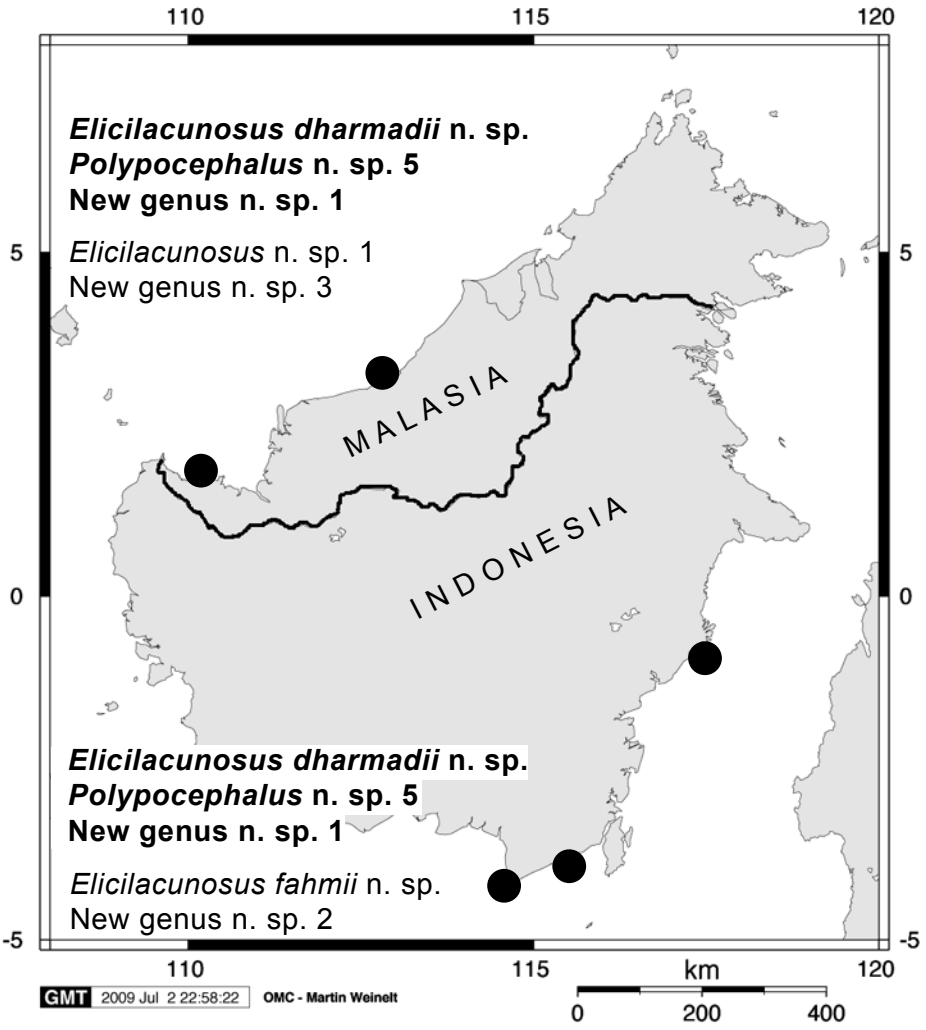

Figure 16. Map indicating specific localities of the 5 *Aetomylaeus niehofii* specimens from Borneo infected with lecanicephalideans and a list of lecanicephalidean species found in either Malaysia or Indonesia; species found in both localities are indicated in bold.

Borneo. The three congeners of the new genus found in *A. niehofii* parasitized rays collected from both Borneo and Northern Australia (Fig. 17). These three species were the only lecanicephalideans found from Northern Australia. The remaining four lecanicephalidean species identified as parasites of *A. niehofii*: *Elicilacunosus dharmadii* n. sp., *E. fahmii* n. sp., *E.* n. sp. 1, and *Polypocephalus* n. sp. 5, were found in rays collected only from Borneo.

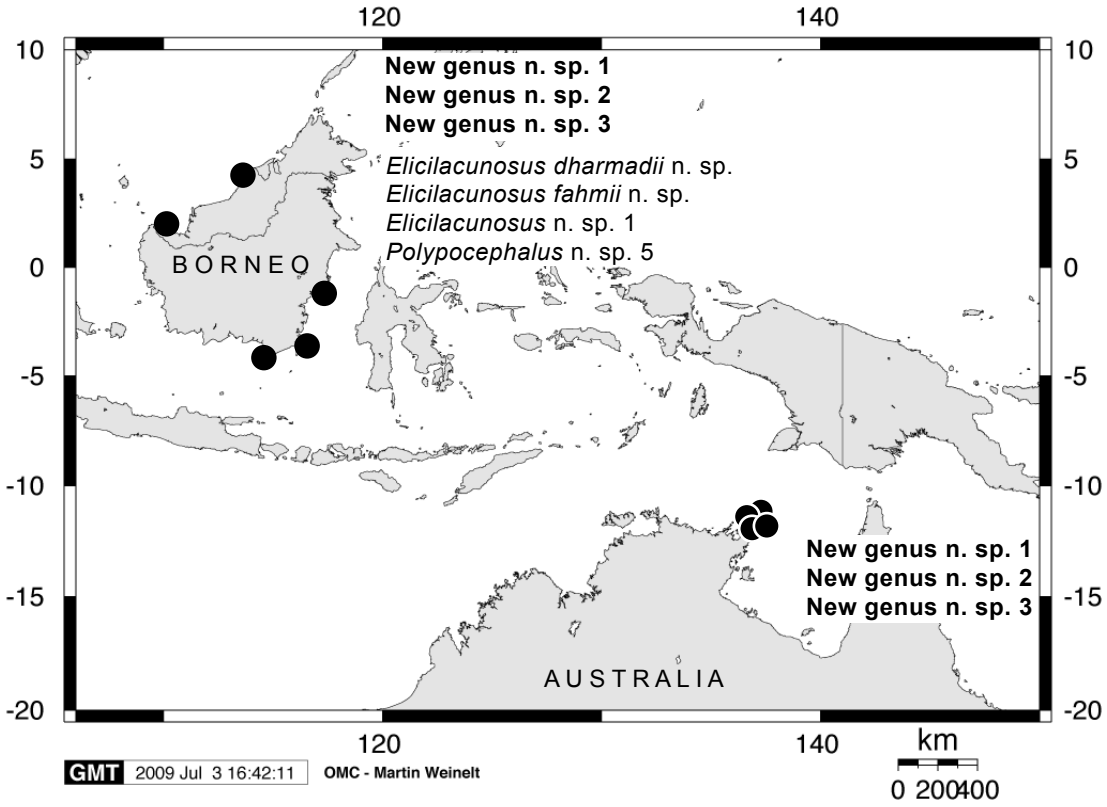

Figure 17. Map indicating specific localities of the 9 total *Aetomylaeus niehofii* specimens infected with lecanicephalideans and a list of lecanicephalidean species found in either Borneo or Northern Australia; species found in both localities are indicated in bold.

Descriptions of New Taxa

Elicilacunosus dharmadii n. sp.

(Figs. 18 and 19)

Description

Based on 11 specimens: 10 whole mounts of mature worms and 1 whole worm prepared for SEM.

Worms 536-906 (689 ± 110; 9) long; maximum width at terminal proglottid,

euapolytic; proglottids 15-26 (20 ± 4; 9) in number. Scolex 43-63 (52 ± 6; 9) long by 47-62 (56 ± 5; 9) wide, consisting of 4 acetabula, apical modificaton of scolex proper, and apical organ. Acetabula in form of suckers, 24-30 (26 ± 2; 9; 17) long by 21-29 (24 ± 2; 9; 17) wide. Apical modification of scolex proper elongate, cylindrical, retractable into scolex proper, with pore-like aperture at center, housing apical organ. Apical organ primarily glandular, retractable; apical modification of scolex proper and apical organ combined 20-29 (25 ± 4; 9) long by 29-34 (32 ± 2; 9) wide when retracted.

Rims of acetabula covered with blade-like spinitriches and long filitriches; blade-like spinitriches absent from posterior margin of rim (Fig. 19C). Scolex proper covered with slightly elongate filiform microtriches (Fig. 19D). Strobila covered with triangular microtriches, increasing in size around column of depressions, becoming shorter and more conical toward posterior margins of each proglottid (Fig. 19E, F, I); anterior region of proglottids with larger, spinitriches (Fig. 19H, I).

