Morphology and Evolution of the Water Scavenger Beetle subfamily Acidocerinae (Coleoptera: Hydrophilidae)

By
© 2019
Jennifer Cristina Girón Duque
M.Sc., University of Puerto Rico, 2012
B.Sc., Universidad del Valle, 2006

Submitted to the graduate degree program in Ecology and Evolutionary Biology and the Graduate Faculty of the University of Kansas in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

_____
Chairperson Dr. Andrew E. Z. Short

_____
Dr. Kirsten Jensen

_____
Dr. Bruce Lieberman

_____
Dr. Jorge Soberón

_____
Dr. Paul Selden

Date Defended: December 10, 2019

The dissertation committee for Jennifer Cristina Girón Duque certifies that this is the approved version of the following dissertation:

Morphology and Evolution of the Water Scavenger Beetle subfamily Acidocerinae (Coleoptera: Hydrophilidae)

_____

Chairperson Dr. Andrew E. Z. Short

Date Approved: December 13, 2019

ABSTRACT

Water scavenger beetles in the subfamily Acidocerinae (Insecta: Coleoptera: Hydrophilidae) are a cosmopolitan group that can be found in a wide range of habitats, including fully aquatic environments, hygropetric habitats, and terrestrial niches. This broad habitat range has resulted in apparently convergent morphologies associated with particular ecologies and caused significant taxonomic confusion across the group. Understanding habitat shifts and their correlation with morphological variation in acidocerine water scavenger beetles was the main objective of this dissertation.

To understand morphological variation in the subfamily Acidocerinae, we revised Quadriops Hansen, the only known terrestrial genus in the subfamily and described three new genera: the aquatic Aulonochares, the hygropetric Ephydrolithus, and the ecologically variable Primocerus. Then, based on a molecular phylogeny, the taxonomy and classification of the entire subfamily was revised, including morphological diagnoses, illustrative images, an identification key for each of the 23 recognized genera, and a catalog (complete to October 2019) containing 469 species of acidocerines with their distributions. The phylogeny was also used for analyzing habitat shifts in the Acidocerinae using phylogenetic comparative methods. We investigated the effect of habitat shifting on the diversification rate of the subfamily, as well as its association with variation in a suite of five morphological traits.

This dissertation constitutes the most comprehensive treatment of a hydrophilid subfamily to date and is the first step towards understanding habitat shifting across the water scavenger beetle family Hydrophilidae.

AUTHOR'S DISCLAIMER

Following the recommendation of Article 8 of the International Code of Zoological Nomenclature, taxonomic acts in this work are disclaimed for nomenclatural purposes.

DEDICATION

This dissertation is dedicated to all the giants who lent me their shoulders.

ACKNOWLEDGMENTS

None of the following pages, nor the publications derived from them would have been put together by me if it wasn't because of my advisor, Andrew Short. I was lucky to be on Twitter to see his ad recruiting grad students (thanks to Guanyang Zhang!), and also lucky that the Department of Ecology and Evolutionary Biology at the University of Kansas (KUEEB) does not require the GRE test, which had prevented me from starting a PhD program before. Andrew chose me from a pool of qualified candidates to work on his CAREER award project, I think partly because of the recommendation of my master's advisor, Nico Franz, to whom I am also grateful. Andrew also took the chance of accepting me into his lab even though I was unable to visit in advance to meet in person, then accommodated my aversion for molecular work, and then accepted that our five-year commitment got shorter because of my need to move away from Lawrence. I will always be grateful for his willingness to reach middle ground despite the stubbornness we have in common. I also recognize his acceptance of my love for broad-nosed weevils.

I'm grateful for the "PSB crew" who took me in and made me feel at home when I came to Lawrence: Stephen Baca, Marianna Simões, Laura Breitkreuz, Mabel Alvarado, Emmanuel Toussaint and Sarah Schmits. You all made it quick and easy for me to get a sense of belonging here. Thanks for all the good times and all the academic and life discussions.

I also want to thank my husband Joe Manthey and his ability to bear with me. We survived two years of long distance relationship and then he considered that starting a new job as assistant professor in Texas, buying a house, starting applying for grants, teaching classes of

his own for the first time, getting married to a Latina wife and adopting a dog, all in a one year period was a reasonable thing to do. He is for me the best example of a brilliant and dedicated scientist and professor, and the most supportive partner I could have ever ask for. He even gave me space in his lab so that I kept working on my dissertation while away from the Short Lab. I thank Pepper for keeping Joe company during the time I've been away this last semester.

I also want to thank my family, especially my mom, Nancy, and sisters Angela and Mónica, who kept me posted on the happenings of their lives through time. We have all supported each other, especially emotionally through difficult times when I have been always away. Thanks for being (and for making me) strong and independent. I would for sure not be here and doing what I do if it wasn't for all your supporting and cheering!

Working on this dissertation remotely would have been even more challenging without the support of Stephen Baca, who let me crash on their couch and fed me more than once during my visits to the lab over the last year. I'm really fortunate that he's always willing to help.

I thank my committee members, Kirsten Jensen, Bruce Lieberman, Jorge Soberón and Paul Selden, who were available for me throughout this time, responding promptly to my requests and were willing to discuss and provide feedback. Same goes for "honorary member" Mark Holder. I also kind of wish I have had more time to enjoy other amazing minds in the department, especially those of John Kelly and Michael Engel.

I also want to recognize the friendly and productive environment of the Short Lab: Andrew Short, Stephen Baca, Grey Gustafson, Rachel Smith and Rachel Neff. Thanks for providing a space where we can all learn together and have a broader and more critical view of the scientific endeavor.

Many deadlines and procedures would have been disastrous without the constant guidance of Aagje Ashe and Dorothy Johanning. It would have been impossible to keep on track without their assistance.

I'm grateful for the occasional interactions and conversations with Fernando Machado, Jacob Hopkins, Johana Goyes, Tina Gustafson, Kaila Colyott, Victor Gonzalez and Jack Hruska.

The phylogeny that is the backbone of Chapters 3 and 4 of this document, was built thanks to the many hours that Stephen Baca, Andrew Short, Emmanuel Toussaint, Katie Allen-Tapondju and Walter Tapondju spent doing extractions, running PCR's, packaging and shipping PCR products, cleaning up sequences and running data analyses. Thank you all.

I would not have been able to compile a lot of the information presented in Chapter 3 without people and institutions that provided access to bibliographic sources. Martin Fikáček (National Museum and Charles University in Prague) built a hydrophiloid-specialized on-line library and made it available for aquatic beetle researchers around the world. Other invaluable resources were available through the Biodiversity Heritage Library, and the amazing Interlibrary Loan team at the University of Kansas Libraries. You all have definitely made my life easier and this work more complete!

I also want to thank Bruce Lieberman for running the macroevolution discussion group especially during my last semester, and also all participants throughout the years, in particular, Kaylee Herzog, Matt Girard and Rene Martin made discussions more fruitful. Alana Alexander and Rich Glor with their initial phylogenetics discussion group opened my perspective about molecular data and the many ways you can look at them.

Jennifer Thomas was always helpful when I had issues with the imaging system over at PSB, and Zack Falin was a great mentor during my time working with the water bug collection.

Lastly, I want to thank my funding sources. I was able to come study at KU thanks to an NSF CAREER grant that Andrew got in 2014. I was supported by KUEEB during one semester as a teaching assistant, and by the KU Natural History Museum as a curatorial assistant for another semester. I got paid during the summers, conference and publication expenses covered and even my entire last semester paid for with resources provided by the Entomology Endowment, including the John M Deal Entomology Scholarship from the University of Kansas.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

The cosmopolitan family Hydrophilidae, known as water scavenger beetles, constitute the largest family of polyphagan aquatic beetles, and the second largest for all aquatic Coleoptera, with more than 3000 described species (Short 2018). Contrary to what the family name may suggest, hydrophilids are not exclusively aquatic and also occur in hygropetric habitats and terrestrial niches such as decaying organic matter and even living in the nests of several ant species.

Traditionally, hydrophilids were classified in two main subfamilies: the predominantly aquatic Hydrophilinae and the predominantly terrestrial Sphaeridiinae, which were considered sister groups based on morphological data (Hansen 1991). Recently, Short and Fikáček (2013) published a reclassification of the Hydrophilidae based on a molecular phylogeny, in which they recognized six subfamilies: Hydrophilinae, Chaetarthriinae, Enochrinae, Acidocerinae, Cylominae (changed from Rygmodinae, see Seidel et al. 2016), and Sphaeridiinae. There is a trend for hygropetric and terrestrial groups to originate from aquatic forms across this phylogeny (see Bloom et al. 2014).

Habitat shifting is one of the most intriguing evolutionary patterns in water scavenger beetles. When did those shifts occur? How common or widespread is habitat shifting across the family? Which groups have shifted or are most likely to shift? Have those shifts had effects on the diversification and morphology of the beetles? To tackle these questions, we focused on the subfamily Acidocerinae, which occupies an intermediate position in the hydrophilid phylogeny, in

sister relationship with the primarily terrestrial Cylominae+Sphaeridiinae; this larger clade (Acidocerinae+Cylominae+Sphaeridiinae) is sister to the primarily aquatic Enochrinae (Short and Fikáček 2013).

When it was first recognized as a subfamily, Acidocerinae contained 300 species in 14 genera (see Hansen 1999, Short and Fikáček 2013). Acidocerines span the entire range of habitats occupied by hydrophilids, which has resulted in recurrent patterns of seemingly convergent morphologies: species from hygropetric and terrestrial environments have shorter maxillary palpi and reduced metafemoral pubescence in comparison with aquatic taxa. In addition, these and other morphological traits (e.g. presence of elytral striae) were traditionally used for taxonomic identifications.

Because of the limited sampling (at the subfamily level) in Short and Fikáček (2013), relationships among genera within the subfamily were not very clear, and inferences about habitat shifting were not possible at the time. In addition, the morphological diversity within Acidocerinae made it difficult to interpret emerging patterns of habitat-driven morphological specialization.

In order to make sense of the morphological diversity within Acidocerinae, we revised the single terrestrial genus known in the subfamily, *Quadriops* Hansen (see chapter 1; Girón and Short 2017) and described three new genera (see chapter 2; Girón and Short 2019): the aquatic

Aulonochares, the hygropetric *Ephydrolithus*, and the variable (both ecologically and morphologically) *Primocerus*.

In parallel, a comprehensive phylogeny of the Acidocerinae was built based on six DNA markers and 206 acidocerine terminals (see Short et al. in prep.). This phylogeny supported the taxonomic reclassification of the subfamily, which is presented in chapter 3. The genera *Colossochares* **gen. nov.** and *Novochares* **gen. nov.** are established as new to accommodate monophyletic groups of species previously assigned to *Helochares* Mulsant. The concept of *Peltochares* Régimbart is redefined to accommodate another group of species previously assigned to *Helochares*. Morphological diagnoses and images are provided for the 23 genera of acidocerines recognized here. In addition, a catalog including the 469 species of acidocerines known to date is presented.

Lastly, the time-calibrated phylogeny by Short et al. (in prep.) was used for analyzing habitat shifts in the Acidocerinae using phylogenetic comparative methods. The most recent common ancestor for the Acidocerinae was recovered as a hygropetric inhabitant with nine antennomeres, with apical abdominal emargination, and without elytral striae; the maxillary palpomere 3 was recovered with an intermediate value and the metafemoral pubescence with an intermediate-to-high value. There are 13 transitions from hygropetric to aquatic habitats, with one reversal, and two transitions from hygropetric to terrestrial habitats. For binary traits, once a character state changed, it did not go back to the former character state, whereas for continuous traits the situation seemed to be more plastic: from the ancestral intermediate

values there are shifts towards either larger or smaller values. Habitat shifts are correlated with changes in morphological traits, but not linked to shifts in diversification rates.

This dissertation constitutes the most comprehensive study of a subfamily of hydrophilids to date. Acidocerines are more diverse than it was previously recognized: six new genera and over a hundred species have been described in the past couple of years. There is considerable morphological diversity within the subfamily, especially in aedeagal traits (see chapter 3). Hygropetric habitats are ancestral for Acidocerinae, with repeated shifts to aquatic and terrestrial habitats across the phylogeny. Habitat shifts do not have an effect in the diversification rates in the subfamily, but are correlated with changes in certain morphological traits of these beetles.

REFERENCES CITED

Bloom DD, Fikáček M, Short AEZ (2014) Clade age and diversification rate variation explain disparity in species richness among water scavenger beetle (Hydrophilidae) lineages. PLOS ONE 9: e98430. https://doi.org/10.1371/journal.pone.0098430

Girón JC, Short AEZ (2017) Revision of the Neotropical water scavenger beetle genus *Quadriops* Hansen, 1999 (Coleoptera: Hydrophilidae: Acidocerinae). ZooKeys 705: 115–141. https://doi.org/10.3897/zookeys.705.19815

Girón JC, Short AEZ (2019) Three additional new genera of acidocerine water scavenger beetles from the Guiana and Brazilian Shield regions of South America (Coleoptera, Hydrophilidae, Acidocerinae). ZooKeys 855: 109–154. https://doi.org/10.3897/zookeys.855.33013

Hansen M (1999) World catalogue of insects. Volume 2: Hydrophiloidea (s. str.) (Coleoptera). Apollo Books, Stenstrup, Denmark, 414 pp.

Seidel M, Arriaga-Varela E, Fikáček M (2016) Establishment of Cylominae Zaitzev, 1908 as a valid name for the subfamily Rygmodinae Orchymont, 1916 with an updated list of genera (Coleoptera: Hydrophilidae). Acta Entomologica Musei Nationalis Pragae 56: 159–165.

Short AEZ (2018) Systematics of aquatic beetles (Coleoptera): current state and future directions. Systematic Entomology 43: 1–18. https://doi.org/10.1111/syen.12270

Short AEZ, Fikáček M (2013) Molecular phylogeny, evolution and classification of the Hydrophilidae (Coleoptera). Systematic Entomology 38: 723–752. https://doi.org/10.1111/syen.12024

Chapter 1. Revision of the Neotropical water scavenger beetle genus *Quadriops* Hansen, 1999 (Coleoptera: Hydrophilidae: Acidocerinae)

Girón, J. C. & A. E. Z. Short. 2017. Revision of the Neotropical water scavenger beetle genus *Quadriops* Hansen, 1999 (Coleoptera: Hydrophilidae: Acidocerinae). ZooKeys 705: 115–141. https://zookeys.pensoft.net/articles.php?id=19815

ABSTRACT

The genus *Quadriops* Hansen, 1999 is revised and redescribed. The genus is found to contain six species, including two that are here described as new: *Quadriops clusia* **n. sp.** (Brazil, Guyana, Suriname) and *Q. acroreius* **n. sp.** (Suriname, French Guiana). Two species are found to be junior subjective synonyms of *Q. depressus* Hansen, 1999: *Q. amazonensis* García, 2000 **syn. n.** and *Q. politus* Hansen, 1999 **syn. n.** The male of *Q. similaris* Hansen, 1999 is described for the first time. New records are provided for *Q. dentatus* Hansen, 1999, *Q. reticulatus* Hansen, 1999, and *Q. similaris*. All species are described and illustrated in detail. Most species are confirmed as having a terrestrial way of life, with several species being found in rotten fruits, sap flows, and dead wood. Furthermore, we discuss ecological trends of the species given their collecting information.

RESUMEN

El género *Quadriops* Hansen, 1999 es revisado y redescrito. El género contiene seis especies, incluyendo dos que se describen aquí como nuevas: *Quadriops clusia* **n. sp.** (Brasil,

Guyana, Surinam) y *Q. acroreius* **n. sp.** (Surinam, Guyana Francesa). Dos especies se sinonimizan *Q. depressus* Hansen, 1999: *Q. amazonensis* García, 2000 **syn. n.** y *Q. politus* Hansen, 1999 **syn. n.** El macho de *Q. similaris* Hansen, 1999 se describe por primera vez. Se proveen nuevos registros para *Q. dentatus* Hansen, 1999, *Q. reticulatus* Hansen, 1999, y *Q. similaris*. Todas las especies son descritas e ilustradas en detalle. La mayoría de las especies presentan un modo de vida terrestre, con varias especies encontradas en frutos podridos, flujos de savia y madera muerta. Además, se discuten tendencias ecológicas de las especies dada su información de colecta.

Keywords: terrestrial aquatic beetles; new species; taxonomy

INTRODUCTION

The water scavenger beetle genus *Quadriops* Hansen, 1999 is endemic to the Neotropical region, with a known distribution from as far north as Costa Rica to as far south as Amazonian Peru (Hansen 1999). When the genus was originally described, Hansen (1999) placed *Quadriops* in the subtribe Acidocerina of the tribe Hydrophilini (*sensu* Hansen 1991), which contemporarily mostly constitutes the subfamily Acidocerinae (Short and Fikáček 2013).

Species of *Quadriops* can be easily recognized by their small size (ca. 2 mm), completely divided eyes, short and stout maxillary palps, mostly glabrous posterior femora, and the rounded apex (as opposed to truncate or emarginate) of the fifth abdominal ventrite. In general terms, and as happens with some other Neotropical acidocerines (e.g., *Globulosi*s García, 2001), the external morphology is highly homogeneous among species. However, the distribution of the elytral punctures constitutes a useful character to recognize species groups.

Previous species descriptions were based on one or a few specimens, all but one of them collected by flight intercept traps. According to Hansen (1999), most diagnostic features that separate species involved the presence, density, and location of microsculpture or reticulation on the clypeus, head and pronotum. Furthermore, by examining the illustrations of the aedeagus provided by Hansen (1999) and García (2000), similarities are evident among the described males.

Recent fieldwork in northern South America has significantly expanded our knowledge of *Quadriops*. This has included increasing the number of known specimens by almost 100-fold, expanding the range of some species, as well as revealing new species and habits of the beetles unknown until now. Based on all the gathered material, here we redescribe the genus and the previously known species, based on morphological characters of the adults. We synonymize *Q. amazonensis* García, 2000 and *Q. politus* Hansen, 1999 with *Q. depressus* Hansen, 1999, based on external morphology as well as on characters of the aedeagus. Additionally, we describe two new species: *Q. acroreius* n. sp. from French Guiana and Suriname, and *Q. clusia* n. sp. from Guyana, Suriname, and Brazil, which has been collected on the rotten fruits of *Clusia* trees. We also discuss the ecology and distribution of the species.

MATERIALS AND METHODS

Depositories of examined material.

CBDG: Center for Biological Diversity, University of Guyana, Georgetown

CMNC: Canadian Museum of Nature, Ottawa, Canada (R. Anderson)

INBio: Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica.

MALUZ: Museo de Artrópodos de la Universidad del Zulia, Maracaibo, Venezuela (J. Camacho, M. García)

MIZA: Museo del Instituto de Zoología Agrícola, Maracay, Venezuela (L. Joly);

NHMUK: United Kingdom, London, The Natural History Museum [formerly British Museum (Natural History BMNH)]

NZCS: National Zoological Collection of Suriname, Paramaribo (P. Ouboter, V. Kadosoe)

SEMC: Snow Entomological Collection, University of Kansas, Lawrence, KS (A. Short)

USNM: U.S. National Museum of Natural History, Smithsonian Institution, Washington, DC (C. Micheli).

Morphological methods.

Specimens were examined using Olympus SZX7 and SZX16 stereo microscopes (magnifications: 0.8x –5.6x with DF PLAPO 1x –4 objective lens and 20x eyepieces; 0.7x – 11.5x, with SDF PLAPO1xPF objective lens and 10x eyepieces, respectively). Genitalia dissections were prepared, in part, by the protocols described by Minoshima et al. (2015), by heating the structures at 60°C in a solution of 10% KOH for 60 minutes. Previous to the KOH treatment, the entire abdomen was removed from the specimen and opened along one side. Afterwards, structures were submerged in glacial acetic acid for 15 minutes, and then rinsed with distilled water. Dissections were performed by placing the cleared parts on a microscope slide with a drop of glycerin. The aedeagi of male holotypes designated by Hansen, originally mounted in Euparal on cards pinned under the specimens, were dismounted by placing the card in 70%

alcohol in a water bath (~60°C, 15-20 min) and then observed on a microscope slide with a drop of glycerin.

Images of internal structures were produced by stacking images taken through an Olympus DP72 camera attached to an Olympus BX51 microscope to 200x magnification. Habitus photographs were taken with a Visionary Digital imaging system, using a Canon MP-E 65mm f/2.8 1-5X Macro Lens mounted on a Canon EOS 6D camera body. All final images were created by stacking multiple individual photographs from different focal planes using the software Zerene Stacker. Scanning electron micrographs were taken by using a FEI Versa 3D Dual Beam Scanning Electron Microscope. Specimens were mounted on carbon tape and coated in gold.

Descriptive sequence and morphological terminology largely follows Hansen (1991) except for the use of meso- and metaventrite instead of meso- and metasternum (see Lawrence and Ślipiński 2013). Terms for the ventral surface of head follow Komarek (2004). Terminology for the metafurca follows Velázquez de Castro (1998). Wing venation follows Lawrence and Ślipiński (2013). The generic description has been modified from Hansen (1999).

In the examined material section of the descriptions, the sex of the specimens is indicated only for those in which the genitalia was exposed. For the remainder specimens the sex was not determined.

RESULTS

List of species and their known distribution

1. *Quadriops acroreius* n. sp.	Suriname, French Guiana
2. *Quadriops clusia* n. sp.	Guyana, Suriname, Brazil
3. *Quadriops dentatus* Hansen, 1999	Venezuela (Bolivar), French Guiana, Suriname
4. *Quadriops depressus* Hansen, 1999	Peru, Ecuador, Venezuela (Amazonas)
Q. amazonensis García, 2000 syn. n.	
Q. politus Hansen, 1999 syn. n.	
5. *Quadriops reticulatus* Hansen, 1999	Costa Rica, Panama
6. *Quadriops similaris* Hansen, 1999	Venezuela (Bolivar), Guyana, Suriname, French Guiana

Characters of taxonomic importance

For the most part, species of *Quadriops* are externally homogeneous (at least within species groups). We also observed very low intraspecific variation, even across large series (hundreds) of specimens. Variation was found mainly in the following characters:

Body shape in lateral view. Though the shape of the body in lateral view might be described as subhemispherical, there is interspecific variation in the degree of convexity. The outline of some species can be described as uniformly convex: *Q. dentatus*, *Q. acroreius*, *Q. reticulatus* and *Q. clusia* (see Fig. 1.1B, 1.1F, 1.3B and 1.3F respectively), whereas *Q. depressus* and *Q. similaris* are more dorsoventrally flattened (Fig. 1.2B and 1.2F).

Coloration. Body coloration, which tends to be uniform across most regions of the beetle, does not represent a diagnostic feature for separating *Quadriops* species. While coloration in

specimens examined ranges from yellowish to reddish to dark brown, this is mostly attributable to intraspecific variation as well as varying degrees of sclerotization. Appendages and the ventral side of the beetles tend to be slightly paler than the dorsal surface of the body.

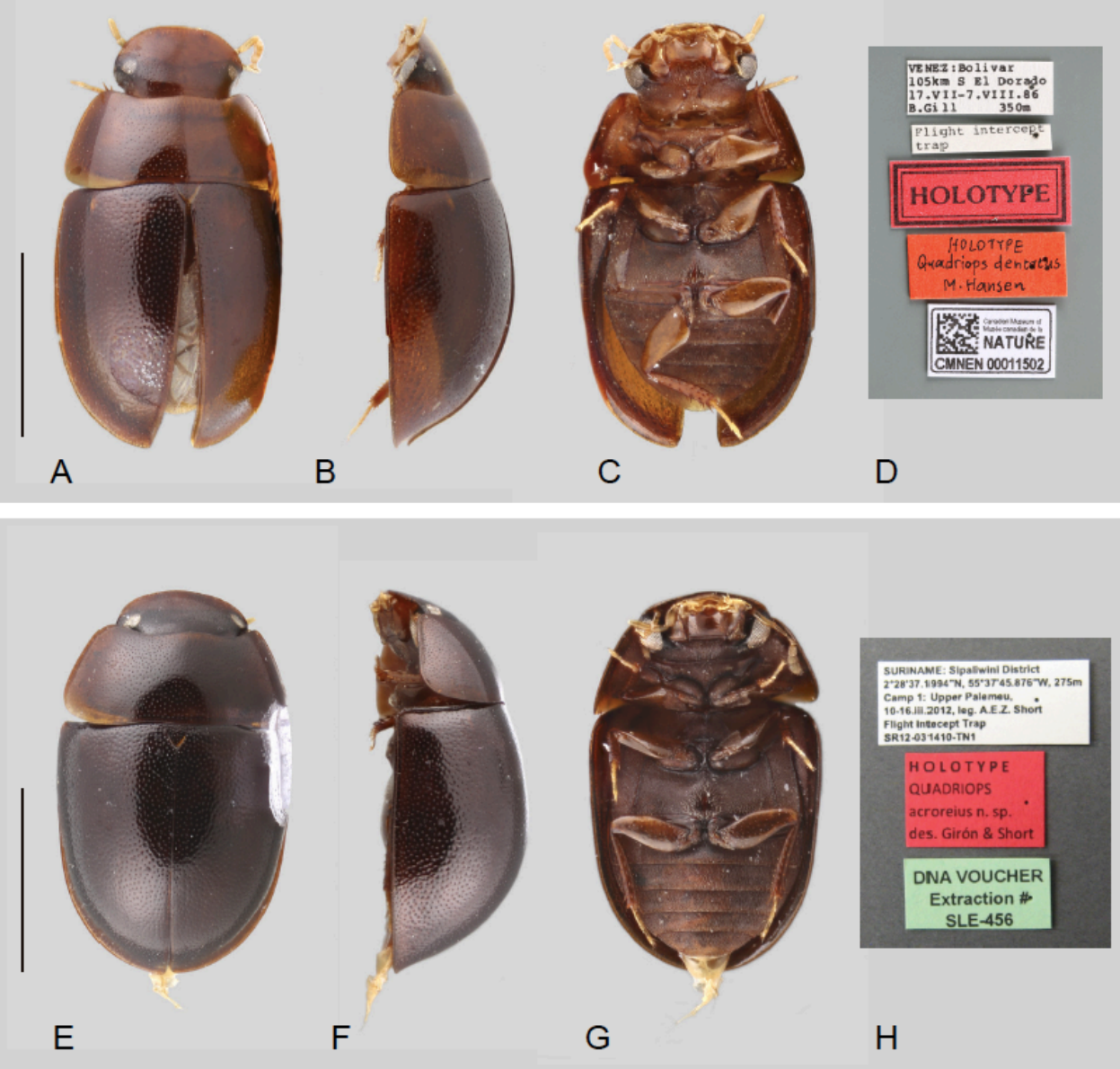


Figure 1.1. Habitus and labels of *Quadriops* spp.: *Q. dentatus* (holotype): **A** dorsal view, **B** lateral view, **C** ventral view, **D** labels; *Q. acroreius* **n. sp.** (holotype): **E** dorsal view, **F** lateral view, **G** ventral view, **H** labels. Scale bar 1 mm.

Microsculpture. One of the main characters used by Hansen (1999) to differentiate species was the presence, density and extension of microreticulations on the head, frons, and pronotum. Even if it might be useful in recognizing particular species (e.g., *Q. acroreius* vs. *Q. dentatus*), by looking at series of specimens, it is a variable character that should not be considered exclusively diagnostic.

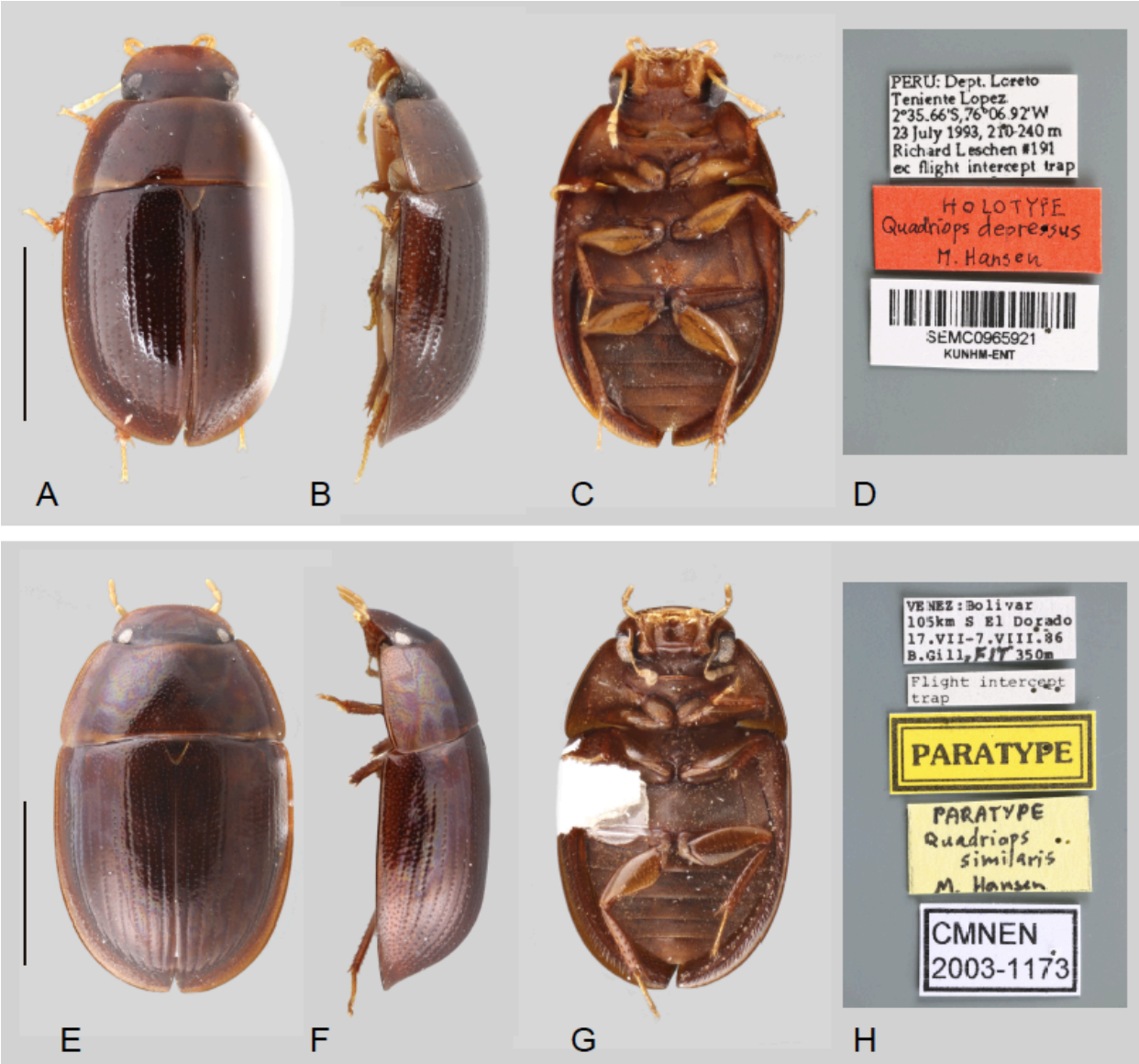


Figure 1.2. Habitus and labels of *Quadriops* spp.: *Q. depressus* (holotype): **A** dorsal view, **B** lateral view, **C** ventral view, **D** labels; *Q. similaris* (paratype): **E** dorsal view, **F** lateral view, **G** ventral view, **H** labels. Scale bar 1 mm.

Elytra. Two main groups of species can be distinguished according to the distribution of the ground and serial punctures of the elytra: those in which the punctures are randomly and uniformly distributed over the surface (*Q. acroreius* and *Q. dentatus*, see Fig. 1.1), and those in which the punctures are serially arranged, forming well defined longitudinal striae (see Figs 1.2 and 1.3). With the exception of *Q. clusia*, in striate species the punctures along the striae are clearly larger than those on the interstria (in *Q. clusia* all elytral punctures are similarly large; see Fig. 1.6). In addition, the elytral punctures can be simple as in *Q. clusia* (Fig. 1.6A) or possess microincisions that radiate from the margins of the puncture as in *Q. reticulatus* (Fig. 1.6B).

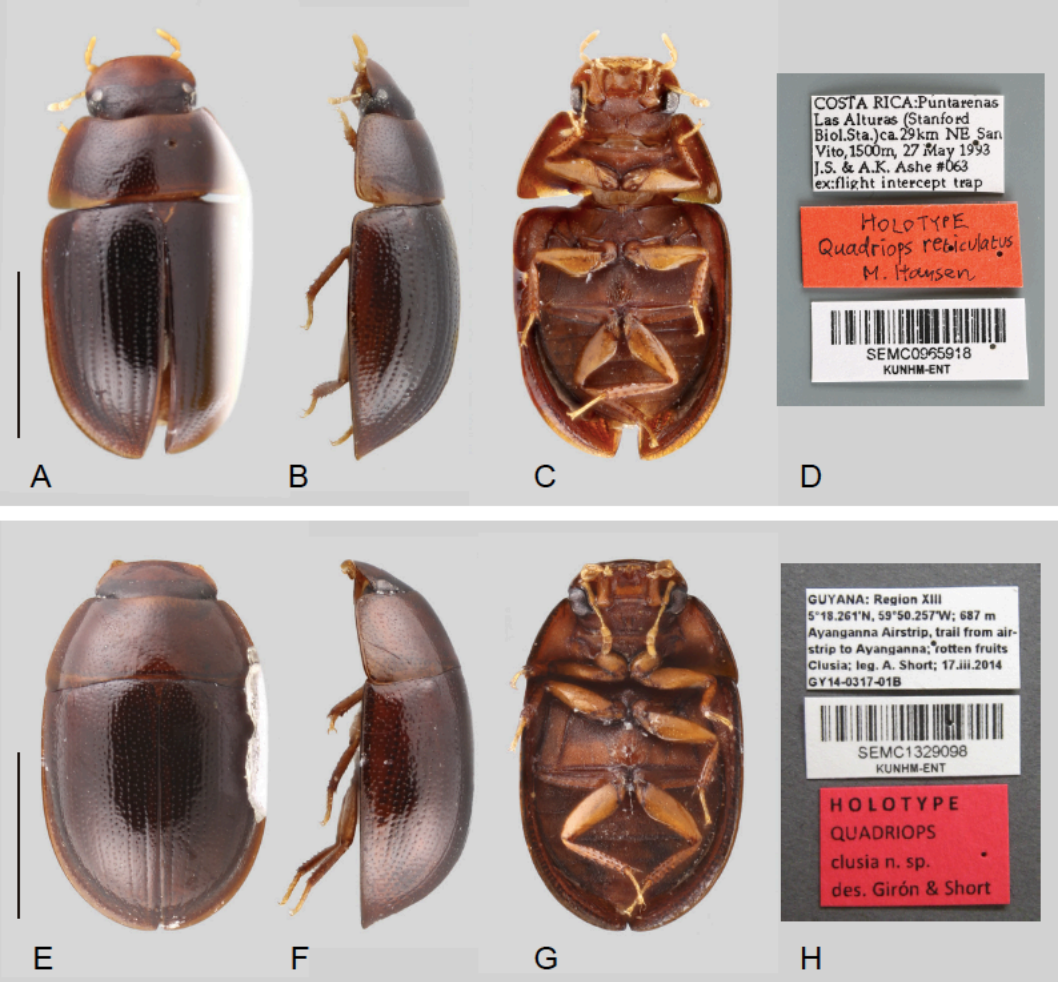


Figure 1.3. Habitus and labels of *Quadriops* spp.: *Q. reticulatus* (holotype): **A** dorsal view, **B** lateral view, **C** ventral view, **D** labels; *Q. clusia* **n. sp.**: **E** dorsal view, **F** lateral view, **G** ventral view, **H** holotype labels. Scale bar 1 mm.

Mesoventrite. In *Quadriops*, the mesoventrite is broadly elevated posteriorly. The wide elevation usually has a transverse ridge, which varies in shape and sharpness. In the known species with irregularly distributed elytral punctures, the transverse ridge is strongly produced. It forms a blunt, vertical, median tooth in *Q. dentatus*, whereas in *Q. acroreius* it forms a wide, transverse, straight and blunt carina. As for species with elytral punctures aligned into striae, the transverse ridge can be simply curved, slightly angulate or bisinuate. For this group of species, the shape of the transverse ridge exhibits more intraspecific variation and is not consistent within series of specimens.

Aedeagus. The general shape of the aedeagus and the length ratio between the basal piece and the median lobe + parameres is generally consistent within species. There is both inter- and intraspecific variation in the outer margins of the basal piece and the shape of the outer margins and apex of the parameres. The gonopore is positioned at the apex of the median lobe, but its shape exhibits intraspecific variation. The shape of the apices of both the median lobe and the parameres tend to be consistent within species. It is important to highlight that some differences observed in the aedeagi presented here may be a result of incomplete clearing, owed to positioning during the photographing process, and/or product of imperfect focus from the stacking process.

Quadriops Hansen, 1999

Quadriops Hansen, 1999: 131.

Type species: *Quadriops depressus* Hansen, 1999 by original designation.

Differential Diagnosis: Small to very small beetles, total body length 1.6–2.6 mm, width 1.1–1.6 mm. Color yellowish to reddish to dark brown. Body shape oval in dorsal view; subhemispherical and sometimes dorsally flattened in lateral view (see Figs 1.1–1.3). Frons lateral and posteriorly expanded, forming a canthus that completely divides the eyes in dorsal and ventral portions (e.g., Figs 1.1B, 1.3B). Antennae with nine antennomeres (e.g., Fig. 1.2C). Maxillary palps curved inward, rather short and stout (e.g., Figs 1.1C, 1.2G). Elytra with punctures either irregularly distributed (Fig. 1.1) or forming ten well defined longitudinal rows, with additional elytral ground punctures along interstriae (Fig. 1.2, 1.3); elytra without sutural striae, narrowly explanate anteriorly, explanation gradually broader towards apex (see Figs 1.1–1.3). Posterior elevation of mesoventrite, usually with a well-defined transverse ridge (except in *Q. dentatus* which possesses an acute tooth). Posterior femora glabrous with the exception of a few very scattered small setae. Fifth abdominal ventrite apically rounded and without stout setae (e.g., Fig. 1.1C).

Description. Body broadly oval, weakly convex, with dorsum distinctly flattened in some species. Head. Eyes completely divided into dorsal and ventral faces by lateral canthus of the frons; dorsal face of eye tear-drop shaped, smaller in size relative to the ventral face. Antennae (see Fig. 1.4A) with 9 antennomeres, usually paler than general coloration of head; antennomere

1 reaching midpoint of ventral face of eye (reaching cardo-stipes joint), nearly 1.5 × longer than antennomere 2; antennomere 3 nearly as long as antennomeres 4–5 combined; antennomere 6 forming a rather small, but well differentiated cupule, antennomeres 7–9 similar in size, slightly flattened, forming a loosely articulated, pubescent club; setae at apex of antennomere 9 longer than general pubescence of club. Temporae forming a rather flat surface behind the eyes, densely covered by setae (hydrofuge pubescence, see Fig. 1.4B). Frons and clypeus (see Fig. 1.4A, 1.4C) with ground punctures uniformly distributed over the surface, accompanied by scattered seta-bearing systematic punctures; setae particularly noticeable on frons anterior to the eye, including lateral canthus, and behind frontoclypeal suture; surface between punctures ranging from smooth to finely reticulated, especially on anterior region of clypeus; anterior corners of clypeus widely rounded; anterior margin of clypeus usually emarginate medially, with distinct bead along entire margin. Labrum reduced, paler, rather short and wide, sometimes appearing deflexed and concealed by clypeus from above (see Fig. 1.4C); dorsal surface convex and finely reticulated; anterior margin mesally widely emarginate and bent inwards; lateral margins bearing a row of long setae. Maxilla (see Fig. 1.4A) usually with sparse setae on ventral surface of cardo and stipes, with a row of stiff decumbent spiniform setae along outer dorsal margin of palpifer; maxillary palps yellowish, shorter than antennae, and somewhat stout; palpomeres similar in size; palpomere 1 shorter than stipes, with inner margin straight, and outer margin distally strongly convex; palpomere 2 conical (narrower at base), with inner margin convex at base and outer margin widely convex; palpomere 3 digitiform, rather elongate (compared to 1 and 2), apically somewhat truncate; apex of palpomere 3 bearing sensilla. Mandibles with apex bifid (examined in *Q. clusia* and *Q. reticulatus*). Labial palps yellowish,

nearly as long as mentum, dorsoventrally flattened; palpomere 2 with inner margin straight, and outer margin distally strongly convex, with a long seta on outer apical corner; palpomere 3 digitiform, usually shorter and markedly narrower than palpomere 2, with a subapical seta on outer corner. Mentum nearly 1.5 × wider than long, parallel sided, moderately to strongly depressed anteromedially; anterior margin with relatively deep median excision, limited from the ventral surface by a U to V shaped transverse carina. Submentum rather flat; ocular ridge (see Komarek 2004, Fig. 1) well developed (see Fig. 1.4A).

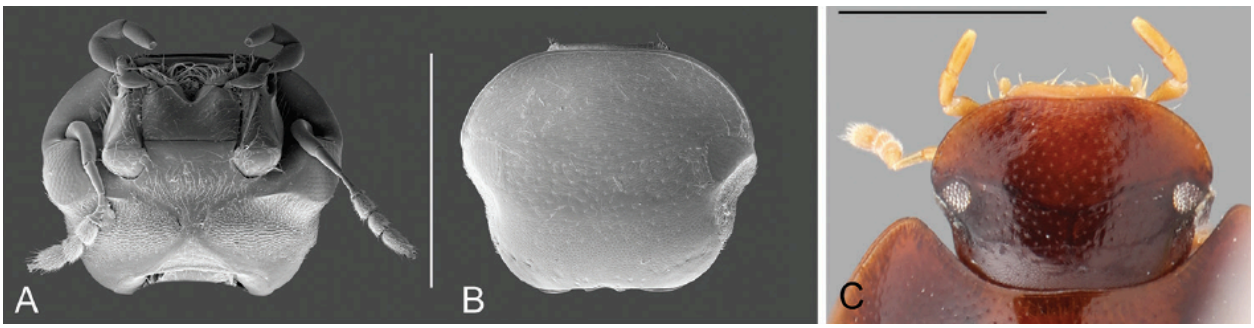


Figure 1.4. Head of *Q. reticulatus*: **A** SEM ventral view, **B** SEM dorsal view, **C** dorsal view. Scale bar 0.5 mm.

Thorax. Pronotum widest at base, narrowed anteriorly, surface rather evenly convex; ground punctation uniform, moderately fine, sometimes ground punctures connected by fine lines; seta bearing systematic punctures scattered through the surface, particularly noticeable as transverse anterolateral bands. Scutellum of moderate size, triangular, nearly as long as wide. Prosternum (Fig. 1.5A) well developed, flat, at most only weakly convex, not carinate; anterior margin of prosternum only slightly convex mesally; intercoxal process somewhat triangular (with base facing posteriorly), with surface posteriorly bifurcated. Mesoventrite not fused to mesepisterna, narrowly reaching anterior mesothoracic margin, posteriorly widely elevated; elevation usually with a transverse ridge, variable in shape and sharpness (in *Q. dentatus* the ridge is produced into a blunt, vertical, median tooth); mesepisternum obliquely widely concave.

Mesofurca (examined in *Q. clusia* and *Q. reticulatus*; see Fig. 1.5B) with short arms, hardly as long as the length of mesocoxae; apex of arms triangular to irregularly explanate. Metaventrite weakly convex, medial posterior portion rather flat, entire metasternum very finely and densely pubescent, without median glabrous patch (reduced in *Q. acroreius* and *Q. dentatus*). Metepisterna approximately three times longer than wide, parallel-sided. Metafurca (examined in *Q. clusia* and *Q. reticulatus*; see Fig. 1.5C) short and stout, with furcal arms slightly longer than stalk; stalk somewhat triangular (wider near the crux, gradually narrowing distally); outer margins of stalk diverging from base towards midpoint of furcal arms; furcal arms somewhat rectangular, with apex (hemiductus) explanate, obliquely positioned; anterior tendons inserted near midpoint of dorsal edge of furcal arms; dorsal sheaths well developed, as wide as to slightly wider than widest point of lateral sheaths.

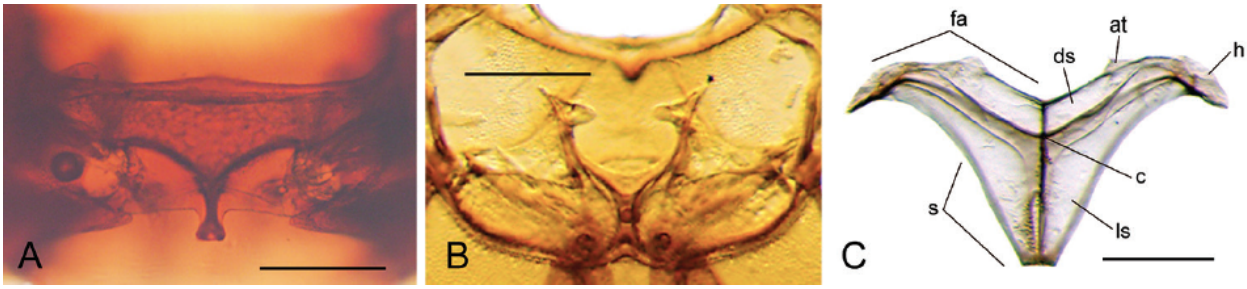


Figure 1.5. Thorax of *Q. reticulatus*: **A** prosternum ventral view, **B** mesofurca dorsal view, **C** metafurca posterior view: (at) anterior tendon, (c) crux, (ds) dorsal sheath, (fa) furcal arm, (h) hemiductus, (ls) lateral sheath, (s) stalk. Scale bar 0.2 mm.

Elytra. Surface even (without elevations or depressions), with 10 well defined longitudinal rows of serial punctures (see Fig. 1.6) (except in *Q. acroreius* and *Q. dentatus* which have irregularly punctate elytra), sutural series rather sharply impressed posteriorly, the remaining series slightly impressed; seta bearing systematic punctures scattered along interstriae; elytral margins slightly explanate anteriorly, increasing to more broadly explanate in posterior third.

Epipleura well developed, densely covered by pubescence, rather weakly oblique, relatively wide anteriorly, gradually narrowing towards level of metacoxae, continued as a somewhat narrow stripe to apex; pseudepipleura glabrous, relatively wide throughout, only slightly narrowed posteriorly; surface of pseudepipleura smooth, undulated, anteriorly reticulate or posteriorly canaliculate. Wings (see Hansen 1999, Fig. 17; Lawrence and Ślipiński 2013, Fig. 23; examined in *Q. clusia* and *Q. reticulatus*) nearly three times longer than wide; radial cell as a pigmented, somewhat triangular area at anterior margin, positioned near mid length of wing; r4, RA_{3+4} and RA_3 reduced; RA_{3+4} not connected to radial cell; RP_2 reduced to a pigmented wide stipe; MP_{3+4}, CuA_2 and AA_3 reaching margin of wing; basal cell long, reaching a little more than halfway towards posterior wing margin; wedge cell absent; anal (jugal) lobe well developed, narrow, demarcated from remainder of wing by a sharp excision at posterior wing margin.

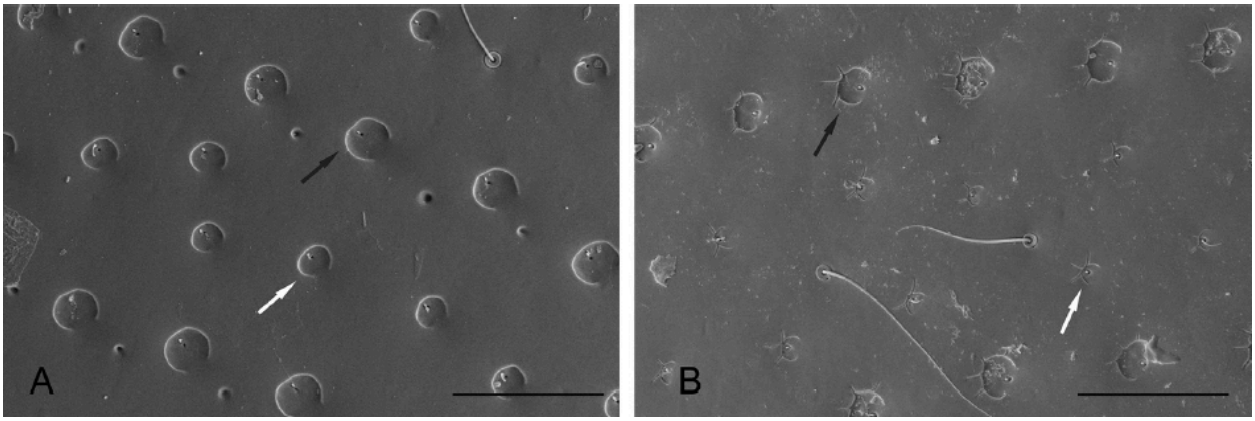


Figure 1.6. SEM of elytral punctures: **A** *Q. clusia*; **B** *Q. reticulatus*. Scale bar: 50 µm. Black arrows point to serial punctures. White arrows point to interstrial punctures.

Legs. Pro- and mesofemora with dense pubescence, at most in about basal half, remainder of surface glabrous and shiny, with subtle reticulations; posterior femora mostly glabrous on ventral face, with only scarce scattered long setae over the surface, sometimes with reduced anterobasal, pubescent patch; all femora with rather sharp tibial grooves on inner face

except basally. Tibiae moderately slender, rather weakly flattened, with moderately fine and sparse spines. All tarsi with five tarsomeres, bearing 2 (tarsomeres 2–4) to a few (tarsomere 5) long apical hair-like setae on dorsal face; tarsomere 5 without setae or spines on ventral face, tarsomeres 1–4 similar in size and shape; pro- and mesotarsi similar in size and proportions, tarsomeres 1–4 with moderately long and rather dense spiniform setae on ventral face, tarsomere 5 approximately as long as tarsomeres 1–4 combined; meta tarsi 1.3 × longer than pro- and mesotarsi, with tarsomeres 1–4 with 1–2 pairs of spines on ventral face, tarsomere 5 approximately as long as tarsomeres 2–4 combined; claws rather large, moderately curved.

Abdomen. Abdomen with 5 ventrites, flat or very weakly convex, all ventrites with uniform, very fine and dense pubescence; first ventrite without median carina, posterior margin of fifth ventrite simply rounded. Aedeagus (Figs 1.7, 1.8) with basal piece about half the length of parameres; median lobe wider than base of each paramere, with a narrow, triangular, longitudinal sclerite, usually extending along apical third; parameres as long as, to longer than median lobe, and nearly half as wide; gonopore preapically situated; basal piece with lateral margins straight to sinuate, apically slightly diverging.

Larvae: The immature stages are unknown.

Distribution: Costa Rica (Cartago, Heredia, Limón, Puntarenas), Panama (Chiriquí, Darién), Ecuador (Napo), Peru (Loreto, Madre de Dios), Venezuela (Amazonas, Bolívar), Guyana, Suriname, French Guiana, Brazil (Amazonas). See Fig. 1.9B.

Biology: Extensive collecting data as well as field observations confirm that the genus is terrestrial. While many specimens have been caught using flight intercept traps, many long series have been collected on decaying *Clusia* fruits. Additional specimens have been collected in

rotten logs, sap flows on freshly cut trees, and in the refuse pile of leafcutter ants. The genus has never been collected from aquatic or semiaquatic habitats. It has been found at elevations from 30 to 1600 m. *Q. acroreius*, *Q. dentatus* and *Q. similaris* are not found higher than 350 m, whereas *Q. reticulatus* is usually found higher than 1000 m.

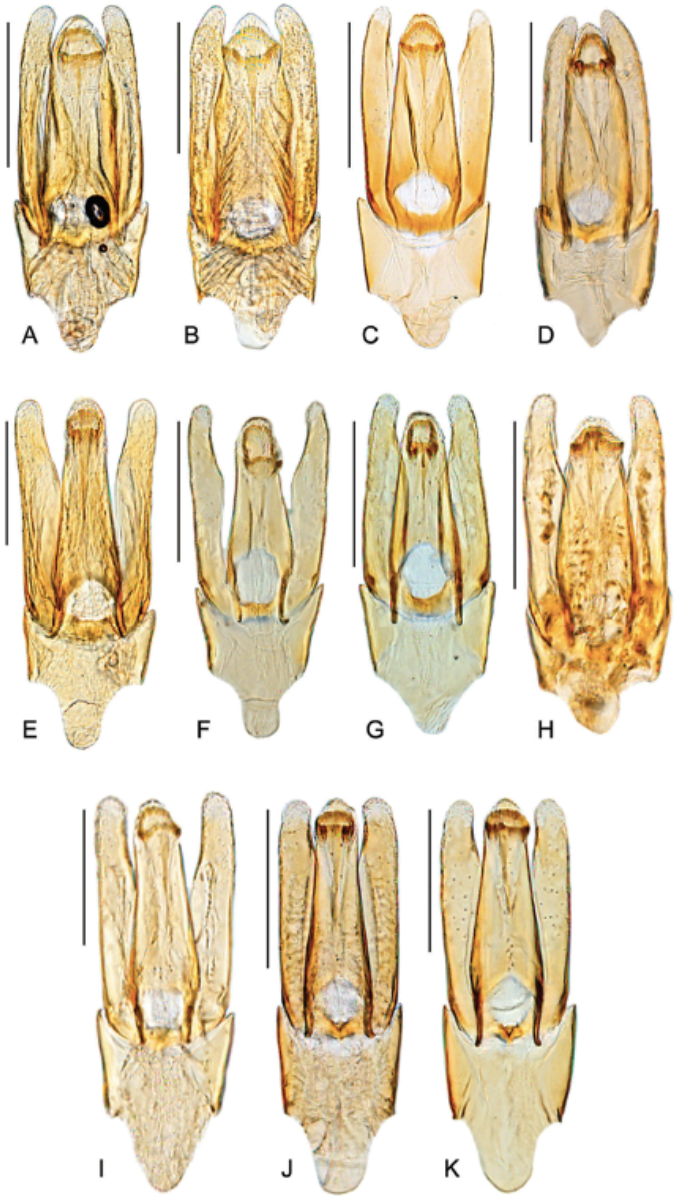


Figure 1.7. Aedeagus of *Quadriops* spp.: Aedeagus of *Quadriops* spp.: *Q. depressus*: **A** holotype, **B** 'politus' holotype, **C** 'amazonensis' holotype, **D** VENEZUELA: Amazonas: Cerro de la Neblina; *Q. reticulatus*: **E** holotype, **F** PANAMA: Chiriquí, **G** COSTA RICA: Puntarenas [CR1ABF00 059], **H** COSTA RICA, Heredia [CR-11TN/16/016]; *Q. clusia*: **I** BRAZIL: Manaus, **J** GUYANA, Upper Potaro [GY14-0312-04A], **K** GUYANA, Ayanganna Airstrip [GY14-0317-01B]. Scale bar 0.1 mm.

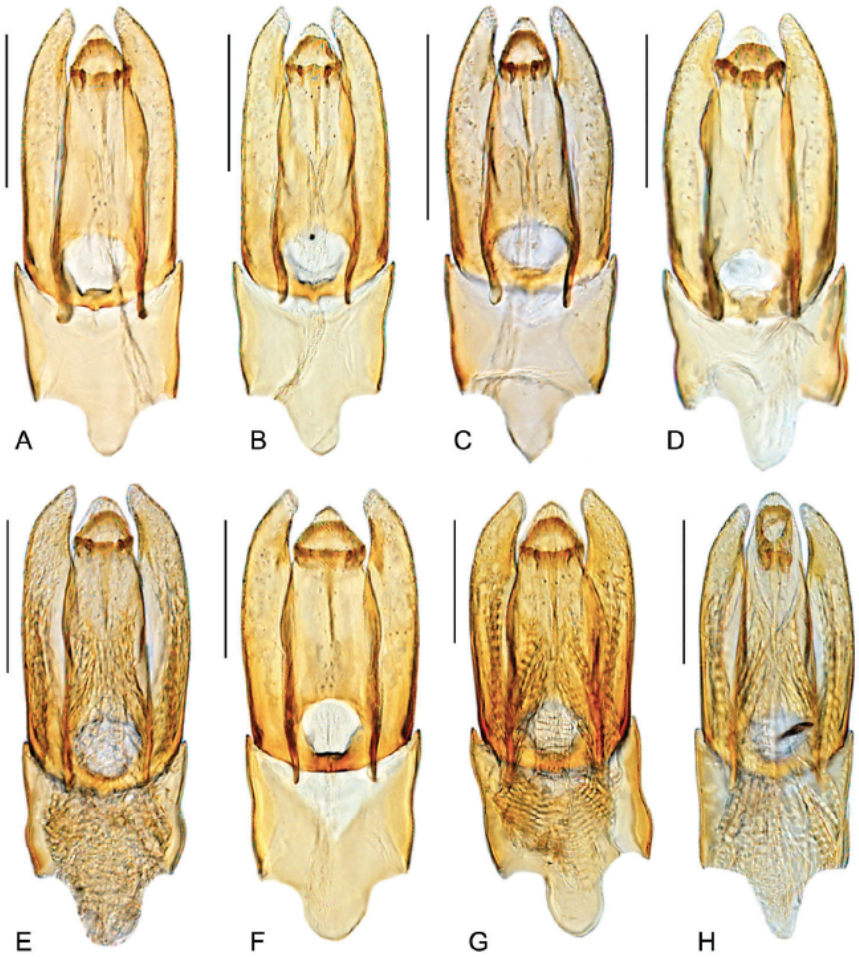


Figure 1.8. Aedeagus of *Quadriops similaris*: **A** SURINAME: Marowijne: Palumeu [SUR1F99 164], **B** GUYANA: Iwokrama Forest [GUY1BF01 005], **C** BRASIL: Manaus, **D** SURINAME: Marowijne: Palumeu [SUR1F99 182], **E** FRENCH GUIANA: Roura [FG1AB97 027], **F** GUYANA: Iwokrama Forest [GUY1BF01 105], **G** FRENCH GUIANA: Cayenne: [FG1AB97 171], **H** SURINAME: Saramacca [SUR1F99 070]. Scale bar 0.1 mm.

Quadriops acroreius n. sp.

Figs 1.1E–H, 1.9B

Type material examined: Holotype (female): "**SURINAME**: Sipaliwini District, 2°28'37.1994"N, 55°37'45.876"W, 275m/ Camp 1: Upper Palemeu,/ 10–16.iii.2012, leg. A.E.Z. Short/ Flight Intercept Trap/ SR12-031410-TN1" (SEMC; voucher SLE456). **Paratype (female):** "**FRENCH GUIANA**, Cayenne, 33.5 km S and 8.4 km NW of Hwy N2 on Hwy D5, 30 m 4°48'18"N,

52°28'41"W, 29 MAY – 9 JUN 1997; J. Ashe, R. Brooks, FG1AB97 171 ex: flight intercept trap" // "Barcode/ SM0102412/ KUNHM-ENT" (SEMC, 1).

Differential Diagnosis: *Quadriops acroreius* is very similar to *Q. dentatus*, both species being moderately convex (as opposed to dorsally flattened) and the serial punctures of the elytra are randomly and uniformly distributed, not aligned to form well-defined longitudinal rows. It can be easily distinguished by the shape of the elevation of the mesoventrite, which is a wide, transverse, straight carina (as opposed to a toothlike projection as in *Q. dentatus*); in addition, the surface of head and clypeus between punctures is smooth (as opposed to reticulated).

Description. Body length 1.9–2.0 mm, width 1.2–1.3 mm. Body elongate oval, moderately convex. General coloration uniform dark brown. Surface of pronotum and elytra, smooth (as opposed to reticulated between punctures), only slightly reticulated on head and clypeus. Elevation of mesoventrite forming a wide, transverse, straight, blunt, strongly raised carina. Metaventrite with a postero median semi triangular glabrous area. Elytra with randomly and uniformly distributed punctures, not aligned into striae; surface of pseudepipleura anteriorly reticulated, posteriorly smooth. Metafemora with basal 1/8 covered by pubescence.

Etymology. Named from the Greek "*akroreia*", meaning mountain ridge (Brown 1956), in reference to the pronounced transverse carina on the elevation of the mesoventrite.

Distribution: Suriname; French Guiana. See Fig. 1.9B.

Biology: The male of the species is not known. Specimens were collected at flight intercept traps.

Quadriops clusia n. sp.

Figs 1.3E–H, 1.6A, 1.7I–K, 1.9B

Material examined: Holotype (male): "SURINAME: Brokopondo District/ 4.95069'N, -55.18599, 470 m/ Brownsberg Nature Park, Leo Val trail, nr. Pump station/ rotting Clusia fruits; 22.iii.2017/ leg. Short et al., SR17-0322-03A // Barcode: SEMC1542023" (NZCS). **Paratypes (210 exs.): BRAZIL: Amazonas:** Reserva Ducke 26 km NE Manaus, Barbosa, M.G.V., Plot B, FIT 1, Feb 1995 (1 male, dissected, NHMUK). **GUYANA: Region XIII:** 5°0.673'N, 59°38.358'W, 500 m, Upper Potaro Camp I (c. 7 km NW Chenapau), near camp, rotten fruits of *Clusia*; leg. A. Short, 12.iii.2014, GY14-0312-04A // Barcodes: SEMC1315733–37, 39, 42–46, 48, 52–55, 57, 60–61, 65, 67–69 (23 ex., incl. 1 female, 7 males [SEMC1315754 dissected]), SEMC1328917–45, 49–60, 62–65, 67-76, 78–85 (SEMC, CBDG, 63 ex., incl. 5 females [SEMC1328965, 78 dissected], 14 males [SEMC1328983 dissected], SEMC1329066–72, 74–75 (SEMC, 9, incl 2 males); 5°18.261'N, 59°50.257'W, 687 m, Ayanganna Airstrip, trail from airstrip to Ayanganna, rotten fruits of *Clusia*; leg. A. Short, 17.iii.2014, GY14-0317-01B // Barcodes: SEMC1329083–84, 86–87, 89–90, 92–93, 96–97 (10, incl. 2 females SEMC1329090 dissected], 5 males [SEMC1329093 dissected], voucher SLE 1003, voucher SLE 1077, voucher SLE 1078; **SURINAME: Brokopondo:** 4.95069'N, -55.18599, 470 m/ Brownsberg Nature Park, Leo Val trail, nr. Pump station/ rotting Clusia fruits; 22.iii.2017, leg. Short et al., SR17-0322-03A // Barcodes: SEMC1541993–2022; 2024 – 2119 (126 ex., SEMC, NZCS, MIZA). **Sipaliwini:** Raleighvallen Nature Reserve/ Lolopasie Area, 14.iii.2016, leg Short et al., *Clusia* fruits, SR16-0314-02B (SEMC; voucher SLE 1054); 4°42'28.8", -56°13'9.5448"; 24 m/

Raleighvallen Nature Reserve/ Lolopasie Area; 18.iii.2016/ *Clusia* fruits; leg. Short/ SR16-0318-01C (SEMC; voucher SLE 1071, female).

Differential Diagnosis: *Quadriops clusia* has well defined longitudinal rows of serial punctures (as opposed to uniform and randomly distributed as in *Q. acroreius* and *Q. dentatus*, see Fig. 1.1). The serial punctures on the striae are simple and similar in size as those on the interstria (Fig. 1.6A) (as opposed to ramified and conspicuously larger than the punctures on the interstrial surface, as on the remainder species, see Fig. 1.6B). Transverse ridge on the elevation of the mesoventrite rather blunt, and slightly bisinuate.

Description. Body length 2.1–2.5 mm, width 1.2–1.4 mm. Body elongate oval, moderately and evenly convex. General coloration reddish brown, with pronotum and clypeus only slightly paler. Surface of head, frons and pronotum reticulated. Clypeus with anterior margin nearly straight. Elevation of mesoventrite with transverse ridge rather broad, and slightly bisinuate. Elytra with ten well defined longitudinal rows of serial punctures; punctures on the interstrial surface similar in size to serial punctures (Fig. 1.6A); surface of pseudepipleura anteriorly undulated, particularly at limit with epipleura, posteriorly smooth. Metafemora with pubescence only along articulation with trochanter, and sometimes along proximal 1/6 of anterior margin. Aedeagus (Fig. 1.7I–K) with parameres as long as median lobe, and nearly as wide at apical 1/4; parameres with outer margins nearly straight, only slightly curved inwards at apical 1/3; apical 1/3 of inner margin of parameres concave; apical 1/3 of parameres rather digitiform and straight, parallel to longitudinal axis of aedeagus. Median lobe with lateral margins straight, converging towards the apex; apex of aedeagus widely rounded; gonopore rather semicircular.

Basal piece as long as 0.5 × the length of the median lobe, with lateral margins straight; manubrium 0.5 times the length and nearly as wide as the base of basal piece.

Etymology. Named after *Clusia*, the genus of plants on whose decomposing fruits the beetles have been collected.

Variation: There is slight variation in the proportions of the aedeagus. Some specimens might have a comparatively wider median lobe (Fig. 1.7K), or seem more slender overall (Fig. 1.7J).

Distribution: Brazil (Amazonas), Guyana, Suriname. See Fig. 1.9B.

Biology: Most known specimens have been collected on rotten fruits of *Clusia* trees, sometimes in series of many hundreds of individuals. In Guyana, this species was found on and beneath rotten fruits of *Clusia grandiflora* (Fig. 1.10A–B). In Suriname, this species was collected on and beneath the rotten fruits of several *Clusia* species, including *C. grandiflora* and *C*. cf. *nemorosa* (Fig. 1.10C–D). The beetles appear most common on fruits in a stage of decay where they are soft and sticky (as opposed to more advanced stages of decay in which the fruits become dry or crumbly). The beetles were also present in leaves beneath the decaying fruits into which rotting fluids had seeped. Most specimens were collected by collecting these fruits and submerging them in pans of water, at which time the beetles float to the surface. We collected hundreds of specimens on several occasions using this method. However, not all rotten *Clusia* patches we examined (some even within 1 km of other patches with *Quadriops* abundance) contained many or any *Quadriops* specimens. We sifted general forest litter and did extensive aquatic collecting at sites in Guyana and Suriname where we found abundant *Quadriops clusia* populations, but no specimens were ever found in these habitats. We also laid baits of other

fruits including bush cashews and bananas but these were not successful in attracting *Quadriops*. We believe the habitat of this species is likely restricted to rotten fruits, and possibly only those from *Clusia*. *Quadriops clusia* has been collected at elevations between 500 and 700 m.

Quadriops dentatus Hansen, 1999

Figs 1.1A–D, 1.9B

Quadriops dentatus Hansen, 1999: 134.

Type material examined: Holotype (female): "VENEZ [Venezuela] : Bolivar/ 105 km S El Dorado/ 17.VII–7.VIII.86/ B. Gill 350m", "Flight intercept/ trap", "HOLOTYPE", "[Handwritten] HOLOTYPE/ Quadriops dentatus/ M. Hansen", "[Barcode] Canadian Museum of/ Musée canadien de la/ NATURE/ CMNEN 0011502" (CMNC).

Additional material examined (5 exs.): FRENCH GUIANA: Matoury: 41.5 km SSW on Hwy N2, 4°37'22"N, 52°22'35W, 50m, 29 May–9 Jun 1997, J. Ashe, R. Brooks, FG1A97 170, ex: flight intercept trap // Barcodes: SM0134289 (SEMC, 1 female), SM0134241 (SEMC, 1 female, dissected); Roura: 8.4 km SSE, 200 m, 4°40'41"N, 52°13'25"W, 25–29 May 1997, J. Ashe, R. Brooks, FG1AB97 088, ex: flight intercept trap // Barcode: SM0096111 (SEMC, 1 female); 13.0 km SSE, 240 m, 4°38'38"N, 52°17'56"W/ 13 Jun 1997; J. Ashe, R. Brooks, FG1AB97 196, ex: miscellaneous collecting // Barcode: SM0100061 (SEMC, 1 female). SURINAME: Sipaliwini: Camp 4 (low), Kasikasima, 2.97731°N, 55.38500°W, 200m, 20–25 mar 2012, leg. Larsen, flight intercept trap, SR12-0320-TN1, 2012 CI-RAP Survey // Barcode: SEMC1089659 (SEMC, 1 female).

Differential Diagnosis: *Quadriops dentatus* is very similar to *Q. acroreius*, both species being moderately convex (as opposed to dorsally flattened) and the serial punctures of the elytra are randomly and uniformly distributed, not aligned to form well defined longitudinal rows. It can be easily distinguished by the toothlike projection of the mesoventrite (as opposed to a wide, transverse, straight, blunt carina as in *Q. acroreius*); in addition, the surface of head and clypeus is smooth between punctures (as opposed to reticulated).

Redescription. Body length 1.6–2.2 mm, width 1.1–1.2 mm. Body elongate oval, moderately convex. General coloration uniform yellowish to dark brown. Surface smooth (as opposed to reticulated between punctures) on head, pronotum and elytra. Elevation of mesoventrite forming a basally transverse acute tooth. Metaventrite with a posterior, short, glabrous and narrow stripe. Elytra with randomly and uniformly distributed punctures, not aligned into striae; surface of pseudepipleura smooth throughout, at most only slightly reticulated at base. Metafemora with pubescence only along dorsal area of articulation to trochanter.

Variation: There is variation in size with the type specimen being the largest.

Distribution: Venezuela (Bolívar), Suriname (Sipaliwini), French Guiana (Matoury, Roura). See Fig. 1.9B.

Biology: The male of this species remains unknown. All known specimens were collected using flight intercept traps, at elevations between 50 and 350 m.

Quadriops depressus Hansen, 1999

Figs 1.2A–D, 1.7A–D, 1.9A

Quadriops amazonensis García, 2000: 59. syn. nov.

Quadriops depressus Hansen, 1999: 136.

Quadriops politus Hansen, 1999: 135. syn. nov.

Type material examined: Holotype (male): *Q. depressus*: "PERU: Dept. [Departamento] Loreto/ 1.5km N Teniente Lopez/ 2°35.66'S,76°06.92'W/ 22 July 1993, 210–240 m/ Richard Leschen #164/ ex: flight intercept trap", "[Handwritten] PARATYPE/ Quadriops depressus/ M. Hansen", "[Barcode]/ SEMC0965921/ KUNHM-ENT" (SEMC). Paratypes: *Q. depressus*: "PERU: Dept. [Departamento] Loreto/ Teniente Lopez/ 2°35.66'S,76°06.94'W/ 23 July 1993, 210–240 m/ Richard Leschen #191/ ex flight intercept trap", "[Handwritten] HOLOTYPE/ Quadriops depressus/ M. Hansen" (SEMC); "PERU: Dept. [Departamento] Loreto/ Campamento San Jacinto/ 2°18.75'S, 75°51.77'W/ 11 July 1993, 175–215 m/ Richard Leschen #84/ ex: flight intercept trap", "[Handwritten] PARATYPE/ Quadriops depressus/ M. Hansen" (SEMC).

Q. amazonensis: Holotype (male): "Venezuela, Amazonas,/ Mcipio. [Municipio] Guinia, Yavita,/ Caño Chivichi, 600 m,/ 29–31 / VIII/ 1996 / Trampa interceptación", "Colector:/ J. Camacho", "Holotipo [male symbol, handwritten]/ [Handwritten] Quadriops/ [Handwritten] amazonensis/ Dcrip. M. García, 1998", "[Barcode]/ MALUZ10158/ LUZ-Venezuela". (MALUZ).

Q. politus: Holotype (male): "PERU: Dept. [Departamento] Loreto/ Campamento San Jacinto/ 2°18.75'S, 75°51.77'W/ 11 July 1993, 175–215 m/ Richard Leschen #83/ ex: flight intercept trap", "[Handwritten] HOLOTYPE/ Quadriops politus/ M. Hansen", "[Barcode]/

SEMC0965917/ KUNHM-ENT" (SEMC). **Paratype:** "PERU: Dept. [Departamento] Loreto/ Campamento San Jacinto/ 2°18.75'S, 75°51.77'W/ 11 July 1993, 175–215 m/ Richard Leschen #83/ ex: flight intercept trap", "[Handwritten] PARATYPE/ Quadriops politus/ M. Hansen", "[Barcode]/ SEMC0965917/ KUNHM-ENT" (SEMC).

Additional material examined (3 exs.): PERU: Loreto: Campamento San Jacinto, 2°18.75'S, 75°51.77'W, 11 July 1993, 175–215 m/ Richard Leschen #82/ ex: flight intercept trap (SEMC, 1); **Madre de Dios:** Pantiacolla Lodge, 8 km NW El Mirador Trail, Alto Madre de Dios River, 800 m, 12°38'30"S, 71°16'41"W, 23–26 OCT 2000, R. Brooks, PERU1B00 102, ex. flight intercept trap // "Barcode/ SM0260334/ KUNHM-ENT" (SEMC, 1 female). **VENEZUELA: Amazonas:** T. F. Amaz. Cerro de la Neblina Basecamp, 140 m, 0°50'N, 66°10'W, 10–20 February 1985// Flight intercept pan trap in rainforest, P. J. & P. M. Spangler, R. A. Faitoute, W. E. Steiner colrs." (1 male, USNM).

Differential Diagnosis: *Quadriops depressus* is externally very similar to *Q. similaris*, and *Q. reticulatus*, as all have well defined longitudinal rows of serial punctures (as opposed to uniform and randomly distributed as in *Q. acroreius* and *Q. dentatus*, see Fig. 1.1), and the serial punctures are conspicuously larger than the punctures on the interstrial surface (as opposed to similarly large as in *Q. clusia*, see Fig. 1.6). It can be separated from *Q. reticulatus* by the dorsal outline of the body being nearly flat (as opposed to moderately convex), and the surface of the pseudepipleura posteriorly markedly canaliculated (see Fig. 1.2C; as opposed to smooth). *Quadriops depressus* can be distinguished from *Q. similaris* by the rounded shape of the apex of the parameres (see Fig. 1.7A–D; as opposed to angulate, as in Fig. 1.8).

Redescription. Body length 2.1–2.5 mm, width 1.3–1.4 mm. Body elongate oval, moderately convex, with dorsal outline nearly flat. General coloration reddish to dark brown,

with pronotum and clypeus only slightly paler. Surface of clypeus smooth to reticulated, usually smooth on frons and pronotum. Elevation of mesoventrite with transverse ridge rather fine and curved (posteriorly concave). Elytra with ten well defined longitudinal rows of serial punctures; punctures on the interstrial surface noticeably smaller than serial punctures; surface of pseudepipleura anteriorly undulated, particularly at limit with epipleura, posteriorly reticulated. Metafemora with pubescence only at base of anterior margin at most. Aedeagus (Fig. 1.7A–D) with parameres slightly longer than median lobe; parameres with outer margins nearly straight, only slightly curved inwards at apical 1/3; apical 1/3 of inner margin of parameres concave; apical 1/6 of parameres digitiform, with rounded apex slightly directed towards longitudinal axis of aedeagus. Median lobe with lateral margins straight, slightly converging from base; apex of aedeagus widely rounded; gonopore rather semicircular. Basal piece as long as 0.4 × the length of the median lobe, with lateral margins straight; manubrium 0.5 × the length and clearly narrower than the base of basal piece.

Variation: There is variation on the density and presence of reticulation on the surface of the frons and clypeus.

Distribution: Peru (Loreto), Ecuador (Napo), Venezuela (Amazonas). See Fig. 1.9B.

Biology: All known specimens were collected with flight intercept traps.

Remarks: It is known that the shape of the aedeagus exhibit intraspecific variation in several acidocerine species (see Short et al. 2017), including *Q. similaris* below. Given the similarity of the illustrations provided by Hansen (1999) and García (2000), and the lack of external characters (beyond the density and presence of reticulation on the surface of the frons and clypeus) to clearly distinguish *Q. amazonensis* and *Q. politus* from *Q. depressus*, we

dismounted the aedeagi of the holotypes of all three species to compare them directly. The aedeaegus of all three type specimens, along with an additional male from Venezuela, share the same overall shape, with only slight variations in proportions that may be due in part to the preparation of the structures. Further, we found the illustration of the aedeagus of the type of *Q. politus* to be incorrectly interpreted (Hansen 1999: Fig. 24); specifically, the apex of the median lobe is drawn to appear very constricted and acutely pointed, while in fact it is broad and blunt as with most other *Quadriops*. This apex of the median lobe was strongly cleared in the type and was not readily visible until we dismounted the genitalia to view it with transmitted light. This mistaken interpretation of the aedeagal shape seems likely to be why Hansen had considered this to be a separate species when in fact it does not appear so. Given the similarity of the aedeagi, coupled with the lack of any detectable external differences, we consider *Q. amazonensis* and *Q. politus* both junior synonyms of *Q. depressus*.

Quadriops reticulatus Hansen, 1999

Figs 1.3A–D, 1.5, 1.6B, 1.7E–H, 1.9A

Quadriops reticulatus Hansen, 1999: 135

Type material examined: Holotype (male): "COSTA RICA: Puntarenas/ Las Alturas (Stanford/ Biol. [Biological] Sta. [Station]) ca. 29km NE San/ Vito, 1500m, 27 May 1993/ J.S. & A.K. Ashe #063/ ex: flight intercept trap", "[Handwritten] HOLOTYPE/ Quadriops reticulatus/ M. Hansen", "[Barcode]/ SEMC0965918/ KUNHM-ENT" (SEMC).

Additional material examined (135 exs.): COSTA RICA: Cartago: 19.3 km NE San José, 17 May 1993, 1010 m, J. & A. Ashe, #105, ex: flight intercept trap (SEMC, 1); Tapanti National Park, 9.776711, -83.792778, Kiri Lodge, 14-19.vii.2011, leg. Short et al., Flight intercept trap, CR11-FIT-Z1-A1 (SEMC; voucher SLE 401). **Guanacaste:** Est. Pitilla, 9 km S. Sta. Cecilia, 700 m, P. N. Guanacaste, P. Ríos, Set. 1991 (INBIO, 1 male); same, 9–20 Nov 1993, C. Moraga, L N 330200_380200 #2449 (INBIO, 1); **Heredia:** 16 km SSE La Virgen, 1070 m, 10°16'N, 84°05'W, 11–20.ii.2001, 11/TN/08/003/ INBio-OET-ALAS transect// Barcodes: SEMC0859232–33 (SEMC, 2 males); same, 11/TN/09/004 // Barcodes: SEMC0859174, 184–185, 203, 206–207 (SEMC, 6 exs., incl. 3 females, 1 male); same, 11/TN/16/006 // Barcodes: SEMC0860054, 58, 68, 73–74, 76 (SEMC, 6 exs., incl. 4 females, 2 males); same, 11/TN/17/007 // Barcodes: SEMC0859642, 827, 836, 840 (SEMC, 4 exs., incl. 2 females, 1 male); same, 11/TN/20/010 // Barcodes: SEMC0860259, 272 (SEMC, 2 exs., incl. 1 female, 1 male); same, 10–21.iii.2001, 11/TN/06/011, // Barcodes: SEMC0859457, 469, 496, 498, 536 (SEMC, 5 males); same, 11/TN/07/012 // Barcodes: SEMC0859353, 363, 374, 385, 389, 599 (6 exs., incl. 2 females, 4 males); same, 11/TN/10/015 // Barcodes: SEMC0859524, 551 (SEMC, 2 exs., incl. 1 female [dissected], 1 male); same, 11/TN/16/016 // Barcodes: SEMC0859973, 975, 979, 0860000, 010, 012 (SEMC, 6 exs., incl. 4 females [SEMC0860000 dissected], 2 males [SEMC0859979 dissected]; same, 11/TN/18/018 // Barcodes: SEMC0859708, 712, 718, 721, 728–729, 733, 738–739, 750, 756, 765, 776, 783, 795 (SEMC, 15 exs., incl. 6 females [SEMC0859712 dissected], 6 males); same, 11/TN/19/019 // Barcodes: SEMC0860511, 515, 527, 531 (SEMC, 4 exs., (2 females, 2 males); same, 11/TN/20/020 // Barcode: SEMC0859935 (SEMC, 1 female); same, 10–21.iv.2001, 11/TN/07/022 // Barcodes: SEMC0860215–216, 220, 226, 233, 254 (SEMC, 6 exs., incl. 4 females, 1 male);

11/TN/08/023 // Barcodes: SEMC0859257, 264, 268–269 (SEMC, 4 exs., incl. 1 female, 2 males [SEMC0859268 and SEMC0859269 dissected]; same, 11/TN/16/026 // Barcodes: SEMC0859406–408, 419, 431, 437 (SEMC, 6 exs., 5 females, 1 dissected male [SEMC0859437]; same, 11/TN/17/027 // Barcodes: SEMC0860628, 630, 641, 652, 663 (SEMC, 5 exs., 1 female, 4 males); same, 11/TN/18/028 // Barcodes: SEMC0860126, 137, 146, 148, 152 (5 exs., 2 females, 3 males); same, 11/TN/19/029 // Barcodes: SEMC0859270, 273, 284, 306, 308, 314, 325 (SEMC, 7 exs., incl. 4 females, 2 males); same, 11/TN/20/030 // Barcodes: SEMC0860573, 599, 602, 606–607, 620, 624–625, 0892500, 502, 511, 578, 583, 590–591, 594 (SEMC, 16 exs., incl. 5 females [SEMC0860599, SEMC0860606 and SEMC0860620 dissected] 5 males [SEMC0860573 and SEMC0860607 dissected]; same, 11–20.iv.2001, 11/TN/18/008 // Barcodes: SEMC0859660, 663–664, 666, 675, 677, 683–684, 704 (SEMC, 9 exs., incl. 4 females, 1 male); same, 12–23.iii.2003, 05/TN/18/020 // Barcode: SEMC0860494 (1 female); same, 10–22.iii.2004, 03/TN/08/015 // Barcode: SEMC0860372 (SEMC, 1); **Limón:** Sector Cerro Cocori, Fca. de E. Rojas, 150 m, E. Rojas, Oct 1991 (INBIO, 1 male); **Puntarenas:** Monteverde Biological Preserve Peñas Blancas Valley-Aleman refugio, 25–29 May 1993, Steve Lingafelter, ex: flight intercept trap (SEMC, 1); Corcovado National Park, Sirena Stn., Corcovado Trail, 150 m, 8°29’7”N 83°34’39”W, 28 JUN–1 JUL 2000, Z. H. Falin, CR1ABF00 059, ex: flight intercept trap // Barcodes: SM0251795 (SEMC, 1 male, dissected), SM0251874 (SEMC, 1 female, dissected), SM0252279 (SEMC, 1 female); Las Cruces Biol. Sta., 1330 m, 08°47.14’N 82°57.58’W, 28–30-V-2004, J. S. Ashe, Z. Falin, I. Hinojosa, ex: flight intercept trap, CR1AFH04 059 // Barcode: SM0625787 (SEMC, 1 male); Altamira Biol. Sta., 1510–1600 m, 09°01.76’N 83°00.49’W, 4–7-VI-2004, J. S. Ashe, Z. Falin, I. Hinojosa, ex: flight intercept trap, CR1AFH04 144 // Barcode: SM0659727 (SEMC, 1). **PANAMA: Chiriqui:** 20 Km N

Gualaca, Finca La Suiza, 1350 m, 08°39'N, 82°12'W, 10 June 1995, J. Ashe & R. Brooks, #167, ex: fogging fungusy log (SEMC, 2 [1 male, dissected]); La Fortuna, "Hydro. Trail", 08°42'N, 82°14'W, 1150 m, 23 V–9 VI 1995, J. Ashe, R. Brooks, #156, ex: flight intercept trap (SEMC, 2 [1 female]); **Darién:** Cana Biological Station, 550 m 7°45'18"N, 77°41'6"W, 07–09 Jun 1996, J. Ashe, R. Brooks, PAN1AB96 114, ex: flight intercept trap // Barcode: SM0049123 (SEMC, 1 female).

Differential Diagnosis: *Quadriops reticulatus* is externally very similar to *Q. depressus*, and *Q. similaris*, as all have well defined longitudinal rows of serial punctures (as opposed to uniform and randomly distributed as in *Q. acroreius* and *Q. dentatus*), and the serial punctures are conspicuously larger than the punctures on the interstrial surface (as opposed to similarly large as in *Q. clusia*, see Fig. 1.6). It can be separated from *Q. depressus* and *Q. similaris* by the dorsal outline of the body being uniformly convex (as opposed to flat), and the smooth surface of the pseudepipleura (as opposed to posteriorly markedly canaliculated, see Fig. 1.2C, G).

Redescription. Body length 2.0–2.4 mm, width 1.2–1.45 mm. Body elongate oval, moderately convex, with dorsal outline only slightly flat. General coloration reddish to dark brown, with margins of pronotum and clypeus only slightly paler. Surface of clypeus, frons and pronotum reticulated. Elevation of mesoventrite with transverse ridge rather fine and curved (posteriorly concave). Elytra with ten well defined longitudinal rows of serial punctures; punctures on the interstrial surface noticeably smaller than serial punctures; surface of pseudepipleura anteriorly undulated, particularly at limit with epipleura, posteriorly smooth. Metafemora with pubescence only on anterior basal corner. Aedeagus (Fig. 1.7E–H) with parameres as long as or longer than median lobe; parameres with outer margins slightly concave near midlength; apical 1/3 of inner margin of parameres concave; apical 1/3 of parameres

digitiform, rather narrow, with rounded apex, slightly pointing towards longitudinal axis of aedeagus. Median lobe with lateral margins usually straight and clearly converging from base; apex of aedeagus widely rounded; gonopore variable in shape. Basal piece as long as 0.5 to 0.7 × the length of the median lobe, with lateral margins straight to sinuate; manubrium 0.3 to 0.6 × the length and clearly narrower than the basal piece at its base.

Variation: The degree of sharpness of the transverse ridge of mesoventrite varies from being blunt and moderately marked to sharp. There is variation on the shape of the aedeagus, even though the overall shape is conserved across the species. Specimens from Panama tend to be smaller.

Distribution: Costa Rica: Cartago, Heredia, Limón, Puntarenas; Panama: Chiriquí, Darién. See Fig. 1.9B.

Biology: Most known specimens have been collected by using flight intercept traps. A few specimens were collected from “fungusy logs”. Additionally, a disassociated note at INBio about one collecting event of *Quadriops* in Costa Rica indicated a series had been collected on the sap of freshly cut trees. Most *Q. reticulatus* specimens have been collected at elevations between 1000 and 1600 m.

Remarks: The female specimen from the Darién of Panama has a differently shaped transversal ridge of the mesoventrite, but no other characters were found to differentiate it from *Q. reticulatus*. However, when males are found it may be shown to represent a distinct species. Several specimens were also observed to have mites on the dorsal surface of the elytra.