Cephalic peduncle absent. Proglottids craspedote, non-laciniate. Immature proglottids 14-25 (19 ± 4; 9) in number, initially wider than long, becoming longer than wide with maturity; posterior-most immature proglottid 65-129 (86 ± 19; 10) long by 40-135 (94 ± 24; 10) wide. Mature proglottids 1 in number, 183-285 (228 ± 31; 10) long by 99-156 (124 ± 17; 10) wide. Testes 12-16 (14 ± 2; 10) in number, 11-38 (26 ± 7; 10; 30) long by 12-51 (32 ± 11; 10; 30) wide, in single field, extending from anterior margin of proglottid to ovary, slightly overlapping anterior margin of ovary, 2 columns in frontal view, 1 row deep. Vas efferens not observed. Vas deferens in form of thin tube, extending along lateral margin of proglottid from ootype region to cirrus sac; external and internal seminal vesicles not observed. Cirrus sac pyriform, slightly angled anteriorly, 28-48 (35 ± 5; 10) long by 26-39 (33 ± 4; 10) wide, containing coiled cirrus. Cirrus microtriches not observed. Ovary H-shaped in frontal view, 29-57 (43 ± 9; 10) long by 62-108 (85 ± 15; 10) wide, lobulated, symmetrical; ovarian bridge

at center of ovary. Mehlis' gland near posterior margin of ovary. Vagina extending laterally from ootype to genital atrium, opening posterior to cirrus sac into genital atrium. Genital pores lateral, irregularly alternating, 44-54% (48 ± 4; 10) of proglottid length from posterior end. Uterus saccate, submedial, extending from just posterior to testes to just posterior of anterior margin of vitellaria. Vitellaria follicular, medullary, lateral, not well-developed in most mature proglottids, in 4 columns, 2 follicles on each side with 1 follicle dorsal and 1 ventral to testes (never lateral to testes), extending from anterior margin of ovary to just posterior to anterior margin of muscular and glandular tissue, slightly overlapping ovary. Single pair of excretory ducts. Eggs not observed.

Taxonomic Summary

Type host: *Aetomylaeus niehofii* (Schneider, 1801), the banded eagle ray (Myliobatiformes: Myliobatidae).

Type locality: Mukah (02°53'N, 112°05'E), Sarawak, Malaysia, South China Sea.

Site of infection: Spiral intestine.

Specimens deposited: Holotype (MZUM No. 00000), 1 paratype (SBC No. 00000); 4 paratypes (USNPC Nos. 00000); 4 paratypes (LRP Nos. 0000 – 0000). Whole worm prepared for SEM retained in the personal collection of Dr. Kirsten Jensen at the University of Kansas.

Prevalence: 11.8% (i.e. in 2 of 17 host individuals examined).

Etymology: This species was named for Dharmadi, Research Centre for Capture Fisheries, Jakarta, Indonesia, for assistance with host collections.

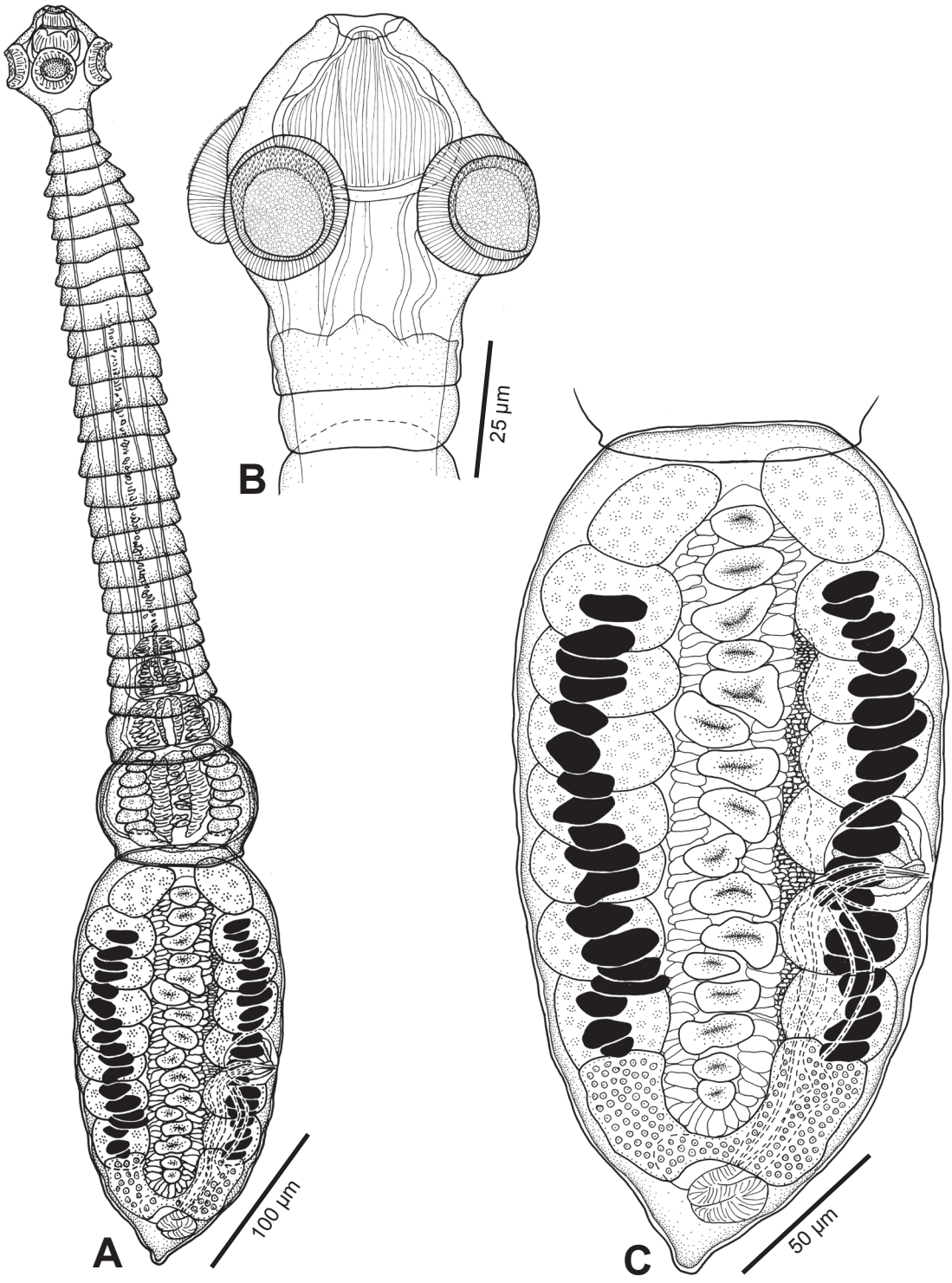

Figure 18. Line drawings of *Elicilacunosus dharmadii* n. sp. (A) Whole worm. (B) Scolex. (C) Mature terminal proglottid.

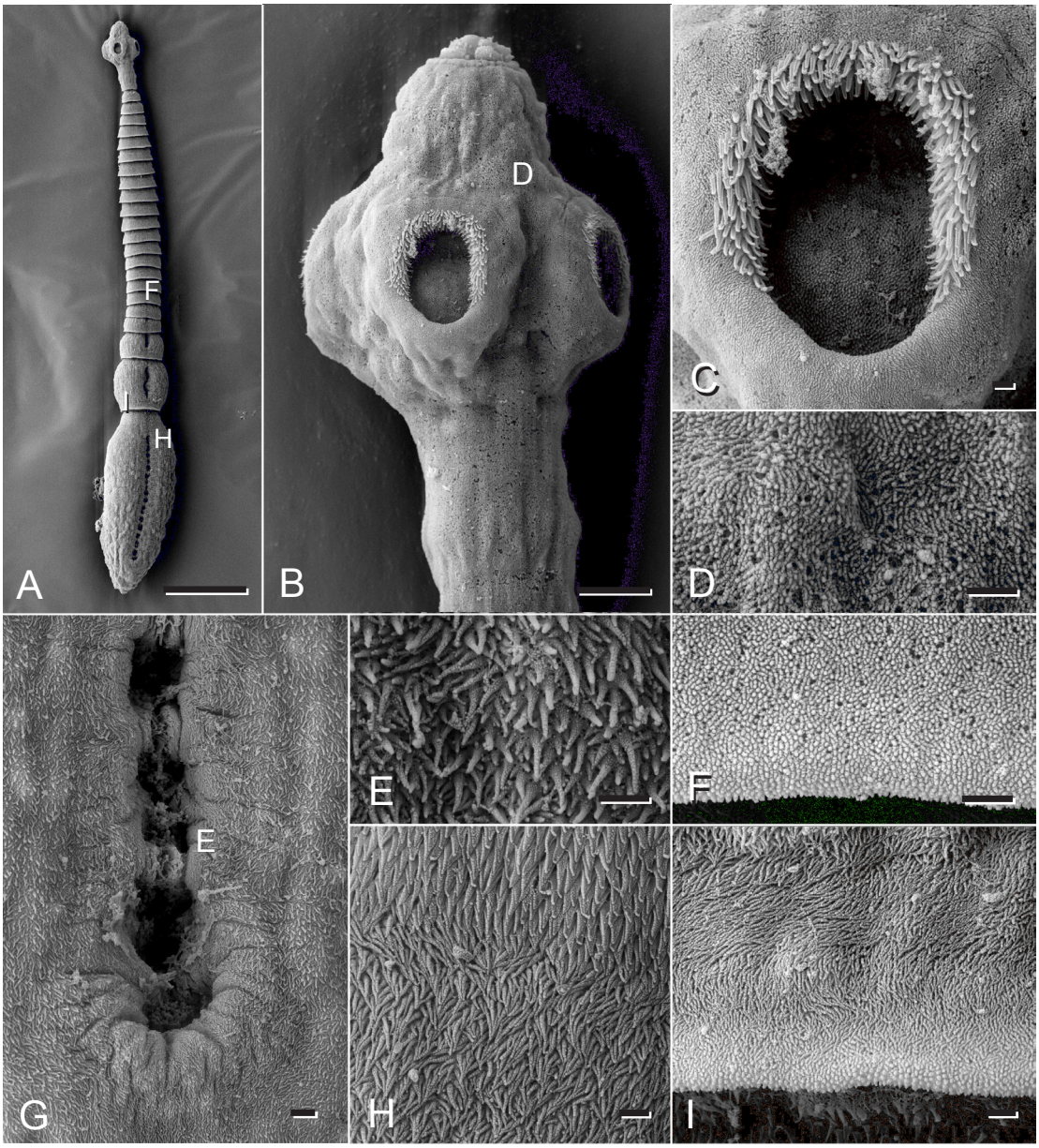

Figure 19. Scanning electron micrographs of *Elicilacunosus dharmadii* n. gen., n. sp. (A) Whole worm. (B) Scolex. Small letter indicates details shown in Fig. D. (C) Enlarged view of sucker. (D) Microtriches on scolex proper. (E) Microtriches along margin of external representation of glandular structures. (F) Microtriches on posterior margin of anterior proglottid. (G) Enlarged view of external representation of glandular structures. (H) Microtriches on anterio of terminal proglottid. (I) Microtriches on posterior margin of subterminal proglottid. Scale bars: A = 100 μm; B = 10 μm; C-F, H-I = 1 μm; G = 2 μm.