Quadriops similaris Hansen, 1999

Figs 1.2E–H, 1.8, 1.9C

Quadriops similaris Hansen, 1999: 136

Type material examined: Paratype (female): "VENEZ [Venezuela]: Bolivar/ 105 km S El Dorado/ 17.VII-7.VIII.86/ B. Gill, FIT [handwritten] 350m", "Flight intercept/ trap", "PARATYPE", "[Handwritten] PARATYPE/ Quadriops/ similaris/ M. Hansen", "CMNEN 2003-1173" (CMNC). [Holotype female from Guyana in NHMUK, not examined].

Additional material examined (34 exs.): BRAZIL: Amazonas: Reserva Ducke 26 km NE Manaus, Barbosa, M.G.V., Plot B, FIT 1, Feb 1995 (2 males (1 dissected); 1 female, NHMUK). GUYANA: Region 8: Iwokrama Forest, Pakatau hills, 70 m, 4°44'54"N, 59°1'36"W, 25–29 MAY 2001, R. Brooks, Z. Falin, GUY1BF01 061, ex: flight intercept trap // Barcode: SM0569493 (SEMC, 1); Iwokrama Forest, 1 km W Kurupukari, Iwokrama Field Stn., 60 m, 4°40'19"N, 58°41'4"W, 21 MAY 2001, R. Brooks, Z. Falin, GUY1BF01 005, ex: *Acromyrmex hystrix* refuse pile // Barcodes: SM0569493 (SEMC, 1); SM0568525 (SEMC, 1 male, dissected); SM0568547 (SEMC, 1 female, dissected); 26–29 MAY 2001, R. Brooks, Z. Falin, GUY1BF01 064, ex: flight intercept trap // Barcode: SM0569493 (SEMC, 1); Iwokrama Forest, 26 km SW Kurupukari, Iwokrama Mt., 300 m, 4°20'2"N, 58°47'18"W, 23–25 MAY 2001, R. Brooks, Z. Falin, GUY1BF01 031, ex: flight intercept trap // Barcode: SM0570965 (SEMC, 1); Iwokrama Forest, Turtle Mt. base camp, 50 m, 4°43'5"N, 58°43'5"W, 1 JUN 2001, R. Brooks, Z. Falin, GUY1BF01 105, ex: fogging splintered tree trunk // Barcodes: SM0564705 (SEMC, 1 male, dissected), SM0564703 (SEMC, 1 male), SM0564690 (SEMC, 1 male), SM0564710 (SEMC, 1), SM0564711 (SEMC, 1), SM0564721 (SEMC, 1). FRENCH

GUIANA: Cayenne: 33.5 km S and 8.4 km NW of Hwy N2 on Hwy D5, 4°48'18"N, 52°28'41"W, 30 m, 26–28 MAY 1997; J. Ashe, R. Brooks, FG1AB97 057, ex: flight intercept trap // Barcode: SM0099106 (SEMC, 1 female, dissected); 29 MAY–9 JUN 1997; J. Ashe, R. Brooks, FG1AB97 171, ex: flight intercept trap // Barcode: SM0102330 (SEMC, 1 male, dissected), SM0101058 (SEMC, 1 female), SM0131132 (SEMC, 1 male, dissected); **Roura:** 8.4 km SSE, 200 m, 4°40'41"N, 52°13'25"W, 22–24 MAY 1997; J. Ashe, R. Brooks, FG1AB97 027, ex: flight intercept trap // Barcodes: SM0101145 (SEMC, 1 female, dissected); SM0101159 (SEMC, 1 male, dissected); 4°40'0"N, 52°13'0"W, 29 MAY–10 JUN 1997; J. Ashe, R. Brooks, FG1AB97 182, ex: flight intercept trap // Barcodes: SM0121078 (SEMC, 1); SM0121118 (SEMC, 1 female); 39.4 km SSE, 270 m, 4°32'43"N, 52°8'26"W, 10 JUN 1997; J. Ashe, R. Brooks, FG1AB97 173, ex: under fermenting bark // Barcode: SM0098799 (SEMC, 1 female). **SURINAME: Saramacca:** West Suriname Road, 178 km WSW Zanderij Airport, 25 m, 4°59'6"N, 56°18'48"W, 13 JUN 1999; Z. H. Falin; SUR1F99 070, ex: splintered tree trunk (pyrethrum fogging) // Barcodes: SM0181529 (SEMC, 1), SM0181531 (SEMC, 1 female, dissected); SM0181968 (SEMC, 1 male, dissected); **Sipaliwini:** Palumeu, 15 km NE, on Tapanahony River, trail to Poti Hill, ca 160 m, 3°27'N, 55°22'W, 6 JUL 1999; Z. H. Falin; SUR1F99 164, ex: splintered tree trunk (pyrethrum fogging) // Barcode: SM0184065 (SEMC, 1 male); Palumeu, ca 160 m, 3°20'56"N, 55°26'18"W, 8 JUL 1999; Z. H. Falin; SUR1F99 182, ex: splintered log (pyrethrum fogging) // Barcodes: SM0180696 (SEMC, 1), SM0180698 (SEMC, 1), SM0180699 (SEMC, 1 female, dissected); N 2.47700°, W 55.62941°, 275 m, Camp 1, Upper Palumeu, leg. A. Short; Flight Intercept Trap, 10–16.iii.2012; SR12-0310-TN1, 2012 CI-RAP Survey // Barcode: SEMC1089282 (SEMC, 1).

Differential Diagnosis: *Quadriops similaris* is externally very similar to *Q. depressus* and *Q. reticulatus*, as all have well defined longitudinal rows of serial punctures (as opposed to uniform and randomly distributed as in *Q. acroreius* and *Q. dentatus*, see Fig. 1.1), and the serial punctures are conspicuously larger than the punctures on the interstrial surface (as opposed to similarly large as in *Q. clusia*, see Fig. 1.6). It can be separated from *Q. reticulatus* by the dorsal outline of the body being nearly flat (as opposed to uniformly convex), and the surface of the pseudepipleura posteriorly markedly canaliculated (see Fig. 1.2G; as opposed to smooth). *Q. similaris* can be distinguished from *Q. depressus* by the angulate shape of the apex of the parameres (see Fig. 1.8; as opposed to rounded, as in Fig. 1.7A–D).

Redescription. Body length 2.2–2.6 mm, width 1.4–1.6 mm. Body elongate oval, moderately convex, with dorsal outline nearly flat. General coloration reddish brown, with sides of pronotum and clypeus only slightly paler. Surface of clypeus, frons and sides of pronotum reticulated. Elevation of mesoventrite with transverse ridge usually rather sharp, curved to somewhat roof-like shaped. Elytra with ten well defined longitudinal rows of serial punctures; punctures on the interstrial surface noticeably smaller than serial punctures; surface of pseudepipleura anteriorly undulated, posteriorly markedly canaliculated. Metafemora with pubescence only along proximal 1/5 of anterior margin. Aedeagus (Fig. 1.8) with parameres usually longer than median lobe; parameres with outer margins straight to slightly convex along basal 3/4, then distinctly curved inwards at apical 1/4, or gradually curved from midlength; preapical area of inner margin of parameres concave; apex narrowly rounded, forming an acute angle pointing towards apex of aedeagus. Median lobe with lateral margins straight to somewhat sinuated, either parallel along basal 2/3 or converging from base; apex of aedeagus variable,

wide to narrow, angulated to rounded; gonopore usually semicircular. Basal piece as long as 0.6 × the length of the median lobe, with lateral margins straight to sinuate; manubrium 0.3 × the length and clearly narrower than the basal piece at its base.

Variation: There is variation in the shape and sharpness of the transverse ridge; the general shape of the aedeagus is consistent within the species, but varies in specific characters: shape of outer margins of parameres, width and shape of apex of parameres, shape of apex of aedeagus. There is one male specimen from Suriname (Collecting event SUR1F99 070) in which the median lobe is longer than the parameres and the gonopore is rather oval.

Distribution: Brazil (Amazonas), French Guiana, Guyana, Suriname, Venezuela (Bolívar). See Fig. 1.9C.

Biology: Most specimens were collected in flight intercept traps. The species was also collected on the refuse pile of the ant *Acromyrmex hystrix*, under fermenting bark and by fogging a splintered tree trunk. *Q. similaris* has been collected at elevations between 25 and 350 m.

Remarks: The male of *Q. similaris* was unknown until now. Specimens collected in Guiana were recognized as belonging to this species by the posteriorly markedly canaliculated pseudepipleura, a character shared with *Q. depressus*. There are no consistent external characters that distinguish both species, but the shape of the apex of the parameres is remarkably different.

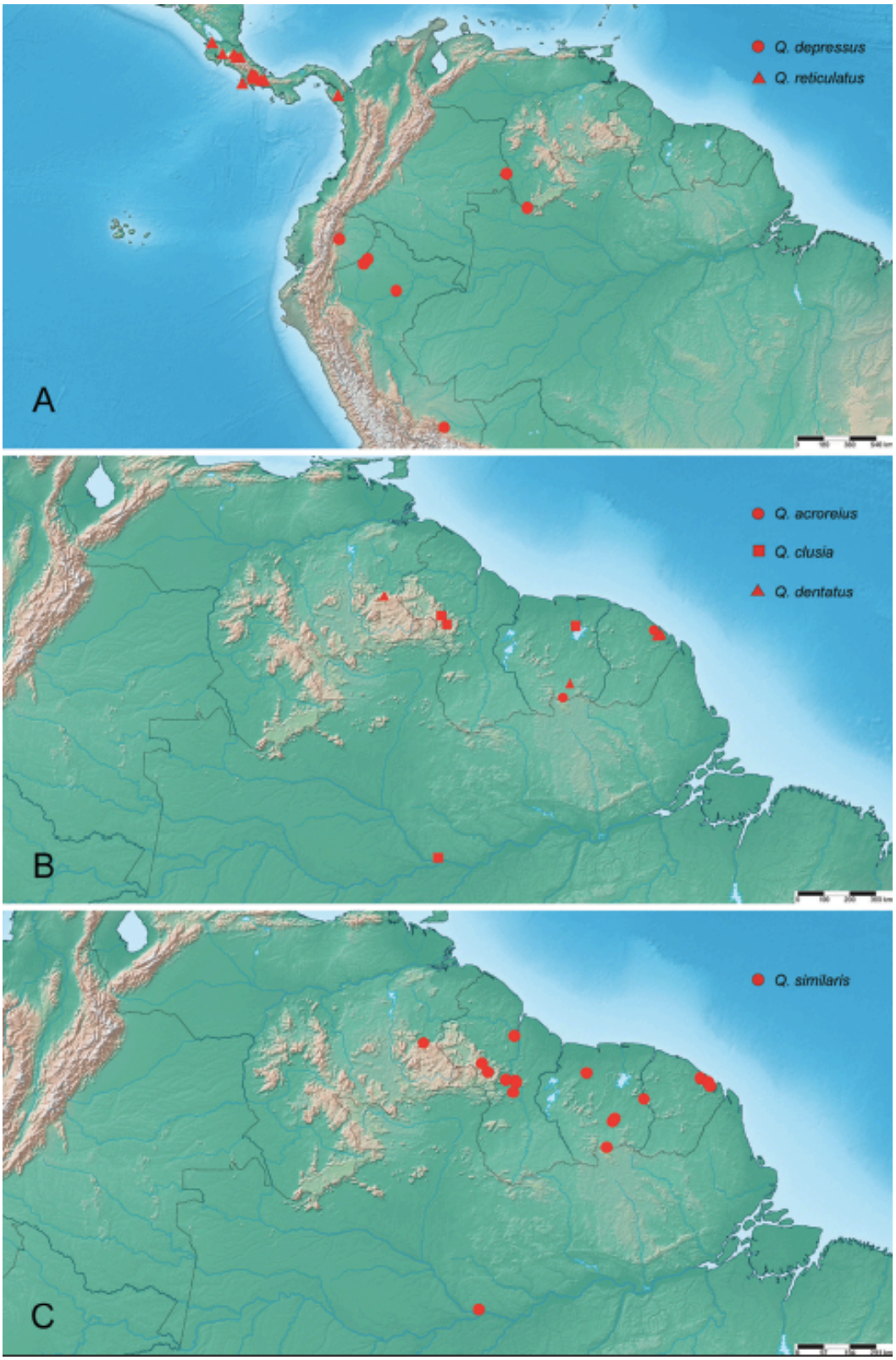


Figure 1.9. Distribution of *Quadriops* spp.: **A** *Q. depressus* (circles), *Q. reticulatus* (triangles); **B** *Q. acroreius* (circles), *Q. clusia* (squares), *Q. dentatus* (triangles); **C** *Q. similaris*.

Figure 1.10. Habitat of *Quadriops clusia* n. sp.: **A** *Clusia* cf. *grandiflora* on the forest floor, collecting event GY14-0312-04A; **B** A specimen of *Quadriops clusia* **n. sp.** crawling on the surface of a rotting *Clusia* fruit, collecting event GY14-0312-04A; **C** *Clusia* cf. *nemorosa* in Brownsberg Nature Park, Suriname on which *Quadriops clusia* **n. sp.** was collected; **D** Collecting *Quadriops* and other terrestrial hydrophilid specimens by submerging collected rotting *Clusia* fruits in pans of water and waiting for the beetles to float to the surface, collecting event SR17-0322-03A.

Key to the species of *Quadriops* Hansen, 1999

1 Elytra with punctures randomly and uniformly distributed (see Fig. 1.1)…**2**

– Elytra with punctures arranged as well defined longitudinal series, forming striae (see Figs 1.2, 1.3) …**3**

2 Elevation of mesoventrite as a narrow toothlike projection…***Q. dentatus*** Hansen (Fig. 1.1A–D)

– Elevation of mesoventrite as a wide, transverse, straight blunt carina…***Q. acroreius*** n. sp. (Fig. 1.1E–H)

3 Serial elytral punctures simple; the ones on striae similar in size as those on the interstrial surface (Figs 1.6A, 1.3E–F)…***Q. clusia*** n. sp.

– Serial elytral punctures ramified; the ones on striae evidently larger in size than those on the interstrial surface (Fig. 1.6B)…4

4 Surface of pseudepipleura smooth throughout; dorsal outline of body in lateral view moderately and uniformly convex…***Q. reticulatus*** Hansen (Fig. 1.3A–D)

– Surface of pseudepipleura posteriorly markedly canaliculated (e.g., Fig. 1.2G), dorsal outline of body in lateral view nearly flat…5

5 Apex of parameres widely to narrowly rounded (Fig. 1.7A–D)…***Q. depressus*** Hansen (Fig. 1.2A–D)

– Apex of parameres angulate (Fig. 1.8)…***Q. similaris*** Hansen (Fig. 1.2E–G)

DISCUSSION

The data now strongly support the conclusion that *Quadriops* is an exclusively terrestrial genus. Previously, all but one specimen were from flight intercept traps, leaving their preferred habitat a mystery. One paratype specimen of *Q. reticulatus* was taken from oak forest litter, leading Hansen to consider them “apparently terrestrial”, though it should be noted that incidental collections of otherwise aquatic or semiaquatic taxa in leaf litter are not rare. We

located older material that confirmed additional collecting events from sifted litter as well as rotten logs and sap flows, further substantiating the terrestrial habits of several species, including *Q. reticulatus* and *Q. similaris*. In 2013, AEZS first observed several *Quadriops clusia* specimens crawling on a rotting *Clusia* fruit in Guyana, and was able to subsequently collect several long series. Since that time, we have actively sought to collect in *Clusia* fruits on subsequent expeditions in Suriname and Guyana. In most of the cases in which we have collected in the fruits, we have been able to find at least one individual, and in some cases have encountered hundreds once again. We have collected hydrophilid larvae from these fruits as well, but we have not yet confirmed that they belong to *Quadriops* (other water scavenger beetles from the tribes Megasternini and Coelostomatini were also collected with *Quadriops* in the fruits). Interestingly, although several *Quadriops* geographically co-occur with *Q. clusia* in Guyana and Suriname, none have been found in *Clusia* fruits. Additionally, no *Quadriops* has been found in any aquatic or semiaquatic habitats despite extensive recent collecting activity in northern South America.

When *Quadriops* was first described from a total of 17 specimens by Hansen (1999), he discussed at relative length his difficulty in placing the taxon in a tribe before ultimately deciding on the (then subtribe) Acidocerina of the Hydrophilini (sensu Hansen 1991). These difficulties in placing *Quadriops* are three-fold: First, the tribe Hydrophilini as Hansen (1991) defined it at the time was in fact not monophyletic, with the acidocerines actually not closely related at all to the remaining groups of Hydrophilini (Short and Fikáček 2013). Second, he misinterpreted several characters: he described *Quadriop*s as having simple (non-bifid) mandibles when in fact they are clearly bifid in the species where the character was examined. Additionally, his assignment of

which taxa had “systematic punctures”, an important character for grouping lineages within the family, was in part erroneous, leading him to code a number of taxa as lacking these punctures when in fact they possessed them (see Short and Fikáček 2013 for a discussion). Third, the derived terrestrial way of life of *Quadriops* has almost certainly been the cause for some of its more atypical morphologies such as reduced palps and lack of femoral pubescence. When these issues are taken into account, *Quadriops* is easily accommodated within the Acidocerinae (Short and Fikáček 2013).

ACKNOWLEDGEMENTS

We are grateful for the assistance and support of many colleagues during fieldwork, including Mauricio García (MALUZ), Jesus Camacho (MALUZ), Luis Joly (MIZA), Vanessa Kadosoe (NZCS), and Paul Ouboter (NZCS), as well as the curators of the collections listed above for the loan of valuable specimens. Angel Solis and Jack Longino assisted AEZS on visits to review material at INBIO and ALAS (La Selva) respectively. This study was supported by US National Science Foundation grant DEB-1453452 to AEZS. Some fieldwork in Suriname and Guyana was partly funded by Conservation International and WWF-Guianas respectively.

REFERENCES CITED

García M (2000) Una nueva especie de *Quadriops* Hansen, 1999 (Coleoptera: Hydrophilidae: Hydrophilinae) de Venezuela. Boletín del Centro de Investigaciones Biológicas 34 (1): 59–65.

García M (2001) Nueva subtribu, género y especie de Hydrophilini (Coleoptera: Hydrophilidae) del extremo suroriental de Venezuela. Boletín del Centro de Investigaciones Biológicas Universidad del Zulia 35: 151–160.

Hansen M (1991) The hydrophiloid beetles. Phylogeny, classification and a revision of the genera (Coleoptera: Hydrophilidae). Biologiske Skrifter 40: 1–367.

Hansen M (1999) Fifteen new genera of Hydrophilidae (Coleoptera), with remarks on the generic classification of the family. Insect Systematics & Evolution 30 (2): 121–172.

Komarek A (2004) Taxonomic revision of *Anacaena* Thomson, 1859. I. Afrotropical species (Coleoptera: Hydrophilidae). Koleopterologische Rundschau 74: 303–350.

Lawrence J, Ślipiński A (2013) *Australian Beetles: morphology, classification and keys*. CSIRO Publishing, Melbourne-Australia, 576 pp.

Minoshima YN, Komarek A, Ôhara M (2015) A revision of *Megagraphydrus* Hansen (Coleoptera, Hydrophilidae): synonymization with *Agraphydrus* Regimbart and description of seven new species. Zootaxa 3930 (1): 1–63.

Short AEZ, Fikáček M (2013) Molecular phylogeny, evolution and classification of the Hydrophilidae (Coleoptera). Systematic Entomology 38 (4): 723–752.

Short AEZ, García M, Girón JC (2017) Revision of the Neotropical water scavenger beetle genus *Globulosis* García, 2001 (Coleoptera: Hydrophilidae: Acidocerinae). Zootaxa 4232 (2): 271–281.

Velázquez de Castro AJ (1998) Morphology and taxonomy of the genus *Sitona* Germar 1817, (I): The metendosternite (Col., Curc.). In: Colonnelli E, Louw S, Osella G (Eds) 2. Taxonomy, ecology and distribution of Curculionoidea (Coleoptera: Polyphaga). XX International Congress of Entomology, Florence (Italy), August 1996. Atti del Museo Regionale di Scienze Naturali, Torino, 109–123.

Chapter 2. Three additional new genera of acidocerine water scavenger beetles from the Guiana and Brazilian Shield regions of South America (Coleoptera: Hydrophilidae: Acidocerinae)

Girón, J. C. & A. E. Z. Short. (2019) Three additional new genera of acidocerine water scavenger beetles from the Guiana and Brazilian Shield regions of South America (Coleoptera: Hydrophilidae: Acidocerinae). ZooKeys, 855: 109–154. https://doi.org/10.3897/zookeys.855.33013

ABSTRACT

Recent study of the water scavenger beetle subfamily Acidocerinae in the Neotropical region has uncovered numerous undescribed species that are not able to be placed in existing genera. Here, we describe three new genera to accommodate 17 of these new species from South America: *Aulonochares* gen. n. for *Aulonochares lingulatus* sp. n. (French Guiana, Suriname), *Aulonochares novoairensis* sp. n. (Brazil), and *Aulonochares tubulus* sp. n. (Brazil, Guyana, Suriname, Venezuela); *Ephydrolithus* gen. n. for *Ephydrolithus hamadae* sp. n. (Brazil), *Ephydrolithus minor* sp. n. (Brazil), *Ephydrolithus ogmos* sp. n. (Brazil), *Ephydrolithus spiculatus* sp. n. (Brazil), and *Ephydrolithus teli* sp. n. (Brazil); and *Primocerus* gen. n. for *Primocerus cuspidis* sp. n. (Venezuela), *Primocerus gigas* sp. n. (Venezuela), *Primocerus neutrum* sp. n. (Guyana, Suriname, Venezuela), *Primocerus ocellatus* sp. n. (Venezuela), *Primocerus petilus* sp. n. (Brazil), *Primocerus pijiguaense* sp. n. (Venezuela), *Primocerus maipure* sp. n. (Venezuela), *Primocerus semipubescens* sp. n. (Guyana), and *Primocerus striatolatus* sp. n. (Suriname). The genus

Ephydrolithus gen. n. is currently restricted to seepages in the mountainous regions of the Brazilian Shield. *Aulonochares* gen. n. and *Primocerus* gen. n. are both currently only known from the Guiana Shield, though widespread in that region where they are associated with streams and seeps. We present differential diagnoses, maps, habitat details, and illustrations of all new genera and species here described.

RESUMEN

El estudio reciente de escarabajos acuáticos de la subfamilia Acidocerinae en la región neotropical, ha revelado numerosas especies no descritas que no pueden ser atribuidas a los géneros existentes. Aquí describimos tres géneros nuevos para acomodar 17 de estas especies nuevas de Suramérica: *Aulonochares* gen. n. para *Aulonochares lingulatus* sp. n. (Guyana Francesa, Surinam), *Aulonochares novoairensis* sp. n. (Brasil), y *Aulonochares tubulus* sp. n. (Brasil, Guyana, Surinam, Venezuela)*; Ephydrolithus* gen. n. para *Ephydrolithus hamadae* sp. n. (Brasil), *Ephydrolithus minor* sp. n. (Brasil), *Ephydrolithus ogmos* sp. n. (Brasil), *Ephydrolithus spiculatus* sp. n. (Brasil), y *Ephydrolithus teli* sp. n. (Brasil); y *Primocerus* gen. n. para *Primocerus cuspidis* sp. n. (Venezuela), *Primocerus gigas* sp. n. (Venezuela), *Primocerus neutrum* sp. n. (Guyana, Surinam, Venezuela), *Primocerus ocellatus* sp. n. (Venezuela), *Primocerus petilus* sp. n. (Brazil), *Primocerus pijiguaense* sp. n. (Venezuela), *Primocerus maipure* sp. n. (Venezuela), *Primocerus semipubescens* sp. n. (Guyana), y *Primocerus striatolatus* sp. n. (Surinam). El género *Ephydrolithus* gen. n. se restringe hasta ahora a hábitats higropétricos en las regiones montañosas del Escudo Brasileño. *Aulonochares* gen. n. y *Primocerus* gen. n. son ambos hasta ahora conocidos del Escudo Guyanés, no obstante, ampliamente distribuidos en esa región en la

que están asociados con corrientes y hábitats higropétricos. Presentamos diagnosis diferenciales, mapas, detalles sobre los hábitats e ilustraciones para todos los géneros y especies que aquí se describen.

Keywords: aquatic beetles; new species; Neotropical region; taxonomy; seepage habitat

INTRODUCTION

The cosmopolitan subfamily Acidocerinae currently includes 16 genera, with eleven of these occurring in the Neotropical region (Short and Fikáček 2013, Minoshima et al. 2015, Girón and Short 2018). Until this century, the number of acidocerine lineages known from South America was relatively modest and their documented distribution quite spotty, particularly in the tropical areas of the region. Recent fieldwork combined with renewed taxonomic efforts over the last two decades have revealed an eye-opening diversity of lineages and forms, resulting in the description of seven of the eleven presently recorded genera since 1999. And still, the discoveries continue unabated: an ongoing review of the Neotropical acidocerine fauna has revealed three additional new genera, which appear biogeographically restricted to the Brazilian and Guiana Shield regions of South America. Most of these new taxa occur in seepage habitats, which likely explains why they have remained hidden until now. Here we describe these three new genera to contain seventeen previously undescribed species.

MATERIALS AND METHODS

Depositories of examined material.

CBDG: Center for Biological Diversity, University of Guyana, Georgetown

INPA: Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (N Hamada)

MALUZ: Museo de Artrópodos de la Universidad del Zulia, Maracaibo, Venezuela (J Camacho, M García)

MIZA: Museo del Instituto de Zoología Agrícola, Maracay, Venezuela (L Joly)

NZCS: National Zoological Collection of Suriname, Paramaribo (P Ouboter, V Kadosoe)

SEMC: Snow Entomological Collection, University of Kansas, Lawrence, KS (A Short)

USNM: US National Museum of Natural History, Smithsonian Institution, Washington, DC (C Micheli).

Morphological methods.

Nearly 280 specimens were examined. Specimen preparation and examination methods are identical to those given in Girón and Short (2017). Descriptive sequence and morphological terminology largely follows Hansen (1991) except for the use of meso- and metaventrite instead of meso- and metasternum, and abdominal ventrites instead of abdominal sternites (see Lawrence and Ślipiński 2013). Terms for the ventral surface of the head follow Komarek (2004). Terminology for the metafurca follows Velázquez de Castro (1998).

Descriptions of genera and species are organized in alphabetical order, whereas in the habitus figures species are grouped by similarity for ease of comparison. Maps were created using SimpleMappr (Shorthouse 2010).

RESULTS

List of species and their known distribution

Aulonochares gen. n.

1. *Aulonochares lingulatus* sp. n. French Guiana, Suriname
2. *Aulonochares novoairensis* sp. n. Brazil (Amazonas)
3. *Aulonochares tubulus* sp. n. Brazil (Roraima), Guyana, Suriname, Venezuela (Amazonas)

Ephydrolithus gen. n.

4. *Ephydrolithus hamadae* sp. n. Brazil (Minas Gerais)
5. *Ephydrolithus minor* sp. n. Brazil (Bahía)
6. *Ephydrolithus ogmos* sp. n. Brazil (Bahía)
7. *Ephydrolithus spiculatus* sp. n. Brazil (Minas Gerais)
8. *Ephydrolithus teli* sp. n. Brazil (Bahía, Minas Gerais)

Primocerus gen. n.

9. *Primocerus cuspidis* sp. n. Venezuela (Amazonas)
10. *Primocerus gigas* sp. n. Venezuela (Amazonas)
11. *Primocerus neutrum* sp. n. Guyana, Suriname, Venezuela (Bolívar)
12. *Primocerus ocellatus* sp. n. Venezuela (Amazonas)

13. *Primocerus petilus* sp. n. Brazil (Pará)

14. *Primocerus pijiguaense* sp. n. Venezuela (Bolívar)

15. *Primocerus maipure* sp. n. Venezuela (Amazonas)

16. *Primocerus semipubescens* sp. n. Guyana

17. *Primocerus striatolatus* sp. n. Suriname

Aulonochares gen. n.

Figs 2.1–2.4

Type species: *Aulonochares tubulus* sp. n.

Differential diagnosis. Medium sized beetles (5.8–7.5 mm), elongate oval in dorsal view, weakly convex in lateral view (see Fig. 2.1B, E, H). Color orange brown to dark brown; ventral surface covered with rather long golden setae, especially on abdominal ventrites. Head subquadrate in dorsal view (see Fig. 2.2A, F, H). Eyes relatively small. Clypeus with anterior margin only slightly narrower than posterior margin. Labrum fully exposed. Mentum and submentum roughly punctate (e.g., Fig. 2.1F). Antennae with nine antennomeres (e.g., Fig. 2.1C). Maxillary palps nearly 1.5 × longer than maximum width of head (e.g., Fig. 2.1A). Elytra without sutural striae, with net-like patterning visible throughout the entire surface (e.g., Fig. 2.1G); ground punctures and systematic punctures similar in size, shallowly impressed; serial punctures absent. Posterior elevation of mesoventrite simple, without carinae or ridges (Fig. 2.2B). Posterior femora glabrous at most along apical seventh. Ventral face of tarsomeres 1–4 densely

covered by stiff setae. Apex of fifth abdominal ventrite strongly emarginate; emargination fringed by stout setae (Fig. 2.2D). Aedeagus (Fig. 2.2E, G, I) somewhat cylindrical, with parameres forming a 5–7 × longer than wide tube; basal piece very short and strongly concave.

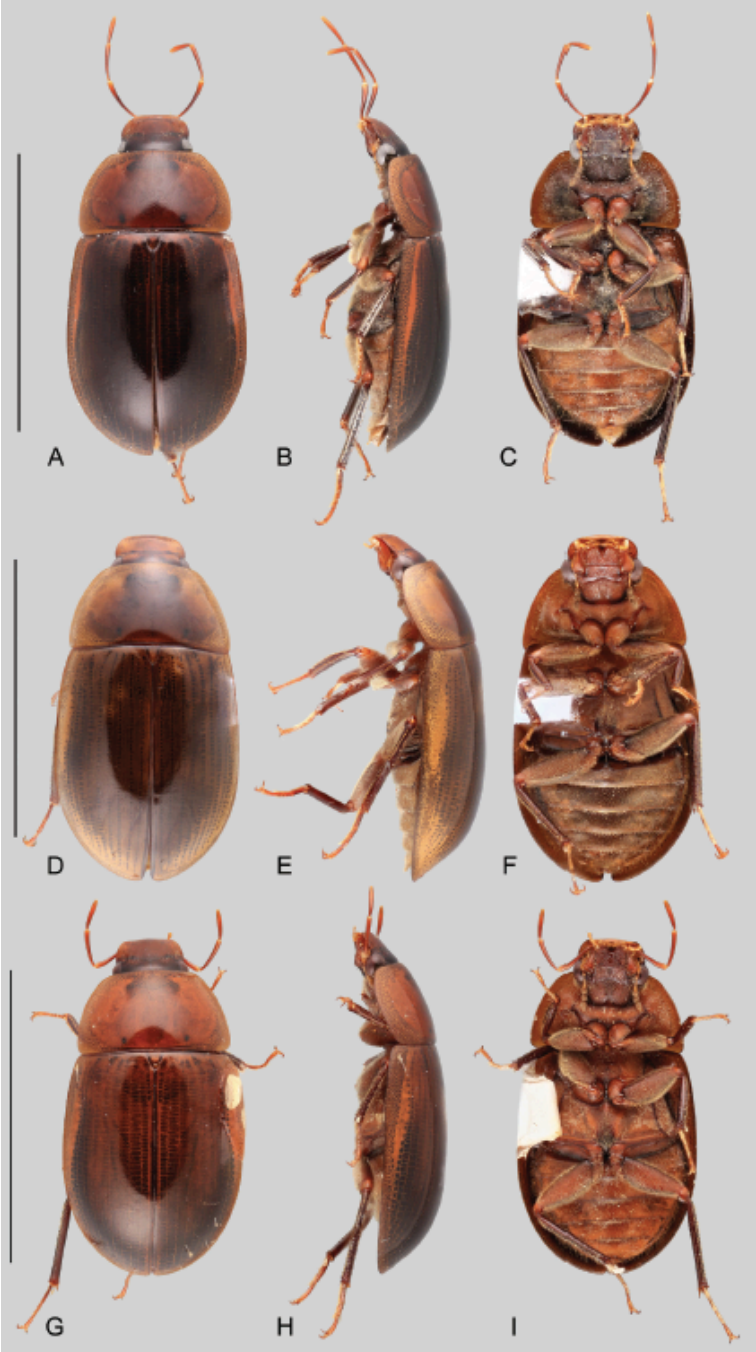


Figure 2.1. Habitus of *Aulonochares* spp.: **A–C** *Aulonochares tubulus*: **A** dorsal view, **B** lateral view, **C** ventral view; **D–F** *Aulonochares novoairensis*: **D** dorsal view, **E** lateral view, **F** ventral view; **G–I** *Aulonochares lingulatus*: **G** dorsal view, **H** lateral view, **I** ventral view. Scale bars 5 mm.

Aulonochares can be easily mistaken for *Helochares*, especially in the field, based on overall body size, shape and coloration, number of antennomeres and apical emargination of the fifth ventrite. *Aulonochares* can be distinguished from other Neotropical acidocerines by the following unique combination of characters: head subquadrate in shape (clypeus with anterior margin only slightly narrower than posterior margin; as opposed to head rather trapezoidal, with anterior margin of clypeus conspicuously narrower than its posterior margin as in Neotropical *Helochares*); eyes relatively small, separated by a distance nearly 6.5 × the maximum width of an eye (as opposed to eyes of moderate size, separated by approximately 4 × the width of one eye as in *Helochares* (see Hansen 1991: 150)); mentum and submentum roughly punctate (submentum usually rather smooth in Neotropical *Helochares*); pubescence covering abdominal ventrites composed of long golden setae (short setae in Neotropical *Helochares*); ventral surface of tarsomeres 1–4 densely setose (tarsomeres bearing two longitudinal rows of denticles in Neotropical *Helochares*); aedeagus narrow and tubular in shape.

Description. Medium sized beetles, total body length 5.8–7.5 mm, width 3.1–4.0 mm; body elongate oval, weakly convex in lateral view (see Fig. 2.1B, E, H), orange brown to dark brown in color (Fig. 2.1), slightly paler on labrum, labial palpi, along lateral margins of pronotum and elytra, on ventral surface (including abdominal ventrites), and tarsi; body setae, including hydrofuge pubescence, setae of systematic punctures, and especially on abdominal ventrites, golden and rather long; hydrofuge pubescence on surface of femora denser, with shorter setae.

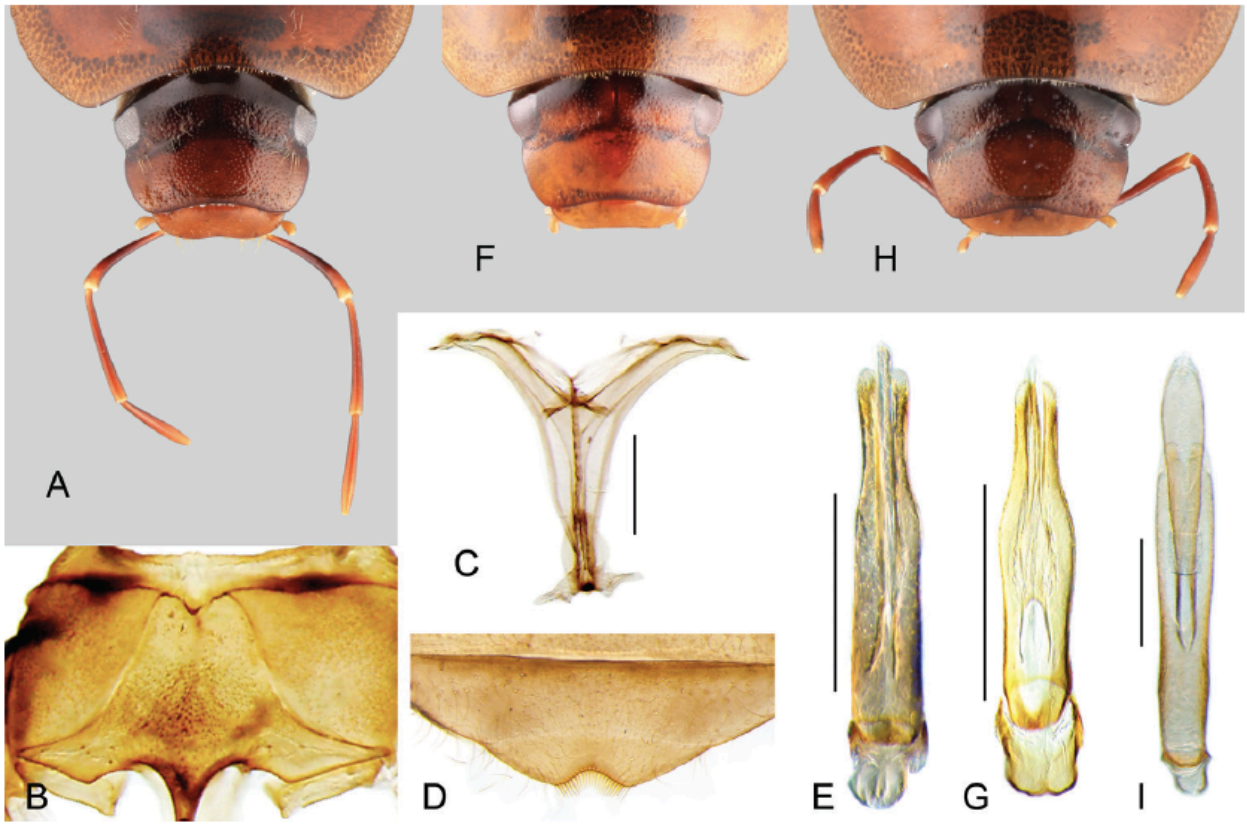


Figure 2.2. Head and internal structures of *Aulonochares* spp.: **A–E** *Aulonochares tubulus*: **A** head, dorsal view, **B** ventral view of mesoventrite with simply convex posterior elevation, **C** posterior view of metafurca, **D** fifth abdominal ventrite, **E** aedeagus; **F–G** *Aulonochares novoairensis*: **F** head, dorsal view, **G** aedeagus; **H–I** *Aulonochares lingulatus*: **H** head, dorsal view, **I** aedeagus. Scale bars 0.5 mm.

Head. Subquadrate in dorsal view, with lateral margins seemingly constricted at anterior margin of eyes (Fig. 2.2A, F, H). Frons and clypeus with moderately marked ground punctures, irregularly and rather densely distributed over the surface, accompanied by scattered seta-bearing systematic punctures, longer and denser on antero-lateral areas of frons and along anterior area of clypeus; surface between punctures smooth and shiny. Frons transversely impressed by anterior margin of pronotum. Frontoclypeal and midcranial sutures well defined, visible as complete, fine grooves; distance between inner anterior corner of eye and frontoclypeal suture approximately 0.5 × maximum length of eye. Clypeus with lateral margins slightly convex, anterior corners roundly angulate, forming a nearly straight angle; anterior

margin of clypeus widely roundly emarginate, only slightly narrower than posterior margin. Eyes relatively small and subquadrate in dorsal view; maximum length of eye 0.5 × distance between anterior margin of eye and anterior margin of clypeus; distance between eyes nearly 6.5 × maximum width of eye. Labrum wide, fully exposed, nearly half as long, and collinear to perpendicular to clypeus; dorsal surface only slightly convex, with scattered fine punctures and few systematic punctures; anterior margin only slightly sinuate, mesally slightly roundly bent inwards, with few denticles along emargination; anterior corners with few setae. Temporae slightly concave, densely covered by rather long and relatively thick setae (hydrofuge pubescence); posteroventral area rather strongly produced. Gular sutures opposite, semicircular, with surface slightly elevated and shiny. Surface of gula and postgenae covered by long fine setae. Mentum (e.g., Fig. 2.1F) parallel sided, with lateral margins fringed by golden setae; surface coarsely punctate, with punctures somewhat obliquely directed; anterior margin with deep U-shaped emargination, sometimes marked by a carina; surface distad of emargination perpendicular to ventral surface of head, smooth, concave, and dorsally directed. Submentum as elevated plate, coarsely punctate, with scattered setae; posterior margin as a low, sinuate, wide ridge; well-developed ocular ridge (e.g., Fig. 2.1F). Maxilla with ventral surface of cardo and stipes with scattered punctures and setae; outer dorsal margin of palpifer with few stiff, spiniform setae; limit between cardo and stipes oblique; maxillary palps curved inward, orange brown, longer than antennae, nearly 1.5 × longer than maximum width of head (e.g., Fig. 2.1A); each palpomere paler towards its apex; apex of palpomere 3 bearing sensilla. Mandibles with apex bifid (examined in *A. tubulus*). Labial palps yellowish, nearly as long as maximum length of mentum, dorsoventrally flattened; palpomere 2 with outer margin only slightly convex near

apex, with several long setae around midlength and at apex; palpomere 3 obovate, with a long subapical seta on outer corner. Antennae (e.g., Fig. 2.1C) with nine antennomeres, paler (yellowish) than general coloration of head; antennomere 1 reaching anterior third of ventral surface of eye (reaching midlength of cardo), nearly 2.5 × longer than antennomere 2, with outer surface densely covered by setae; antennomere 2 thicker, and nearly as long as antennomere 3; antennomere 3 cylindrical, 4 and 5 trapezoid; antennomere 6 forming a well differentiated, asymmetric cupule; antennomeres 7–9 slightly flattened, forming a loosely articulated, pubescent club, with antennomeres 7 and 8 similar in shape and length, and antennomere 9 1.5 × longer than 7; apex of antennomere 9 with a few longer setae compared to general pubescence of club. **Thorax.** Pronotum widest at base, narrowed anteriorly, surface evenly convex, with internal structural reticulations visible along lateral areas; ground punctation shallow, uniformly sparse, with surface between punctures smooth and shiny; seta bearing systematic punctures forming paired anterolateral semicircles; anterior margin of pronotum fringed by short, rather sparse setae; lateral and anterior areas of pronotum translucent, with inner reticulations. Scutellar shield of moderate size, triangular, posteriorly rounded, nearly as long as wide, with punctation as in pronotum. Prosternum (e.g., Fig. 2.1I) nearly as long as half the length of a procoxa; anterior margin of prosternum mesally projected as a wide triangle, slightly carinate along longitudinal midline; surface of median area of prosternum slightly elevated, somewhat densely covered by rather long, fine setae; intercoxal process projected from posterior margin of procoxal cavities, rectangularly shaped in outline, mesally longitudinally carinate. Mesoventrite (Fig. 2.2B) not fused to mesepisterna, densely setose for the most part, with posterolateral smooth and glabrous areas; anterior margin nearly 0.3 × as wide as anterior

margin of mesepisternum; anterior rib of mesoventrite bearing paired oblique to parallel pearlescent maculae; posterior elevation of mesoventrite simply convex, without carinae or ridges (Fig. 2.2B); mesepisternum with surface nearly flat, densely covered by fine setae; mesepimeron trapezoid, with densely pubescent surface. Mesofurca (examined in *A. tubulus*) with short arms, 0.7 × length of mesocoxae; apical half of arms free, somewhat triangular at apex. Metaventrite mesally elevated, narrowly anteriorly, widely and flat posteriorly; surface of metaventrite densely and uniformly pubescent; mesal region of posterior margin rounded to truncate. Metepisterna approximately 3 × longer than wide, with posterior margin oblique. Metepimeron triangular, elongate to short. Metafurca (examined in *A. tubulus*, Fig. 2.2C) 1.46 × wider than long, with furcal arms as long as stalk; stalk triangular (wider near the crux, gradually narrowing ventrally), with paired longitudinal keels extending along basal third of posterior face, fusing together towards crux; with a well-developed median keel on anterior face extending to anterior margin of dorsal sheets; outer margins of stalk diverging towards crux, more strongly so along basal third; each furcal arm sickle-shaped, with apex (hemiductus) explanate in dorsal view, with apical region sinuate, pointing laterally; anterior tendons inserted nearly at mid length of dorsal edge of furcal arms; well-developed dorsal sheaths, wider than widest point of lateral sheaths. **Elytra.** Surface even (without elevations or depressions) and smooth, without sutural striae; ground punctures and systematic punctures very shallowly marked, all similar in size and degree of impression, and evenly distributed across surface; seta bearing systematic punctures rather scarce, at most only distinguishable as rows along midline, third outer fourth, and near outer margin of each elytron, more evident along posterior fourth; serial punctures absent; elytral margins slightly flared; net-like patterning visible throughout the entire surface, especially

along outer margins (e.g., Fig. 2.1G), with a pale lateral band extending from anterior margin up to apical third on each elytron. Epipleura well-developed, surface flat, with sparse fine setae and irregular sculpture, anteriorly wide, gradually narrowing posteriorly, extending up to line of posterior margin of first abdominal ventrite; inner margin of epipleura at most slightly bent at anterior outer corner of metepisternum; well-developed pseudepipleura, perpendicularly positioned, nearly as wide as anterior portion of epipleura, extending along entire outer margin of elytra, with rather smooth surface. Hind wings well developed. **Legs.** All coxae, trochanters and femora with dense pubescence, except on (at most) apical seventh of femora, in which surface is mostly glabrous, shiny and slightly reticulated. Anterior surface of mesocoxae with interspersed small denticles. All femora antero-posteriorly flattened; metafemora with rather well-developed tibial grooves, at most glabrous along apical seventh. Tibiae slender, cylindrical; spines forming longitudinal rows along tibiae rather small, accompanied by conspicuous and somewhat dense golden setae; protibiae with median longitudinal row of small, appressed spines along anterior surface; apical spurs of protibiae very short (not exceeding length of tarsomere 1) and stout; apical spurs of metatibiae asymmetrical, inner posterior spur largest, nearly as long as metatersomere 1, 2 × longer than shorter spur (inner anterior). All tarsi with five tarsomeres, bearing numerous long hair-like setae on dorsal face, and densely covered by stiff setae on ventral face of tarsomeres 1–4; pro- and mesotarsomeres 1–4 similar in size and shape, with tarsomere 5 approximately as long as tarsomeres 2–4 combined, with few setae on ventral face; metatarsomeres 2, 3+4, and 5 similar in length; metatarsomere 4 shortest; claws rather large, curved; well-developed empodium, bearing a pair of long, curved apical setae. **Abdomen.** Abdomen with five ventrites, all uniformly and rather densely covered by fine and

rather long, fine, golden setae, particularly longer along lateral margins; first ventrite medially convex, remainder ventrites rather flat; posterior margin of fifth ventrite with a medial triangular emargination, fringed by thick, flat spine-like setae (Fig. 2.2D); ninth tergite with transverse V-shaped impression, lateral margins deeply emarginate near midlength, and posterior margin rounded to mesally emarginate; ninth ventrite as fully sclerotized plate, with lateral margins posteriorly diverging, and posterior margin widely, roundly emarginate. Aedeagus (Fig. 2.2E, G, I) with well-developed basal piece, 0.1–0.25 × the length of parameres, longitudinally strongly convex; parameres basally fused together into a rather cylindrical tube, 5–7 × longer than wide, with basal margin rounded to truncate, and lateral margins straight to sinuate; median lobe nearly as long as parameres, with well-developed lateral basal apodemes; median lobe rounded at apex, either as a narrow tube throughout, or tongue-like and distally widened; gonopore reduced (inconspicuous), situated near apex of median lobe.