Remarks

Elicilacunosus dharmadii n. sp. can be distinguished from *Elicilacunosus lasti* based on the presence of only one proglottid close to maturity rather than two to three proglottids that are either mature or approaching maturity. *Elicilacunosus dharmadii* n. sp. can be further distinguished from the type species by its shorter ovary (29-57 *vs* 60-146 long). Unfortunately, the apical modification of the scolex proper and the apical organ was not everted in any of the specimens examined; descriptions of the apical structure in this taxon requires confirmation.

***Elicilacunosus fahmii* n. sp.**

(Figs. 20-22)

Description

Based on 28 specimens: 3 whole mounts of complete mature worms, 5 whole mounts of mature and 3 whole mounts of immature worms without scolex, 1 whole mount of scolex, 11 whole mounts of detached mature proglottids, cross-sections of 4 mature proglottids (2 PAS stained), and 1 scolex prepared for SEM.

Worms 2,117-2,662 (2,450 ± 292; 3) long; maximum width at terminal proglottid, euapolytic; proglottids 34-51 (42 ± 6; 7) in number. Scolex 152-249 (205 ± 49; 3) long by 65-125 (105 ± 27; 4) wide, consisting of 4 acetabula, apical modificaton of scolex proper, and apical organ. Acetabula in form of suckers, 37-60 (53 ± 8; 4; 8) long by 34-61 (50 ± 9; 4; 8) wide. Apical modification of scolex proper long, cylindrical, retractable into scolex proper, with pore-like aperture at center, housing apical organ. Apical organ primarily glandular, retractable; apical modification of scolex proper and apical organ combined 145 long by 63 wide.

Rims of acetabula covered with blade-like spinitriches and elongate filitriches (Fig. 21B, C). Distal acetabular surface covered with short and elongate filitriches. Scolex proper and cephalic peduncle densely covered with long filitriches, giving worms "fuzzy" appearance (Fig. 21A, D). Apical modification of scolex proper and apical organ covered with short filitriches (Fig. 21F). Strobila covered with short, more widely dispersed filitriches (Fig. 21G).

Cephalic peduncle present. Proglottids craspedote, non-laciniate. Immature proglottids 34-51 (42 ± 6; 7) in number, initially wider than long, becoming longer than wide with maturity; posterior-most immature proglottid 218-378 (277 ± 52; 11) long by 180-319 (235 ± 48; 11) wide. Mature proglottids 1 in number, 311-1,024 (465 ± 168; 19) long by 171-467 (249 ± 71; 19) wide. Testes 14-33 (24 ± 6; 17) in number, 16-52 (33 ± 9; 17; 51) long by 28-119 (65 ± 20; 17; 51) wide, in single field, extending from anterior margin of proglottid to ovary, slightly overlapping anterior margin of ovary, 2 columns in frontal view, 1 row deep in cross-section (Fig. 22A). Vas efferens not observed. Vas deferens in mature proglottids in form of thick tube, extending laterally from ootype region to cirrus sac; external and internal seminal vesicles not observed. Cirrus sac pyriform, perpendicular to genital pore, 51-152 (86 ± 29; 19) long by 29-144 (56 ± 25; 19) wide, containing coiled cirrus. Cirrus microtriches not observed. Ovary H-shaped in frontal view, bilobed in cross-section (Fig. 22B), 45-229 (103 ± 46; 18) long by 131-354 (188 ± 53; 18) wide, lobulated, symmetrical; ovarian bridge at center of ovary. Mehlis' gland near posterior margin of ovary. Vagina extending laterally from ootype to genital atrium, opening posterior to cirrus sac into genital atrium. Genital pores lateral, irregularly alternating, 39-55% (48 ± 5; 19) of proglottid length from posterior end. Uterus saccate, submedial, extending from ootype to just posterior of anterior margin of muscular and glandular tissues. Vitellaria follicular, medullary, lateral, in 4 columns (Fig. 22A), 2 follicles on each side with 1 follicle dorsal and 1 ventral to testes (never lateral to

testes), extending from anterior margin of ovary nearly to anterior margin of proglottid, slightly overlapping ovary; vitelline follicles 8-53 (16 ± 8; 16; 48) long by 25-150 (47 ± 23; 16; 48) wide. Single pair of excretory ducts (Fig. 22B). Eggs not observed.

Taxonomic Summary

Type host: *Aetomylaeus niehofii* (Schneider, 1801), the banded eagle ray (Myliobatiformes: Myliobatidae).

Type locality: Sepuk Laut (00°12'S, 109°05'E), West Kalimantan, Indonesia, South China Sea.

Site of infection: Spiral intestine.

Specimens deposited: Holotype (MZB No. 00000), 4 paratypes (2 whole mounts of worms without scoleces and 2 detached mature proglottids) (MZB Nos. 00000); 12 paratypes (2 whole mounts of worms with scolex, 1 whole mount of mature worm without scolex, 2 whole mounts of immature worms without scoleces, 5 detached mature proglottids, cross-sections of 2 mature proglottids [1 PAS stained]) (USNPC Nos. 000000); 10 paratypes (1 whole mount of scolex, and 2 whole mounts of mature worms without scoleces, 1 whole mount of immature worm without scolex, 4 detached proglottids, and cross-sections of 2 mature proglottids [1 PAS stained]) (LRP Nos. 00000). Scolex prepared for SEM with voucher retained in the personal collection of Dr. Kirsten Jensen at the University of Kansas.

Prevalence: 5.9% (i.e. in 1 of 17 host individuals examined).

Etymology: This species was named for Fahmi, Pusat Penelitian Oseanografi, LIPI, Jakarta, Indonesia, for assistance with host collections.

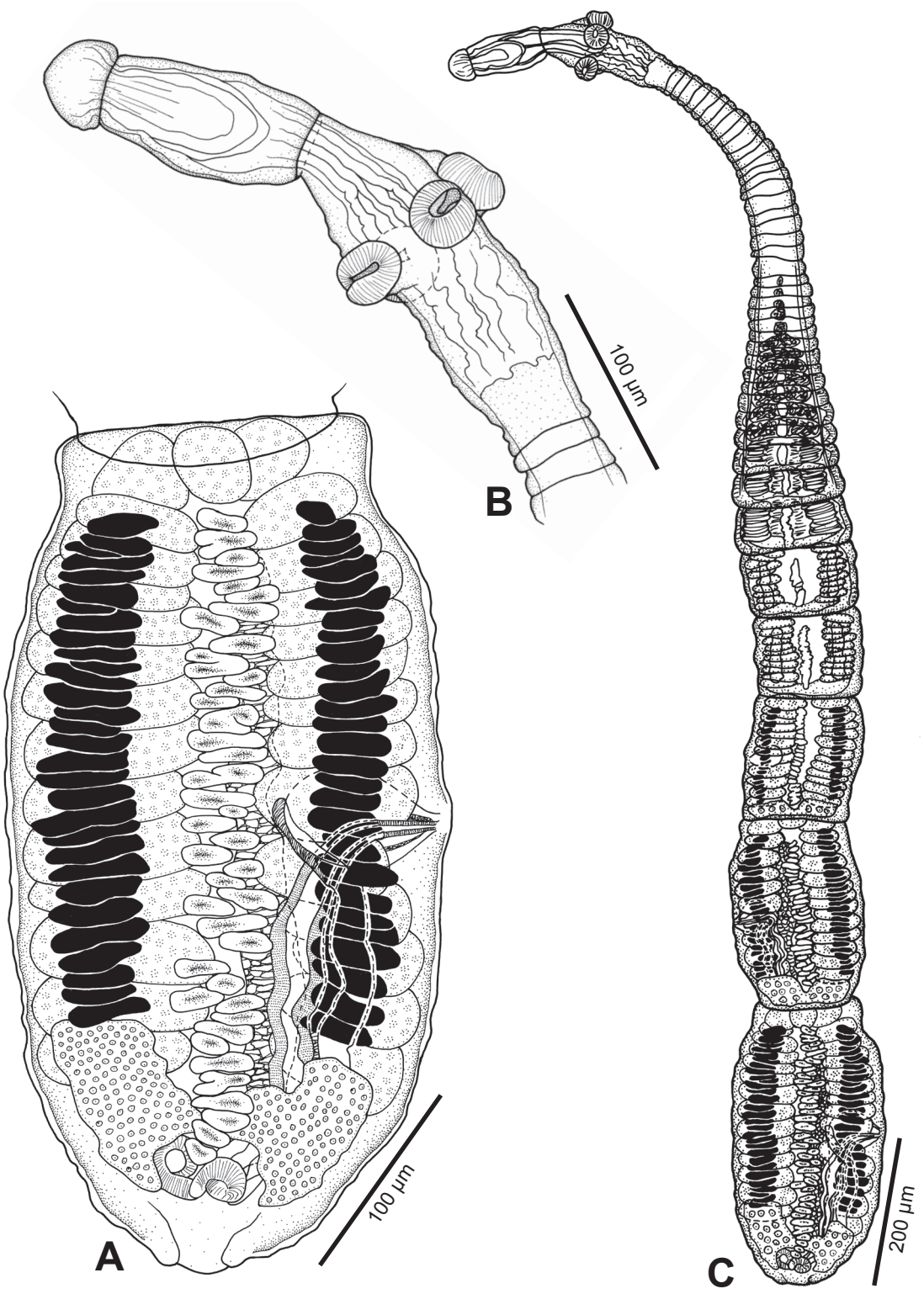

Figure 20. Line drawings of *Elicilacunosus fahmii* n. sp. (A) Whole worm. (B) Scolex. (C) Mature terminal proglottid.