Larvae. The immature stages are unknown.

Etymology. Named from the Greek *aulon*, meaning pipe, tube, in reference to the unique tubular shape of the aedeagus of the species in the genus, combined with the ending -*chares*, as a reference to the general similarity with *Helochares* in the Acidocerinae. To be treated as masculine.

Distribution. To date known only from the Guiana Shield region of South America, where it is broadly distributed from southern Venezuela to French Guiana (Fig. 2.3).

Remarks. All known species are associated with small forested streams, typically with sand and detritus substrate where they are found along the margins (see Fig. 2.4). Adult females

of *Aulonochares tubulus* have been observed to carry their egg case attached to the ventral side of their abdomen as other closely-related genera such as *Helochares* and *Helobata*.

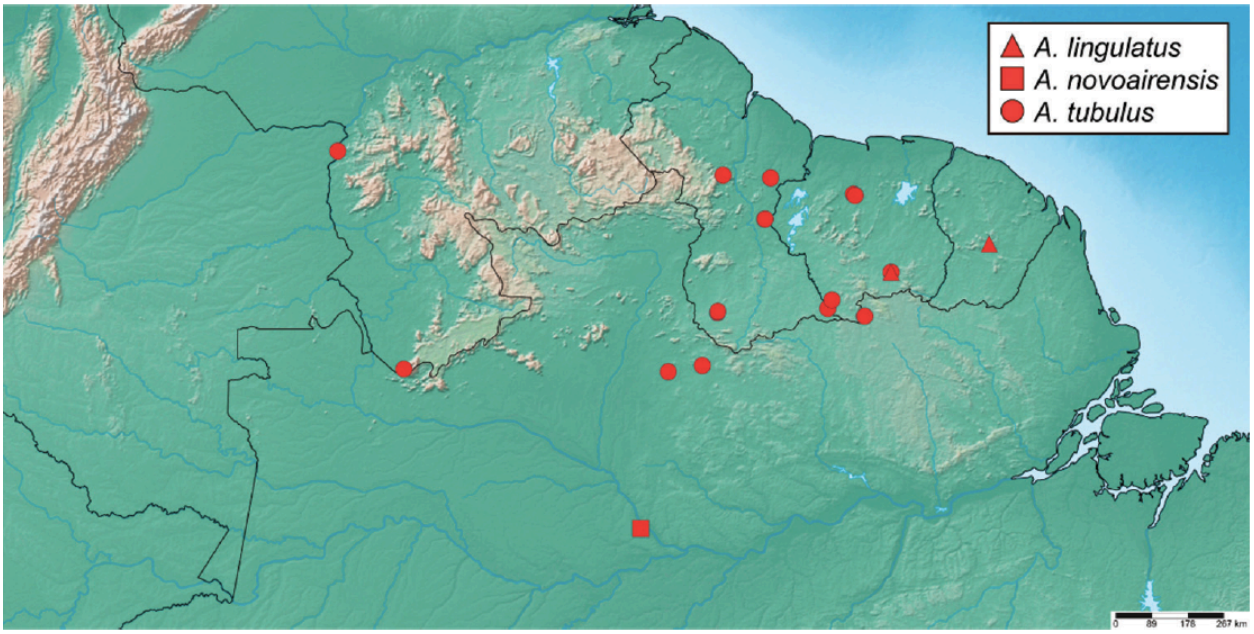


Figure 2.3. Distribution of *Aulonochares* spp.

Characters of taxonomic importance for *Aulonochares*

The external morphology of *Aulonochares* is extremely uniform across species.

Coloration. Even though coloration is not typically a reliable diagnostic feature in acidocerines, the dorsal coloration in *Aulonochares* is helpful for recognizing the species described here: *A. tubulus* is typically dark brown, *A. lingulatus* is orange brown and *A. novoairensis* is yellowish brown (see Fig. 2.1). Because teneral specimens may appear paler, the color of a specimen should not alone be considered as diagnostic. Specimens that have been extracted for DNA become uniformly dark brown in coloration.

Aedeagus. In all the known species of *Aulonochares* the aedeagus has basally fused parameres forming a tube which is 5–7 × longer than wide and becomes dorsoventrally flattened

along the apical half; the median lobe is either cylindrical or broad and flat, and can slide within the parameres, so its extension beyond the apex of the parameres cannot be considered a diagnostic feature to distinguish species. The apex of the parameres can also be cylindrical or flattened. The basal piece is very short. The general form of the aedeagus of *Aulonochares* is unique among the Acidocerinae.

Key to the species of *Aulonochares*

1 General coloration orange brown (Fig. 2.1G–I); median lobe of aedeagus broad and flat, wider than apical portion of a paramere (Fig. 2.2I).... ***A. lingulatus***

– General coloration dark brown to yellowish brown; median lobe of aedeagus cylindrical, as wide as apical portion of a paramere … 2

2 General coloration dark brown (Fig. 2.1A–C); aedeagus parallel sided along basal 2/3 (Fig. 2.2E).... ***A. tubulus***

– General coloration yellowish brown (Fig. 2.1D–F); aedeagus widened at 2/3 (Fig. 2.2G).... ***A. novoairensis***

Aulonochares lingulatus sp. n.

Figs 2.1G–I, 2.2H, I, 2.3, 2.4A

Type material. Holotype (male): "SURINAME: Sipaliwini District; N 2.97731°, W 55.38500°; 200 m; Camp 4 (low), Kasikasima; sandy stream on trail to METS camp; 20.iii.2012; leg. A. Short; SR12-0320-02A" (NZCS). **Paratypes (12): FRENCH GUIANA:** "Unnamed Trib. To Crique Nouvelle France, N 3.59627°, W 53.17637°, above Courant double; 09.xi.2016, leg. D. Post" (SEMC, 1, DNA voucher specimen SLE 1173). **SURINAME: Sipaliwini District:** Same data as holotype (NZCS, SEMC, 10, including DNA voucher SLE 415); same, except "sandy creek, trail to Kasikasima; flotation; 22.iii.2012; SR12-0322-02A" (SEMC, 1).

Differential diagnosis. *Aulonochares lingulatus* can be distinguished by its orange brown general coloration (Fig. 2.1G–I), and the shape of the median lobe of aedeagus, which is broad and flat (Fig. 2.2I).

Description. Body length 6.0–6.5 mm, width 3.2–3.6 mm. General coloration orange brown (Fig. 2.1G–I). Aedeagus (Fig. 2.2I) with outer margins of parameres subparallel, slightly diverging apically; median lobe flat, gradually widening towards apical region, widely rounded at apex.

Etymology. Named with the Latin word *lingulatus* meaning tongue-like, after the shape of the median lobe of the aedeagus in this species.

Distribution. *Aulonochares lingulatus* is known from the area surrounding Mt. Kasikasima in Suriname and a locality in central French Guiana (Fig. 2.3).

Remarks. All specimens were collected in densely forested sandy streams (Fig. 2.4A).

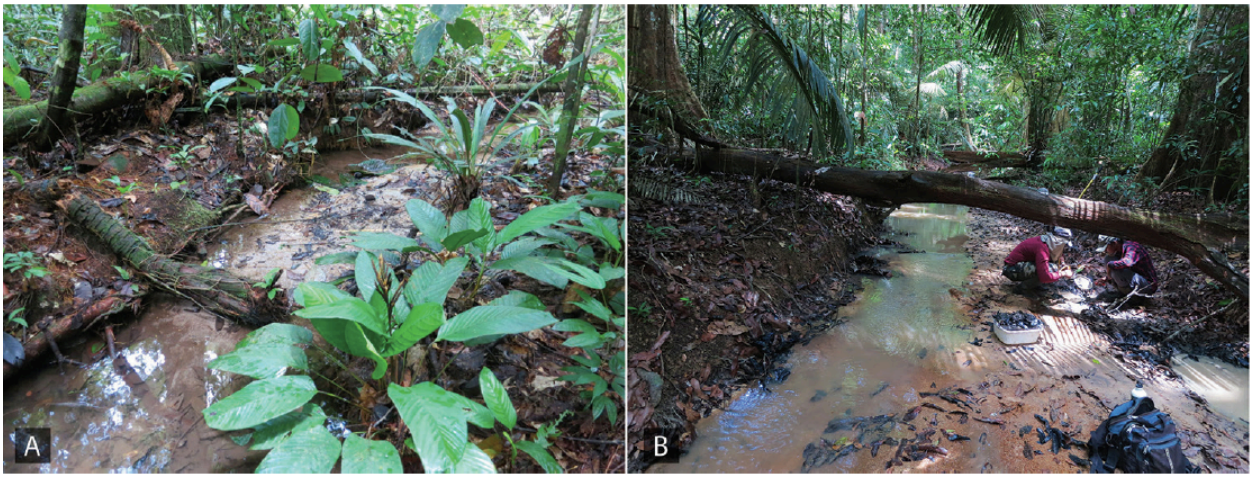


Figure 2.4. Habitat of *Aulonochares* spp.: **A** habitat and type locality for *A. lingulatus*, Suriname: Kasikasima, collecting event SR12-0320-02A, **B** habitat for *A. tubulus*, Guyana: Upper Berbice, collecting event GY14-0921-03H.

Aulonochares novoairensis sp. n.

Figs 2.1D–F, 2.2F, G, 2.3

Type material. Holotype (male): "BRAZIL: Amazonas: Novo Airão; 2°41'2.2878"S, 60°56'18.24"W; 60 m; detrital pools in forest along sides of blackwater creek; 9.vi.2017; leg. Benetti; BR17-0609-04B" (INPA). **Paratype (1):** Same data as holotype (SEMC, DNA voucher specimen SLE 1268).

Differential diagnosis. *Aulonochares novoairensis* can be distinguished by its yellowish brown general coloration (Fig. 2.1D–F), and the shape of the aedeagus, which is widened at 2/3, with cylindrical median lobe (Fig. 2.2G).

Description. Body length 6.3–6.9 mm, width 3.4–3.6 mm. General coloration yellowish brown (Fig. 2.1D–F). Aedeagus (Fig. 2.2G) with outer margins of parameres sinuate, widest along 2/3; median lobe cylindrical, somewhat acute at apex.

Etymology. Named after Novo Airão municipality in the state of Amazonas in Brazil.

Distribution. Currently only known from a single locality in the central Amazon near Manaus (Fig. 2.3).

Remarks. The single collection of this species was from densely forested, shallow detrital pools immediately adjacent to a blackwater stream.

Aulonochares tubulus sp. n.

Figs 2.1A–C, 2.2A–E, 2.3, 2.4B

Type material. Holotype (male): "SURINAME: Sipaliwini District; 2°00.342'N, 55°58.149'W; 337 m; Sipaliwini Savanna nature Res., 4-Brothers Mts.; clearwater stream, sandy with emergent vegetation; at night; 31.iii.2017; leg. A. Short; SR17-0331-01F" (NZCS). **Paratypes (156): BRAZIL: Roraima:** "00°46'35.1"N, 60°19'58.7"W; 97 m; Rorainópolis, Recanto da Cachoeira, vicinal 12; creek flowing through gallery forest; 10.1.2018; leg. A. Short; BR18-0110-04A" (SEMC, 3); "00°54.786'N, 59°34.397'W; 150 m; Caroebe, Rio Caroebe, ca. 13 Km NE of Caroebe; margins of sandy river; 17.i.2018; leg. A. Short & Benetti; BR18-0117-04A" (SEMC, 1). **GUYANA: Region 6:** "4°09.143'N, 58°11.207'W; 105 m; Upper Berbice, c. 1 Km W Basecamp 1; small sandy stream; 21.ix.2014; leg. A. Short; GY14-0921-03A" (SEMC, 2); same, except "margins of creek; 22.iv.2014; leg. Short, Salisbury, La Cruz; GY14-0921-03H" (SEMC, 4); same, except "4°09.136'N, 58°11.365'W; 106 m; Upper Berbice, ca. 1.1 Km W of basecamp 1; stream detrital pool; 23.ix.2014; GY14-0923-02A" (SEMC, 1); same, except "4°09.289'N, 58°10.717'W; 95 m; Upper Berbice, Basecamp 1; margins of basecamp creek; 24.ix.2014; GY14-0924-01A" (SEMC, 1); same,

except “4°09.241'N, 58°10.627'W; 109 m; puddles along road; GY14-0924-02A” (SEMC, 4); same, except “margins of creek with leaf packs and mud; 25.ix.2014; leg. Short & La Cruz; GY14-0925-01B” (SEMC, 1); same, except “detritus pools in dry creekbed; leg. Short, Salisbury, La Cruz; GY14-0925-01D” (SEMC, 1); same, except “5°03.892'N, 58°03.303'W; 71 m; Upper Berbice, Logging Road Km 1; marsh and creek; 29.ix.2014; GY14-0929-01B” (CBDG, SEMC, 12). **Region 8:** “5°07.539'N, 59°06.732'W; 80 m; Konawaruk River, basecamp 2 (NARIL basecamp); unnamed clearwater creek, slow flowing, shallow; 15.ix.2014; leg. Salisbury & La Cruz; GY14-0915-02” (SEMC, 6). **Region 9:** “2°05.095'N, 59°14.174'W; 250 m; Parabara, trail to mines; detrital pools in forest; 2.xi.2013; leg. Short, Isaacs, Salisbury; GY13-1102-01A” (CBDG, SEMC, 8); same, except “2°06.492'N, 59°13.653'W;274 m; Parabara, N side of river; small flowing forested creek, detritus margins & leaf packs; 3.xi.2013; GY13-1103-02A” (SEMC, 2). **SURINAME: Sipaliwini District:** “2°10.521'N, 56°47.244'W; 228 m, Camp 1, on Kutari River; forest swamp; 22.viii.2010; leg. Short & Kadosoe; SR10-0822-02A; 2010 CI-RAP Survey” (SEMC, 2); same, except “2°21.776'N, 56°41.861'W; 237 m; Camp 3, Wehepai; sandy forest creek; 4-6.ix.2010; SR10-0904-01A” (SEMC, 7); “N 2.97731°, W 55.38500°; 200 m; Camp 4 (low), Kasikasima; sandy stream on trail to METS camp; 20.iii.2012; leg. A. Short; SR12-0320-02A; 2010 CI-RAP Survey” (SEMC, 2); same, except “detrital pools along trail to METS camp; 20-25.iii.2012; SR12-0320-03A” (SEMC, 3); same, except “sandy creek, trail to Kasikasima; flotation; 22.iii.2012; SR12-0322-02A” (SEMC, 7); “04°40.910'N, 56°11.138'W; 78 m; Raleighvallen Nature Reserve, Voltzberg Station; stream margins; 29.vii.2012; leg. Short, Maier, McIntosh, Kadosoe; SR12-0729-02A” (SEMC, 1); same, except “detrital side pool; leg. Short & McIntosh; SR12-0729-02B” (SEMC, 1); same, except “margin of stream; 30.vii.2012; leg. Maier & Kadosoe; SR12-0730-01A” (SEMC, 1); same, except “detrital

pools along stream; leg. Short & McIntosh; SR12-0730-01B" (NZCS, SEMC, 10); "4°42.48'N, 56°13.15908'W; 24 m; Raleighvallen Nature Reserve, Lolopaise area; side pool of creek; 14.iii.2016; leg. Short et al.; SR16-0314-02D" (SEMC, 1); "4°40.432'N, 56°11.079'W; 86 m; Raleighvallen Nature Reserve, base of Voltzberg; pooled up stream; 16.iii.2016; SR16-0316-01B" (SEMC, 1); "Raleighvallen Nature Reserve, trail from plateau to Voltzberg stream with roots, mud; 17.iii.2016; leg. J. Girón; SR16-0317-04A" (SEMC, 4); "4°42.48'N, 56°13.15908'W; 24 m; Raleighvallen Nature Reserve, Lolopaise area; intermittent stream margins; flotation; 18.iii.2016; leg. Short et al.; SR16-0318-01D" (SEMC, 2); same, except "intermittent stream pools; pan/screen method; 18.iii.2016; leg. Toussaint et al.; SR16-0318-01E" (SEMC, 1); "Raleighvallen Nature Reserve, Copename River, Voltzberg trail; detrital pools in stream bed; 17.iii.2016; leg. A. Short; SR16-0319-01A" (SEMC, 1); "4°42.48'N, 56°13.15908'W; 24 m; Raleighvallen Nature Reserve, Lolopaise area; intermittent stream pools; 19.iii.2016; leg. Toussaint et al.; SR16-0319-02C" (SEMC, 2); "2°00.397'N, 55°58.371'W; 306 m; Sipaliwini Savanna nature Res., palm swamp nr. 4-Brothers Mts.; mud/detritus; 30.iii.2017; leg. Short & Baca; SR17-0330-03A" (SEMC, 1); same, except "2°00.342'N, 55°58.149'W; 337 m; 4-Brothers Mts.; clearwater stream, sandy with emergent vegetation; 31.iii.2017; SR17-0331-01C" (SEMC, 23); same, except "sandy pools in creek; leg. S. Baca; SR17-0331-01E" (SEMC, 10); same data as holotype (NZCS, SEMC, 23).

VENEZUELA: Amazonas: "0°50'N, 66°10'W; 140 m; Cerro de la Neblina, 1 Km S Basecamp; along small whitewater stream; pools of dead leaves and sticks; 17.ii.1985; leg. P.J. & P.M. Spangler, R. Faitoute, W. Steiner" (USNM, 2); "Puerto Ayacucho; in small ponds full of dead leaves; 22.i.1985; leg. G.E. Ball" (SEMC, USNM, 5).

Differential diagnosis. *Aulonochares tubulus* can be distinguished by its dark brown general coloration (Fig. 2.1A–C), and the shape of the aedeagus, which is parallel sided along its basal 2/3, with cylindrical median lobe (Fig. 2.2E).

Description. Body length 5.8–7.5 mm, width 3.1–4.0 mm. General coloration dark brown (Fig. 2.1A–C). Aedeagus (Fig. 2.2E) with outer margins of parameres subparallel along basal 2/3, slightly concave along apical third; median lobe cylindrical, rounded at apex.

Etymology. Named with the Latin word *tubulus* meaning pipe, after the shape of the median lobe of the aedeagus in this species.

Distribution. Broadly distributed in the Guiana Shield region, from the Orinoco River to central Suriname (Fig. 2.3).

Remarks. The majority of collecting events of this species are from forested streams, including those actively flowing as well as pooled up, or from isolated marginal pools in the stream bed (Fig. 2.4B). A few collections were made in forested detrital pools, although most if not all of these were near or associated with riparian corridors. They are usually found in habitats with abundant detritus or decaying organic matter. Females have been observed on numerous occasions to carry their egg case beneath their abdomen.

Ephydrolithus gen. n.

Figs 2.5–2.9

Type species: *Ephydrolithus hamadae* sp. n.

Differential diagnosis. Small beetles (1.8–3.3 mm), oval in dorsal view, moderate to strongly convex in lateral view (e.g., Figs 2.5B, 2.6F), yellowish brown to dark brown. Antennae with nine antennomeres (e.g., Fig. 2.6C). Maxillary palps short (e.g., nearly two thirds the width of the head) and stout (e.g., Fig. 2.6H). Elytra without sutural striae, and only rarely with impressed striae (e.g., *Ephydrolithus ogmos*); ground punctures sharply marked, uniformly and rather densely distributed; systematic punctures slightly larger and deeper than remainder punctures; serial punctures usually absent (present but reduced in *E. ogmos*). Prosternum flat (e.g., Figs 2.5C, 2.6C), sometimes only slightly elevated along longitudinal midline. Posterior elevation of mesoventrite usually with a transverse ridge (Fig. 2.7A; except in *E. ogmos* and *E. spiculatus* which bear a well-developed tooth, e.g., Fig. 2.6C). Metaventrite densely pubescent, except for a large median teardrop-shaped glabrous patch. Posterior femora glabrous for the most part, with few scattered setae along basal half to basal two thirds, with hydrofuge pubescence along anterodorsal margin; well-developed tibial grooves, sometimes covered by hydrofuge pubescence. Fifth abdominal ventrite apically truncate, with stout setae (e.g., Fig. 2.7C).

Among Neotropical acidocerines, *Ephydrolithus* has a general resemblance to *Katasophistes* (see Girón and Short 2018), especially by characters of the elytral punctation, which exhibits five rows of deep/large systematic punctures. *Ephydrolithus* can be easily recognized from *Katasophistes* by the mostly glabrous metafemora, with only few scattered setae on anterior surface, as opposed to at most glabrous along apical third in *Katasophistes*. *Ephydrolithus* might also resemble some species of *Chasmogenus*; nevertheless, the absence of sutural striae in *Ephydrolithus* allows its recognition.

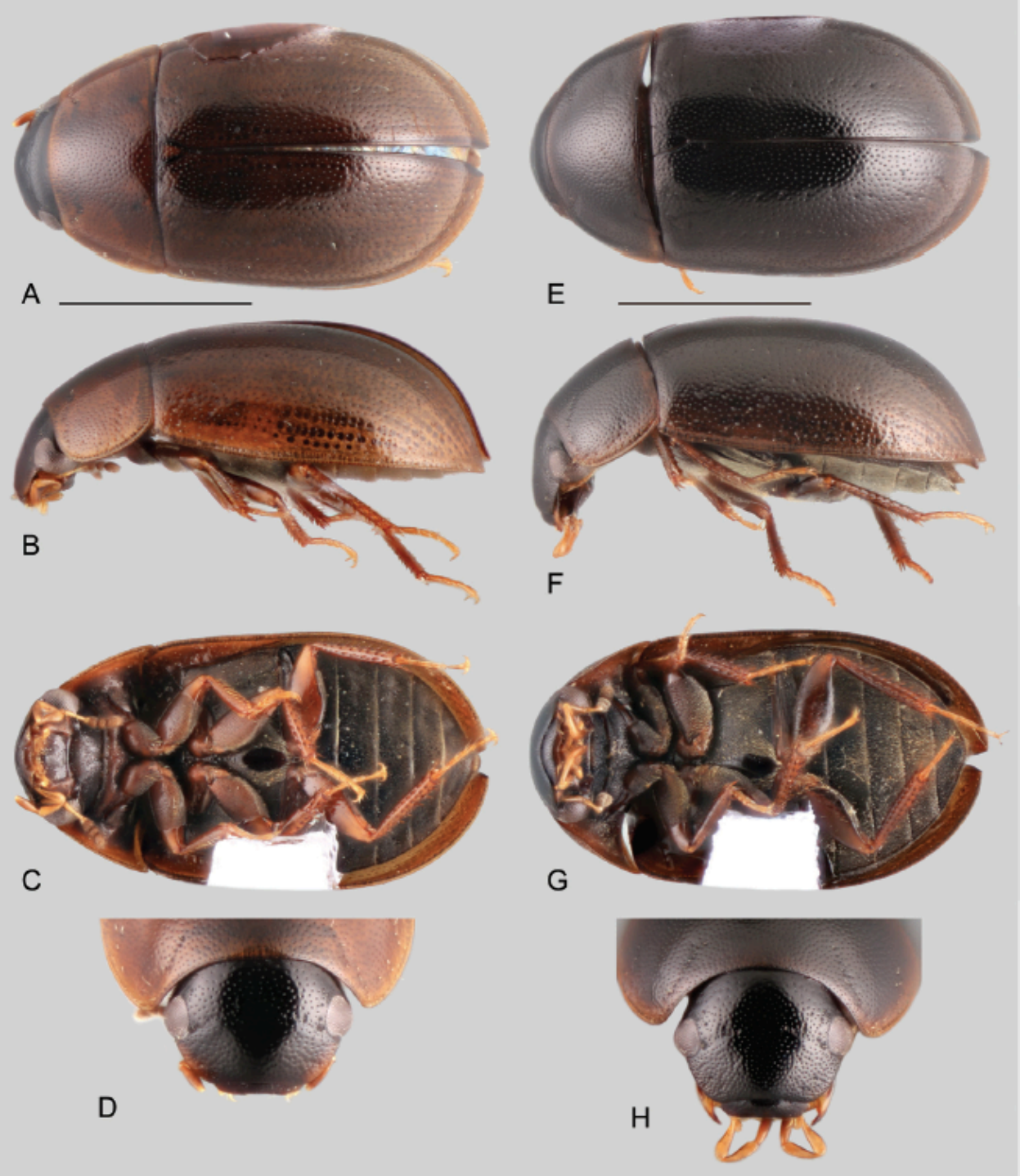


Figure 2.5. Habitus of *Ephydrolithus* spp.: **A–D** *Ephydrolithus hamadae*: **A** dorsal view, **B** lateral view, **C** ventral view, **D** head, dorsal view; **E–H** *Ephydrolithus teli*: **E** dorsal view, **F** lateral view, **G** ventral view; **H** head, dorsal view. Scale bars 1 mm.

Ephydrolithus can be distinguished from other Neotropical acidocerines with mostly glabrous metafemora such as *Quadriops* (e.g., Girón and Short 2017) by the entire (as opposed

to divided) eyes. From *Tobochares* (e.g., Kohlenberg and Short 2017) *Ephydrolithus* can be distinguished by the number of antennomeres (nine in *Ephydrolithus*, eight in *Tobochares*). In addition, in some species of *Ephydrolithus* the tibial grooves of the metafemora are covered by hydrofuge pubescence, which is an unusual condition among Neotropical acidocerines with mostly glabrous metafemora.

The smaller members of *Ephydrolithus* might resemble species of *Crucisternum* (see Girón and Short 2018), but the prosternal keel of *Crucisternum* easily separates them.

Description. Small beetles, total body length 1.8–3.3 mm; body elongate oval, moderate to strongly convex in lateral view (e.g., Figs 2.5B, 2.6F), yellowish brown to dark brown in color, sometimes paler along lateral margins of pronotum and elytra, legs (especially tarsi), mouthparts and antennae. **Head.** Frons and clypeus (e.g., Fig. 2.5H) with moderately marked ground punctures, irregularly and rather densely distributed over the surface, with only few seta-bearing systematic punctures along lateral areas of frons and clypeus; surface between punctures smooth and shiny. Eyes oval in dorsal view, separated by nearly 5 × width of one eye; in lateral view, anterior margin slightly emarginate. Clypeus trapezoid, with medial surface moderately convex, and anterior corners forming widely rounded obtuse angles; anterior margin of clypeus widely roundly emarginate, 0.7 × width of posterior margin; membranous preclypeal area absent. Labrum 0.7 × as wide as anterior margin of clypeus, fully exposed, nearly 1/3 as long, and usually collinear to clypeus (e.g., Fig. 2.6D); dorsal surface convex, with fine punctures; anterior margin roundly bent inwards, mesally emarginate and with tiny denticles along emargination; anterior corners fringed by setae. Temporae densely covered by very short and fine setae (hydrofuge pubescence). Mentum parallel sided, with surface mostly smooth and undulated,

sometimes anteromesally depressed; anterior margin mesally depressed, usually depression marked by a u-shaped transverse carina. Submentum sunken and pubescent at base, glabrous, shiny, and ascending at apex; well-developed ocular ridge. Maxilla (see Fig. 2.6C) with ventral surface of cardo and stipes smooth and shiny, at most with few scattered and shallow punctures; cardo positioned collinear to oblique to ventral surface of head; outer dorsal margin of palpifer with a row of stiff, decumbent, spiniform setae; limit between cardo and stipes parallel to posterior margin of mentum; maxillary palps curved inward, yellowish, nearly as long as antennae, short (e.g., nearly two thirds the width of the head) and stout (e.g., Fig. 2.6H); palpomere 1 strongly widened near apex (with outer apical margin strongly convex); palpomere 2 gradually widening towards apex; palpomere 3 fusiform, bearing apical sensilla; all palpomeres similar in length. Mandibles with apex bifid (examined in *E. ogmos*). Labial palps yellow, slightly shorter than mentum, dorsoventrally flattened; palpomere 2 with outer margin strongly convex apicad of midpoint, sometimes with one preapical seta on outer surface; palpomere 3 digitiform, with a long subapical seta on outer corner. Antennae (see Fig. 2.6C) with nine antennomeres, usually yellow with darker club; antennomere 1 with surface evenly convex near base, reaching midpoint of ventral surface of eye (reaching cardo-stipes joint), 1.5–2.5 × longer than antennomere 2; antennomere 2 nearly as long as antennomeres 3–5 combined; antennomere 6 forming a well differentiated, asymmetric cupule; antennomeres 7–9 each wider than long, slightly flattened, forming a loosely articulated, pubescent club (antennomere 8 shortest, 9 longest); pubescence of antennomere 9 with few scattered longer setae on apical area.

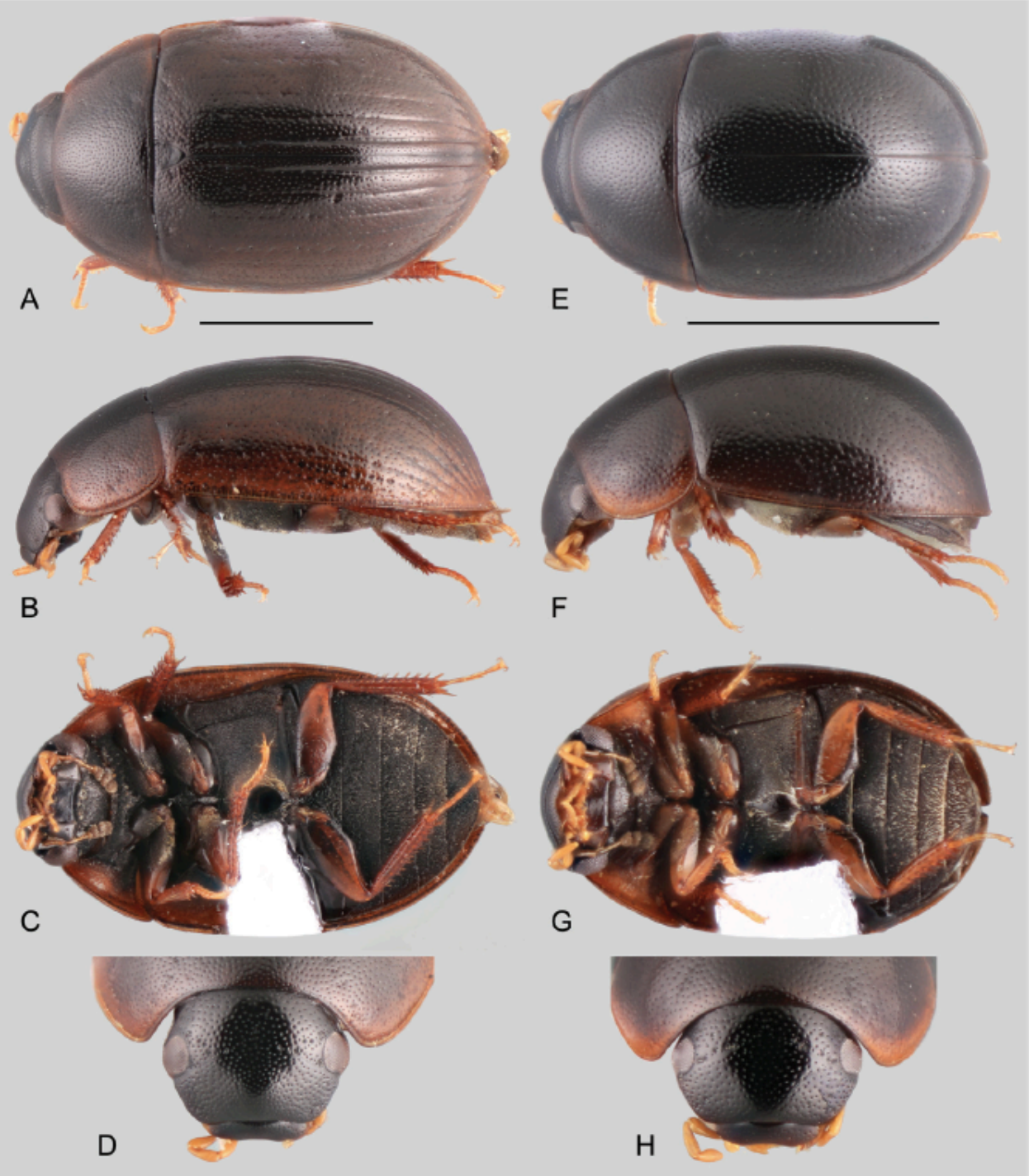


Figure 2.6. Habitus of *Ephydrolithus* spp.: **A–D** *Ephydrolithus ogmos*: **A** dorsal view, **B** lateral view, **C** ventral view, **D** head, dorsal view; **E–H** *Ephydrolithus minor*: **E** dorsal view, **F** lateral view, **G** ventral view; **H** head, dorsal view. Scale bars 1 mm.

Thorax. Pronotum widest at base, narrowed anteriorly, surface evenly convex; ground punctation moderate, uniformly dense, with surface between punctures smooth and shiny; seta

bearing systematic punctures forming paired anterolateral semicircles, and paired short posterolateral transverse bands. Scutellar shield of moderate size, triangular, nearly as long as wide, with punctation as in pronotum. Prosternum flat (e.g., Figs 2.5C, 2.6C), sometimes only slightly elevated along longitudinal midline (e.g., Fig. 2.5G), nearly as long as half the length of a procoxa; anterior margin of prosternum straight to slightly convex; surface finely crenulate, with scattered fine setae, slightly impressed along procoxal area; intercoxal process projected from posterior margin of procoxal cavities, rectangularly shaped in outline, mesally longitudinally carinate. Mesoventrite (Fig. 2.7A, G) not fused to mesepisterna, with anterior margin 0.2–0.4 × as wide as anterior margin of mesepisternum; anterior rib of mesoventrite with median, triangular, pale macula; posterior elevation of mesoventrite either with a sharp, low, transverse, curved ridge (Figs 2.5C, 2.7A), or bearing a basally transverse, well-developed tooth that extends anteriorly as a longitudinal carina (Figs 2.6C, 2.7G); surface of mesoventrite with posterolateral smooth and glabrous areas; mesepisternum obliquely widely concave; mesepimeron trapezoid, with pubescent surface. Mesofurca (examined in *E. hamadae*) with short arms, 0.9 X length of mesocoxae; apical half of arms free, somewhat triangular at apex. Metaventrite posteromesally elevated, with elevation somewhat narrow anteriorly, widening posteriorly; surface of metaventrite densely pubescent, except for a median to posteromedian, large teardrop-shaped glabrous patch; anteromedian area of metaventrite with a deep and narrow transverse depression before anterior intercoxal process. Metepisterna nearly 4 × longer than wide, slightly narrowing at posterior end. Metepimeron triangular and posteriorly slightly projected. Metafurca (examined in *E. hamadae*, Fig. 2.7B) 1.3 × wider than long, with furcal arms 0.8 × the length of stalk; stalk triangular (wider near the crux, gradually narrowing ventrally), with paired

longitudinal keels extending along basal third of posterior face, fusing together towards crux, with a well-developed median keel on anterior face extending to anterior margin of dorsal sheets; outer margins of stalk diverging from basal third towards crux; furcal arms somewhat trapezoid, with apex (hemiductus) roundly explanate, with apex pointing laterally; anterior tendons inserted at basal third of dorsal edge of furcal arms; well-developed dorsal sheaths, wider than widest point of lateral sheaths.

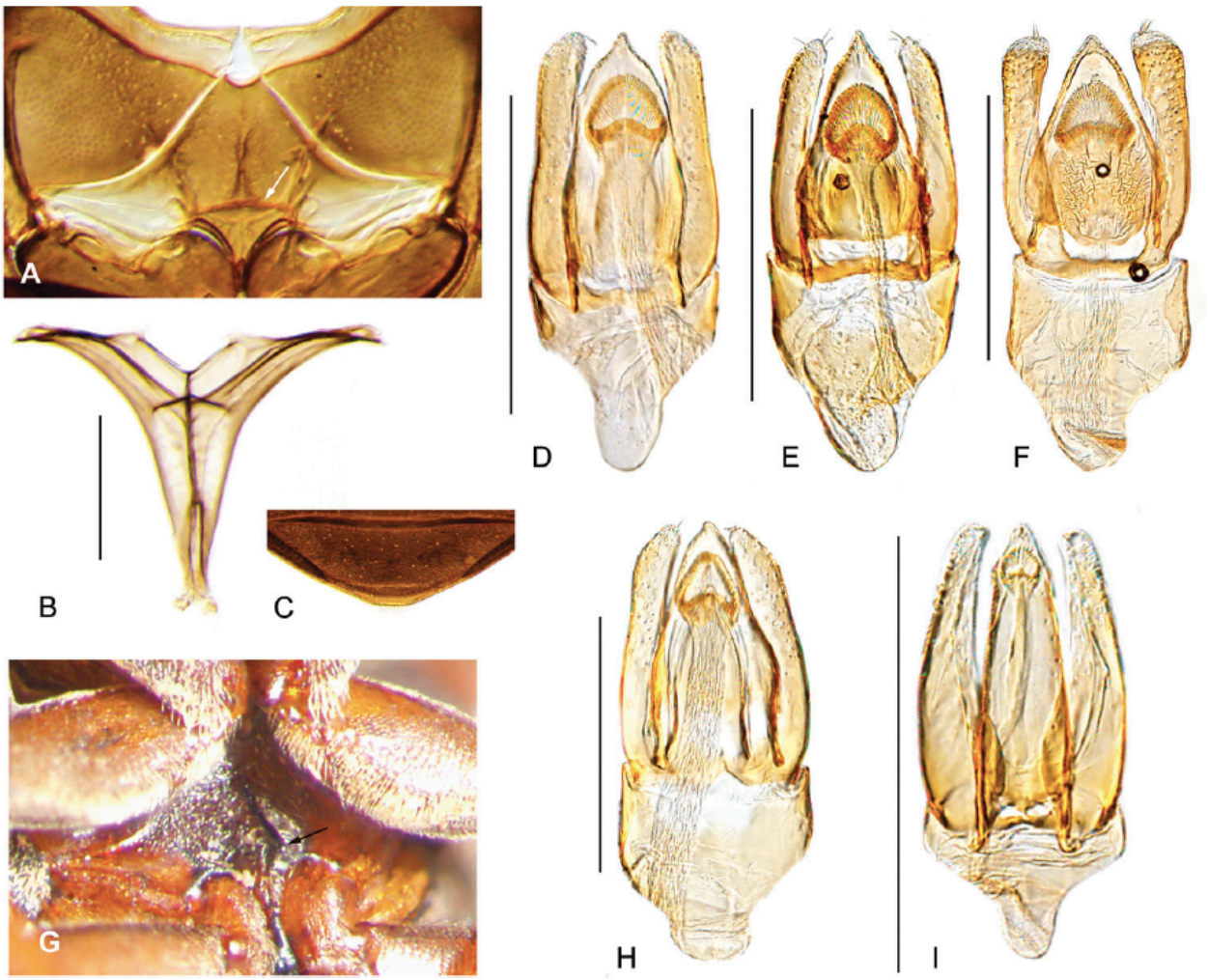


Figure 2.7. Thorax, abdomen and genitalia of *Ephydrolithus* spp.: **A–D** *Ephydrolithus hamadae*: **A** ventral view of mesoventrite (white arrow pointing transverse ridge), **B** posterior view of metafurca, **C** fifth abdominal ventrite, **D** aedeagus; **E** aedeagus of *Ephydrolithus teli*; **E–F** *Ephydrolithus spiculatus*: **F** aedeagus, **F** oblique view of mesoventrite (black arrow pointing well-developed tooth); **H** aedeagus of *Ephydrolithus ogmos*, **I** aedeagus of *Ephydrolithus minor*. Scale bars 0.25 mm.