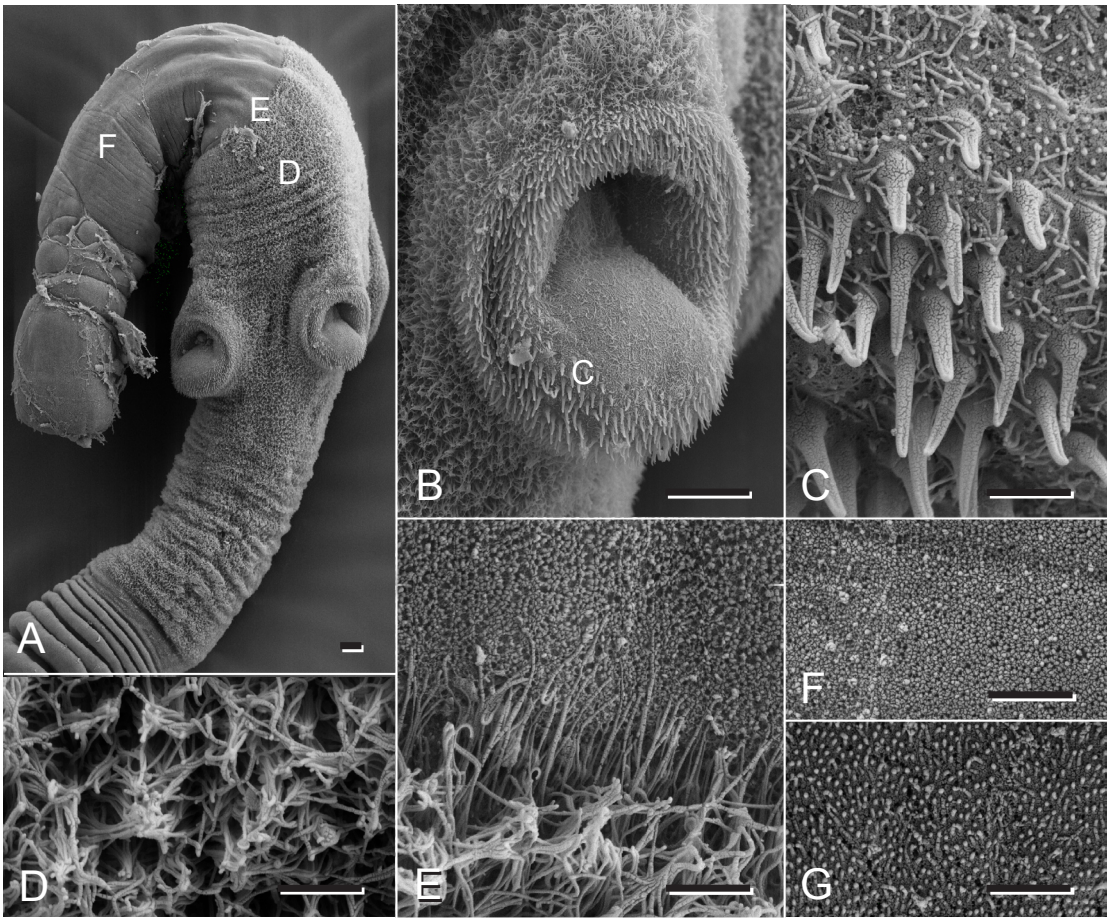

Figure 21. Scanning electron micrographs of *Elicilacunosus fahmii* n. gen., n. sp. (A) Scolex. Small letters indicate details shown in Figs. D, E, and F. (B) Enlarged view of sucker. Small letter indicates details shown in Fig. C (C) Microtriches on sucker rim. (D) Microtriches on scolex proper. (E) Microtriches at interface between scolex proper and apical organ. (F) Microtriches on apical organ. (G) Microtriches on strobila. Scale bars: A, B = 10 μm; C-G = 1 μm.

Remarks

Elicilacunosus fahmii n. sp. can be easily distinguished from *E. lasti* and *E. dharmadii* based on its larger size (2,117-2,662 *vs* 536-906, and 890-1,830, respectively) as well as its greater number of proglottids (34-51 *vs* 15-26, and 18-24, respectively). In addition, blade-like spinitriches only cover the anterior margin of the rim of the acetabulae of *E. lasti* and *E. dharmadi*, while they are present on the entire rim of the acetabulae in *E.*

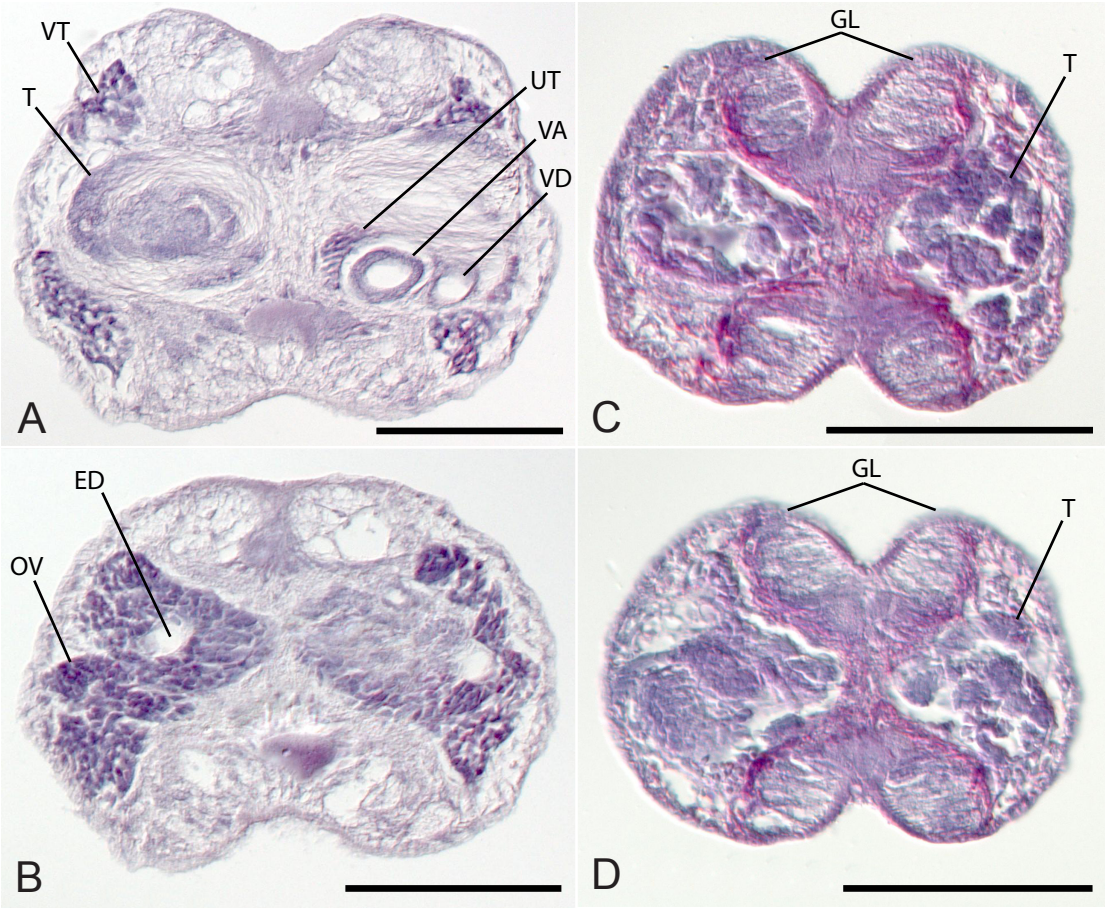

Figure 22. *Elicilacunosus fahmii* n. gen., n. sp. (A) Cross-section through mature proglottid at level of testes. (B) Cross-section through mature proglottid at level of ovary. (C) Cross-section through mature proglottid at level of testes (PAS stained), showing dorsal and ventral muscular and glandular tissues. (D) Cross-section through mature proglottid at level of testes (PAS stained), showing dorsal and ventral muscular and glandular tissues. Abbreviations: ED, excretory duct; GL, glandular and muscular tissues; OV, ovary; T, testis; UT, uterus; VA, vagina; VD, vas deferens; VT, vitelline follicle. Scale bars: A-D = 100 μm.

fahmii n. sp. Moreover, the apical organ is most extensive in this species as compared to those of its two congeners. Also, the long filitriches covering the entire scolex proper, which convey a fuzzy appearance, are only slightly elongate in the two congeners. The unusual glandular and muscular tissues possessed by all congeners of this genus were investigated in *E. fahmii* n. sp. using conventional staining techniques as well as staining with McManus' periodic acid-Shiff (PAS) reaction in order to determine their potential function (see Fig. 22C,

D). PAS selectively stains glycoproteins or mucopolysaccharides, evidence for the presence of adhesive substances. This staining method applied to proglottid cross-sections of *E. fahmii* revealed PAS-positive staining of the region surrounding what appears to be muscular tissue, especially towards the internal region of the proglottid (see Fig. 22C, D)

Other Lecanicephalidean Species of *Aetomylaeus niehofii*

Of the seven new lecanicephalidean species in three genera hosted by *Aetomylaeus niehofii*, five are not formally described in this study. These included a fourth species of *Elicilacunosus*, three species representing a new genus, and one species of *Polypocephalus*.

Elicilacunosus n. sp. 1 (Fig. 23A) is clearly a member of this genus based on its possession of the glandular and muscular regions along the length of the proglottids, the

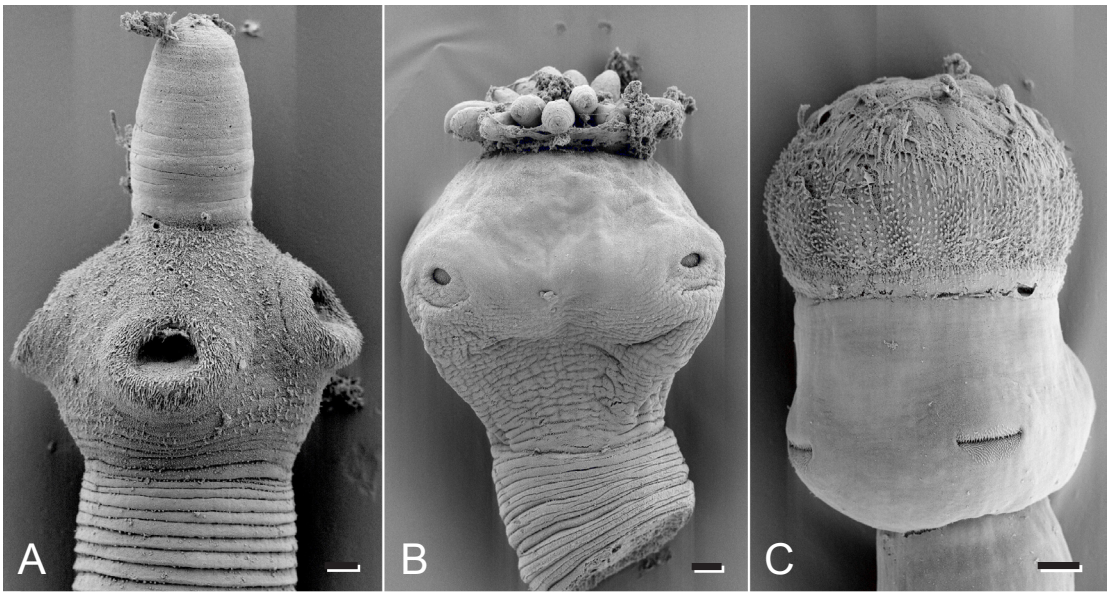

Figure 23. Scanning electron micrographs of scoleces from representatives of other lecanicephalidean taxa from *Aetomylaeus niehofii*. (A) *Elicilacunosus* new species 1. (B) *Polypocephalus* new species 5. (C) New genus new species 2. Scale bars: A = 10 μm; B = 20 μm; C = 10 μm.

presence of an elongate apical modification of the scolex proper housing the apical organ, and the distribution of vitelline follicles dorsal and ventral to, but never outside of, the columns of testes. However, this species can be easily distinguished from the three species described in this study based on the presence of blade-like spinitriches covering the entire scolex proper and the rims of the acetabulae, rather than being restricted to the acetabular rims (Fig. 23A).

Polypocephalus new species 5 (Fig. 23B) possesses a slightly thick strobila and six testes in each proglottid.

The three new species representing a new genus, similar to *Tylocephalum* but with a retractable apical organ, are each very distinct. New genus new species 1 is a tiny worm (~ 1 mm) with a robust and broad scolex. Its neck is short and thick, with few segments, followed by only a few developing proglottids. Only the terminal proglottid is mature. New genus new species 2 (Fig. 23C) is a larger, longer worm (~ 4-5 mm) with a long neck consisting of several immature segments. The terminal proglottid is several times longer than wide. New genus new species 3 possesses a long, thin neck that suddenly widens at the point where internal anatomy becomes visible in the proglottids. These proglottids are consistently wider than long and the terminal proglottid is hardly elongate.

DISCUSSION

Lecanicephalidean Diversity

This study revealed the genus *Aetomylaeus* as host to a great diversity of cestodes of the order Lecanicephalidea. This diversity is well represented on both the generic and species levels in each of the three host species. All lecanicephalidean species reported in this study were determined to be unique and non-overlapping among the three congeners of *Aetomylaeus*. Moreover, all 30 species collectively found to parasitize *Aetomylaeus* were lecanicephalidean species new to science. The new species not officially described here were determined to be morphologically distinct from one another both within and among the three host species. Previously, only one lecanicephalidean species had been described from any of the species of *Aetomylaeus*. Shipley and Hornell (1906) described *Tylocephalum dierama* from *A. maculatus* (as *Myliobatis maculata*) from Sri Lanka. *Tylocephalum dierama* is currently considered a *species inquirendum* (Jensen, 2005). None of the twelve species of *Tylocephalum* found parasitizing *Aetomylaeus* species in this study were found to match the original description of *T. dierama*.

Based on Jensen (2005), as well as taking into account species that have since been described (Jensen, 2006; Pramanik and Manna, 2007), a total of 79 species are currently recognized in the Lecanicephalidea. The 30 lecanicephalidean species found in this study contribute much to the knowledge of this cestode order. Based on the results of this study, the total number of lecanicephalidean species known is increased by over one third. Aside from the sheer number of new species, the number of previously undescribed lecanicephalidean genera represented in *Aetomylaeus* is remarkable. Prior to this study, 12 lecanicephalidean genera were recognized. Including the three new genera diagnosed above, i.e., *Rexapex, Collicocephalus*, and *Elicilacunosus*, a total of 15 genera can now be recognized. Moreover, taking into account the two unidentified genera in *A. vespertilio* and the new genus

parasitizing *A. niehofii*, the lecanicephalidean generic diversity is clearly even higher.

Most remarkable is that with these new genera, novel scolex and proglottid morphologies could be demonstrated for the lecanicephalideans. The crown-like, retractable apical organ of *Rexapex* n. gen. from *A. vespertilio*, with its finger-like projections, is a form never before observed in the Lecanicephalidea. This unique apical organ morphology, along with the combination of bothridiate acetabula and a laterally expanded anterior strobila set this genus apart from all other known lecanicephalideans. The new genus from *A. niehofii* not diagnosed here is yet another new form due to its retractable, globular apical organ, in combination with its *Tylocephalum*-like proglottid anatomy. Most notable, however, was the discovery of a unique proglottid feature exhibited by *Elicilacunosus* n. gen. from the hosts *A. maculatus* and *A. niehofii*. The unusual glandular and muscular tissues possessed by all congeners of this genus appear to be unique not only among the Lecanicephalidea or elasmobranch tapeworm orders, but among all cestodes. This morphological feature was investigated in some detail to determine its potential function using conventional staining techniques as well as staining with McManus' periodic acid-Shiff (PAS) reaction (see Fig. 21C, D). PAS selectively stains glycoproteins or mucopolysaccharides, evidence for the presence of adhesive substances. This staining method applied to proglottid cross-sections of the largest species of *Elicilacunosus, E. fahmii*, showed PAS-positive staining of the region surrounding the, what appears to be muscular tissue, especially towards the internal region of the proglottid (see Fig. 21C, D). An adhesive function can only be speculated.

Given that little to nothing was known about lecanicephalideans from *Aetomylaeus*, prior to this study, the lecanicephalideans encountered represent new host records for all genera, with the exception of *Tylocephalum* (of which *T. dierama* was described from *Myliobatis maculata* by Shipley and Hornell [1906]); these genera are reported for the first time from the genus *Aetomylaeus*. *Aberrapex* had previously been reported from species of

another myliobatid genus, *Myliobatis* (Brooks *et al*., 1981; Jensen, 2001), as well as from *Taeniura lymma* (Forsskål, 1775) (Dasyatidae) (Jensen, 2006); *Lecanicephalum* was only known from species of *Dasyatis* Gray (Dasyatidae) from the Atlantic Ocean. This is in contrast to *Polypocephalus* which had been reported from several families of rays, including the Myliobatidae.