Elytra. Surface even (without elevations or depressions), without sutural striae (in *E. ogmos* elytral striae well-marked, more strongly so along stria 1); ground punctures sharply marked, uniformly and rather densely distributed; seta bearing systematic punctures rather enlarged and deep, forming five longitudinal rows along each elytron, fifth row very close to outer margin of elytron; serial punctures usually absent (present but reduced in *E. ogmos*); elytral margins slightly flared. Epipleura well developed, surface rather oblique, with fine setae, anteriorly wide, gradually narrowing posteriorly, extending up to line of posterior margin of metaventrite; inner margin of epipleura slightly concave at articulation of anterior outer corner of metepisternum; well-developed pseudepipleura, rather obliquely positioned, anteriorly nearly as wide as anterior portion of epipleura, narrowing towards line of posterior margin of metaventrite, extending as narrow band along remainder outer margin of elytron. Hind wings well developed (examined in *E. hamadae* and *E. teli*). **Legs.** Pro- and mesofemora covered with hydrofuge pubescence along at least basal half; metafemora with hydrofuge pubescence as a narrow stripe along basal 2/3 of anterodorsal margin, remainder anterior surface usually smooth and shiny, with only few scattered setae; all femora antero-posteriorly flattened, with sharp tibial grooves; sometimes tibial grooves with hydrofuge pubescence (in *E. hamadae* and *E. teli*). Tibiae slender, weakly flattened, with well-developed spines; protibiae with a median longitudinal row of long setae along anterior surface; apical spurs of protibiae rather large and slender. All tarsi with five tarsomeres, bearing long apical hair-like setae on dorsal face, and two lateral rows of hair-like spines on ventral face of tarsomeres 2–4; pro- and mesotarsomeres 1–4 similar in size and shape; pro- and mesotarsomere 5 similar in size to pro- and mesotarsomeres 1–4 combined; metatarsomere 2 nearly as long as tarsomeres 3–4 combined; metatarsomere 5

similar in size to metatarsomere 2, without spines on ventral face; claws rather large, curved; well-developed empodium, bearing a pair of long, curved apical setae. **Abdomen.** Abdomen with five ventrites, very weakly convex medially; all ventrites with uniform, dense, fine pubescence; posterior margin of fifth ventrite truncate, set with a row of thick, flat spine-like setae (Fig. 2.7C). Aedeagus (Fig. 2.7D–F, H, I) with outer margins convex, straight or sinuate, with basal piece between 0.45 and 0.9 × the length of parameres; median lobe somewhat triangular in shape, with well-developed lateral basal apodemes; widest point of median lobe wider than widest point of each paramere; apex of median lobe widely to narrowly acute, sometimes "pinched" (e.g., *E. hamadae*, Fig. 2.7D); parameres nearly as long as median lobe, with greatest width near base, bearing apical setae; well-developed gonopore, preapically situated.

Larvae. The immature stages are unknown.

Etymology. Named by the combination of the Greek words *ephydros* meaning wet, and *lithus* meaning rock, in reference to the seepage habitat in which the genus has been collected. To be treated as neuter.

Distribution. The genus is currently only known from the northeastern highlands of Brazil (Bahía, Minas Gerais) on the Brazilian Shield (Fig. 2.8).

Remarks. Species of *Ephydrolithus* have been collected in an altitudinal range between 568 and 1705 m. All known species are exclusively associated with rock seepages (see Fig. 2.9).

Figure 2.8. Distribution of *Ephydrolithus* spp.

Figure 2.9. Habitat of *Ephydrolithus* spp. **A–B** Habitat and type locality for *E. minor* and *E. ogmos*, Brazil, Pico do Barbado, collecting event BR18-0226-01C, **C** Habitat and type locality for *E. hamadae* and *E. spiculatus*, Brazil, Cachoeira da Palmeira, collecting event BR18-0302-04A, **D** Habitat and type locality for E. *teli*, Brazil, Pico do Barbado, collecting event BR18-0226-01B.

Characters of taxonomic importance for *Ephydrolithus*

Even though members of *Ephydrolithus* are externally relatively homogeneous, there are some useful characters for species identification.

Body size. Most *Ephydrolithus* species range in size from 2.6 to 3.3 mm. *Ephydrolithus minor* is the smallest species, with body size ranging from 1.8 to 2.2 mm.

Elytral surface. Most species of *Ephydrolithus* lack elytral striae; only *E. ogmos* has impressed striae along almost the entire length of the elytra.

Tibial grooves of metafemora. In some species of *Ephydrolithus* the tibial grooves of the metafemora are covered by hydrofuge pubescence. Only *E. minor* and *E. ogmos* have glabrous metafemoral tibial grooves.

Posterior elevation of mesoventrite. Usually the elevation bears a sharp, low, transverse, curved ridge. Only *E. ogmos* and *E. spiculatus* bear a pointed spine.

Aedeagus. The overall forms and proportions of the aedeagus of *Ephydrolithus* species are very similar among species, except for *E. minor*, which has a comparatively shorter basal piece and narrower median lobe (see Fig. 2.7I).

Key to the species of *Ephydrolithus*

1 Elytra with well-defined and impressed striae (Fig. 2.6A, B)… ***E. ogmos***

– Elytral without impressed striae (Figs 2.5A, E, 2.6E)… **2**

2 Body strongly convex, 1.8–2.2 mm in length; anterior surface of pro- and mesofemora covered by hydrofuge pubescence along basal half (Fig. 2.6G)… ***E. minor***

– Body moderately convex, 2.4–2.9 mm in length; anterior surface of pro- and mesofemora covered by hydrofuge pubescence along basal two thirds (Fig. 2.5C, G)… **3**

3 Posterior elevation of mesoventrite bearing a pointed spine (Fig. 2.7G)… ***E. spiculatus***

– Posterior elevation of mesoventrite with a sharp, low, transverse, curved ridge (Figs 2.5C, 2.7A)… **4**

4 Parameres of aedeagus 1.2–1.3 × longer than basal piece; median lobe 2 × longer than its greatest width; outer margins of apex of median lobe straight to slightly sinuate (apex of median lobe triangular) (Fig. 2.7E)… ***E. teli***

– Parameres of aedeagus 1.5–1.6 × longer than basal piece; median lobe nearly 2.5 × longer than its greatest width; outer margins of apex of median lobe clearly sinuate (apex of median lobe "pinched") (Fig. 2.7D)… ***E. hamadae***

Ephydrolithus hamadae sp. n.

Figs 2.5A–D, 2.7A–D, 2.8, 2.9C

Type material. Holotype (male): "BRAZIL: Minas Gerais: Lassance; -17.83384, -44.50515; 568 m; Cachoeira da Palmeira; flotation of root mats and moss from side of waterfall & seepage; 2.iii.2018; leg. Benetti & team; BR18-0302-04A" (INPA). **Paratypes (7): BRAZIL: Minas Gerais:** Same data as holotype (INPA, SEMC, 7 including DNA voucher SLE 1506).

Differential diagnosis. *Ephydrolithus hamadae* is very similar to *E. teli*. Both species can only be distinguished from each other by characteristics of the aedeagus.

Description. Body length 2.6–3.2 mm, width 1.5–1.7 mm. Body elongate oval, moderately convex (Fig. 2.5B). General coloration yellowish to dark brown, slightly paler along margins of pronotum and elytra. Posterior elevation of mesoventrite with well-defined, curved transverse ridge. Elytra without striae or serial punctures. Pro- and mesofemora covered with hydrofuge pubescence along basal 2/3; metafemora with hydrofuge pubescence on tibial grooves. Apex of fifth abdominal ventrite truncate (Fig. 2.7C). Aedeagus (Fig. 2.7D) with basal piece 0.6 × the length of parameres; parameres nearly 0.5 × greatest width of median lobe, with outer margins slightly sinuate; apex of parameres rounded, obliquely directed; apex of median lobe "pinched", narrowly rounded.

Etymology. Named after Neusa Hamada from the Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA), in recognition of her support on recent expeditions collecting aquatic beetles in Brazil.

Distribution: Known only from the type locality (Fig. 2.8).

Remarks: This species was collected by gathering moss and roots from bottom and margin of a seepage that was next to a large waterfall (Fig. 2.9C). Specimens were collected by placing the moss and roots in a pan with water, where they floated to the surface along with one specimen of *E. spiculatus*.

Ephydrolithus minor sp. n.

Figs 2.6E–H, 2.7I, 2.8, 2.9A, B

Type material. Holotype (male): "BRAZIL: Bahia: Abaíra; -13.29053, -41.90489; 1705 m; Pico do Barbado W of Catolés; vertical seep on rock; 26.ii.2018; leg. Benetti & team; BR18-0226-01C" (INPA). **Paratypes (15): BRAZIL: Bahia:** Same data as holotype (SEMC, 8 including DNA vouchers SLE-1511, SLE-1512; INPA, 7).

Differential diagnosis. *Ephydrolithus minor* is easily recognized among its congeners by its small size.

Description. Body length 1.8–2.2 mm, width 0.9–1.3 mm. Body elongate oval, strongly convex (Fig. 2.6F). General coloration dark brown, slightly paler along margins of pronotum. Posterior elevation of mesoventrite with well-defined, curved transverse ridge. Elytra without striae or serial punctures. Pro- and mesofemora covered with hydrofuge pubescence along basal half; metafemora with glabrous tibial grooves. Apex of fifth abdominal ventrite rounded. Aedeagus (Fig. 2.7I) with basal piece 0.45 × the length of parameres; greatest width of parameres similar to greatest width of median lobe, with outer margins evenly convex; apex of parameres truncate, obliquely directed; apex of median lobe rather widely rounded.

Etymology. Named with the Latin word *minor* meaning small, in reference to the species being the smallest member of the genus.

Distribution. Only known from the type locality, Pico do Barbado (Fig. 2.8).

Remarks. The type series was collected on a high-elevation seepage over a vertical cliff. The rock face had moss and algal growth on same areas (Fig. 2.9A, B).

Ephydrolithus ogmos sp. n.

Figs 2.6A–D, 2.7H, 2.8, 2.9A, B

Type material. Holotype (male): "BRAZIL: Bahia: Abaíra; -13.29053, -41.90489; 1705 m; Pico do Barbado, W of Catolés; vertical seep on rock; 26.ii.2018; leg. Benetti & team; BR18-0226-01C" (INPA). **Paratypes (4): BRAZIL: Bahia:** Same data as holotype (SEMC, 2 including DNA voucher SLE-1510; INPA, 2).

Differential diagnosis. *Ephydrolithus ogmos* is easily distinguished from all the other known species by its well-defined striae along the posterior third of the elytra.

Description. Body length 3.1–3.3 mm, width 1.8–2.0 mm. Body elongate oval, strongly convex (Fig. 2.6B). General coloration brown, slightly paler along margins of pronotum and elytra. Posterior elevation of mesoventrite with well-developed spine, forming high anterior carina. Elytra with well-developed striae along posterior half and reduced serial punctures. Pro- and mesofemora covered with hydrofuge pubescence along basal half; metafemora with glabrous tibial grooves. Apex of fifth abdominal ventrite truncate. Aedeagus (Fig. 2.7H) with basal piece 0.7 × the length of parameres; parameres nearly 0.7 × greatest width of median lobe, with outer margins slightly sinuate; apex of parameres rounded, obliquely directed; apex of median lobe broadly acute.

Etymology. Named with the Greek word *ogmos* meaning furrow, in reference to the well-defined elytral striae of the species.

Distribution. Only known from the type locality, Pico do Barbado (Fig. 2.8).

Life history. The type series was collected on a high-elevation seepage over a vertical cliff. The rock face had moss and algal growth on same areas (Fig. 2.9A, B).

Ephydrolithus spiculatus sp. n.

Figs 2.7F, G, 2.8, 2.9C

Type material. Holotype (male): "BRAZIL: Minas Gerais: Lassance; -17.83384, -44.50515; 568 m; Cachoeira da Palmeira; flotation of root mats and moss from side of waterfall and seepage; 2.iii.2018; leg. Benetti & team; BR18-0302-04A" (INPA).

Differential diagnosis. *Ephydrolithus spiculatus* is very similar to *E. hamadae* and *E. teli*. It can be easily distinguished from both by the presence of a pointed spine on the posterior elevation of the mesoventrite (see Fig. 2.7G).

Description. Body length 3.2 mm, width 1.7 mm. Body elongate oval, moderately convex. General coloration brown, slightly paler on pronotum and along margins of elytra, with dark brown head. Posterior elevation of mesoventrite with a pointed spine (Fig. 2.7G). Elytra without striae or serial punctures. Pro- and mesofemora covered with hydrofuge pubescence along basal 2/3; metafemora with hydrofuge pubescence along basal 2/3 of anterior margin, and on tibial grooves. Apex of fifth abdominal ventrite truncate. Aedeagus (Fig. 2.7F) with basal piece 0.9 × the length of parameres; parameres nearly 0.3 × greatest width of median lobe, with outer margins nearly straight for most of their length; apex of parameres truncate, with outer corners broadly rounded; apex of median lobe widely acute.

Etymology. Named with the Latin word *spiculatus* meaning sharpen to a point, in reference to the pointed spine on the posterior elevation of the mesoventrite.

Distribution. Known only from the type locality (Fig. 2.8).

Remarks. This species was collected by gathering moss and roots from bottom and margin of a seepage that was next to a large waterfall (Fig. 2.9C). The only known specimen was collected by placing the moss and roots in a pan of water, where it floated to the surface along with several specimens of *E. hamadae*.

Ephydrolithus teli sp. n.

Figs 2.5E–H, 2.7E, 2.8, 2.9D

Type material. Holotype (male): "BRAZIL: Bahia: Abaíra; -13.29053, -41.90489; 1705 m; Pico do Barbado, W of Catolés; flotation of mud and moss from seepage; 26.ii.2018; leg. Benetti & team; BR18-0226-01B" (INPA). **Paratypes (8): BRAZIL: Bahia:** Same data as holotype (SEMC, 6 including DNA voucher SLE-1486). **Minas Gerais:** "Monte Azul; -15.17067, -42.80351; 970 m; Serra do Espinhaço, c. 7 Km E of Monte Azul; seepage areas in stream on rock; 28.ii.2018; leg. Benetti & team; BR18-0228-02B" (SEMC, 3 including DNA voucher SLE-1509).

Differential diagnosis. *Ephydrolithus teli* is very similar to *E. hamadae*. Both species can only be distinguished from each other by characteristics of the aedeagus.

Description. Body length 2.8–3.3 mm, width 1.5–1.9 mm. Body elongate oval, moderately convex (Fig. 2.5F). General coloration dark brown. Posterior elevation of mesoventrite with well-

defined, curved transverse ridge. Elytra without striae or serial punctures. Pro- and mesofemora covered with hydrofuge pubescence along basal 2/3; metafemora with hydrofuge pubescence on tibial grooves. Apex of fifth abdominal ventrite truncate. Aedeagus (Fig. 2.7E) with basal piece 0.85 × the length of parameres; parameres nearly 0.4 × greatest width of median lobe, with outer margins only slightly convex; apex of parameres truncate, obliquely directed; apex of median lobe triangular, very narrowly rounded.

Etymology. Named with the Latin word *teli* meaning spear, in reference to the shape of the median lobe of the aedeagus of the species.

Distribution. Known from two localities in the highlands of northeastern Brazil (Fig. 2.8).

Remarks. Both collections of this species were taken from rocky seepage habitats (e.g., Fig. 2.9D).

Primocerus gen. n.

Figs 2.10–2.16

Type species: *Primocerus neutrum* sp. n.

Differential diagnosis. Small to medium sized beetles (2.4–4.9 mm), elongate oval in dorsal view, moderate to strongly convex in lateral view (e.g., Figs 2.11F, 2.12B), brown, dark brown, reddish brown, or rather orange. Antennae with eight antennomeres (e.g., Fig. 2.10G). Maxillary palps short to moderately long (e.g., shorter to nearly as long as the width of the head; e.g., Figs 2.10H, 2.12H). Elytra with sutural striae; elytral punctures from shallow to sharply

marked (e.g., Figs 2.11E, 2.12E); serial punctures, ground punctures and systematic punctures similar in size and degree of impression throughout elytra; all punctures seemingly arranged in rows, sometimes evidently so. Prosternum flat to mesally only slightly produced. Posterior elevation of mesoventrite with a curved transverse ridge, rather sharp and low (Fig. 2.14A), except in *P. cuspidis* which bears a sharp, pyramidal (triangular) projection. Posteromesal glabrous patch on metaventrite nearly as wide as long. Pubescence on anterior surface of metafemora ranging from sparse to densely covering basal three fourths of the femur (e.g., Figs 2.12C, 2.10G, 2.11G). Fifth abdominal ventrite apically rounded, truncate or slightly emarginate, usually with stout setae (e.g., Fig. 2.14C). Basal piece of aedeagus as long as or longer than parameres; median lobe triangular, nearly as wide at base as basal width of one paramere, with apical projection (Fig. 2.14D–L); gonopore absent (Fig. 2.14D–L).

At first sight, the dorsally smoother members of *Primocerus* (Figs 2.10, 2.11) can be mistaken for *Chasmogenus*, given that both genera exhibit sutural striae. The presence of a transverse curved ridge (sometimes very low) on the posterior elevation of the mesoventrite distinguishes *Primocerus* from *Chasmogenus*, in which the mesoventrite is either flat, broadly elevated or with a longitudinal elevation (e.g., figs 2, 4 in Clarkson and Ferreira 2014). In addition, the maxillary palps of most *Chasmogenus* species are nearly 1.5 × longer than the maximum width of the head, whereas in *Primocerus* the maxillary palps are nearly as long as the width of the head.

Punctate members of *Primocerus* (in particular *P. maipure* and *P. pijiguaense*, Fig. 2.12) may resemble some species of *Tobochares* (e.g., *T. canthus*, *T. pallidus*; Kohenberg and Short 2017); striate *Primocerus* may resemble a very small *Radicitus* (see Short and García 2014). In

those cases, *Primocerus* can be easily recognized by the presence of sutural striae. Some *Primocerus* may also superficially resemble certain New World cylomine genera, such as *Andotypus* (see Fikáček et al. 2014), from which it may be distinguished by the fully exposed labrum of *Primocerus*.

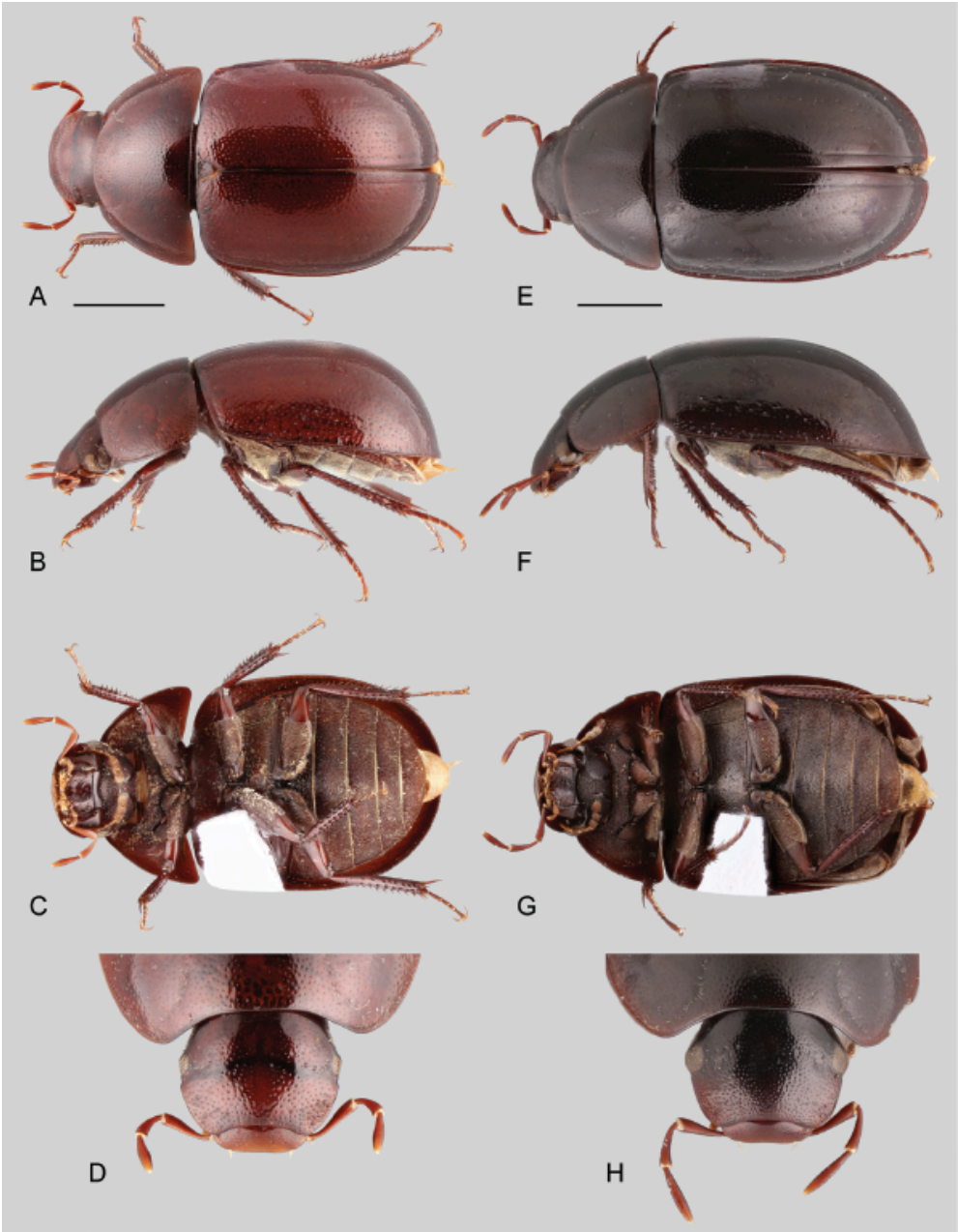


Figure 2 10. Habitus of *Primocerus* spp.: **A–D** *Primocerus ocellatus*: **A** dorsal view, **B** lateral view, **C** ventral view, **D** head, dorsal view. E – H *Primocerus gigas*: (E) dorsal view, (F) lateral view, (G) ventral view; (H) head, dorsal view. Scale bars 1 mm.

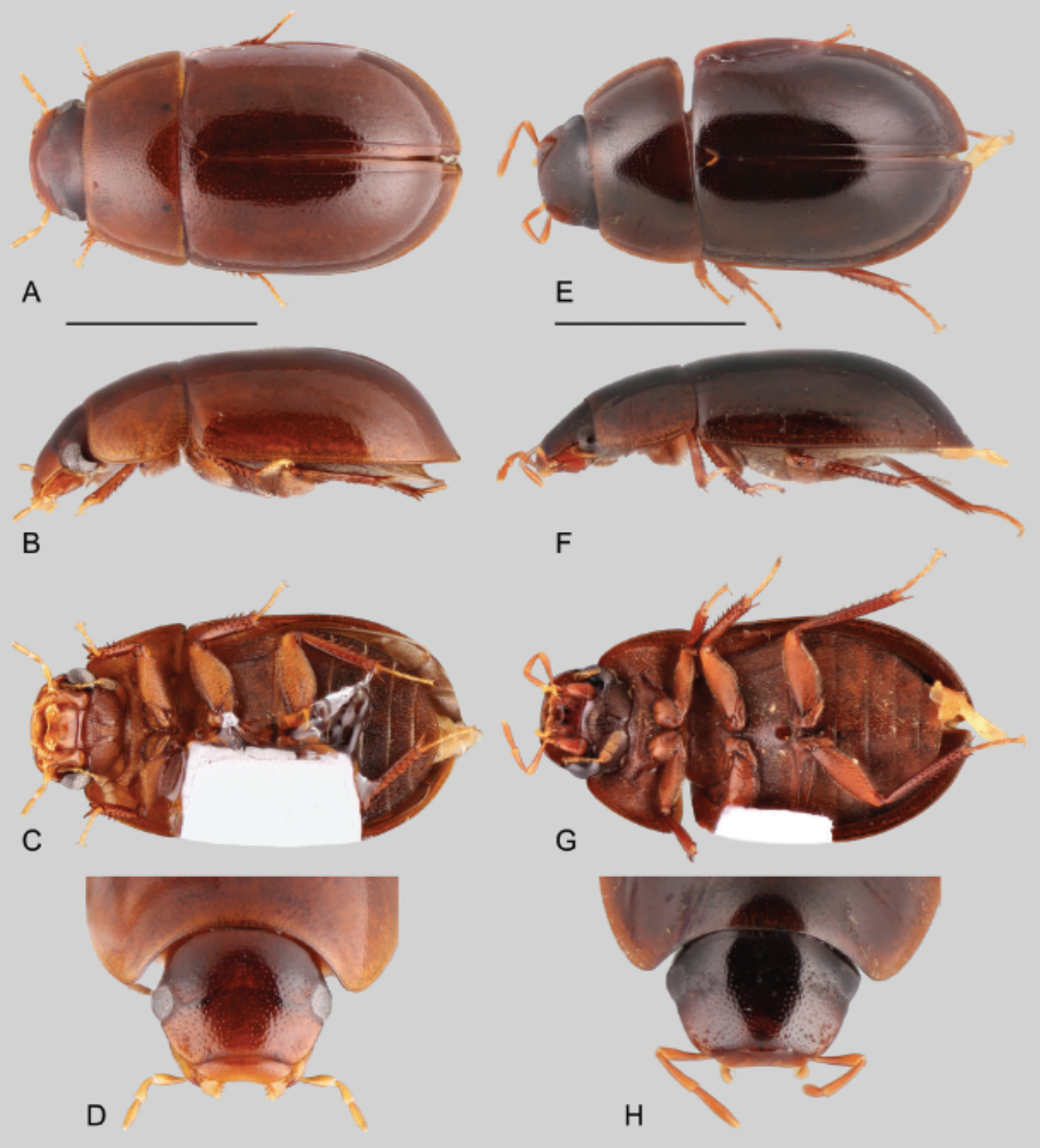


Figure 2.11. Habitus of *Primocerus* spp.: **A–D** *Primocerus cuspidis*: **A** dorsal view, **B** lateral view, **C** ventral view, **D** head, dorsal view; **E–H** *Primocerus neutrum*: **E** dorsal view, **F** lateral view, **G** ventral view, **H** head, dorsal view. Scale bars 1 mm.

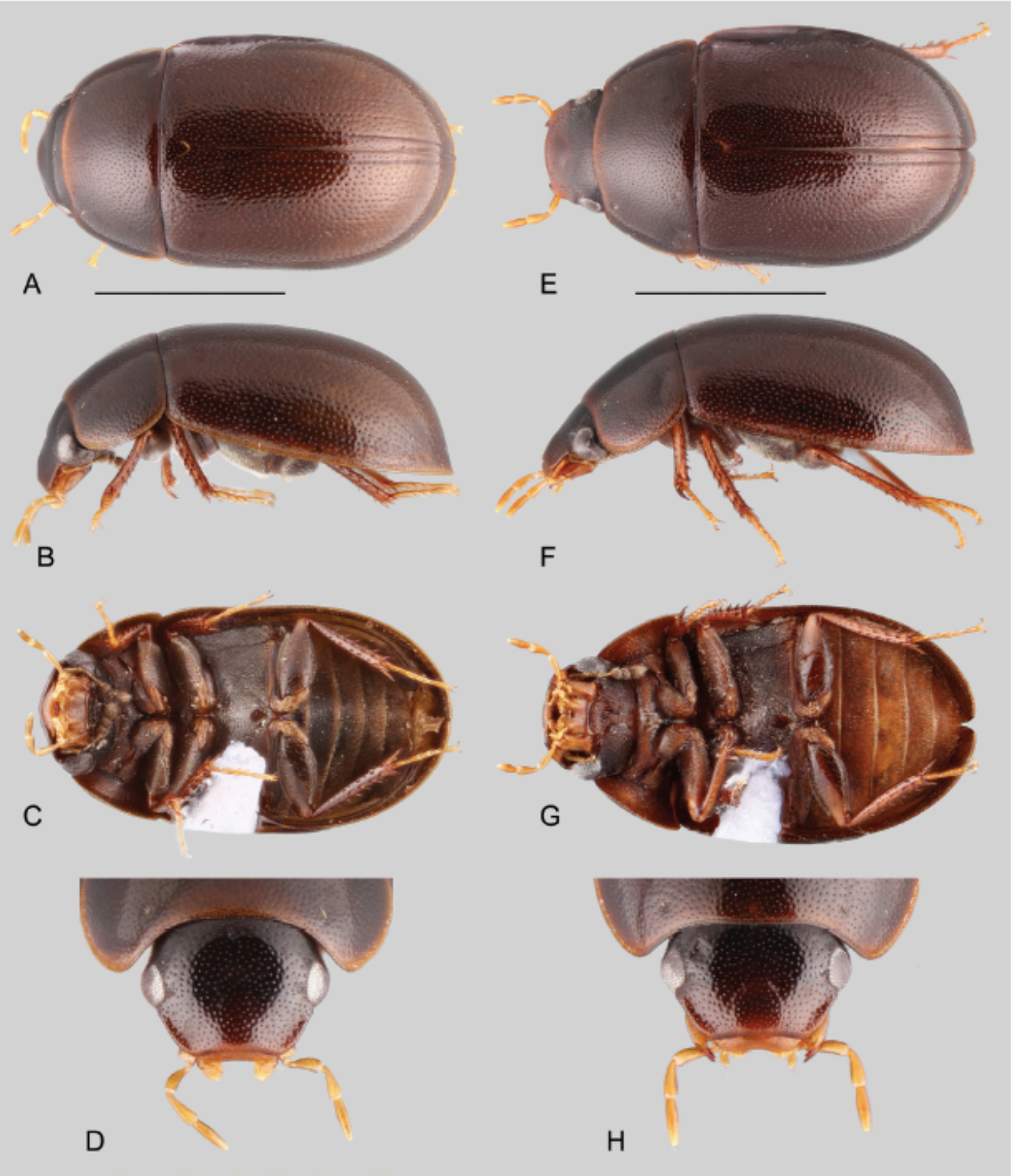


Figure 2.12. Habitus of *Primocerus* spp.: **A–D** *Primocerus maipure*: **A** dorsal view, **B** lateral view, **C** ventral view, **D** head, dorsal view; **E–H** *Primocerus pijiguaense*: **E** dorsal view, **F** lateral view, **G** ventral view, **H** head, dorsal view. Scale bars 1 mm.

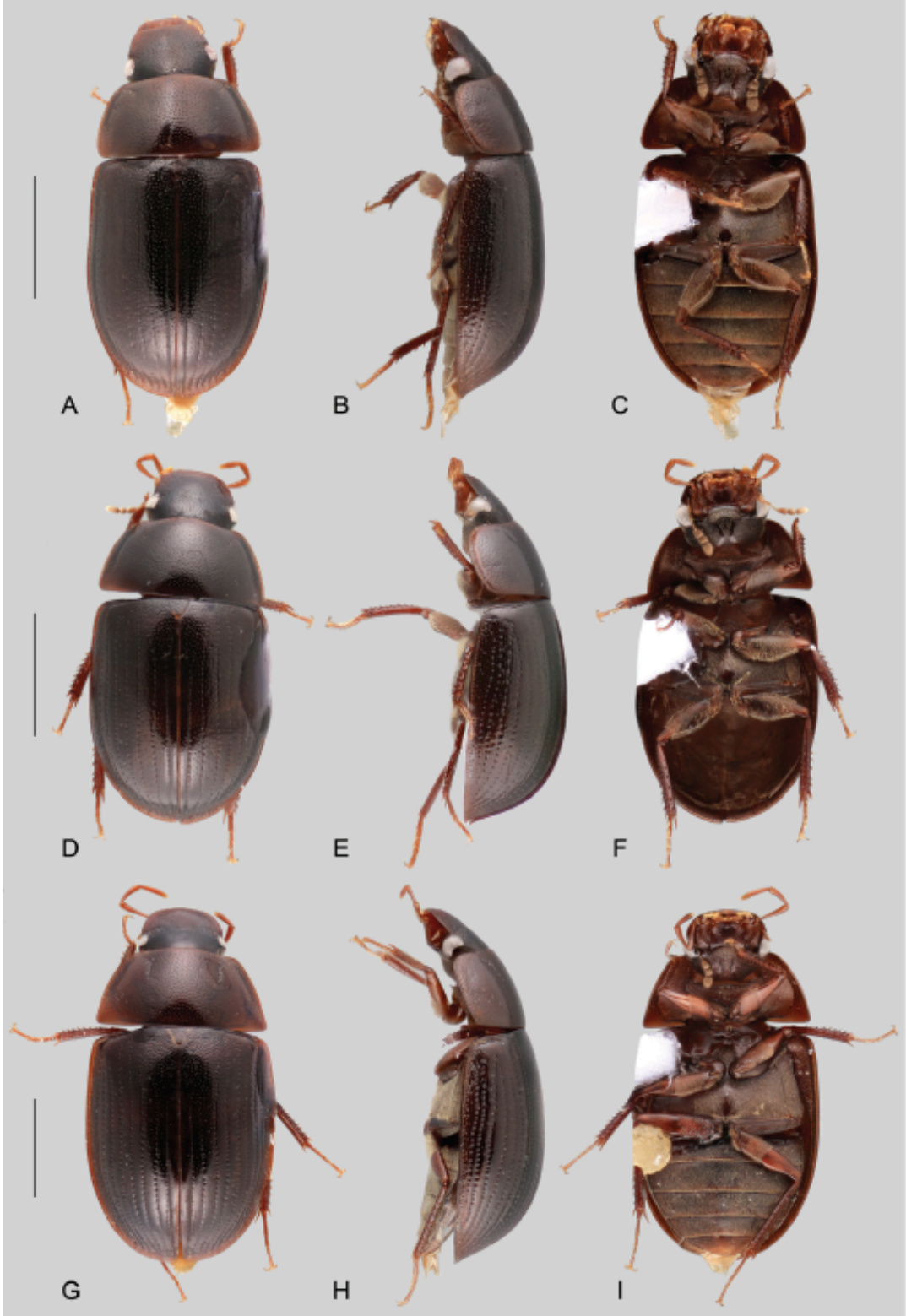


Figure 2.13. Habitus of *Primocerus* spp.: **A–C** *Primocerus semipubescens*: **A** dorsal view, **B** lateral view, **C** ventral view, **D–F** *Primocerus petilus*: **D** dorsal view, **E** lateral view, **F** ventral view; **G–I** *Primocerus striatolatus*: **G** dorsal view, **H** lateral view, **I** ventral view. Scale bars 1 mm.

In addition, the presence of sutural striae and the relative size of the basal piece of the aedeagus resemble some species of *Enochrus* (Enochrinae) in that the basal piece is as long as or longer than the median lobe + parameres (e.g., see figs 11 and 14 in Fernández 2006). The maxillary palps curved inwards in *Primocerus* (as opposed to zig-zag-like as in *Enochrus*) allows for its recognition.

The aedeagus of *Primocerus* is so far unique among the Acidocerinae in the lack of a well-developed gonopore, and the presence of a lightly sclerotized projection beyond the apex of the median lobe.

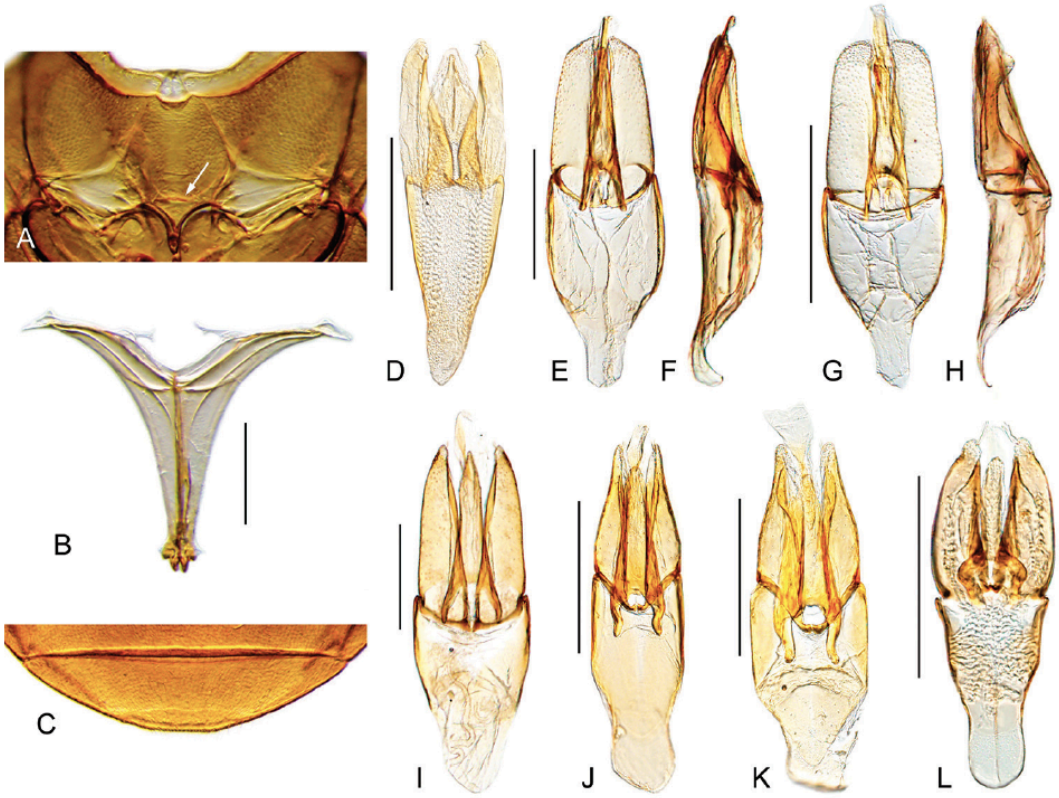


Figure 2.14. Thorax, abdomen and aedeagus of *Primocerus* spp.: **A–D** *Primocerus neutrum*: **A** ventral view of mesoventrite (white arrow pointing transverse ridge, **B** posterior view of metafurca, **C** fifth abdominal ventrite, **D** aedeagus; **E–L** aedeagus: **E, F** *Primocerus maipure*: **E** dorsal view, **F** lateral view, **G, H** *Primocerus pijiguaense*: **G** dorsal view, **H** lateral view, **I** *Primocerus gigas*, **J** *Primocerus petilus*, **K** *Primocerus striatolatus*, **L** *Primocerus cuspidis.* Scale bars 0.25 mm.

Description. Small to medium sized beetles, total body length 2.4–4.9 mm; body elongate oval, moderate to strongly convex in lateral view (e.g., Figs 2.11F, 2.12B); orange brown (Fig. 2.11A–D), reddish brown (Fig. 2.10 A–D), to dark brown in coloration (e.g., Fig. 2.13), usually uniform along body regions, sometimes slightly paler along margins, pronotum, ventral surfaces, and appendages, particularly maxillary palps and tarsi. **Head.** Frons and clypeus with either shallow (e.g., Fig. 2.10D) or sharply marked (e.g., Fig. 2.12D) ground punctures, irregularly and rather densely distributed over the surface, accompanied by scattered seta-bearing systematic punctures, particularly noticeable along anterior and inner margins of eyes, and lateral areas of clypeus; surface between punctures smooth and shiny. Clypeus roughly trapezoid, with posterior margin wider than anterior margin; anterior corners roundly angulated, anterior margin widely roundly emarginate; membranous preclypeal area not visible (visible in *Chasmogenus*; e.g., fig. 28 in Clarkson and Ferreira 2014); surface mesally moderately convex, laterally flattened to slightly concave (Fig. 2.12D, H). Eyes subquadrate in dorsal view, usually protruding from outer outline of head. Labrum wide, fully exposed, collinear to perpendicular to clypeus, and usually around 0.3 × as long as clypeus (e.g., Fig. 2.10D); dorsal surface flat to convex, with scattered fine punctures; anterior margin markedly roundly bent inwards, mesally emarginate, with tiny denticles along emargination, and setae on lateral areas of anterior margin. Temporae densely covered by very short and fine setae (hydrofuge pubescence). Mentum parallel sided, often with lateral margins densely fringed by short setae; surface rather flat, smooth, and glabrous, sometimes with lateral oblique longitudinal ridges, and few crenulations; anterior margin with wide, deep, concave median impression, sometimes marked by a transverse carina. Submentum sunken, concave, and pubescent at base, glabrous, shiny, flat and ascending at apex; ocular ridge

of variable development. Maxilla (e.g., Fig. 2.10G) with ventral surface of cardo and stipes smooth, shiny, and glabrous; outer dorsal margin of palpifer with a row of stiff, decumbent, spiniform setae; limit between cardo and stipes oblique; maxillary palps curved inward, brown to orange or yellow, longer than antennae, short to moderately long (e.g., shorter to nearly as long as the width of the head; e.g., Figs 2.10H, 2.12H); maxillary palpomere 1 gradually broadening towards apex, with inner margin straight and outer margin apically convex; apex of palpomere 3 bearing sensilla; palpomeres 1 and 3 similar in length, palpomere 2 only slightly shorter. Mandibles with apex bifid (observed in *P. gigas*, *P. pijiguaense*, *P. striatolatus* and *P. petilus*; e.g., Fig. 2.12H). Labial palps yellowish to brown, usually nearly as long as mentum, dorsoventrally flattened; palpomere 2 with outer margin convex apicad of midpoint, sometimes with setae near apex; palpomere 3 digitiform to somewhat kidney-shaped, with one or two long subapical setae on outer margin. Antennae (e.g., Fig. 2.10G) with eight antennomeres, slightly paler than general coloration of head; antennomere 1 anteriorly projected near base, at most reaching midpoint of ventral surface of eye, reaching to surpassing cardo-stipes joint, nearly 2.0 × longer than antennomere 2; antennomere 2 nearly as long as antennomeres 3–4 combined; antennomere 5 forming a well differentiated, symmetric cupule; antennomeres 6–8 slightly flattened, forming a loosely articulated, pubescent club (antennomere 7 shortest, 8 longest); apex of antennomere 8 with longer setae than general pubescence of club. **Thorax.** Pronotum widest at base, narrowed anteriorly, surface evenly convex; anterior and posterior corners widely rounded, sometimes posterior corners almost forming a sharp straight angle (e.g., Fig. 2.10G); anterior and posterior margins nearly straight; ground punctation either shallow or sharp, uniformly dense, with surface between punctures smooth and shiny; seta bearing systematic punctures forming paired

anterolateral semicircles. Scutellar shield of moderate size, triangular, nearly as long as wide, with punctation as in pronotum. Prosternum nearly as long as 0.7 × the length of a procoxa; anterior margin of prosternum mesally projected as a wide triangle, apically either acute or rounded (except in *P. ocellatus*); surface of prosternum flat to only weakly broadly convex, covered by scattered, fine, rather long setae; intercoxal process projected from posterior margin of procoxal cavities, rectangular in outline, mesally longitudinally carinate. Mesoventrite (Fig. 2.14A) not fused to mesepisterna, with anterior margin nearly 0.3 × as wide as anterior margin of mesepisternum; anterior rib of mesoventrite bearing paired medial teardrop-shaped, pearlescent maculae; posterior elevation of mesoventrite with a transverse curved ridge, rather sharp and low, reduced in *P. maipure*, *P. pijiguaense* and *P. ocellatus*, with a sharp, pyramidal (triangular) spine-like projection in *P. cuspidis* (Fig. 2.11C); surface of mesoventrite reticulated for the most part, covered by scattered, fine and rather long setae, with anteromedial depression, and posterolateral smooth and glabrous areas; mesepisternum obliquely widely concave, with reticulated surface; mesepimeron trapezoid, with reticulate and pubescent surface. Mesofurca (examined in *P. neutrum*) with short arms, 0.75 × length of mesocoxae; apical half of arms free, explanate at apex, somewhat square. Metaventrite mesally widely elevated, rather wide throughout and flat posteromesally; surface densely pubescent, except for posteromesal nearly as wide as long glabrous patch, and soemtimes postero-lateral areas (Fig. 2.10G; except in *P. ocellatus*, Fig. 2.10D). Metepisterna 3–4 × longer than wide, narrowing only at posterior end. Metepimeron clearly visible, triangular. Metafurca (examined in *P. neutrum*, Fig. 2.14B) 1.3 × wider than long, with furcal arms slightly shorter than stalk; stalk triangular (wider near the crux, gradually narrowing ventrally), with paired longitudinal keels extending along

basal third of posterior face, fusing together towards crux, with a well-developed median keel on anterior face extending to anterior margin of dorsal sheets; outer margins of stalk gradually diverging from base towards basal third of furcal arms; furcal arms somewhat parallelogram-shaped, with apex (hemiductus) only slightly explanate, with apex pointing obliquely; anterior tendons inserted basad of mid length of dorsal edge of furcal arms; well-developed dorsal sheaths, narrower than widest point of lateral sheaths. **Elytra.** Surface even (without elevations or depressions), with sutural striae; ground punctures and systematic punctures either shallow or sharply marked (e.g., Figs 2.11E, 2.12E), similar in size and degree of impression throughout elytra, seemingly arranged in rows; serial punctures, when present (e.g., Fig. 2.13A, D, G), larger and deeper than ground punctures, and clearly arranged in longitudinal rows (striae); serial punctures only very slightly impressed into grooves along posterior half of elytra in striate species (e.g., *P. petilus*, *P. striatolatus*, and *P. semipubescens*; see Fig. 2.13); seta bearing systematic punctures rather scarce; elytral outer margins flared, usually along entire length. Epipleura usually well developed, surface either flat or oblique, with sparse setae and irregular sculpture, anteriorly wide, gradually narrowing posteriorly, extending up to midlength of first abdominal ventrite; inner margin of epipleura only slightly indented at anterior outer corner of metepisternum; pseudepipleura usually well developed and perpendicularly positioned, ranging in width from nearly as wide as anterior portion of epipleura, to half as wide, extending up to basal half of abdomen along outer margin of elytra. Hind wings well developed. **Legs.** Pubescence on anterior surface of metafemora ranging from scarce and limited to anterior margin (e.g., Fig. 2.12C), to densely covering most surface up to apical fifth (e.g., Fig. 2.11G); glabrous area of metafemur with shiny and sometimes slightly reticulated surface; all femora

antero-posteriorly flattened; metafemora usually with sharply marked tibial grooves. Tibiae slender, rather cylindrical; longitudinal rows of well-developed spines along pro-, meso- and metatibiae, composed of rather sharp and stout spines, slightly sparser along metatibiae; protibiae with a median longitudinal row of rather long and thick setae along anterior surface; protibial apical spurs large, extending beyond apex of protarsomere 2, sometimes reaching apex of protarsomere 3. All tarsi with five tarsomeres, bearing long apical hair-like setae on dorsal face, and spines-like or hair-like setae on ventral face of tarsomeres 2–4, sometimes also tarsomere 5; pro- and mesotarsomeres 1–4 similar in size and shape; pro- and mesotarsomere 5 approximately as long as 3–4 combined; metatarsomere 2 similar in length to metatarsomere 5; claws rather large, curved; well-developed empodium, bearing a pair of long, curved apical setae. **Abdomen.** Abdomen with five ventrites, rather flat to medially convex; all ventrites with uniform, dense, fine pubescence; posterior margin of fifth ventrite either rounded, truncate, or slightly emarginate, usually fringed with spine-like setae (Fig. 2.14C). Aedeagus (Fig. 2.14D–L) with basal piece as long or longer than parameres; median lobe triangular, with base nearly as wide as base of a paramere, with well-developed lateral basal apodemes; apex of median lobe variable, with a membranous to sclerotized apical projection; gonopore not differentiated; parameres nearly as long as median lobe, with outer margins usually straight along basal 3/4, with setae at apex.