Atlantic and Pacific Forms of *Tylocephalum*

The genus represented by the greatest number of species in this system was *Tylocephalum*. Both, *Aetomylaeus vespertilio* and *A. maculatus* hosted six congeners, while members of *Tylocephalum* were not encountered in the 17 specimens of *A. niehofii* examined. Twelve species of *Tylocephalum* are currently recognized (Jensen, 2005), comprised of species from the Atlantic Ocean, and the Pacific and Indian Oceans. Comparison of the species resulting from this study and the original descriptions of those described from the Atlantic Ocean (e.g., *T. pingue* Linton, 1890, from Woods Hole, Massachusetts, *T. bonasum* Campbell and Williams, 1984 from Sakonnet Point, Rhode Island, and *T. brooksi* Ivanov and Campbell, 2000, from the Gulf of Venezuela), as well as the detailed treatment of Atlantic *Tylocephalum* by Ivanov and Campbell (2000), showed what appear to be two distinctive forms of the genus *Tylocephalum* (Linton, 1890; Campbell and Williams, 1984; Ivanov and Campbell, 2000). The type species, *T. pingue, T. bonasum*, and *T. brooksi* exhibit only slightly craspedote proglottids, possess many testes arranged in four columns, and possess vitelline follicles that are circumcortical and represent the Atlantic form. This is compared to the Pacific form, exemplified by *Tylocephalum* species 1-12 from this study, and, for example, *T. koenneckeorum* Jensen, 2005, which possesses more craspedote proglottids, testes arranged in fewer columns and vitelline follicles that are restrictd to the lateral margins of the proglottids. A revision of the genus might be in order, ideally supported by a phylogenetic hypothesis

based on molecular data, to determine whether these two groups actually comprise separate genera.

Host Specificity

Elasmobranch tapeworms in general, with the exception of the Trypanorhyncha, appear to exhibit oioxenous specificity (Caira *et al*., 2001; 2003). Oioxenous specificity has been demonstrated for the Lecanicephalidea (Jensen, 2005). This present study further supports the persuasion of oioxenous specificity of this cestode order. All of the 30 lecanicephalidean species identified during this study were determined to parasitize only a single species of *Aetomylaeus*. Even congeners among the three host species were distinct from one another.

Such a relationship between elasmobranch species and their unique assemblages of cestode parasites suggests a long-lived association (Hoberg and Klassen, 2002). One explanation previously proposed for these tight relationships are tied to host diet, i.e. the particular intermediate hosts ingested (Bush *et al*., 1993; Marcogliese, 2002; Caira and Reyda, 2005). Certain rays may only prey upon certain types of intermediate hosts, thereby encountering a limited assortment of cestode species present in these intermediate hosts as larvae. Another explanation of this oioxenous specificity in elasmobranch cestodes could involve a host's internal environmental pressures on the parasite, including the immune system, nutrients, and microhabitat of the spiral intestine, etc. (e.g., Brooks, 1979; Mitter and Brooks, 1983). For example, areas of the spiral intestine may differ structurally among species and unique arrangements of microvilli may be present, allowing only species with a particular scolex morphology to attach. Considering these host factors, certain cestode species may have evolved specialization for occupation of a unique microhabitat within the spiral intestine (Caira and Reyda, 2005) and may thus be restricted to a single elasmobranch host species.

Comparision of Lecanicephalidean Faunas Among Host Species

The total diversity of 30 lecanicephalidean species identified across ten genera parasitizing *Aetomylaeus* is somewhat differently distributed among the host species; *Aetomylaeus vespertilio* hosted the greatest diversity with 13 species, while *A. maculatus* and *A. niehofii* hosted ten and seven species, respectively. The generic diversity showed a similar pattern. *Aetomylaeus vespertilio* hosted lecanicephalideans representing seven genera, while *A. maculatus* and *A. niehofii* were host to nearly half that generic diversity (i.e., four and three genera, respectively).

No complete life cycle of any elasmobranch cestode has been described, with the exception of the experimental life cycles of two species of trypanorhynchs by Sakanari and Moser (1989). A typical life cycle must include at least one invertebrate intermediate host with potentially one to two additional intermediate hosts, which may be invertebrates or vertebrates (see, e.g., Caira, 1990; Caira and Reyda, 2005). The Lecanicephalidea are thought to potentially utilize two intermediate hosts in their life cycle, a copepod and another invertebrate or vertebrate host (Caira and Reyda, 2005).

Given that elasmobranch tapeworms are transmitted from their final intermediate host to their definitive host, the elasmobranch, via the food chain, information on the diet of the three species of *Aetomylaeus* could shed light on the possible transmission route of their tapeworms. Unfortunately, very little is known about the diet. Basically, the food habits of *Aetomylaeus vespertilio* and *A. maculatus* are unknown, but are thought to consist of bivalves and other bottom-dwelling invertebrates (White et al., 2006). The food habits of *A. niehofii* have been reported to consist of worms, snails, crustaceans, and bony fishes (Michael, 1993), and also bivalves (White et al., 2006).

In this study, *Aetomylaeus vespertilio* hosted the greatest diversity of lecanicephalideans, a total of 13 species in seven genera. Perhaps the higher

lecanicephalidean diversity in *A. vespertilio* can be attributed to the fact that this host attains the largest in size of the three congeners of *Aetomylaeus*. *Aetomylaeus vespertilio* can attain a disc width of up to 350 centimeters (White et al., 2006) and can venture into waters up to 110 meters in depth (Compagno, 1999b). It is classified as a benthopelagic ray, and also said to be a strong and agile swimmer in comparison to *A. maculatus* and *A. niehofii* (White *et al*., 2006). These biological factors may allow *A. vespertilio* the opportunity to exploit a wider array of food items as well as a higher volume of diet than its two sister species, and in turn, a greater opportunity for encountering a higher diversity of intermediate hosts of lecanicephalidean cestodes.

Biogeographical patterns

The Lecanicephalidea are especially diverse in the tropics (Caira and Reyda, 2005; Jensen, 2005). The waters off of Borneo and Northern Australia have been demonstrated to exhibit a high diversity of elasmobranch cestodes (e.g., Fyler and Caira, 2006; Reyda and Caira, 2006; Healy, 2006; Twohig *et al*., 2008). However, few studies have addressed whether the same cestode species parasitize hosts across a broad geographic range. While specimens of *Aetomylaeus vespertilio* were collected only off of Northern Australia, and specimens of *A. maculatus* were collected only off of Malaysian and Indonesian Borneo, specimens of *A. niehofii* were collected from both Malaysian and Indonesian Borneo and Northern Australia. A comparison of lecanicephalidean species parasitizing *A. niehofii* from both Malaysian and Indonesian Borneo and Northern Australia is addressed below. At a smaller scale, comparison of the lecanicephalidean fauna of *A. maculatus* and *A. niehofii* collected from Malaysian versus Indonesian Borneo is also of interest. The data in this study suggest a possible difference in the lecanicephalidean biotas of Malaysian versus Indonesian Borneo with regard to certain genera and species. *Aetomylaeus maculatus*, in particular, appears to host only

certain lecanicephalidean species depending on its locality.

Of the five total specimens of *A. maculatus* available, three were collected from Malaysian Borneo (specimens indicated by BO in Table 4) and two from Indonesian Borneo (specimens indicated by KA in Table 4). Only one lecanicephalidean species, *Tylocephalum* new species 11, was present in both localities, while eight, *Elicilacunosus lasti, Tylocephalum* new species 8, 9, 10, and 12, *Polypocephalus* new species 3 and 4, and *Lecanicephalum* new species 1, were found only in Malaysian Borneo, and one species, *Tylocephalum* new species 7, only in Indonesian Borneo (see Fig. 12). Perhaps individuals of *A. maculatus* have a more limited range of movement and thus, the lecanicephalidean species of *A. maculatus* of Malaysian Borneo and Indonesian Borneo are more restricted locally. While suggestive of a pattern with a greater diversity in the waters off Malaysian Borneo, cestode data from additional host specimens are needed.

Contrastingly, *Aetomylaeus niehofii* exhibited greater overlap in its lecanicephalidean fauna among specimens from Malaysian and Indonesian Borneo. Of the seventeen total specimens of *A. niehofii* collected, five were from Malaysian Borneo and five were from Indonesian Borneo (seven were from off of Northern Australia); three of the seven lecanicephalidean species were found in host specimens from both Malaysian (specimens indicated by BO in Table 5) and Indonesian (specimens indicated by KA in Table 5) Borneo. The other four species parasitizing this ray were present in only one of these collection localities. and *Elicilacunosus* new species 1 and new genus new species 3 were present in *A. niehofii* collected only from Malaysian Borneo. *Elicilacunosus fahmii* and new genus new species 2 were collected only from Indonesian Borneo. *Elicilacunosus dharmadii, Polypocephalus* new species 5, and new genus new species 1 were present in *A. niehofii* from both Malaysian and Indonesian Borneo (see Fig. 16). These data suggest that this ray may cover greater areas and distances in its movements and thus rays from different localities may

share more similar lecanicephalidean faunas.

Aetomylaeus niehofii was the only species of *Aetomylaeus* to be collected from both Malaysian and Indonesian Borneo and Northern Australia. The separation of these two distant areas is amplified by the presence of the deepwater trench in the Makassar Strait. Little is known of the biology of *A. niehofii* and whether it is capable or in the habit of traveling long distances across deep water. If this ray does move between Northern Australia and Borneo, it is more likely for the cestode faunas of specimens from Northern Australia and those from Borneo to be homogenous. If, however, *A. niehofii* is more restricted in its movements and does not cross over into the opposite biogeographic realm, the cestode faunas of specimens from these two disjunct areas may differ from one another, for historical and/or biological reasons.