Larvae. The immature stages are unknown.

Etymology. Named from the Latin *primus*, meaning first, with the ending -*cerus*, in reference to the belonging of the genus to the Acidocerinae. To be treated as masculine.

Distribution. Broadly distributed across the Guiana Shield region of South America, including Brazil (Pará), Guyana, Suriname and southern Venezuela (Amazonas, Bolívar) (Fig. 2.15).

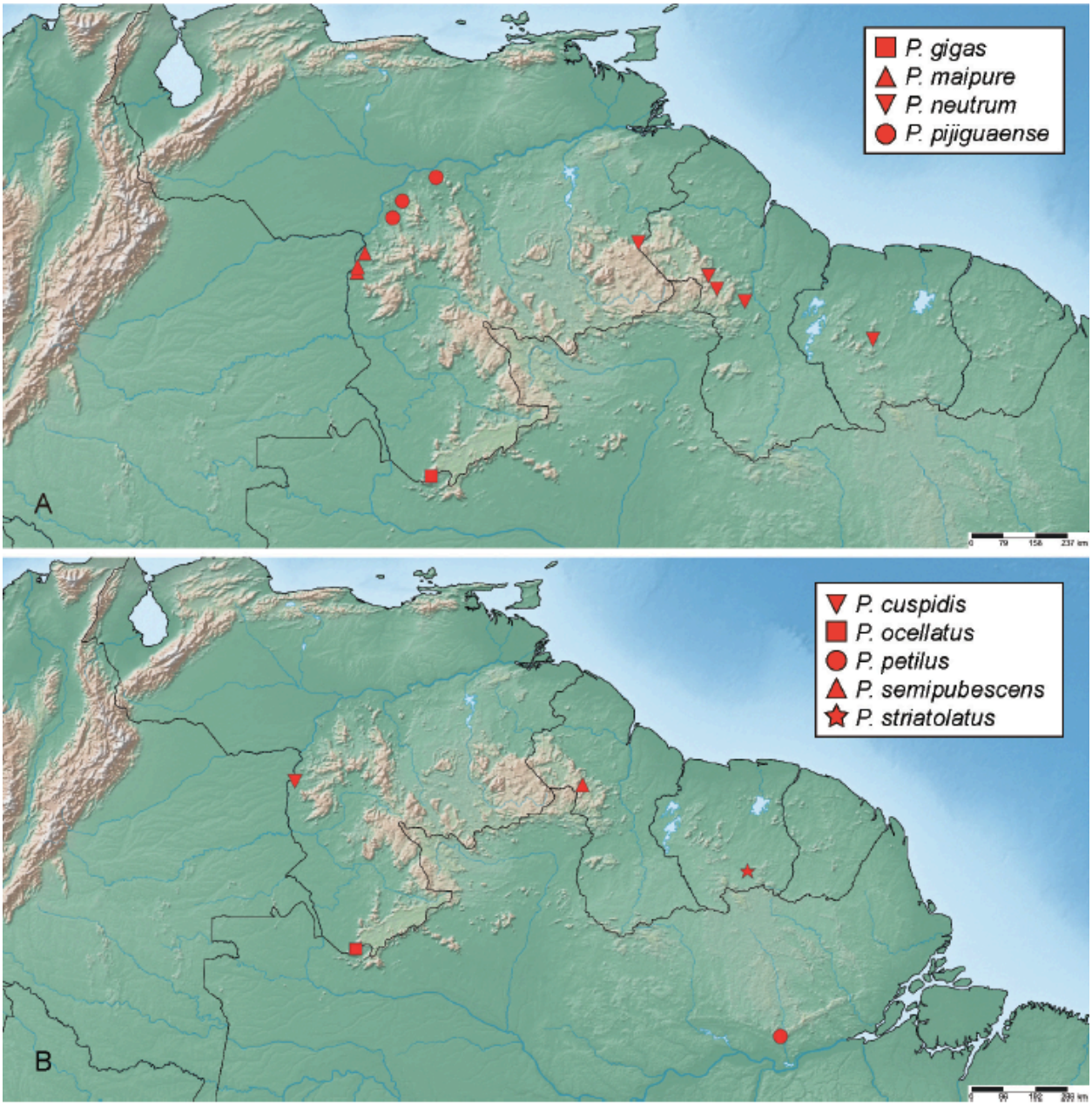


Figure 2.15. Distribution of *Primocerus* spp.

Remarks. The habitats occupied by members of *Primocerus* range from forested pools to seepages (Fig. 2.16), in an elevational range from 80 to 1950 m. Only one specimen has been collected with a flight intercept trap. Specimens of *Primocerus* are relatively rare, given that so far have only been found in low numbers of specimens per collecting event.

Figure 2.16. Habitat of *Primocerus* spp. **A** habitat and type locality for *P. cuspidis*, Venezuela, Tobogán de la Selva, collecting event AS-08-080b, **B** habitat and type locality for *P. pijiguaense*, Venezuela, Los Pijiguaos, collecting event AS-07-015, **C** habitat and type locality for *P. neutrum*, Venezuela, along La Escalera, collecting event AS-08-058, **D** habitat and type locality for *P. petilus*, Brazil, Vale do Paraiso, collecting event BR18-0203-01G.

Characters of taxonomic importance for *Primocerus*

The external morphology of *Primocerus* species may be considered very heterogeneous in comparison with other acidocerine genera (e.g., *Globulosis* García, 2001, *Quadriops* Hansen, 1999 (see Girón and Short 2017), *Crucisternum* Girón and Short, 2018).

Body size. Species of *Primocerus* measure approximately 3.0–3.5 mm, except for the largest species *Primocerus grandis* approximately 5.0 mm.

Elytral punctation. Two main groups of species can be recognized by the degree of impression of the ground punctures: the smooth group (with shallowly impressed elytral punctures: *P. cuspidis*, *P. gigas*, *P. neutrum*, *P. ocellatus*; Figs 2.10, 2.11) and the punctate group (with sharply marked punctures: *P. maipure*, *P. pijiguaense*, *P. petilus*, *P. semipubescens*, *P. striatolatus*; Figs 2.12, 2.13). Within the punctate group, two groups of species can be distinguished by how evident the longitudinal rows of serial punctures are: the homogeneous group (with serial punctures only slightly distinguishable from ground and systematic punctures: *P. maipure*, *P. pijiguaense*, Fig. 2.12) and the striate group (with serial punctures larger than the ground punctures and clearly organized into rows: *P. petilus*, *P. semipubescens*, *P. striatolatus*; Fig. 2.13).

In some cases (*P. petilus* (Fig. 2.13A, B) and *P. striatolatus* (Figs 2.13D, E)), the striae are very slightly impressed along the posterior half of the elytra.

Coloration. The general coloration of *Primocerus* specimens range from orange and reddish brown to dark brown, although there is not much variation within species groups. Teneral specimens are significantly paler than fully sclerotized ones. Specimens that have been extracted for DNA are darker. Coloration should not alone be taken as a diagnostic feature.

Hydrofuge pubescence on metafemora. The extent of coverage of hydrofuge pubescence of the anterior surface of the metafemora varies across species. Most species have at least the basal half of the surface covered, but in some the coverage is limited to the dorsal margin (*P. maipure*, *P. pijiguaense*, Fig. 2.12C, G).

Aedeagus. As it is usual for the subfamily, the general configuration of the aedeagus (e.g., large basal piece, median lobe at base nearly as wide as base of a paramere, median lobe rather triangularly shaped, and nearly as long as parameres) is conserved across the genus, with specific diagnostic features (e.g., shape of parameres) at the species group and species level. Species groups distinguishable by characters of the elytra can also be recognized by aedeagal traits.

Key to the species of *Primocerus*

1 Elytra with ground punctures shallowly to very weakly marked (Figs 2.10A, E, 2.11A, E) … 2

– Elytra with ground punctures sharply marked (e.g., Figs 2.12A, E, 2.13A, D, G)… 5

2 Body length equal to or larger than 4.0 mm... 3

– Body length smaller than 4.0 mm… 4

3 Eyes in dorsal view of the head, very small (distance separating eyes 17 × the width of an eye) (Fig. 2.10D)… ***Primocerus ocellatus***

– Eyes in dorsal view of the head, of normal size (distance separating eyes 7.5 × the width of an eye) (Fig. 2.10H)… *Primocerus gigas*

4 Posterior elevation of mesoventrite with a sharply pointed pyramidal (triangular) spine (Fig. 2.11C) *Primocerus cuspidis*

– Posterior elevation of mesoventrite with a curved transverse ridge, rather sharp and low (Fig. 2.14A)… *Primocerus neutrum*

5 Hydrofuge pubescence on metafemora limited to dorsal margin of anterior surface (Fig. 2.12C, G)… 6

– Hydrofuge pubescence on metafemora covering at least the entire basal third of anterior surface (Fig. 2.13C, F, I)… 7

6 Apex of median lobe of aedeagus simply rounded in lateral view; base of parameres in lateral view oblique (Fig. 2.14F)… *Primocerus maipure*

– Apex of median lobe of aedeagus carinate (dorsally projected in lateral view, Fig. 2.14H); base of parameres in lateral view perpendicular to longitudinal axis of aedeagus (Fig. 2.14H)… *Primocerus pijiguaense*

7 Hydrofuge pubescence covering slightly less than the basal half of the anterior surface of all femora (Fig. 2.13I)… *Primocerus semipubescens*

– Hydrofuge pubescence covering at least basal 3/4 of the anterior surface of all femora Fig. 2.13C, F)… **8**

8 Elytra in dorsal view 3 × longer than wide; serial punctures not well differentiated along basal fourth of elytral striae 9 and 10 (Fig. 2.13A, B)… ***Primocerus petilus***

– Elytra in dorsal view nearly 2.6 × longer than wide; serial punctures of elytral striae 9 and 10 well developed along entire length (Fig. 2.13D, E)… ***Primocerus striatolatus***

Primocerus cuspidis **sp. n.**

Figs 2.11A–D, 2.14L, 2.15B, 2.16A

Type material. Holotype (male): "VENEZUELA: Amazonas/ 5°23.207'N, 67°36.922'W; 125 m/ Tobogán de la Selva, old "Tobogancito"/ on seepage area with detritus/ 8.viii.2008; leg. A. Short, M. García, / L. Joly; AS-08-080b" (MIZA). **Paratypes (3): VENEZUELA: Amazonas:** same data das holotype (SEMC).

Differential diagnosis. *Primocerus cuspidis* belongs to the group of species with shallowly impressed, rather irregularly distributed, and undifferentiated elytral punctures. It can be easily distinguished among its congeners by its paler (orange) coloration, and the presence of a sharp, pyramidal (triangular) projection on the posterior elevation of the mesoventrite.

Description. Body length 2.4 mm, width 1.5 mm. Body elongate oval, moderately convex (Fig. 2.11B). General coloration orange-brown. Elytra with ground punctures shallowly marked;

serial punctures absent. Posterior elevation of mesoventrite with sharply pointed pyramidal (triangular) spine. Metafemora with hydrofuge pubescence covering basal 4/5. Apex of fifth abdominal ventrite slightly emarginate. Aedeagus (Fig. 2.14L) with basal piece 1.3 × longer than parameres; parameres 1.15 × longer than median lobe; distal end of parameres with anteapical constriction, apex rounded and obliquely directed; apex of median lobe widely rounded.

Etymology. Named with the Latin word *cuspidis* meaning point, in reference to the sharp projection on the posterior elevation of the mesoventrite.

Distribution. *Primocerus cuspidis* has only been collected at Tobogán de la Selva in the Venezuelan Amazon, at an elevation of 125 m (Fig. 2.15B).

Remarks. The type series was collected in a flat, horizontal seepage area that was formed from water seeping from the banks of the Rio Coromoto (Fig. 2.16A).

Primocerus gigas **sp. n.**

Figs 2.10E–H, 2.14I, 2.15A

Type material. Holotype (male): "VENEZUELA: Amazonas/ 0°50'N, 65°59'W; 2100 m/ Cerro de la Neblina, camp II; beetles in flight over sunlit stream/ 16:00hrs. 31.i.1985/ leg. W.E. Steiner et al." (USNM). **Paratypes (8): VENEZUELA: Amazonas:** Same data as holotype (SEMC, USNM, 7, including DNA voucher SLE 1374); same except 0°52'N, 65°58'W, 1450 m, camp XI, 25-28.ii.1985, seine of rapids in small mountain stream, leg. P.J. & P.M. Spangler, R. Faitoute (USNM, 1).

Differential diagnosis. *Primocerus gigas* is among the largest species of the genus. It can be distinguished from similarly sized species by the eyes being separated by a distance of 7.5 × the width of an eye (Fig. 2.10H).

Description. Body length 4.9 mm, width 2.8 mm. Body elongate oval, moderately convex (Fig. 2.10F). General coloration dark brown. Elytra with ground punctures shallowly marked, systematic punctures slightly enlarged, and serial punctures absent. Posterior elevation of mesoventrite with simple transverse ridge. Metafemora with hydrofuge pubescence covering slightly more than basal half of anterior surface. Apex of fifth abdominal ventrite truncate. Aedeagus (Fig. 2.14I) with basal piece nearly 1.1 × longer than parameres; parameres slightly longer than median lobe, truncate and obliquely directed at apex; apex of median lobe narrowly pointed.

Etymology. Named with the Latin word *gigas* meaning giant, in reference to the large size of this species compared to most remainder members of the genus.

Distribution. *Primocerus gigas* is only known from Cerro de la Neblina in the Venezuelan Amazon, at elevations between 1450 and 2100 m (Fig. 2.15A).

Remarks. Label data indicates the beetles were collected “in flight”, with one specimen collected by seining rapids in a mountain stream.

Primocerus maipure **sp. n.**

Figs 2.12A–D, 2.14E, F, 2.15A

Type material. Holotype (male): “VENEZUELA: Amazonas: 5°30.623'N, 67°36.109'W; 100 m; ca. 15 Km S. of Puerto Ayacucho; rock pools on top; 14.ix.2007; leg. A. Short; AS-07-011b” (MIZA). **Paratypes (10): VENEZUELA: Amazonas:** 5°23.207'N, 67°36.922'W; 125 m/ Tobogán de la selva, old "Tobogancito"/ upstream at small slide; 12.ix.2007/ leg. M. García; AS-07-007b (SEMC, 1); "5°30.518'N, 67°36.079'W; 100 m/ ca. 15 Km S. of Puerto Ayacucho; isolated seepage/ 13.ix.2007; leg. A. Short; AS-07-009a" (SEMC, 1); same data as holotype (SEMC, 2, including DNA voucher specimen SLE 1034); same except "pools at outcrop base, AS-07-011x" (SEMC, 2); "110 m; rock outcrop pools; 8.ix.2007; leg. A. Short, M. García; AS-08-081b" (SEMC, 1); 5°48.414'N, 67°26.313'W; 80 m/ nr. Iboruwa, "Tobogancito"/ 7.viii.2008; leg. A. Short, M. García, L. Joly/ AS-08-078" (SEMC, 3).

Differential diagnosis. *Primocerus maipure* can be differentiated by the presence of sharply impressed elytral punctures, with serial punctures only slightly differentiated, longitudinally aligned (more evidently so along posterior half of elytra, Fig. 2.12A, B). It is very similar to *P. pijiguaense*, from which it can be distinguished by its simple median lobe and the oblique and rather angulate outer margins of the apical region of the parameres (Fig. 2.14E, F; apical region of median lobe dorsally keeled along apical region, and widely rounded outer margins of the apical region of the parameres in *P. pijiguaense*, Fig. 2.14G, H).

Description. Body length 2.6 mm, width 1.5 mm. Body elongate oval, strongly convex (Fig. 12A, B). General coloration brown. Elytra with ground punctures sharply marked, with serial punctures only slightly differentiated, longitudinally aligned, more evidently so along posterior half of elytra (Fig. 2.12A, B). Posterior elevation of mesoventrite with simple, very lowly raised curved transverse ridge. Metafemora with hydrofuge pubescence limited to anterodorsal

surface. Apex of fifth abdominal ventrite truncate. Aedeagus (Fig. 2.14E, F) with basal piece nearly 1.2 × longer than parameres; parameres nearly as long as median lobe, in lateral view with base oblique to longitudinal axis of aedeagus; outer margin of apical region of parameres oblique and rather angulate; apical region of median lobe simple, non-carinate.

Etymology. Noun in apposition. Named after the Maipure, one of the pre-Columbian indigenous tribes that inhabited the "Spanish Guyana" region, and the language they spoke.

Distribution. *Primocerus maipure* has been collected at localities south of Puerto Ayacucho in the Venezuelan Amazon, at elevations between 80 and 125 m (Fig. 2.15A).

Remarks. All collections of this species were made either on small seepages over granite outcrops, or in small rock pools that had formed on the outcrops.

Primocerus neutrum sp. n.

Figs 2.11E–H, 2.14D, 2.15A, 2.16C

Type material. Holotype (male): "VENEZUELA: Bolívar/ 6°2'10.5"N, 61°23'57.8'W; 630 m/ along La Escalera; rocky stream/ 31.vii.2008; leg. A. Short, M. García, L. Joly/ AS-08-058" (MIZA). **Paratypes (20): GUYANA: Region 8**: "4°43'49"N, 59°1'35"W; 300 m/ Iwokrama Forest, Pakatau hills/ flight intercept trap; 26-29.v.2001/ leg. R. Brooks & Z. Falin; GUY1BF01 063" (SEMC, 1); "5°0.730'N, 59°38.965'W; 585 m/ Upper Potaro camp I, c. 7 km NW Chenapau, Ridge Trail/ 11.iii.2014; leg. Short, Baca, Salisbury; GY14-0311-02A" (CBDG, SEMC, 11); "5°18.261'N, 59°50.257'W; 687 m/ Ayanganna Airstrip, trail from airstrip to Ayanganna/ forest detrital pools;

17.iii.2014/ leg. A. Short; GY14-0317-01A" (SEMC, 1); same except "18.iii.2014, GY14-0318-01B" (SEMC, 1); same except "seepage area over rocks in forest flowing into stream, GY14-0318-01C" (SEMC, 1). **SURINAME: Sipaliwini District:** "3°53.942'N, 56°10.849'W; 733 m/ CSNR: Tafelberg Summit, nr. Caiman Creek Camp/ pools in forest; 19.viii.2013/ leg. Short & Bloom; SR13-0819-05B" (SEMC, DNA voucher specimen SLE 1085). **VENEZUELA: Amazonas:** Same data as holotype (MIZA, SEMC, 8, including DNA voucher SLE 529).

Differential diagnosis. *Primocerus neutrum* can be regarded as very plain in appearance, lacking remarkable features. It can be distinguished among similarly sized species with shallowly punctured elytra by its dark brown coloration and simple transverse ridge on the posterior elevation of the metaventrite.

Description. Body length 2.6–3.5 mm, width 1.4–1.9 mm. Body elongate oval, moderately convex (Fig. 2.11F). General coloration brown. Elytra with ground punctures very shallowly marked. Posterior elevation of mesoventrite with simple curved transverse ridge. Metafemora with hydrofuge pubescence covering nearly basal 4/5 of anterior surface. Apex of fifth abdominal ventrite slightly emarginate. Aedeagus (Fig. 2.14D) with basal piece nearly 1.25–1.35 × longer than parameres; parameres slightly longer than median lobe, truncate to rounded and obliquely directed at apex; apex of median lobe somewhat "pinched" and narrowly pointed.

Etymology. Named with the Latin word *neutrum* meaning neutral, in reference to the comparatively unremarkable appearance of the species.

Distribution. *Primocerus neutrum* has only been collected at the locality known as La Escalera in the Venezuelan Amazon, the Upper Potaro region and the Iwokrama Forest in

Guyana, and the Tafelberg summit in Suriname. Specimens have been collected at elevations of 300–733 m (Fig. 2.15A).

Remarks. This species has been collected in detrital pools in densely forested areas, typically associated with streams (Fig. 2.16C).

Primocerus ocellatus sp. n.

Figs 2.10A–D, 2.15B

Type material. Holotype (female): "VENEZUELA: Amazonas/ Cerro de la Neblina/ Camp XII, 1950 m/ near Pico Phelps/26.ii.1985// from leaf packs and wood pieces in small stream/ leg. W. Steiner, W. Buck, B. Boom, C. Brewer" (USNM).

Differential diagnosis. *Primocerus ocellatus* can be easily recognized by its large size (4.4 mm), reddish coloration, and very small eyes in dorsal view (separated by a distance 17 × larger than the width of an eye).

Description. Body length 4.4 mm, width 2.4 mm. Body elongate oval, strongly convex (Fig. 2.10B). General coloration reddish brown. Elytra with ground punctures shallowly marked, systematic punctures slightly enlarged, and serial punctures absent. Posterior elevation of mesoventrite with very lowly raised transverse ridge. Metafemora with hydrofuge pubescence covering slightly more than basal half of anterior surface. Apex of fifth abdominal ventrite rounded.

Etymology. Named from the Latin word *ocellatus* which means "having little eyes", in reference to the unusually small eyes of the species.

Distribution. *Primocerus ocellatus* has only been collected at Cerro de la Neblina in the Venezuelan Amazon, at an elevation of 125 m (Fig. 2.15B).

Remarks. The single known specimen is a female that was found in "leaf packs and wood pieces in a small stream".

Primocerus petilus sp. n.

Figs 2.13A–C, 2.14J, 2.15B, 2.16D

Type material. Holotype (male): "BRAZIL: Pará: Alenquer/ -1.49292, -54.51566; 150 m/ Vale do Paraíso, ca. 55 km N. of Alenquer/ tiny wet rock/seepage on trail; 3.ii.2018/ leg. A. Short; BR18-0203-01G" (INPA, DNA voucher specimen SLE 1498).

Differential diagnosis. *Primocerus petilus* can be recognized by the presence of sharply impressed elytral punctures, with serial punctures well differentiated (larger and deeper than remainder punctures), longitudinally aligned to form elytral striae. It is similar to *P. semipubescens*, from which it can be differentiated by the hydrofuge pubescence of the metafemora covering basal 3/4 of the anterior surface (covering less than basal half in *P. semipubescens*). It is also very similar to *P. striatolatus*, from which it can be differentiated by the undefined elytral striae 9 and 10 along the basal fourth of the elytra (Fig. 2.13B; elytral striae 9 and 10 clearly impressed along their entire length in *P. striatolatus*, Fig. 2.13E).

Description. Body length 3.4 mm, width 1.6 mm. Body elongate oval, moderately convex (Fig. 2.12A, B). General coloration dark brown. Elytra with ground punctures sharply marked, and well-defined rows of serial punctures (forming elytral striae); elytral striae very slightly impressed along posterior half of elytra. Posterior elevation of mesoventrite with simple, curved transverse ridge. Metafemora with hydrofuge pubescence covering basal 4/5 of anterior surface. Apex of fifth abdominal ventrite rounded. Aedeagus (Fig. 2.14J) with basal piece nearly 1.3 × longer than parameres; parameres nearly as long as median lobe (median lobe inserted further into basal piece, thus appearing shorter than parameres); apex of parameres narrowly rounded; apex of median lobe widely rounded.

Etymology. Named with the Latin word *petilus* meaning slender, in reference to the relative slenderness of the body in this species.

Distribution. *Primocerus petilus* has only been collected at one locality in the north Brazil, at an elevation of 150 m (Fig. 2.15B).

Remarks. The single known specimen is missing the maxillary palps. It was collected on a temporary wet spot on an exposed forested rock outcrop. The rock was wet when the specimen was collected due to recent rains but was dry by the following day (Fig. 2.16D).

Primocerus pijiguaense sp. n.

Figs 2.12E–H, 2.14G, H, 2.15A, 2.16B

Type material. Holotype (male): "VENEZUELA: Bolívar: 6°35.617'N, 66°49.238'W; 80 m; Los Pijiguaos; morichal/rock outcrop; 14.ix.2007; leg. A. Short, M. García, L. Joly; AS-07-015" (MIZA). **Paratypes (14): VENEZUELA: Bolívar:** same data as holotype (MALUZ, SEMC, 7, including DNA voucher specimen SLE 1029); same, except "6.viii.2008, AS-08-076" (SEMC, 1); same, except "at rock outcrop, seeps and streams at night, 9.vii.2010, leg. Short, Tellez, Arias, VZ10-0709-03A" (SEMC, 1); same, except "rock pools, 7.vii.2010, VZ10-0707-01A" (SEMC, 3, including DNA voucher specimen SLE 444); "6°57.904'N, 66°36.392'W, 51 m, Outcrop ca. 15 Km NE. of los Pijiguaos, detritus flotation, 9.vii.2010, leg. Short & Tellez, VZ10-0709-01B" (SEMC, 1); "7°29'47.3"N, 65°51'44.8"W, 45 m, 2 Km E. of Río Cuchivero, rock outcrop seeps, 6.viii.2008, leg. A. Short, M. García, L. Joly, AS-08-075" (SEMC, 1).

Differential diagnosis. *Primocerus pijiguaense* can be differentiated by the presence of sharply impressed elytral punctures, with serial punctures not differentiated (e.g., they look similar to the ground punctures). It is very similar to *P. maipure*, from which it can be distinguished by the dorsal keel on the apical region of the median lobe and the widely rounded outer margins of the apical region of the parameres (Fig. 2.14G, H; apical region of median lobe simple, non-keeled, and oblique and rather angulate outer margins of the apical region of the parameres in *P. maipure*, Fig. 2.14E, F).

Description. Body length 2.6–3.1 mm, width 0.9–1.7 mm. Body elongate oval, strongly convex (Fig. 2.12F). General coloration dark brown. Elytra with ground punctures sharply marked; serial punctures not differentiated (similar to ground punctation). Posterior elevation of mesoventrite with simple, very lowly raised curved transverse ridge. Metafemora with hydrofuge pubescence limited to anterodorsal surface. Apex of fifth abdominal ventrite rounded. Aedeagus

(Fig. 2.14G, H) with basal piece nearly 1.2 × longer than parameres; parameres nearly as long as median lobe, in lateral view with base perpendicular to longitudinal axis of aedeagus; outer margin of apical region of parameres widely rounded; apical region of median lobe with well-developed dorsal carina.

Etymology. Named after Los Pijiguaos, the type locality for the species.

Distribution. *Primocerus pijiguaense* has been collected at Los Pijiguaos and a few other localities north from it, at elevations between 45 and 80 m (Fig. 2.15A).

Remarks. All collections of this species were made either on small seepages over granite outcrops, or in small rock pools that had formed on the outcrops (e.g., Fig. 2.16B).

Primocerus semipubescens sp. n.

Figs 2.13G–I, 2.15B

Type material. Holotype (male): "GUYANA: Region VIII/ 5°17.823'N, 59°50.000'W; 684 m/ Ayanganna Airstrip, trail from Blackwater Creek Camp to Potaro River/ small forested creek with lots of detritus/ 20.iii.2014; leg. A. Short/ GY14-0320-01A" (CBDG). **Paratypes (1): GUYANA: Region VIII:** 5°18.261'N, 59°50.257'W, 687 m, Ayanganna Airstrip, trail from airstrip to Ayanganna, rotten fruits of *Clusia*; leg. A. Short, 17.iii.2014, GY14-0317-01B (SEMC, DNA voucher SLE 1079).

Differential diagnosis. *Primocerus semipubescens* can be recognized by the presence of sharply impressed elytral punctures, with serial punctures well differentiated (larger and deeper

than remainder punctures), longitudinally aligned to form elytral striae. It can be differentiated by the hydrofuge pubescence of the metafemora covering less than basal half of the anterior surface (covering at least basal 3/4 in *P. petilus* and *P. striatolatus*).

Description. Body length 3.7 mm, width 2.0 mm. Body elongate oval, strongly convex (Fig. 2.13G, H). General coloration dark brown. Elytra with ground punctures sharply marked, and well-defined rows of serial punctures (forming elytral striae); elytral striae not impressed along elytra. Posterior elevation of mesoventrite with simple transverse ridge. Metafemora with hydrofuge pubescence covering less than basal half of anterior surface (Fig. 2.13I). Apex of fifth abdominal ventrite truncate.

Etymology. Named from the Latin word *semis*, meaning half, combined with the word *pubescens*, in reference to the hydrofuge pubescence covering only half of the anterior surface of the metafemora in this species.

Distribution. *Primocerus semipubescens* has only been collected around the Ayanganna airstrip in Guyana, 684–687 m in elevation (Fig. 2.15B).

Remarks. The unique male specimen was collected along the margins of a sandy creek that had lots of detritus.

Primocerus striatolatus sp. n.

Figs 2.13D–F, 2.14K, 2.15B

Type material. Holotype (male): "SURINAME: Sipaliwini District/ 2°58'36.7782"N, 55°24'40.986"W; 400 m/ Camp 4 (high) Kasikasima; White Rock/ seepage area on trail; 24.iii.2012/ leg. A. Short; SR12-0324-01B" (NZCS). **Paratypes (1): SURINAME: Sipaliwini District:** Same data as holotype (SEMC).

Differential diagnosis. *Primocerus striatolatus* can be recognized by the presence of sharply impressed elytral punctures, with serial punctures well differentiated (larger and deeper than remainder punctures), longitudinally aligned to form elytral striae. It is similar to *P. semipubescens*, from which it can be differentiated by the hydrofuge pubescence of the metafemora covering basal 3/4 of the anterior surface (covering less than basal half in *P. semipubescens*). It is also very similar to *P. petilus*, from which it can be differentiated by the elytral striae 9 and 10 clearly impressed along their entire length (Fig. 2.13E; elytral striae 9 and 10 undefined along their basal fourth in *P. petilus*, Fig. 2.13B).

Description. Body length 3.1 mm, width 1.6 mm. Body elongate oval, strongly convex (Fig. 2.13D, E). General coloration dark brown. Elytra with ground punctures sharply marked, and well-defined rows of serial punctures (forming elytral striae); elytral striae very slightly impressed along posterior half of elytra. Posterior elevation of mesoventrite with simple, curved, transverse ridge. Metafemora with hydrofuge pubescence covering basal 4/5 of anterior surface. Apex of fifth abdominal ventrite rounded. Aedeagus (Fig. 2.14K) with basal piece nearly as long as parameres; parameres nearly as long as median lobe (median lobe inserted further into basal piece, thus appearing shorter than parameres); apex of parameres rounded; apex of median lobe rounded.

Etymology. Named from the word *stria*, combined with the Latin word *latus* meaning broad, in reference to the comparatively broad shape of the body and the clearly defined elytral striae in this species.

Distribution. *Primocerus striatolatus* has only been collected at one locality in the Kasikasima region in Suriname, at an elevation of 400 m (Fig. 2.15B).

Remarks. Collected on a forested seepage that had lots of detritus.

ACKNOWLEDGEMENTS

We are grateful for the assistance and support of many colleagues during fieldwork, including Mauricio García (MALUZ), Jesus Camacho (MALUZ), Luis Joly (MIZA), Neusa Hamada (INPA), Cesar Benetti (INPA), Vanessa Kadosoe (NZCS), and Paul Ouboter (NZCS), as well as the curators of the collections listed above for the loan of valuable specimens. We are particularly thankful to the continued assistance of Charyn Micheli (USNM) for access to the Spangler collection and backlog. Fernando Machado (Venezuela) and Vanessa Kadosoe (Suriname) provided name ideas for the new species. Alex Kohlenberg pre-sorted specimens of *Primocerus* from large series of small acidocerines. Albrecht Komarek provided critical reviews, contributing to improve the manuscript. This study was supported by US National Science Foundation grants DEB-0816904 and DEB-1453452 to AEZS. Fieldwork in Suriname and Guyana was partly funded by Conservation International and WWF-Guianas respectively. Fieldwork in Brazil was partly funded by a Fulbright fellowship to AEZS. The expedition to Tafelberg Tepui (Suriname) was

funded by grant #9286-13 from the National Geographic Society Committee for Research and Exploration to AEZS.

REFERENCES CITED

Clarkson B, Ferreira-Jr N (2014b) Four new species and first nominal record of *Chasmogenus* Sharp, 1882 (Coleoptera: Hydrophilidae) from Brazil. Zootaxa 3765(5): 481–494. https://biotaxa.org/Zootaxa/article/view/zootaxa.3765.5.6

García M (2001) Nueva subtribu, género y especie de Hydrophilini (Coleoptera: Hydrophilidae) del extremo suroriental de Venezuela. Boletín del Centro de Investigaciones Biológicas Universidad del Zulia 35: 151–160. http://produccioncientificaluz.org/index.php/boletin/article/view/3978

Girón JC, Short AEZ (2017) Revision of the Neotropical water scavenger beetle genus *Quadriops* Hansen, 1999 (Coleoptera: Hydrophilidae: Acidocerinae). ZooKeys 705: 115–141. https://doi.org/10.3897/zookeys.705.19815

Girón JC, Short AEZ (2018) Three new genera of acidocerine water scavenger beetles from tropical South America (Coleoptera, Hydrophilidae, Acidocerinae). ZooKeys 768: 113–158. https://doi.org/10.3897/zookeys.768.24423

Hansen M (1991) The hydrophiloid beetles. Phylogeny, classification and a revision of the genera (Coleoptera: Hydrophilidae). Biologiske Skrifter 40: 1–367.

Hansen M (1999) Fifteen new genera of Hydrophilidae (Coleoptera), with remarks on the generic classification of the family. Insect Systematics & Evolution 30(2): 121–172. https://doi.org/10.1163/187631200X00228

Fernández LA (2006) Two new species of *Enochrus* Thomson (Coleoptera, Hydrophilidae) from the Neotropical Region. Transactions of the American Entomological Society 132(3): 279-284. https://doi.org/10.3157/0002-8320(2006)132[279:TNSOET]2.0.CO;2

Fikáček M, YN Minoshima, AF Newton (2104) A review of *Andotypus* and *Austrotypus* gen. nov., Rygmodine genera with an Austral disjunction (Hydrophilidae: Rygmodinae). Annales Zoologici 64(4): 557-597. https://doi.org/10.3161/000345414X685893

Kohlenberg, AT, Short AEZ (2017) Revision of the Neotropical water scavenger beetle genus *Tobochares* Short & García, 2007 (Coleoptera, Hydrophilidae, Acidocerinae). ZooKeys 669: 113–146. https://doi.org/10.3897/zookeys.669.11773

Komarek A (2004) Taxonomic revision of *Anacaena* Thomson, 1859. I. Afrotropical species (Coleoptera: Hydrophilidae). Koleopterologische Rundschau 74: 303–350.

Lawrence J, Ślipiński A (2013) Australian Beetles: morphology, classification and keys. CSIRO Publishing, Melbourne, Australia, 576 pp.

Minoshima, YN, Komarek, A, Ôhara, M (2015) A revision of *Megagraphydrus* Hansen (Coleoptera, Hydrophilidae): synonymization with *Agraphydrus* Régimbart and description of seven new species. Zootaxa 3930: 1–63. http://dx.doi.org/10.11646/zootaxa.3930.1.1

Short AEZ, M García (2014) A new genus of egg case-carrying water scavenger beetle from the Guiana Shield (Coleoptera: Hydrophilidae: Acidocerinae). Zootaxa 3835(2): 251–262. https://biotaxa.org/Zootaxa/article/view/zootaxa.3835.2.5

Short AEZ, Fikáček M (2013) Molecular Phylogeny, Evolution, and Classification of the Hydrophilidae (Coleoptera). Systematic Entomology 38: 723–752. https://doi.org/10.1111/syen.12024

Shorthouse, DP (2010) SimpleMappr, an online tool to produce publication-quality point maps. [Retrieved from http://www.simplemappr.net, accessed November 26, 2018].

Velázquez de Castro AJ (1998) Morphology and taxonomy of the genus *Sitona* Germar 1817, (I): The metendosternite (Col., Curc.). In: Colonnelli E, Louw S, Osella G (Eds) 2. Taxonomy, ecology and distribution of Curculionoidea (Coleoptera: Polyphaga). XX International Congress of Entomology, Florence (Italy), August 1996. Atti del Museo Regionale di Scienze Naturali, Torino, 109–123.

Chapter 3: Taxonomy, Classification, and Catalog of the subfamily Acidocerinae (Coleoptera: Hydrophilidae)

ABSTRACT

The cosmopolitan subfamily Acidocerinae (Coleoptera: Hydrophilidae) is one of the largest and most taxonomically challenging lineages of water scavenger beetles. Recent phylogenetic studies have substantially advanced our understanding of acidocerine relationships but also illuminated the twin challenges of (1) poorly delineated generic concepts, and (2) a classification broadly incompatible with the phylogeny. Here, we address these two challenges by comprehensively reviewing and morphologically circumscribing all 23 genera currently recognized within the Acidocerinae. The following nomenclatural acts are proposed to bring the phylogeny and classification in alignment: *Colossochares* **gen. nov.** is established to accommodate two African species previously described as *Helochares* (s. str.). *Novochares* **gen. nov.** is newly established to accommodate 15 Neotropical species previously included in *Helochares* (s. str.). *Peltochares* is hereby redefined to include eight Old World species previously included in *Helochares* (s. str.). A lectotype is designated for *Peltochares conspicuus*, the type species of the genus. The taxonomic and morphological circumscription of *Helochares* is narrowed and redefined. Generic diagnoses, habitus images, and summarized information, including distributions, are presented. A taxonomic catalog is provided for the 469 species of acidocerines recognized as of 1 November 2019, including synonymy lists, published distributions, and associated references.

RESUMEN

La cosmopolita subfamilia Acidocerinae (Coleoptera: Hydrophilidae) es uno de los linajes más diversos y taxonómicamente más desafiantes de escarabajos acuáticos detritívoros. Estudios filogenéticos recientes han avanzado sustancialmente nuestro entendimiento de las relaciones entre acidocerinos, así como iluminado nuevos desafíos: (1) conceptos genéricos pobremente delineados, y (2) una clasificación ampliamente incompatible con la filogenia. Aquí abordamos estos dos desafíos mediante una revisión comprehensiva y una circunscripción morfológica de los 23 géneros actualmente reconocidos en Acidocerinae. Se proponen los siguientes actos taxonómicos para alinear la filogenia y la clasificación: *Colossochares* **gen. nov.** se establece para acomodar dos especies africanas descritas previamente como *Helochares* (s. str.). *Novochares* **gen. nov.** se establece como nuevo para acomodar 15 especies neotropicales previamente incluidas en *Helochares* (s. str.). *Peltochares* **sensu nov.** es redefinido para incluir ocho especies del viejo mundo previamente incluidas en *Helochares* (s. str.). Un lectotipo se designa para *Peltochares conspicuus*, la especie tipo del género. La circunscripción taxonómica y morfológica de *Helochares* **sensu nov.** se reduce y redefine. Se presentan diagnosis genéricas, imágenes del hábito y resúmenes de información, incluyendo distribuciones. Se provee un catálogo para las 469 especies de acidocerinos reconocidas a noviembre 1 de 2019, incluyendo listas de sinónimos, distribuciones publicadas y referencias asociadas.

Keywords: aquatic beetles; taxonomy; new taxa; nomenclature

INTRODUCTION

Water scavenger beetles in the family Hydrophilidae Latreille, with nearly 3,000 described species, comprise the most diverse family of polyphagan aquatic beetles, and the second largest for all aquatic Coleoptera (Short 2018). This diversity is reflected not just in their species richness but also in their ecological habits: members of the family are associated not only with aquatic, but also various hygropetric and terrestrial habitats. Relatively recently, Short and Fikáček (2013) inferred a comprehensive molecular phylogeny for the family in which six subfamilies were recognized: Hydrophilinae Latreille, Chaetarthriinae Bedel, Enochrinae Thomson, Acidocerinae Zaitzev, Cylominae Zaitzev (changed from Rygmodinae d'Orchymont, see Seidel et al. 2016), and Sphaeridiinae Latreille. We focus here on the subfamily Acidocerinae, which occupies an intermediate position in the phylogeny, descending from the primarily aquatic Hydrophilinae, Chaetarthriinae and Enochrinae, and in sister relationship with the mostly terrestrial Cylominae+Sphaeridiinae.

In morphological terms, Acidocerinae is a fairly heterogeneous assemblage on a broad scale, as a subfamily, given the variety of sizes, colorations and body shapes that can be found in the group (see Figs. 3.1, 3.2). They range in size from 1.2 mm (*Nanosaphes* Girón and Short; see Figs 3.2J, 3.41) to 14 mm (*Colossochares* **gen. nov.**; see Figs 3.1A, 3.24), range in color from pale yellowish and orange brown to nearly black, with body shapes from compact and convex (e.g., *Globulosis* García; see Figs 3.2G, 3.31) to broadly explanate and dorsoventrally compressed (e.g., *Helobata* Bergroth (see Figs 3.1J, 33), *Helopeltarium* d'Orchymont (see Figs 1H, 38). Most genera

are relatively easy to tell apart, however, within a genus, the external morphology ranges from extremely homogeneous (e.g., *Aulonochares* Girón and Short; see Figs 3.1D, 3.18) to highly variable (e.g., *Primocerus* Girón and Short (see Figs 3.2D, 3.46), *Agraphydrus* Régimbart (see Figs 3.2A–C, 3.15, 3.16)).

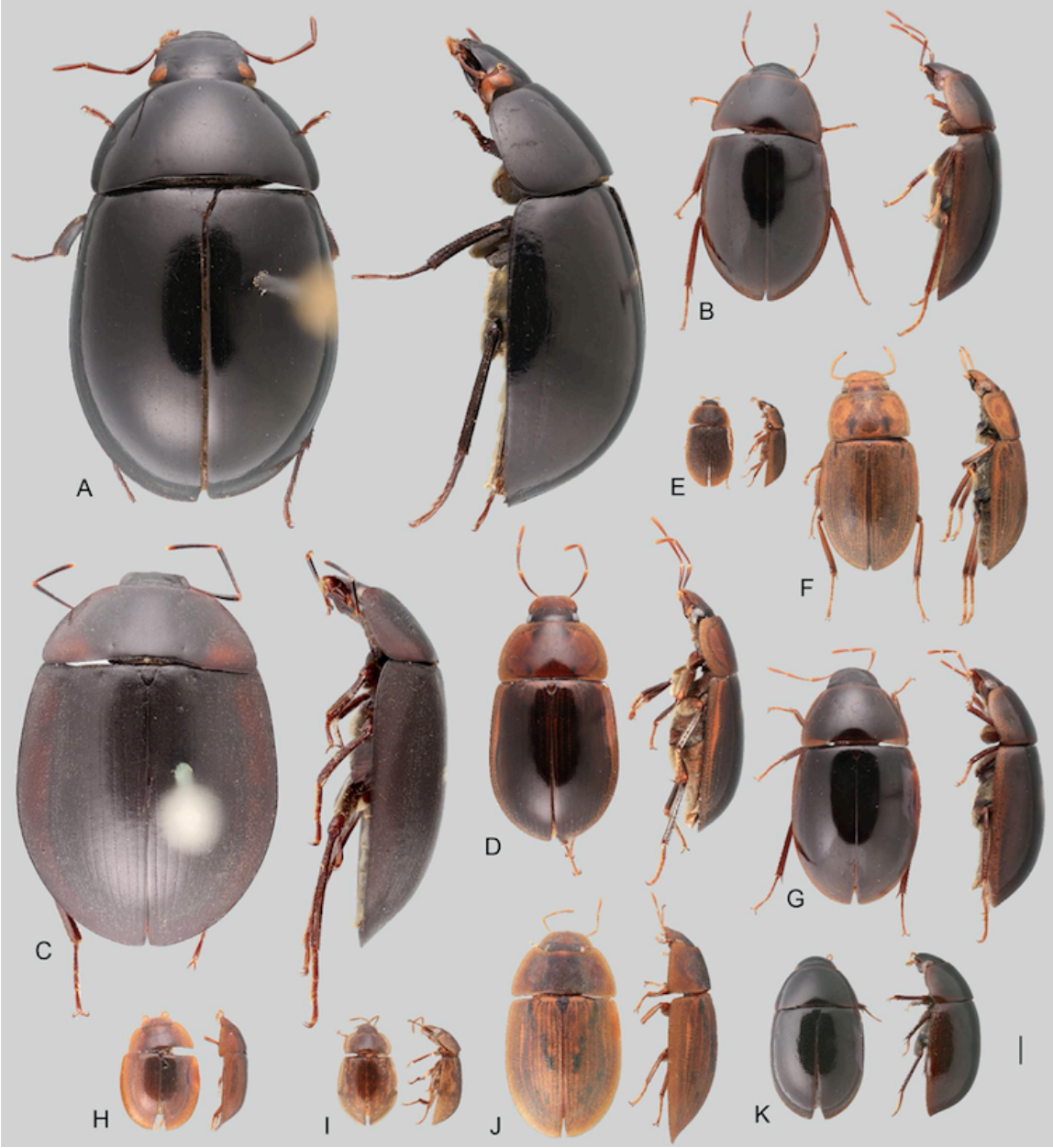


Figure 3.1. Variation across Acidocerinae, dorsal and lateral views: *Helochares*-group: **A** *Colossochares ellipticus*, **B** *Peltochares* sp., **C** *Peltochares conspicuus*, **D** *Aulonochares tubulus*, **E** *Helochares* sp., **F** *Helochares tristis*, **G** *Novochares* sp., **H** *Helopeltarium ferrugineum*, **I** *Batochares* sp., **J** *Helobata larvalis*, **K** *Radicitus* sp. Scale bar 1 mm.

Figure 3.2. Variation across Acidocerinae, dorsal and lateral views: *Agraphydrus*- **(A–C)**, *Primocerus*- **(D)**, *Chasmogenus*- **(E)**, and *Tobochares*- **(F–J)** groups: **A** *Agraphydrus* cf. *attenuatus*, **B** *Agraphydrus coomani*, **C** *Agraphydrus* sp., **D** *Primocerus neutrum*, **E** *Crephelochares nitescens*, **F** *Quadriops similaris*, **G** *Globulosis flavus*, **H** *Tobochares* sp., **I** *Tobochares sulcatus*, **J** *Nanosaphes tricolor*. Scale bar 1 mm.

Although the circumscription of the subfamily is well supported by several molecular studies (Short and Fikáček 2013, Short et al. in prep.) the morphological diversity of acidocerines has complicated defining generalizations, as every putative synapomorphy for the lineage has at least one exception. This morphological diversity may be a consequence of the broad range of

habitats where acidocerines can be found, and compounded by the widespread distribution of some taxa, which has resulted in confusion in terms of taxonomic classification. Acidocerine species can be found across the wide variety of environments described above for the Hydrophilidae, including fully aquatic settings like ponds, streams and river margins, hygropetric habitats like rock seepages, or terrestrial niches like rotting fruits.

Taxonomic history and composition of the Acidocerinae

Horn (1873) established the monogeneric tribe Helopeltini for the newly established genus *Helopeltis* (now *Helobata*; see Figs. 3.1J, 3.33). Horn (1873) viewed the genus as quite different and warranting its own tribe based on the broadly explanate body form, concealed labrum, and long maxillary palpi (he retained *Helochares*, the only other Acidocerine [in the current sense] in North America at the time, as within the Hydrobiini with most other hydrophilids). However, Helopeltini was unavailable due to its type genus *Helopeltis* being a preoccupied name (Hansen 1999b). Later, Zaitzev (1908) placed the genus *Acidocerus* Klug (see Fig. 3.14) into its own “subfamily” under the new name Acidocerini without comment. It is unclear why he considered the taxon so unique as to give it such a prominent rank in his classification, which placed it equal to the rank he considered for Epimetopidae, Spercheidae, and other currently recognized hydrophilid families. A decade later, d’Orchymont (1919c), either unaware or unconcerned with the Acidocerini of Zaitzev, proposed the subtribe Helocharae for *Helochares*, *Enochrus* and their apparent relatives (including *Acidocerus*). Unlike Helopeltini and Acidocerini, the erection of Helocharae was not done to bestow recognition on a single bizarre

taxon, but to unite a morphologically similar collection of genera. The name and concept of the Helocharae (either as a subtribe of Hydrobiini or as the tribe Helocharini (of Hydrobiinae) remained in use for the next 70 years.

Hansen (1991) was the first to both recognize Zaitzev's Acidocerini as having priority over Helocharae and to affirm the circumscription of the lineage in a phylogenetic context (as the subtribe Acidocerina of Hydrophilini). Twenty years later, Short and Fikáček (2011), elevated the Acidocerini to tribal level, citing accumulating evidence that the Hydrophilini *sensu* Hansen was not monophyletic. In a subsequent comprehensive molecular phylogeny and reclassification of the Hydrophilidae, Short and Fikáček (2013) elevated the lineage further to its current subfamily rank, while transferring *Enochrus* Thomson, *Cymbiodyta* Bedel, and *Helocombus* Horn from the Acidocerinae into the newly defined subfamily Enochrinae. This circumscription has remained unchanged to date.

In terms of diversity, Acidocerinae included nearly 300 species grouped in 14 genera when it was first recognized as a subfamily (*Acidocerus*, *Agraphydrus*, *Chasmogenus* Sharp, *Dieroxenus* Spangler, *Globulosis*, *Helochares*, *Helobata*, *Helopeltarium*, *Horelophopsis* Hansen, *Megagraphydrus* Hansen, *Peltochares*, *Quadriops* Hansen, *Tobochares* Short and García, and *Troglochares* Spangler; Short and Fikáček 2013). Since then, six genera have been described (*Crucisternum* Girón and Short , *Katasophistes* Girón and Short, and *Nanosaphes*, see Girón and Short 2018; *Aulonochares*, *Primocerus*, and *Ephydrolithus* Girón and Short, see Girón and Short

2019), and two genera have been synonymized (*Dieroxenus* syn. of *Chasmogenus*; see Girón and Short 2018; *Horelophopsis* syn. of *Agraphydrus*; see Short et al. in prep.).

The most comprehensive molecular phylogenetic analyses of the subfamily Acidocerinae were recently conducted (Short et al. in prep.). The dataset included DNA sequence data for the mitochondrial gene COI, and the nuclear genes 18S, 28S, H3, and CAD, for 206 acidocerine and eleven outgroup terminals (Short et al. in prep.). These analyses confirmed the monophyly of the subfamily, as well as of most genera, with the unsurprising exception of a polyphyletic *Helochares* (see Figs. 3.3–3.6).

The *Helochares* problem

At the time Acidocerinae was elevated to subfamily, *Helochares* was its largest and most widespread genus, grouping nearly two thirds of the species in the subfamily. *Helochares* has been traditionally divided into five subgenera: *Batochares* Hansen (e.g., Figs. 3.1I, 3.20), *Helochares* (e.g., Fig. 3.1B), *Helocharimorphus* Kuwert (e.g., Fig. 3.35), *Hydrobaticus* MacLeay (e.g., Figs. 3.34, 3.36A–C) and *Sindolus* Sharp (e.g., Fig. 3.52), some of which were recognized mostly by the absence (*Helochares* (s. str.)) or presence (*Helochares* (*Hydrobaticus*)) of rows of serial punctures along the elytra.

The phylogeny presented by Short et al. (in prep.; see Figs. 3.3–3.6) provided evidence for elevating *Batochares* and *Sindolus* to full generic status, as well as for synonymizing

Helocharimorphus and *Hydrobaticus* with *Helochares*. Nevertheless, there are several taxonomic issues within *Helochares* left unresolved, which we aim to sort out here. In addition, it is now clear that the presence of rows of serial punctures along the elytra is not necessarily a reliable character to recognize genera (or subgenera) within Acidocerinae, whereas the configuration of the male genitalia, which is much more conserved within clades, is very useful for recognizing allied species.

Updating the classification of the Acidocerinae

Based on their phylogeny, Short et al. (in prep.) defined five monophyletic genus-groups within the Acidocerinae: the *Primocerus*-group (including only *Primocerus*; see Fig. 3.3), *Helochares*-group (including *Helochares* (see Fig. 3.3), *Colossochares* gen. nov., *Batochares*, *Aulonochares*, *Peltochares*, *Helobata*, *Radicitus*, *Sindolus*, and *Novochares* gen. nov.; see Fig. 3.4), *Agraphydrus*-group (including only *Agraphydrus*; see Fig. 3.5), *Chasmogenus*-group (*Chasmogenus* and *Crephelochares*; see Fig. 3.5), and *Tobochares*-group (*Katasophistes*, *Ephydrolithus*, *Globulosis*, *Quadriops*, *Nanosaphes*, *Crucisternum*, and *Tobochares*; see Fig. 3.6).

Here, we recognize 23 genera within Acidocerinae. We summarize information for each genus including diagnoses, habitus images, biological and ecological information, as well as distributions. We also include a full catalog for the 469 species of acidocerines described to date, including synonyms, distributions, and references.

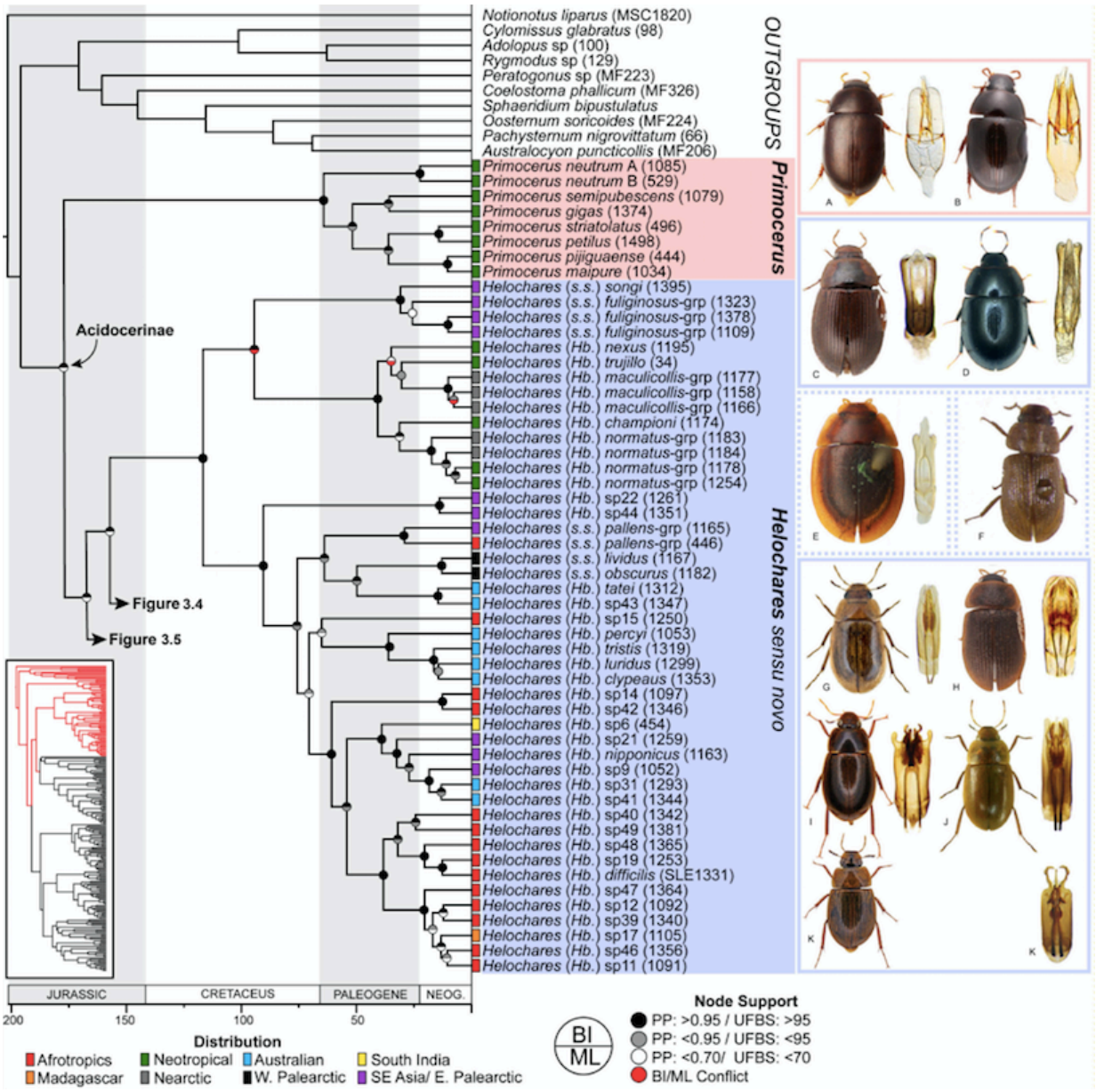


Figure 3.3. Part one of the time-calibrated Bayesian phylogeny by Short et al. (in prep.): *Primocerus* and *Helochares*. Right panel illustrates dorsal views and genitalias of representative species of major clades: **A** *Primocerus pijigueanse*, **B** *Primocerus petilus*, **C** *Helochares maculicollis*, **D** *Helochares songi* (taken from Jia and Tang 2018), **E** *Helopeltarium ferrugineum*, **F** *Acidocerus aphodiodes*, **G** *Helochares pallens*, **H** *Helochares* sp., **I** *Helochares dilutus*, **J** *Helochares lividus*, **K** *Helochares* sp. Bottom panel includes key for distribution and node support.

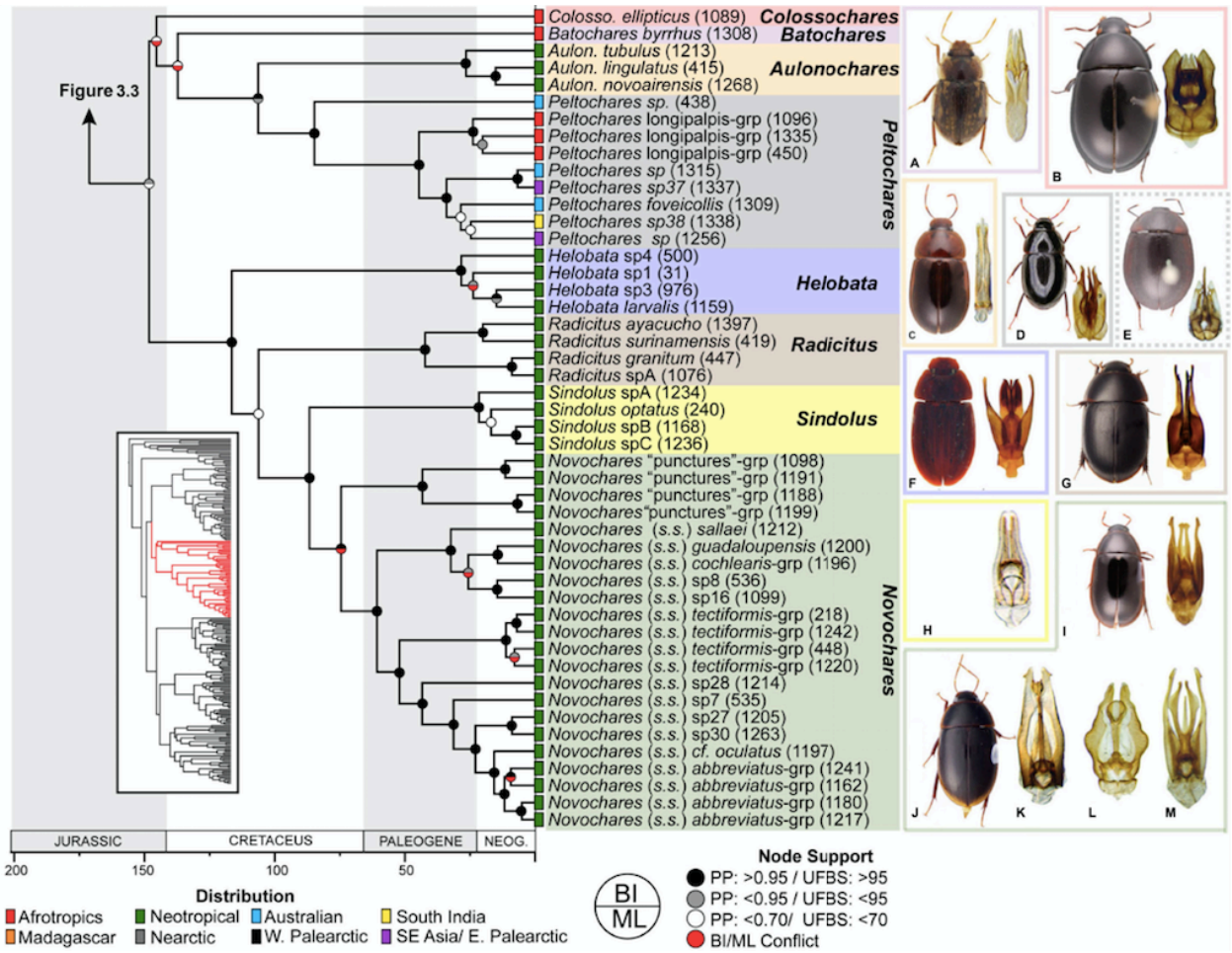


Figure 3.4. Part two of the time-calibrated Bayesian phylogeny by Short et al. (in prep.): *Colossochares* through *Novochares*. Right panel illustrates dorsal views and genitalias of representative species of major clades: A *Batochares* sp., B *Colossochares ellipticus*, C *Aulonochares tubulus*, D *Helochares* sp., E *Peltochares conspicuus*, F *Helobata quatipuru* (taken from Clarkson et al. 2016), G *Radicitus ayacucho*, H *Sindolus* sp., I *Novochares* sp., J *Novochares* sp., K *Novochares* sp., L *Novochares* sp., M *Novochares* sp. Bottom panel includes key for distribution and node support.

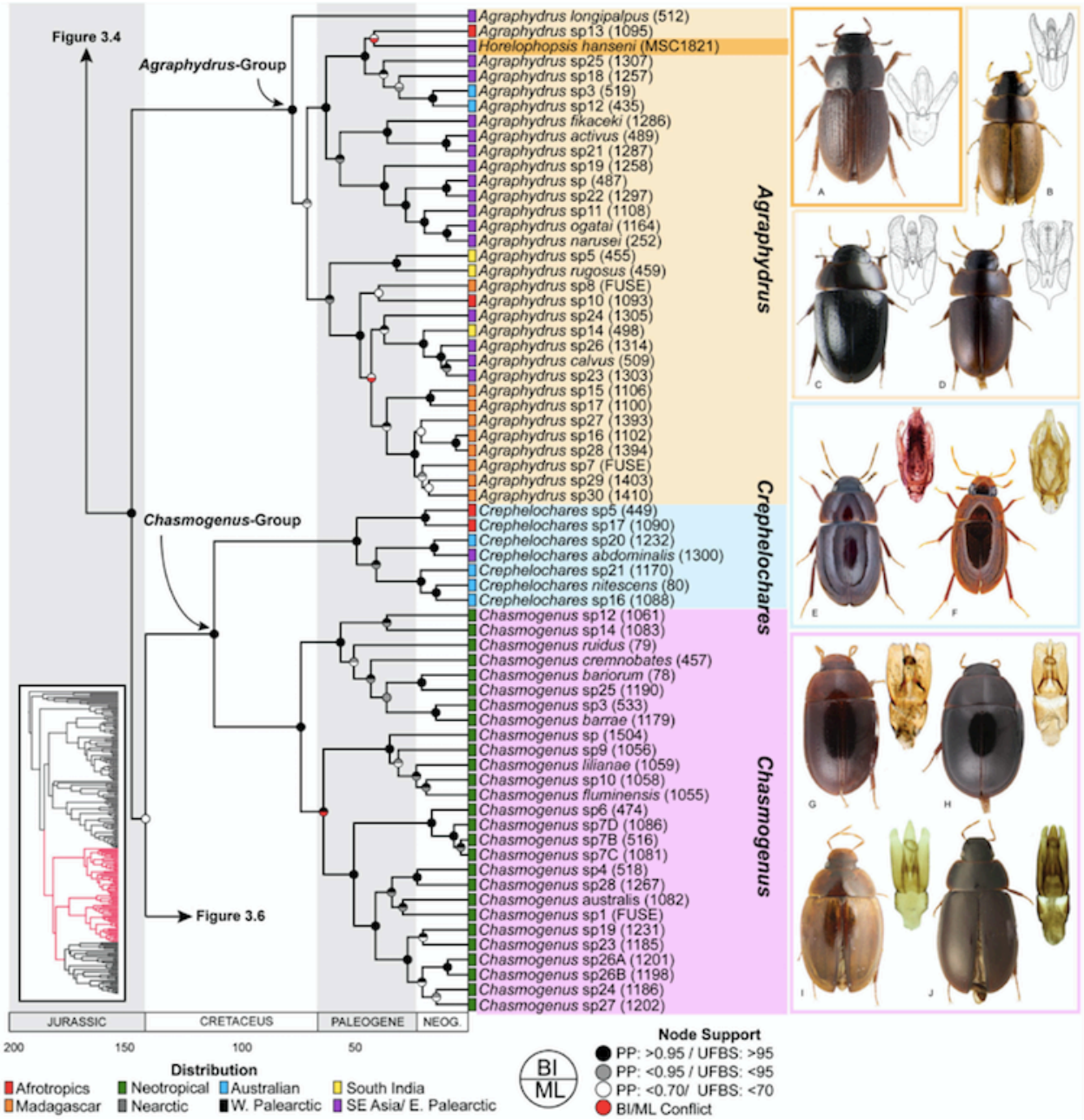


Figure 3.5. Part three of the time-calibrated Bayesian phylogeny by Short et al. (in prep.). Right panel illustrates dorsal views and genitalias of representative species of major clades: *Agraphydrus*, *Crephelochares* and *Chasmogenus*: **A** *Horelophopsis hanseni*, **B** *Agraphydrus coomani*, **C** *Agraphydrus insidiator*, **D** *Agraphydrus ogatai*, **E** *Crephelochares abdominalis*, **F** *Crephelochares* sp., **G** *Chasmogenus ruidus*, **H** *Chasmogenus cremnobates*, **I** *Chasmogenus fluminensis*, **J** *Chasmogenus itatiaia*. Images B–D taken from Minoshima et al. (2015). Images I, J taken from Clarkson and Ferreira-Jr (2014b). Bottom panel includes key for distribution and node support.

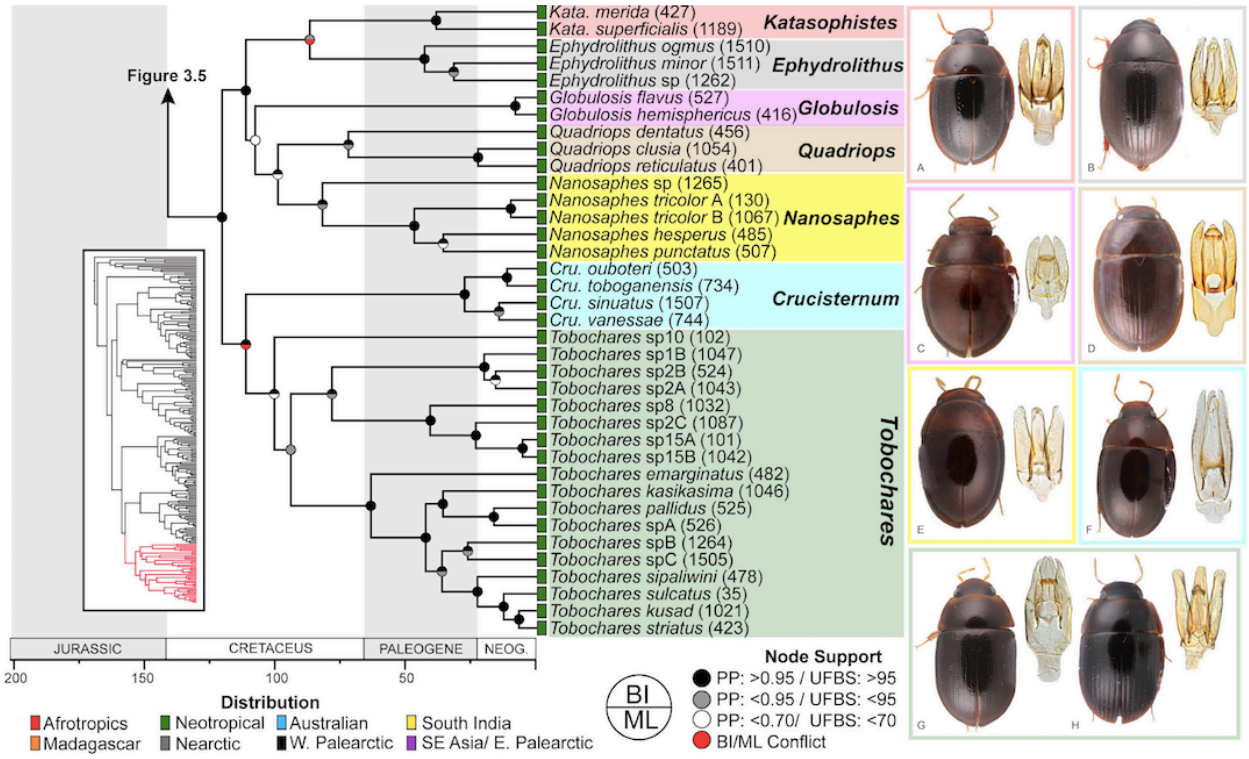


Figure 3.6. Part four of the time-calibrated Bayesian phylogeny by Short et al. (in prep.). Right panel illustrates dorsal views and genitalias of representative species of major clades: *Katasophistes* through *Tobochares*: **A** *Katasophistes merida*, **B** *Ephydrolithus ogmus*, **C** *Globulosis hemisphericus*, **D** *Quadriops similaris*, **E** *Nanosaphes punctatus*, **F** *Crucisternum ouboteri*, **G** *Tobochares* sp., **H** *Tobochares sipaliwini*. Bottom panel includes key for distribution and node support.

Novochares **gen. nov.** is newly established to accommodate 15 Neotropical species previously described as *Helochares* (s. str.) (see Fig. 3.4; *Helochares* Clade D in Short et al. in prep.). *Colossochares* **gen. nov.** is established to accommodate two African species previously described as *Helochares* (s. str.) (see Fig. 3.4; *Helochares* Clade B in Short et al. in prep.). *Peltochares* is hereby redefined to include eight Old World species previously described as *Helochares* (s. str.) (*Helochares* Clade C in Short et al. in prep.; see Fig. 3.4); a lectotype is designated for its type species *P. conspicuus* Régimbart. *Helochares* is redefined, including 153 species world-wide distributed (see Fig. 3.3, *Helochares* Clade A in Short et al. in prep.). After the

publication of a series of revisions of the genus *Agraphydrus* (see Komarek and Hebauer 2018, Komarek 2018, Komarek 2019), *Helochares* is now the second largest genus in number of species only by a few.

MATERIALS AND METHODS

Morphological methods. Specimen preparation and examination methods are identical to those given in Girón and Short (2017). For each genus, a list of diagnostic character states is provided, followed by notes comparing it to similar genera. Morphological terminology largely follows Hansen (1991) except for the use of meso- and metaventrite instead of meso- and metasternum, and terminology for veins and areas of the hind wings (see Lawrence and Ślipiński 2013). Diagnoses of genera and species lists are organized in alphabetical order. Figures illustrating each genus are arranged in alphabetical sequence, but within each plate, images are organized to display variation.

Distributional data. For consistency, we followed the biogeographic regions as delimited by Hansen (1999b) with the following exceptions for convenience: Saudi Arabia is here treated entirely as Afrotropical (rather than split between Afrotropical and Palearctic regions), and India is considered entirely Indo-Malayan (rather than being split between the Indo-Malayan and Palearctic regions) (Fig. 3.7).

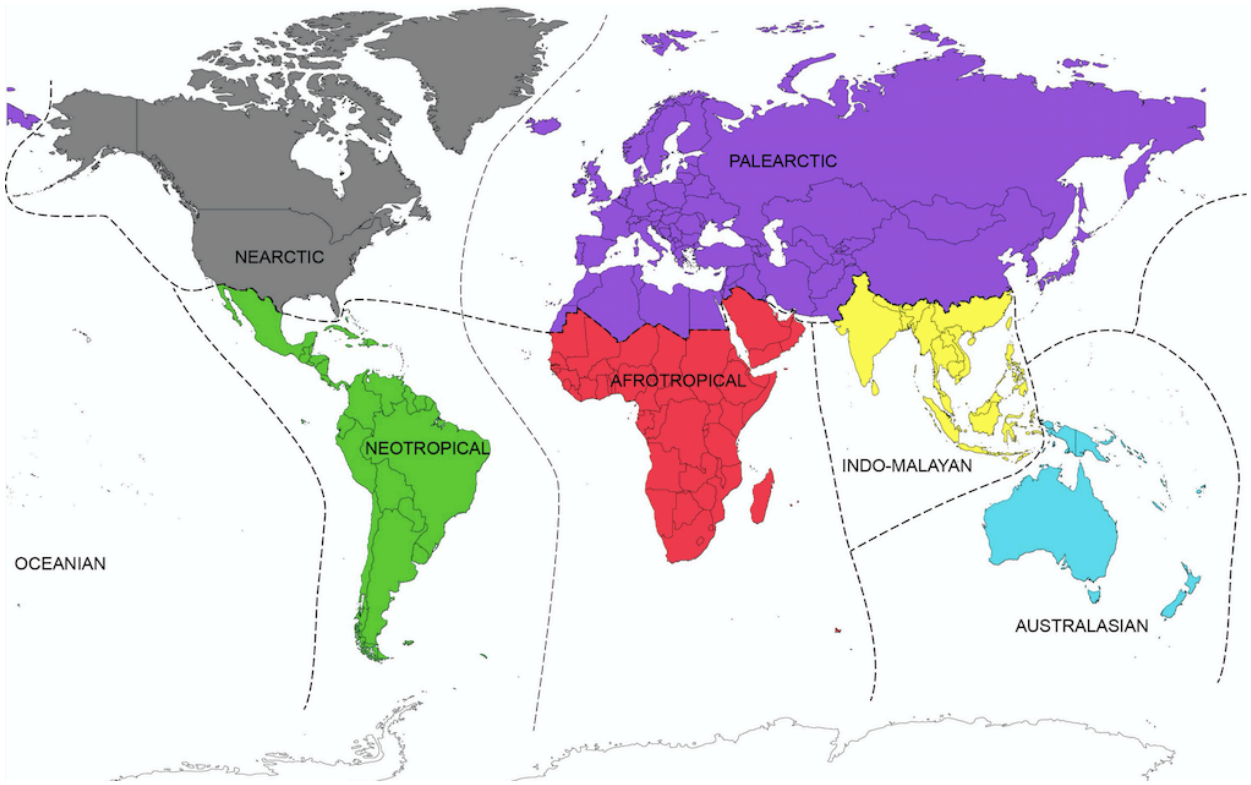


Figure 3.7. World map with biogeographic regions modified from Hansen (1999b).

Current numbers of species per genus have been consolidated and are presented for each of the regions where acidocerines occur. Known distributional information obtained from the literature has been summarized for each species and included in the catalog.

Catalog. Each current genus or species name is followed by its original name including its full reference. A list of subsequent names and references, in chronological order, is also included where appropriate, indicating in square brackets the kind of reference involved, for example, [checklist], [redescription], [taxonomic treatment], etc. Page numbers where the taxon name appears in the text are given for each reference using colon ":" after the publication year. For the

most part, the list of names is based on Hansen's (1999b) catalogue; additional references are also listed. Species described between 1999 and November 2019 are added to this catalog.

RESULTS

Subfamily Acidocerinae Zaitzev, 1908

Acidocerini Zaitzev, 1908: 353, as subfamily.

as subtribe Acidocerina [of tribe Hydrophilini, subfamily Hydrophilinae] in Hansen (1991: 282; 1999b: 155).

as tribe [of subfamily Hydrophilinae] in Short and Fikáček (2011: 85).

as subfamily in Short and Fikáček (2013: 741).

Helopeltini Horn, 1873: 118; synonymized by Hansen (1991: 282); unavailable: generic name is preoccupied (ICZN 1999, Code Art. 39).

Type genus: *Helopeltis* Horn, 1873: 137 [syn. of *Helobata* Bergroth, 1888: 221].

Helocharae d'Orchymont, 1919c: 147; described as subtribe, synonymized by Hansen (1991: 282).

Type genus: *Helochares* Mulsant, 1844a: 197.

Horelophopsinae Hansen, 1997: 108.

Type genus: *Horelophopsis* Hansen, 1997: 109; synonymized by Short and Fikáček (2013: 15, in table, discussed along the text).

Globulina García, 2001: 153; emended to Globulosina by Short and Hebauer (2006: 338); synonymized with tribe Acidocerini by Short and Fikáček 2011: 84.

Type genus: *Globulosis* García, 2001: 153.

Type genus. *Acidocerus* Klug, 1855: 649.

Diagnosis. Body length 1.2–14.0 mm. Body shape oval in dorsal view, dorsoventrally flattened, or weakly to strongly convex in lateral view (Figs. 3.1, 3.2); surface even (without elevations or depressions), granulate (e.g., Figs. 3.14, 3.33) or smooth on head and pronotum. From yellowish to dark brown in coloration (Figs. 3.1, 3.2), usually uniform, sometimes different regions of body colored differently. Shape of head variable (trapezoid, subquadrate, round; see Fig. 3.9E–L). Anterior corners of frons sometimes extended posteriorly forming canthus and emarginating anterior margin of eyes (e.g., *Tobochares*, *Helobata*; e.g., Fig. 3.9B, C). Eyes varying in size, shape, degree of emargination, and degree of projection from outline of head (Fig. 3.9E–L); absent only in cavernicolous genus *Troglochares* Spangler, 1981a. Clypeus variable in shape (rectangular to trapezoid; Fig. 3.9E–L), with anterior margin from straight to mesally emarginate. Labrum usually exposed; concealed by clypeus in *Helobata* (Fig. 3.9L) and *Helopeltarium*. Mentum usually wider than long, with strong median anterior depression, may be limited by low transverse carina (Fig. 3.10A–C); surface of mentum with variable sculpture, ranging from smooth (Fig. 3.10A) to roughly puncturate or obliquely strigate (Fig. 3.10B). Antennae with eight or nine antennomeres (Fig. 3.10D, E), with cupule varying in symmetry and shape. Maxillary palpi curved inward, ranging from very short (nearly half width of the head; e.g., *Quadriops reticulatus*, see Fig. 3.10C) and stout, to very long and slender (nearly twice the width of the head; e.g., *Peltochares*, see Fig. 3.9K). Pronotum evenly convex, usually with systematic punctures forming paired anterolateral semicircles and paired short posterolateral transverse

bands. Elytra with or without sutural striae, with outer margins simple, slightly flared, or laterally explanate; elytral punctation variable (see Fig. 3.8). Hindwings usually well developed (see Fig. 3.12). Surface of prosternum flat (e.g., Fig. 3.11A, B), convex or rarely medially carinate (e.g., *Crucisternum*; see Fig. 3.27C), with anterior margin straight or anteriorly projected. Posterior elevation of mesoventrite either only weakly bulging or with transverse or longitudinal ridge (e.g., Fig. 3.11E, G; with strongly produced, anteriorly pointed and longitudinally carinate transverse ridge in *Crucisternum*; see Fig. 3.11C). Anapleural sutures variable in shape and orientation. Metaventrite rather uniformly covered by hydrofuge pubescence (e.g., Fig. 3.11E), sometimes with posteromesal glabrous patch (e.g., *Tobochares*, Fig. 3.11F, G), sometimes also with posterolateral glabrous patches (e.g., *Nanosaphes*, Fig. 3.11D). Protibiae with anterior row of spines varying in shape and development; apical spurs of protibiae varying in development. Metafemora with tibial grooves of varying development; hydrofuge pubescence on anterior surface of metafemora absent, reduced to only basal or dorsal patch, or increasingly covering most of surface. Tarsomeres 5-5-5; metatarsomeres variable in size, proportions, and dorsal and ventral coverage. Abdomen with five pubescent ventrites, density of setae ranging from sparse to very dense. Fifth abdominal ventrite with apex either rounded, truncate, or emarginate; apex with or without fringe of flat and stout setae. Aedeagus usually symmetrical (see Fig. 3.13), with basal piece varying in size from longer than parameres (e.g., *Primocerus* (see Fig. 3.47), *Batochares* (see Fig. 3.21A)), to reduced and virtually absent (e.g., *Peltochares*; see Fig. 3.45); parameres highly variable in shape, either slender and only connected to each other at base of ventral surface, or fused together forming tube-like structure (see Fig. 3.13K–O; e.g., New World *Helochares* see Short and Girón (2018)); apex of parameres either simple, or bifurcated and

modified with hooks and spines; median lobe either simple or with dorsal and ventral lobes, with well-developed lateral basal apodemes; further modifications (longitudinal divisions, presence of internal hooks and spines, development of gonopore) widespread.

Differential diagnosis. Acidocerines can be generally recognized by their oval and moderately convex body shapes with slender maxillary palpi and uniformly slender tibiae (usually strongly convex and sometimes rounded in Cylominae and Sphaeridiinae, with short and stout maxillary palpi and stout to apically broadened tibiae). The maxillary palpi are always curved inwards in Acidocerinae (maxillary palpomere 2 with inner margin straight to concave), with all palpomeres similar in length and proportions (curved outwards, zig-zag oriented, or with shorter palpomere 3 in most Enochrinae and Chaetarthriinae). In addition, Acidocerines always bear five tarsomeres on the meso- and metatarsi (four in some enochrines).

Distribution. Acidocerines can be found in all biogeographic regions except the Antarctic.

Natural history. Members of the subfamily can be found in a broad range of habitats. In aquatic habitats such as ponds, marshes, forest pools, waterfalls, streams and their margins, the beetles can be found freely swimming in the water column or clinging to submerged vegetation. In hygropetric habitats (rock seepages), the beetles usually crawl over the surface of rocks while submerged in a thin layer of flowing water. They can also be found in terrestrial habitats like rotten fruits, which are usually wet. Females of the *Helochares*-group are known to carry their egg-sac below the abdomen.

Larvae. From the 469 acidocerine species, immature stages are only known for 19 species in seven different genera until now. Information is summarized in Table 3.1.

Table 3.1. Summary of information on immature stages of Acidocerinae. Origin refers to the country where the adults, eggs, or larvae were collected according to the provided references.