The differences between the lecanicephalidean faunas of *Aetomylaeus niehofii* collected from Borneo and those of Northern Australia were curious. All seven species were encountered in rays from Borneo (specimens with numbers beginning with BO and KA in Table 5). The three congeners of *Elicilacunosus* and the sole species of *Polypocephalus* were present only in *A. niehofii* specimens collected from Borneo and absent from the specimens from Northern Australia (see Fig. 17). These prevalence data suggest that the genera *Elicilacunosus* and *Polypocephalus* potentially do not occur off of Northern Australia in *A. niehofii*. Interestingly, the three congeners of the new, undiagnosed genus (found only in *A. niehofii*) were the only lecanicephalidean species parasitizing the specimens from Northern Australia (see Fig. 17). Each of these species was also found in *A. niehofii* collected from Borneo in much higher intensities, but relatively lower prevalence; while all rays from Northern Australia were infected with at least one species of the new genus, only three out of five rays from Borneo were parasitized by this genus.

Because the four specimens of *Aetomylaeus niehofii* collected from Northern

Australia that were infected came from a single locality, the understanding of the lecanicephalidean fauna from this region is limited. An additional factor might have influenced the relatively low diversity (and relatively low number of worms encountered in general) in rays from Northern Australia. These *A. niehofii* specimens were infected with (often several) large nematodes in the family Gnathosomatidae at 100% prevalence, also occupying the spiral intestine. Such an infection is uncommon in rays from other localities (Jensen, personal communication) and none of the other *Aetomylaeus* spiral intestines in this study yielded metazoan parasites other than cestodes. The presence of these nematodes could have affected the establishement and/or presence of cestodes in these hosts. Perhaps this nematode infection explains the low intensities of cestodes found in these host specimens. Cestodes (diphyllideans, trypanorhynchs, tetraphylldieans, rhinebothriideans or lecanicephalideans) were found to parasitize all seven *A. niehofii* specimens from Northern Australia, however, their numbers were much lower than in hosts from other regions.

These data indicate possible causes influencing, and confounding, the distribution of lecanicephalidean genera and species parasitizing *A. niehofii* on either side of Wallace's line. A connection of faunal differences to the biogeographic history of the greater IndoMalaysian and Australasian realms cannot clearly be made at this point

Future Directions

A surprising diversity, in number and forms, resulted from this work into the lecanicephalidean fauna of the three species of *Aetomylaeus* collected from Borneo and/or Northern Australia. Additional specimens from these localities might shed light on faunal differences observed within and among species of *Aetomylaeus*. It would be interesting to determine whether the 30 lecanicephalideans reported here are representative of lecanicephalideans parasitizing *A. vespertilio, A. maculatus*, and *A. niehofii* from

throughout their range. It is likely that additional new species (and genera) may be present in *Aetomylaeus* from localities not sampled here. Also, collection of the putative fourth species, *Aetomylaeus milvus,* from the Red Sea or Persian Gulf would be of interest. Additionally, aside from *Aetobatus*, which has been documented as a major host for lecanicephalidean diversity (see Jensen, 2005), only few lecanicephalideans (see Shipley and Hornell, 1906; Dailey and Mudry, 1968; Brooks *et al*., 1981; Jensen, 2001) have been reported from *Myliobatis*; no lecanicephalideans are known from the fourth genus in the Myliobatidae, *Pteromylaeus*. Further exploration of the lecanicephalidean faunas of these hosts would likely be valuable towards further increasing the knowledge of lecanicephalidean diversity.

LITERATURE CITED

Barber, P. H., S. T. Palumbi, M. V. Erdmann, and M. K. Moosa (2000). A marine Wallace's line? *Nature* 406: 692-693.

Benz, G. W., B. E. Smith, S. A. Bullard, and J. S. Braswell (2007). New genus and species of eudactylinid (Siphonostomatoida: Copepoda) from gill lamellae of ornate eagle rays, *Aetomylaeus vespertilio* (Myliobatidae), collected in the Beagle Gulf off Northern Australia. *Journal of Parasitology* 93(1): 32-38.

Brooks, D. R. (1979). Testing the context and extent of host-parasite coevolution. *Systematic Zoology* 28: 299-307.

Brooks, D. R., M. A. Mayes, and T. B. Thorson (1981). Cestode parasites in *Myliobatis goodie* Garman (Myliobatiformes: Myliobatidae) from Rio de la Plata, Uruguay, with a summary of cestodes collected from South American elasmobranchs during 1975-1979. *Proceedings of the Biological Society of Washington* 93: 1239-1252.

Bush, A. O., R. W. Heard, R. M. Overstreet (1993). Intermediate hosts as source communities. *Canadian Journal of Zoology* 71: 1358-1363.

Bush, A. O., K. D. Lafferty, J. M. Lotz, and A. W. Shostak (1997). Parasitology meets ecology on its own terms: Margolis *et al*. revisited. *The Journal of Parasitology* 83(4): 575-583.

Caira, J. N. (1990). Metazoan Parasites as Indicators of Elasmobranch Biology. In: H. L. Pratt Jr., S. H. Gruber, and T. Taniuchi (eds.), *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of Fisheries*. NOAA Technical Report 90. pp. 71-96.

Caira, J. N., K. Jensen, and C. J. Healy (1999). On the phylogenetic relationships among tetraphyllidean, lecanicephalidean and diphyllidean tapeworm tapeworm genera. *Systematic Parasitology* 42: 77-151.

Caira, J. N., K. Jensen, and C. J. Healy (2001). Interrelationships among tetraphyllidean and lecanicephalidean cestodes. In: Littlewood, D. T. J. and R. A. Bray (eds.), *Interrelationships of the Platyhelminthes*. Taylor & Francis, London. pp. 135-158.

Caira, J. N. and D. T. J. Littlewood (2001). Worms, Platyhelminthes. In: *Encyclopedia of Biodiversity, Vol. 5*. Academic Press. pp. 863-899.

Caira, J. N., K. Jensen, and K. Holsinger (2003). On a new index of host specificity. In: Tome, I., C. Combes, and J. Jordan (eds.), *Taxonomy, Ecology, and Evolution of Metazoan Parasites*. PUP, Perpignan France. Presses Universitaires de Perpignan, France. pp. 161-201.

Caira, J. N. and C. J. Healy (2004). Elasmobranchs as hosts of metazoan parasites. In: J. C. Carrier, J. A. Musick, M. R. Heithaus (eds.), *Biology of Sharks and Their Relatives*. CRC Press, Boca Raton, Florida. pp. 524-545.

Caira, J. N. and F. B. Reyda. (2005). In: K. Rohde (ed), *Marine Parasitology*. CABI Publishing and CSIRO Publishing. pp. 92-104.

Caira, J. N., K. Jensen, and C. J. Healy (Eds.). The Global Cestode Database (online). Accessed June, 2009 at www.cestodedatabase.org.

Campbell, R. A. and I. Beveridge (2002). The genus *Acanthobothrium* (Cestoda: Tetraphyllidea: Onchobothriidae) parasitic in Australian elasmobranch fishes. *Invertebrate Systematics* 16(2): 237-344.

Campbell, R. A. and A. D. Williams (1984). *Tylocephalum* Linton, 1890 (Cestoda: Lecanicephalidea) from the Cownose Ray, *Rhinoptera bonasus* (Mitchill, 1815) with a discussion of its validity and systematic relationships. *Proceedings of the Helminthological Society of Washington* 51(1): 121-134.

Chisholm, L. A. and I. D. Whittington (2004). Two new species of *Myliocotyle* (Monogenea: Monocotylidae) from the gills of *Aetomylaeus maculatus* and *A. nichofii* (Elasmobranchii: Myliobatidae) from Sarawak, Borneo, Malaysia. *Folia Parasitologica* 51: 304-310.

Chisholm, L. A. and I. D. Whittington (2009). *Malalophus jensenae* n. g., n. sp. (Monogenea: Monocotylidae) from the gills of *Aetomylaeus vespertilio* (Myliobatidae) off northern Australia. *Systematic Parasitology* 73(2): 81-86.

Compagno, L. J. V. (1999a). Checklist of living elasmobranchs. In: W. C. Hamlett (ed.), *Sharks, Skates, and Rays: The Biology of Elasmobranch Fishes*. The John Hopkins University Press, Baltimore, Maryland. pp. 471-498.

Compagno, L. J. V. (1999b). Myliobatidae. Eagle rays. In: K. E. Carpenter and V. Niem (eds.), *FAO Identification Guide for Fishery Purposes. The living marine resources of the Western Central Pacific*. Vol. 3. Batoid Fishes, chimaeras and bony fishes part 1 (Elopidae to Linophrynidae). FAO, Rome. pp. 1398-1537.

Compagno, L. J. V. (2005). Sharks, rays and chimaeras: The status of chondrichthyan fishes. In: Fowler, S. L. (ed.), *Global Checklist of Living Chondrichthyan Fishes*. pp. 401-423.

Dailey, M. D. and D. R. Mudry (1968). Two new species of Cestoda from California rays. *Journal of Parasitology* 54: 1141-1143.

Faliex, E., G. Tyler, and L. Euzet (2000). A new species of *Ditrachybothridium* (Cestoda: Diphyllidea) from *Galeus* sp. (Selachii, Scyliorhynidae) from the South Pacific Ocean, with a revision of the diagnosis of the order, family, and genus and notes on descriptive terminology of microtriches. *Journal of Parasitology* 86(5): 1078-1084.

Forsskål, P. (1775). *Descriptiones Animalium, Avium, Amphibiorum, Iscium, Insectorum, Vermium; Quae in Itirene Orientali Observavit*. Molleri, Hauniae, 164 pp.

Fyler, C. A. and J.N. Caira (2006). Five new species of *Acanthobothrium* (Tetraphyllidea: Onchobothriidae) from the freshwater stingray *Himantura chaophraya* (Batoidea: Dasyatidae) in Malaysian Borneo. *Journal of Parasitology* 92(1): 105-125.

Gonzalez-Isais, M. and H. M. M. Dominguez (2004). Comparative anatomy of the Superfamily Myliobatoidea (Chondricthyes) with some comments on phylogeny. *Journal of Morphology* 262: 517-535.

Gray, J. E. (1834). *Illustrations of Indian zoology; chiefly selected from the collection of Major-General Hardwicke*. London.

Healy, C. J. (2006). Three new species of *Rhinebothrium* (Cestoda: Tetraphyllidea) from the freshwater whipray, *Himantura chaophraya*, in Malaysian Borneo. *Journal of Parasitology* 92(2): 364-374.

Hoberg, E. P. and G. J. Klassen (2002). Revealing the faunal tapestry: co-evolution and historical biogeography of hosts and parasites in marine systems. *Parasitology* 124: 3-g

Ivanov, V. A. and R. A. Campbell (2000). Emendation of the generic diagnosis of *Tylocephalum* (Cestoda: Lecanicephalidea: Tetragonocephalidea), and description of *Tylocephalum brooksi* n. sp. *Journal of Parasitology* 86(5): 1085-1092.

Jensen, K. (2001). Four new genera and five new species of lecanicephalideans (Cestoda: Lecanicephalidea) from elasmobranches in the Gulf of California, Mexico. *Journal of Parasitology* 87: 845-861.

Jensen, K. (2005). Tapeworms of Elasmobranchs (Part 1). A monograph on the Lecanicephalidea (Platyhelminthes, Cestoda). *Bulletin of the University of Nebraska State Museum* 18: 241 pp.

Jensen, K. (2006). A new species of *Aberrapex* Jensen, 2001 (Cestoda: Lecanicephalidea) from *Taeniura lymma* (Forsskal) (Myliobatiformes: Dasyatidae) from off Sabah, Malaysia. *Systematic Parasitology* 64: 117-123.

Jensen, K. and J. N. Caira (2006). The status of *Rhoptrobothrium* Shipley et Hornell, 1906 (Cestoda: Tetraphyllidea), with redescription of the type species, *R. myliobatidis*, and description of three new species from two species of *Aetomylaeus* (Myliobatiformes: Myliobatidae) from Malaysian Borneo. *Folia Parasitologica* 53: 189-207.

Last, P. R. and J. D. Stevens (2009). *Sharks and Rays of Australia, Second Edition*. Australia: CSIRO. 513 pp.

Lomolino, M. V., B. R. Riddle, and J. H. Brown (2006). *Biogeography*, 3rd ed. Sinauer Associates, Inc., Sunderland, Massachusetts. 845 pp.

Lourie, S.A. Vincent, A.C.J. (2004). A marine fish follows Wallace's Line: the phylogeography of the three-spot seahorse (*Hippocampus trimaculatus*, Syngnathidae, Teleostei) in Southeast Asia. *Journal of Biogeography* 31: 1975-1985.

Marcogliese, D. J. (2002). Food webs and transmission of parasites to marine fish. *Parasitology* 124: S83-S99.

Michael, S. W. (1993). *Reef sharks and rays of the world. A guide to their identification, behavior, and ecology*. Sea Challengers, Monterey, California. 107 pp.

Mitter, C. M. and D. R. Brooks (1983). Phylogenetic aspects of coevolution. In: Futuyma, D. J. and M. Slatkin (eds.) *Coevolution*. Sinauer Associates: Sunderland. pp. 65-98.

Muller, J. and F. G. J. Henle (1841). *Systematische Beschreibung der plagiostomen*. Veti & Co: Berlin. pp. 103-200.

Myers, R. F. (1999). *Micronesian reef fishes: a comprehensive guide to the coral reef fishes of Micronesia*, 3rd revised and expanded edition. Coral Graphics, Barrigada, Guam. 330 pp.

Nishida, K. (1990). Phylogeny of the Superorder Myliobatidoidei. *Memoirs of the Faculty of Fisheries*, Hokkaido University 37(1, 2): 108 pp.

Palm, H. W., A. Waeschenbach, P. D. Olson, D. T. J. Littlewood (2009). Molecular phylogeny and evolution of the Trypanorhyncha Diesing, 1863 (Platyhelminthes: Cestoda). *Molecular Phylogenetics and Evolution* 52(2): 351-367.

Pramanik, P. B. and B. Manna (2007). Six new species of the Genus *Tylocephalum* Linton, 1890 (Cestoida: Lecanicephalidea) in cartilagenous fishes from Bay of Bengal at Digha coastal waters, West Bengal, India. *Journal of Natural History* 3(2): 12-33.

Rao, V. (1977). *Acanthobothrium hanumantharaoi* sp. n. (Cestoda: Tetraphyllidea, Onchobothriidae) from the Niehof's eagle ray, *Myliobatis nieuhofii* (Bloch and Schneider) of Waltair Coast, Bay of Bengal. *Rivista di Parassitologia* 38: 277-283.

Reyda, F. B. and J. N. Caira (2006). Five new species of *Acanthobothrium* (Cestoda: Tetraphyllidea) from *Himantura uarnacoides* (Myliobatiformes: Dasyatidae) in Malaysian Borneo. *Comparative Parasitology* 73(1): 49-71.

Ride, W. D. L., H. G. Cogger, C. Dupuis, O. Kraus, A. Minella, F. C. Thompson, and P. K. Tubbs (1999). *International Code of Zoological Nomenclature*. 4th Edition. The International Trust for Zoological Nomenclature, The Natural History Museum, London, 306 pp.

Sakanari, J. A. and M. Moser (1989). Complete life cycle of the elasmobranch cestode, *Lacistorhynchus dollfusi* Beveridge and Sakanari, 1987 (Trypanorhyncha). *Journal of Parasitology* 75(5): 806-808.

Sarwade, D. V., G. B. Shinde, E. S. Pawar, and M. A. Mahajan (1995). On a new species of the genus *Myliobatibothrium* Mohekar and Shinde from *Myliobatis nieullofii* [sic] at Aurangabad, M. S. India, Muller and Henle. *Rivista di Parassitologia* 12: 87-89.

Schneider, J. G. (1801). In: *M. E. Blochii, Systema ichthyologiae iconibus ex illustratum. Post orbitum auctoris opus inchoatum absolvit, correxit, interpolavit J. G. Schneider, Saxo.* Berolini. 584 pp.

Sheehan, D. C. and B. B. Hrapchak (1987). *Theory and Practice of Histotechnology*, 2nd Edition. Battelle Memorial Institute, Columbus, Ohio.

Shipley, A. E. and J. Hornell (1906). Report on the cestode and nematode parasites from the marine fishes of Ceylon. *Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar (Herdman),* Part 5: 43-96.

Shipley, A. E. (1909). *Anthobothrium crispum*. *Zoologischer Anzeiger* 34: 641.

Shinde, G. B. and A. D. Mohekar (1983) *Myliobatibothrium alii* gen. et sp. n. (Cestoda: Tetraphyllidea) from ray, *Myliobatis nieuhofii* (Muller and Henle). *Rivista di Parassitologia*. 44: 247-251.

Sommer, C., W. Schneider, and J. M. Poutiers (1996). *FAO species identification field guide for fishery purposes*. *The living marine resources of Somalia*. FAO, Rome. 376 pp.

Srivastav, A. K., S. Lohia, and N. Mathur (1995). *Acanthobothrium myliomaculata* sp. nov. (Onchobothriidae, Cestoda) form the *Myliobates maculata* from Madras (India). *Flora and Fauna* 1: 43-45.

Subhapradha, C. K. (1951). On the genus *Polypocephalus* Braun, 1878 (Cestoda), together with descriptions of six new species from Madras. *Proceedings of the Zoological Society of London* 121(2): 205-235.

Subhapradha, C. K. (1955). Cestode parasite of fishes of Madras Coast. *Indian Journal of Helminthology* 7: 41-132.

Twohig, M. E., J. N. Caira, and C. A. Fyler (2008). Two new cestode species from the Dwarf Whipray *Himantura walga* (Batoidea: Dasyatidae), from Borneo, with comments on site and mode of attachment. *Journal of Parasitology* 94(5): 1118-1127.

Voris, H.K. (2000). Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography* 27: 1153-1167.

Wardle, R. A. and J. A. McLeod (1952). *The Zoology of Tapeworms*. University of Minnesota Press, Minneapolis. 780 pp.

Wessel, P. and W. H. F. Smith (1998). New, improved version of the Generic Mapping Tools released. *EOS, Transactions of the American Geophysical Union* 79: 579.

White, W. T., P. R. Last, J. D. Stevens, G. K. Yearsley, Fahmi, Dharmadi (2006). *Economically Important Sharks & Rays of Indonesia*. Australian Centre for International Agricultural Research, Canberra, Australia. 327 pp.