Species	Origin	Described stages	References
Agraphydrus hanseni (Satô and Yoshitomi)	Japan	Third larval instar	Minoshima et al. 2013
Agraphydrus narusei (Satô)	Japan	First and third larval instars	Minoshima and Hayashi 2011
Crephelochares nitescens (Fauvel) [as *Helochares nitescens*; *Chasmogenus nitescens*]	Australia	Eggs, egg case, first and third instar larvae, pupa	Anderson 1976; Archangelsky 1997
Helobata larvalis (Horn)	Guatemala	Egg case, first larval instar	Spangler and Cross 1972; Archangelsky 1997
Helochares anchoralis Sharp	Japan	First instar larva	Minoshima and Hayashi 2011
Helochares clypeatus (Blackburn)	Australia	Third instar larva	Watts 2002
Helochares foveicollis (Montrouzier)	Australia	Third instar larva	Watts 2002
Helochares lividus (Forster)	Unknown (Palearctic)	Unknown stage larva in d'Orchymont 1913b; first, second and third instar larvae in Panzera 1932	d'Orchymont 1913b; Panzera 1932
Helochares luridus (MacLeay)	Australia	Third instar larva	Watts 2002
Helochares maculicollis Mulsant	USA	Eggs, first and third instar larvae, pupa	Richmond 1920; Archangelsky 1997
Helochares nipponicus Hebauer	Japan	First, second and third instar larvae	Minoshima and Hayashi 2011
Helochares obscurus (Müller) [as *Helochares griseus*]	Italy	First, second and third instar larvae	Panzera 1932
Helochares pallens (MacLeay)	Japan	First, second and third instar larvae	Minoshima and Hayashi 2011
Helochares tenuistriatus Régimbart	Australia	Third instar larva	Watts 2002
Helochares tristis (MacLeay)	Australia	Eggs, first, second and third instar larvae, pupa	Anderson 1976; Watts 2002
Novochares pallipes (Brullé) [as *Helochares* (s. str.) *pallipes*]	Argentina	Egg sac, first, second and third instar larvae, pupa	Fernández 1983
Peltochares conspicuus Régimbart*	Madagascar	Unknown stage larva	Bertrand 1962
Sindolus femoratus (Fernández) [as *Helochares* (*Sindolus*) *femoratus*]	Argentina	Egg case, first, second and third instar larvae, pupae	Fernández 2004
Sindolus talarum (Fernández) [as *Helochares* (*Sindolus*) *talarum*]	Argentina	Egg case, first, second and third instar larvae, pupae	Fernández 1983

* *Peltochares conspicuus* has never been reported from Madagascar. The species identification is likely incorrect.

Females lay between 18 (*Crephelochares nitescens* **comb. nov.**; see Anderson 1976) and 103 eggs (*Novochares pallipes* **comb. nov.**; see Fernández 1983) per egg case or nest. In observations from rearing experiments, it has been described that the larvae emerging from egg sacs carried by the females, the larvae seem to emerge towards the mother's air bubble to capture their own first air bubble (Anderson 1976). For *Crephelochares nitescens*, it was described that the females deposit their eggs in cavities built by the adults in damp soil (Anderson 1976). Larvae of *Sindolus talarum* have been described to perforate and enter the aerenchyma of *Spirodella intermedia* (Araceae) and staying in the plant tissue for some time, apparently breathing the air stored in the plant tissues (Fernández 1983).

Selected references. Hansen 1991: diagnosis of the group (at the time as a subtribe, and including some genera now placed in the subfamily Enochrinae), list of genera and subgenera with synonyms, key to genera, and description of each genus (8 out of the 23 recognized in this paper). Hansen 1999b: catalog with full list of species at the time (nearly 300), synonyms and references. Short and Fikáček 2013: Acidocerinae as a subfamily excluding enochrine genera, with Horelophopsinae as synonym, list of genera, general diagnosis. Short et al. (in prep.): molecular phylogeny and biogeography of the subfamily.

Remarks. The subfamily Acidocerinae is a group with many contrasts. It includes some of the largest as well as smallest hydrophilids; some genera are either strikingly different from, or extremely similar to, others; the external morphology of some genera is extremely uniform and species can only be recognized by characters of the male genitalia, or so variable that is difficult

to diagnose the group as a unit; at the species level, the distributions can be very narrow and restricted to one or a few fairly close localities, or very broadly widespread across several continents. There is a trend for species living in the same kind of habitats to have certain shared morphological features. For example, species that live in aquatic habitats tend to have slender and relatively long maxillary palpi and metafemora mostly covered by hydrofuge pubescence, whereas species living in hygropetric habitats tend to have shorter and stouter maxillary palpi and reduced or absent coverage of hydrofuge pubescence on the metafemora.

List of genera and their general distributions

A summary of the distributional information of each acidocerine genus is presented in Table 3.2. Regions correspond to those in Fig. 3.7. The total number of species are given per genus, per region; in parenthesis the number of species that are shared with other regions. En-dash is used to indicate that there are no species recorded for a given genus in a given region.

Table 3.2. Distributional information for Acidocerinae. Numbers in parentheses correspond to the number of species from the region that are shared with other regions. En-dash (–) indicates that no species of the genus are recorded from that particular region.

	Afrotropical	Australasian	Indo-Malayan	Nearctic	Neotropical	Palearctic	Total
Acidocerus Klug, 1855	1	–	–	–	–	–	1
Agraphydrus Régimbart, 1903	5 (1)	5 (1)	152 (13)	–	–	21 (15)	167
Aulonochares Girón and Short 2019	–	–	–	–	3	–	3
Batochares Hansen, 1991	3	–	–	–	–	–	3
Chasmogenus Sharp, 1882	–	–	–	–	16	–	16
Colossochares Girón and Short **gen. nov.**	2	–	–	–	–	–	2
Crephelochares Kuwert, 1890	18	3	7 (2)	–	–	3(2)	29

Crucisternum Girón and Short, 2018	–	–	–	–	7	–	7
Ephydrolithus Girón and Short, 2019	–	–	–	–	5	–	5
Globulosis García, 2001	–	–	–	–	3	–	3
Helobata Bergroth, 1888	–	–	–	1(1)	13(1)	–	13
Helochares Mulsant, 1844	90 (2)	14(3*)	31(3)	2(2)	8(2)	12(4)	153
Helopeltarium d'Orchymont, 1943	–	–	1	–	–	–	1
Katasophistes Girón and Short, 2018	–	–	–	–	4	–	4
Nanosaphes Girón and Short, 2018	–	–	–	–	4	–	4
Novochares Girón and Short **gen. nov.**	–	–	–	–	15	(1)	15
Peltochares Régimbart, 1907	2(1)	3(1)	4(1)	–	–	(1)	8
Primocerus Girón and Short, 2019	–	–	–	–	9	–	9
Quadriops Hansen, 1999	–	–	–	–	6	–	6
Radicitus Short and García, 2014	–	–	–	–	3	–	3
Sindolus Sharp, 1882	–	–	–	–	8	–	8
Tobochares Short and García, 2007	–	–	–	–	8	–	8
Troglochares Spangler, 1981	–	–	–	–	1	–	1
TOTAL by Region	121	25	195	3	113	36	469

* Only one species has been recorded from the Oceanian region (Samoa, Tonga).

Morphological variation in Acidocerinae and its taxonomic importance

The Acidocerinae have been described as "relatively uniform and difficult to characterize" (Short and Fikáček 2013), mostly because for each proposed synapomorphy, there are taxa that exhibit exceptional character states. The phylogeny presented by Short et al. (in prep.) revealed a high recurrence of morphological convergence across the phylogeny of the Acidocerinae that seem to track ecologies rather than phylogenetic relationships. Here we present an account of morphological features, how they vary in the subfamily, and their usefulness for recognizing taxonomic units.

Size and shape of body. This subfamily includes members among the largest (nearly 14.0 mm) and smallest (nearly 1.2 mm) hydrophilids (see Figs 3.1 and 3.2). In general terms,

acidocerines can very roughly be grouped by their size: most genera in the *Helochares*-group (*sensu* Short et al. in prep.) are larger than 4 mm (see Fig. 3.1), whereas *Agraphydrus*, *Chasmogenus*, *Crephelochares*, *Primocerus*, and members of the *Tobochares*-group are smaller than 4.5 mm (see Fig. 3.2). The body is usually oval and parallel-sided, occasionally slightly broader anteriorly or posteriorly; it can also be rather dorsoventrally flattened (e.g., *Helobata* (see Fig. 3.1J), *Peltochares* (see Fig. 3.1C), *Helopeltarium* (see Fig. 3.1H)), or strongly convex (e.g., *Globulosis* (see Fig. 3.2G), *Colossochares* (see Fig. 3.1A), *Radicitus* (see Fig. 3.1K)), but it is generally moderately convex. The outline of the body in dorsal view is continuous (not interrupted between pronotum and elytra) when the specimens are in natural resting position; when the specimen is card-mounted the outline of the body may appear interrupted.

Coloration. Body color ranges from very pale (yellowish) to very dark brown (appearing almost black), and it is usually uniform along the dorsal surfaces of the body, although sometimes the margins of the pronotum and elytra may be slightly paler than the disc (see Figs 3.1 and 3.2). The ventral surface of the body and the appendages (or parts of appendages) tend to be paler than the dorsum. In *Batochares* (e.g., Fig. 3.1I) and *Helobata* (e.g., Fig. 3.1J), there are alternating areas of darker/paler colorations along the elytra, giving specimens a flecked or speckled appearance. In some species of *Nanosaphes*, different regions of the body (head, pronotum, elytra) have different colorations (e.g., Fig. 3.2J); in some species of *Tobochares*, the lateral margins of the clypeus are paler (e.g., Fig. 3.2H); in both cases, coloration can be used for species-group recognition. In some genera, internal structural reticulations are visible throughout the surface (mostly on the elytra), giving the beetles a “checkered” appearance of

darker spots over a paler background (e.g., *Aulonochares* (Fig. 3.18), New World *Helochares* (Fig. 3.36A–C; see also Short and Girón 2018)).

Punctation. Three kinds of punctures can be recognized along the dorsal surface of the body in Acidocerinae that may be shallowly to moderately or sharply (strongly) marked. Ground punctures are usually fine and uniformly distributed along the entire body. Systematic punctures (*sensu* Hansen 1991), those bearing a seta inserted in a doughnut-shaped socket (thrichobothria *sensu* Short and Fikáček 2013; see Fig. 3.8A–C), are usually well developed and can also be found along the entire body, being more densely distributed in particular areas of the head, pronotum and elytra. The seta on a systematic puncture is usually fine and can be short or long; sometimes these setae may be lost by abrasion but are usually visible along the lateral and posterior areas of the elytra. Systematic punctures usually form well defined rows along the elytra; quite a few species in some genera exhibit four or five rows of systematic punctures clearly enlarged in comparison with the remainder elytral punctation (e.g., *Agraphydrus* (see Fig. 3.2A–C), *Ephydrolithus* (see Fig. 3.29), *Katasophistes* (see Fig. 3.38)). Serial punctures are only present along the elytra and can only be recognized when well-developed (larger and usually more impressed than ground punctures), as they form usually ten well-defined rows, at least along the posterior third of each elytron (e.g., *Radicitus*; see Fig. 3.50A–C); some *Agraphydrus* species have strongly enlarged and irregular elytral series of punctures (e.g., Fig. 3.15D–F). Serial punctures were traditionally used for the recognition of subgenera within *Helochares sensu* Hansen (1999b), but it has been shown that the presence or absence of this kind of punctures has taxonomic value only at the species or species-group level in certain genera (e.g., *Primocerus*

(see Fig. 3.46), *Tobochares* (see Fig. 3.53)). The presence, size, density, degree of impression and development/differentiation of punctures on the dorsal surface of the body are useful for recognition of certain genera and species, but there are no general character states that cover the entire subfamily.

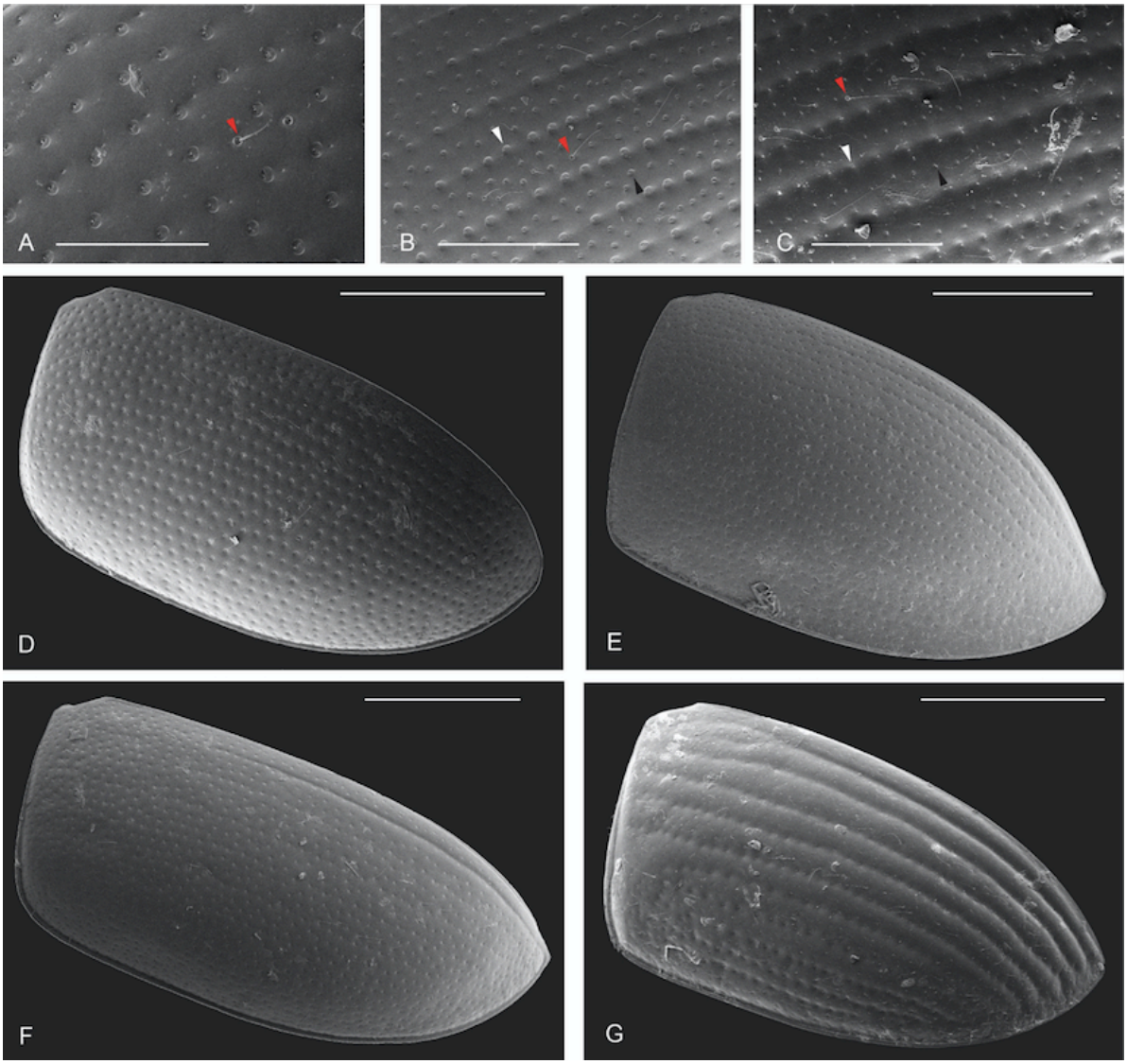


Figure 3.8. Elytral punctation: **A** *Tobochares* sp. with red arrow pointing to systematic puncture (scale bar 100 µm), **B** *Tobochares sipaliwini* with red arrow pointing to systematic puncture, white arrow pointing to serial puncture, and black arrow pointing to ground/interserial puncture (scale bar 200 µm), **C** *Tobochares striatus* with red arrow pointing to systematic puncture, white arrow pointing to serial puncture, and black arrow pointing to ground/interserial puncture (scale bar 200 µm), **D** *Tobochares* sp. elytron with all kinds of punctures similar in size and degree of impression, seemingly evenly distributed (to longitudinally aligned) (scale bar 500 µm), **E** *Quadriops similaris* with serial punctures longitudinally aligned (scale bar 500 µm), **F** *Primocerus maipure* with sutural stria (scale bar 500 µm), **G** *Tobochares striatus* with impressed serial striae (scale bar 500 µm).

Eyes. The only known species of hydrophilid lacking eyes (i.e., *Troglochares*) is a member of the Acidocerinae. Eyes range in shape from subquadrate to oval and are usually of moderate size (see Fig. 3.9E–L), although in some species the eyes are relatively small (e.g., *Primocerus ocellatus*). In some genera, the posterior corners of the frons extend posteriorly forming a canthus that emarginates the anterior margin of the eyes (see Fig. 3.9B), which is more evident in lateral view (e.g., *Tobochares*, *Helobata*). There is only one known acidocerine genus in which the canthus reaches the posterior margin of the eye, thus completely dividing the eye in dorsal and ventral faces (*Quadriops*; see Fig. 3.9C). In some genera the eyes are protruding, interrupting the outline of the head (e.g., *Aulonochares*; see Fig. 3.9J). In most cases the proportion between the width of an eye and the distance between eyes remain constant across congeneric species. The shape, size, and degree of protrusion of the eyes are useful for generic recognition.

Clypeus. It is usually roughly trapezoid (clearly wider at base; see Fig. 3.9F–I) and relatively flat or antero-medially convex. In some genera, it fully conceals the labrum (e.g., *Helobata* (see Fig. 3.9L), *Helopeltarium*). The shape of the anterior margin of the clypeus, and the development of a membranous preclypeal area (see Fig. 3.9H) are useful for diagnosing species within some genera (e.g., *Chasmogenus*). In some *Helochares* the surfaces surrounding the lateral margins of the clypeus are slightly bent upwards.

Maxillary palpi. In general the maxillary palpi in Acidocerinae have been described as ‘curved inward’ (e.g., Hansen 1991), which means that the outer margin of the maxillary palpomere 2 is apically or medially curved towards the midline of the body, and the apex of

palpomere 3 is oblique, so that the palpomere 4 articulates pointing towards the midline of the body. The inner margin of maxillary palpomere 2 ranges from straight (e.g., *Agraphydrus*; see Fig. 3.10G) to slightly and uniformly curved (concave; e.g., Fig. 3.10I). All palpomeres tend to be of somewhat similar proportions among them, and are usually similar in length as well, although it is common that the maxillary palpomere 2 is slightly longer. The comparative length of maxillary palpomeres 3 and 4 may be useful as a supporting diagnostic feature. According to the diagnosis of the Acidocerinae offered by Hansen (1991) and by Short and Fikáček (2013), the maxillary palpi are at least as long or usually longer than the width of the head (except for some *Agraphydrus* and *Quadriops*). The number of exceptions to this rule keeps growing, the more seepage taxa are found (e.g., *Ephydrolithus*, *Radicitus*, some *Tobochares*). The length of the maxillary palpomeres in Acidocerinae ranges from very short and stout (nearly half width of the head), to very long and slender (nearly 2 × width of the head) (see Fig. 3.10F–J).

Mentum. The anterior margin of the mentum is usually laterally emarginated by the base of the palpigers and mesally emarginated and deeply depressed on ventral view (projected upwards) (see Fig. 3.10A–C); this antero-medial depression varies in width and depth and may be demarcated by a transverse crest or carina (see Fig. 3.10A). The surface of the mentum may be flat, medially depressed or bear oblique elevations (see Fig. 3.10B); the surface may further range from smooth (see Fig. 3.10A) to punctate, to anteriorly strigate, with little or no variation within genera. Characteristics of the mentum and submentum may be useful as supporting diagnostic features.

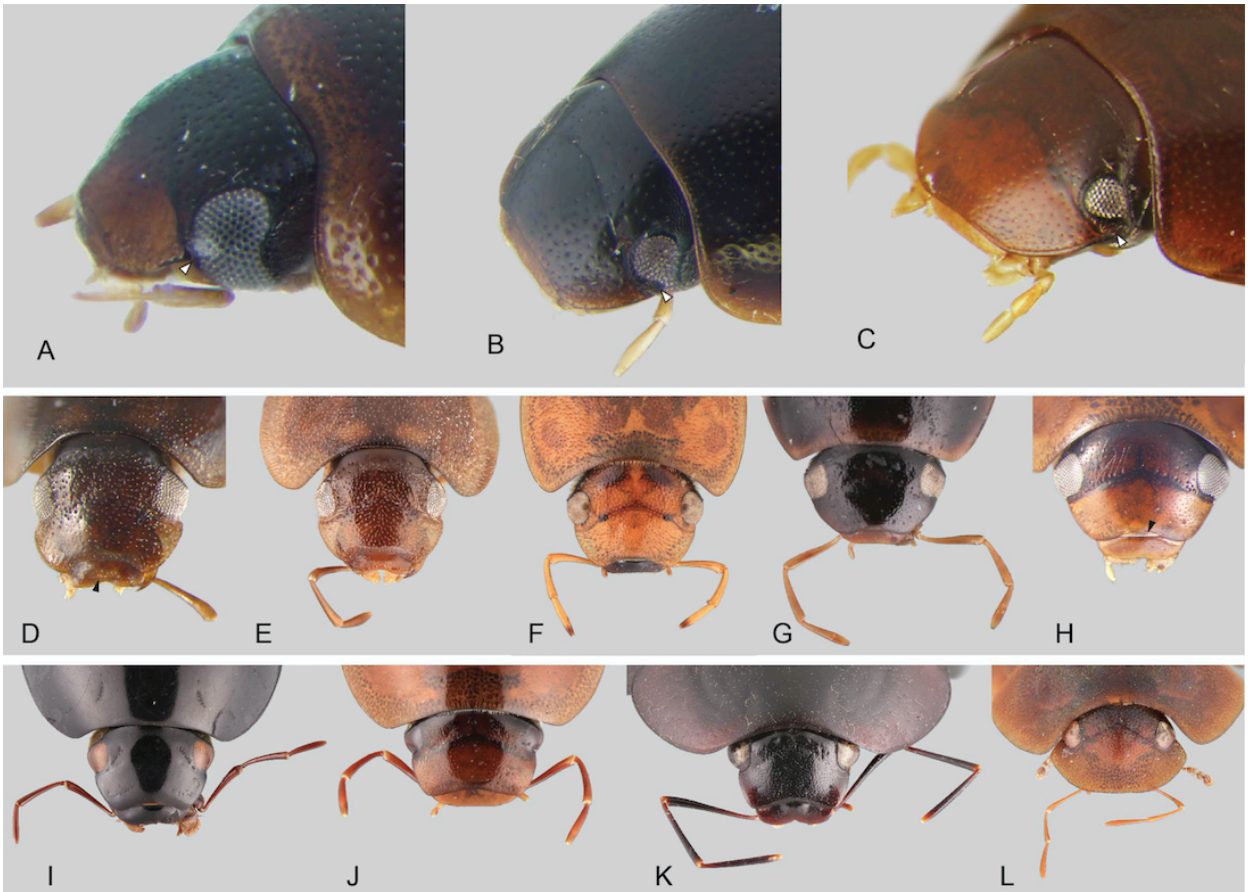


Figure 3.9. Head: A–D antero-lateral view of head: A *Tobochares* sp. with white arrow pointing straight anterior margin of eye, B *Tobochares emarginatus* with white arrow pointing to canthus emarginating anterior margin of eye, C *Quadriops politus* with white arrow pointing to canthus fully dividing the eye in dorsal and ventral faces, D *Batochares* sp. black arrow pointing to transverse carina on labrum, E–L dorsal view of head: E *Batochares* sp., F *Helochares tristis*, G *Crephelochares nitescens*, H *Chasmogenus australis* with black arrow pointing to preclypeal membrane, I *Colossochares ellipticus*, J *Aulonochares tubulus*, K *Peltochares conspicuus*, L *Helobata larvalis*.

Antennae. The number of antennomeres is either nine (the ancestral state in Hydrophilidae; Hansen 1991; see Fig. 3.20D) or reduced to 8 (see Fig. 3.10E). The cupule can be symmetric, or slightly to strongly asymmetric. The three-part pubescent antennal club is always loosely articulated, and the proportions of the club antennomeres have been used in the past to recognize some groups.

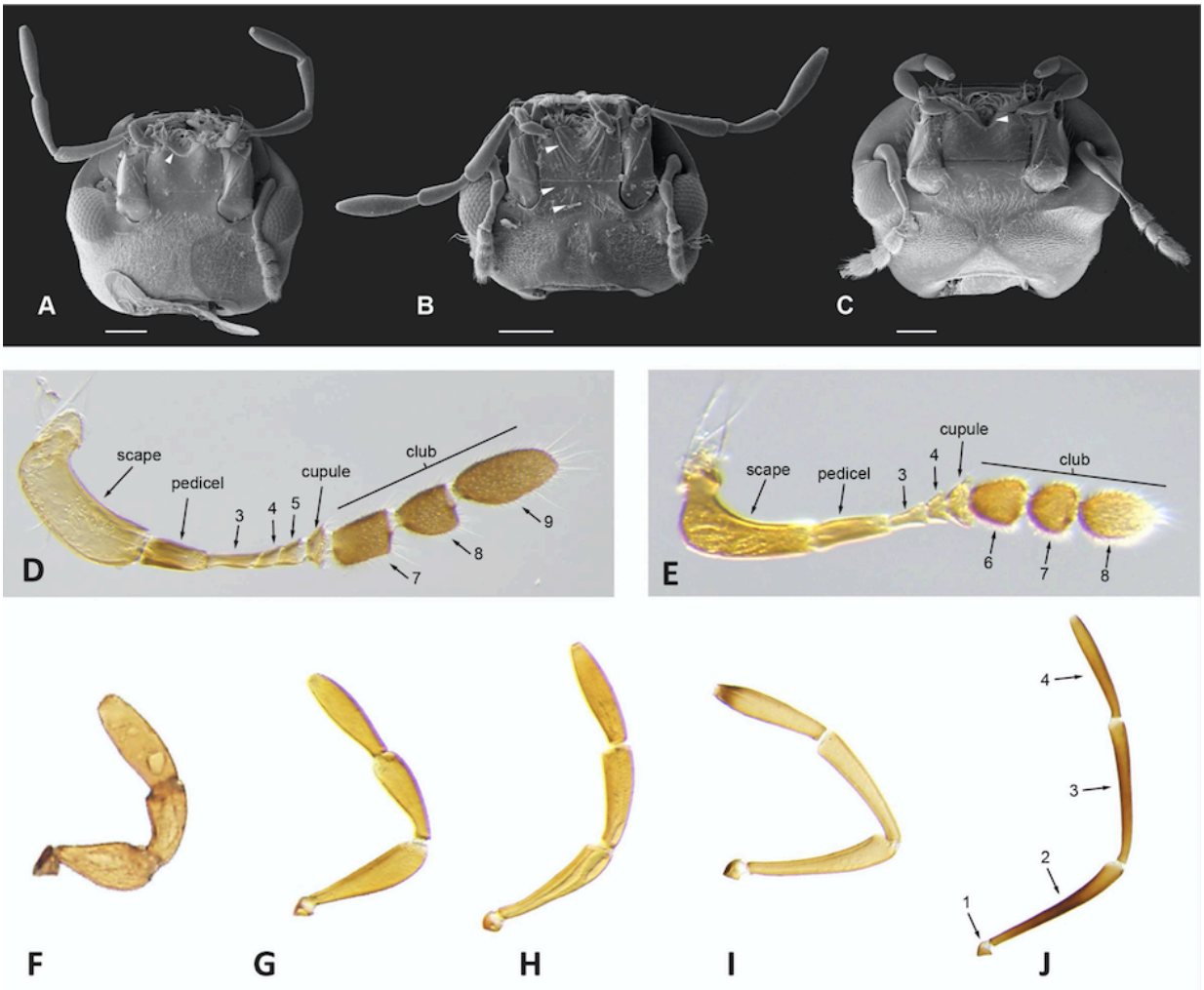


Figure 3.10. Head structures: A–C scanning electron micrographs of ventral view of head (scale bars 100 µm): A *Tobochares pallidus* with smooth mentum and white arrow pointing to transverse carina limiting posterior margin of antero-medial depression, B *Nanosaphes tricolor* with top white arrow pointing to oblique crenulations, mid white arrow pointing to flat and smooth anterior surface of submentum, and bottom white arrow pointing to concave posterior surface of submentum, C *Quadriops reticulatus* with white arrow pointing to antero-medial depression, D–E light micrographs of antenna: D *Aulonochares tubulus* (9 antennomeres), E *Chasmogenus crenmobates* (8 antennomeres), F–J light micrographs of maxillary palpi: F *Quadriops reticulatus*, G *Agraphydrus insidiator*, H *Helochares* sp., I *Helochares lividus*, J *Aulonochares tubulus*.

Thoracic venter. The prosternum in Acidocerinae is usually rather flat (see Fig. 3.11A, B), at most medially tectiform or broadly bulging, except in *Acidocerus* and *Crucisternum* which bear a medial longitudinal carina. The surface of the posterior elevation of the mesoventrite is taxonomically important; it may be projected in various forms: as a longitudinal carina (see Fig.

3.11D, F), cruciform projection (see Fig. 3.11C), transverse ridge (see Fig. 3.11E, G) or acute spine. The shape of the projection on the posterior elevation can sometimes be used for recognition of genera, but it may also vary among congeneric species (e.g., *Ephydrolithus*, *Nanosaphes*). The shape of the anapleural sutures ranges from angulate (forming an obtuse angle; e.g., *Primocerus, Troglochares* (see fig. 8 in Spangler 1981a) to only slightly curved (e.g., *Katasophistes*, *Nanosaphes* (see figs 11A and 17A, respectively, in Girón and Short 2018); the orientation along their anterior section may be nearly parallel (e.g., *Helobata*; see fig. 8 in Clarkson et al. 2016) or anteriorly converging; they may be widely separated anteriorly (anterior margin of mesoventrite nearly as wide as anterior margin of mesepisternum; e.g., *Globulosis*, *Nanosaphes* (see fig. 17A in Girón and Short 2018), or very closely converging (anterior margin of mesoventrite 0.2 × the width of the anterior margin of mesepisternum; e.g., *Ephydrolithus* (see fig. 7A in Girón and Short 2019), *Katasophistes* (see fig. 11A in Girón and Short 2018). The metaventrite is usually densely and uniformly covered by hydrofuge pubescence; a posteromedian glabrous patch and/or posterolateral glabrous patches may also be present (see Fig. 3.11C–G). The size and shape of the posteromedian glabrous patch is useful for recognition of some genera and subgenera (e.g., *Tobochares*).

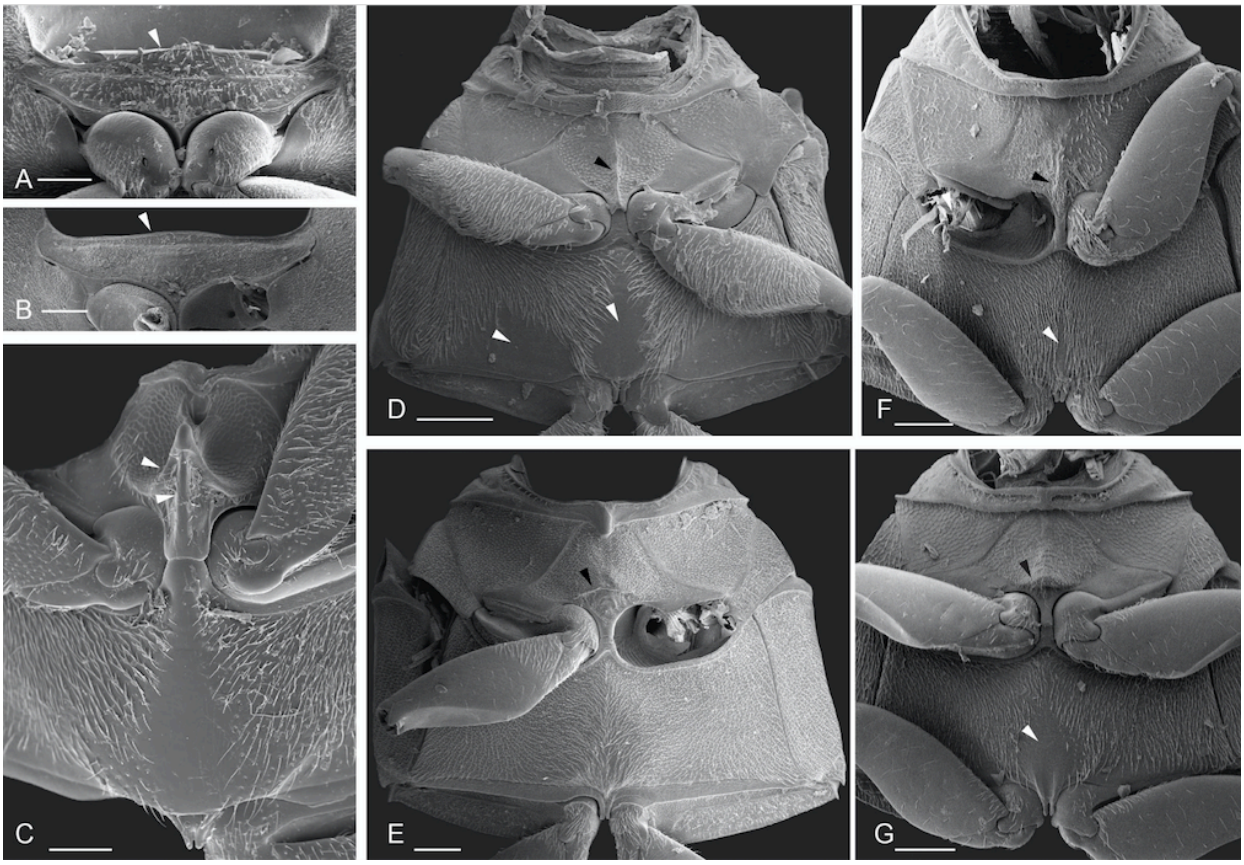


Figure 3.11. Scanning electron micrographs of thorax in ventral view: **A–B** prosternum: **A** *Tobochares striatus* with white arrow pointing to anterior projection, **B** *Quadriops reticulatus* with white arrow pointing to anterior projection, **C–G** mesoventrite and metaventrite: **C** *Crucisternum ouboteri* with white arrows pointing to anteriorly pointed transverse ridge and longitudinal carina, metaventrite with median glabrous patch, **D** *Nanosaphes tricolor* with black arrow pointing to longitudinal carina along mesoventrite and white arrows pointing to median and postero-lateral glabrous patches, **E** *Quadriops reticulatus* with black arrow pointing to transverse carina across mesoventrite and metasternum uniformly pubescent, **F** *Tobochares* sp. with black arrow pointing to longitudinal carina along mesoventrite and white arrow pointing to narrow postero-medial glabrous patch on metasternum, **G** *Tobochares kasikasima* with black arrow pointing to transverse elevation across mesoventrite and white arrow pointing to broad postero-medial glabrous patch on metasternum. Scale bars 100 µm.

Elytra. The shape and punctation of the elytra are highly variable in the Acidocerinae. The elytra may be evenly convex (e.g., *Radicitus*, see Fig. 3.1K) or with nearly flat dorsal outline (e.g., *Helopeltarium*, Fig. 3.1H), with outer margins slightly flared or broadly explanate (e.g., *Helobata*, Fig. 3.1J); the surface is usually smooth, but can also be granulate (e.g., *Acidocerus* (Fig. 3.14), *Helobata* (Fig. 3.33)). Sutural striae are only present in *Chasmogenus* (Fig. 3.22), *Crephelochares*

(Fig. 3.25), and *Primocerus* (Fig. 3.46). The elytral punctation has been traditionally considered as a diagnostic feature at the subgenus level, in *Helochares* for example, but it is clear now that this character system can be variable among congeneric species (e.g., *Ephydrolithus* (Fig. 3.29), *Katasophistes* (Fig. 3.39), and *Primocerus* (Fig. 3.46)). In some cases, all kinds of punctures (ground punctures, systematic punctures, and serial punctures) are well-developed and therefore easily recognized (e.g., Fig. 3.8B, C), but in other instances they can be virtually indistinguishable from each other (e.g., Fig. 3.8A). In some species, or even groups of species within a genus, the serial punctures are impressed forming longitudinal grooves that can extend from the anterior to the posterior margins of the elytra (e.g., *Tobochares sulcatus*, see Fig. 3.53), or at least along the posterior third of each elytron (e.g., *Tobochares*). When serial punctures are well developed, the ground punctures between series have been called "interserial punctures" (see Fig. 3.8B, C; e.g., *Tobochares* (*Tobocharoides*) see Girón et al. in prep.), and their distribution may be informative at the species level.

Hind wings. The hind wings of the Acidocerinae are usually well developed, with most of the general venation clearly visible. The posterior margin of the wing usually has a well-defined anal notch, demarcating a noticeable "jugal lobe" (see fig. 285 in Hansen 1991) that is either broad (Fig. 3.12B, C) or narrow (Fig. 3.12D–G). AP3+4 can be either thick and curved (Fig. 3.12AB, C), or evanescent and angulate (Fig. 3.12B, D–G). One species of *Tobochares* was found to have reduced hindwings (Fig. 3.12G), in which most of the veins are still well developed, but the entire apical region of the wing is reduced.

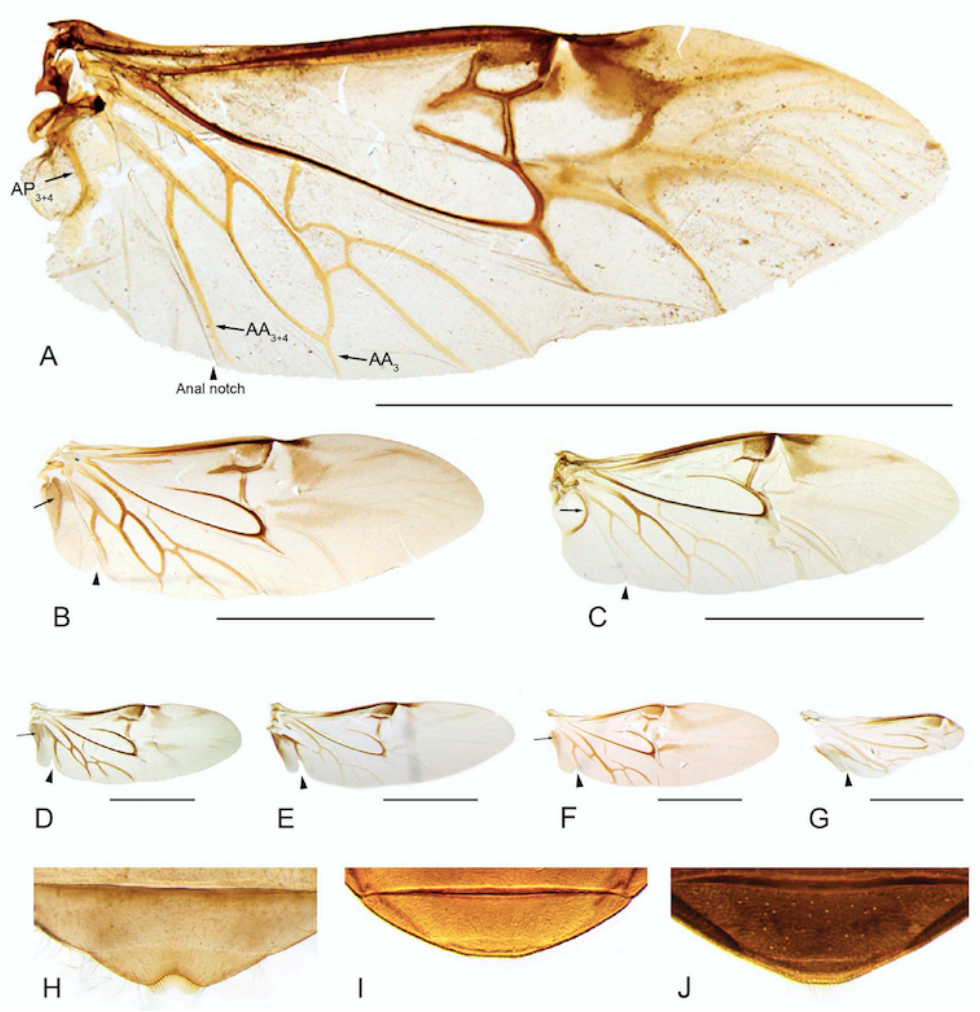


Figure 3.12. Hindwings and abdominal ventrite 5: **A–G** hind wings: **A** *Colossochares ellipticus* (scale bar 1 cm), **B** *Primocerus gigas* (scale bar 3 mm), **C** *Helobata larvalis* (scale bar 3 mm), **D** *Crucisternum ouboteri* (scale bar 1 mm), **E** *Tobochares sipaliwini* (scale bar 1 mm), **F** *Quadriops similaris* (scale bar 1 mm), **G** *Tobochares* sp. (scale bar 0.5 mm); **H–J** abdominal ventrite 5: **H** *Aulonochares tubulus*, **J** *Primocerus neutrum*, **J** *Ephydrolithus hamadae*.

Protibiae. Two main features of the protibia are taxonomically relevant: the shape and size of the apical spurs and the characteristics of the spines composing the median longitudinal anterior row. The apical spurs are usually large and slender (longer than protarsomere 1) but can be relatively short and stout (as long as or shorter than protarsomere 1; e.g., *Aulonochares*). The spines composing the median longitudinal anterior row can be very short, stout, and appressed

to the surface of the tibia in most members of the *Helochares*-group (*sensu* Short et al. in prep.), or be long, relatively thick and seta-like, and semi-erect.

Metafemora. In Acidocerinae the metafemora are moderate to strongly antero-posteriorly compressed. The anterior surface of the metafemur may be covered to a variable degree with hydrofuge pubescence. Usually species found in typical fully aquatic habitats (streams, ponds, marshes) have the anterior surface of the metafemora mostly covered by pubescence, whereas species found in hygropetric habitats (seepages) exhibit a reduced coverage (about half the surface or less) and fully terrestrial species (on rotten fruits) lack any pubescence. The degree of coverage may be useful for generic identifications in many cases, and it is also known to vary among species of *Agraphydrus* and *Primocerus*. The degree of development of the tibial grooves (ventral surface that is either flat or concave) of the metafemora can also be used as a supporting character for identifications; they may be well developed, when at least the posterior edge is sharply marked, or reduced, or absent when the ventral surface of the metafemur is convex or only relatively flattened, without any sharp edges.

Tarsi. The tarsal formula of acidocerine beetles is always 5-5-5, with tarsomeres 1–4 usually similar in shape and length and tarsomere 5 longer and slender; tarsomere 2 is the most variable in length, ranging from similar to tarsomere 1 to as long as tarsomere 5. The coverage of the ventral surface of the tarsomeres is variable. Usually the protarsomeres will have a dense and uniform coverage of thick setae; the coverage of meso- and metatarsomeres 1 may be asymmetric, with thick setae only along its outer margin. Tarsomeres 2, 3 and 4 may be densely

covered ventrally, but more frequently bear a pair of lateral rows of denticles, spines or spiniform setae. Tarsomeres 5 are usually glabrous ventrally, rarely bear a ventral medial row of tiny denticles or fine setae. Very fine and relatively long natatorial setae (swimming hairs *sensu* Hansen 1991) may be present on the dorsal face of meso- and metatarsomeres but are scarce and do not form a fringe. The length of metatarsomeres 5 relative to the length of all or some of the remaining tarsomeres may be useful as a supporting character to recognize genera.

Apical margin of fifth abdominal ventrite. The apical margin of the fifth abdominal ventrite usually bears a mesal emargination that varies in depth and is usually fringed by flat and stout setae (see Fig. 3.12H). There is a trend for taxa from seepages or terrestrial habitats to have a rounded or truncate posterior margin of the fifth abdominal ventrite (see Fig. 3.12I, J); in these cases, the flat and stout setae are reduced or absent.

Aedeagus. The general configuration of the aedeagus in acidocerines is highly variable across the subfamily (see Fig. 3.13), yet strongly conserved within genera and even groups of genera. An attempt to group African species of *Helochares* (*Hydrobaticus*) by aedeagal categories was made by Hebauer (1996).

For merely practical purposes, here we propose four main aedeagal forms in Acidocerinae. These categories are very general and by no means exhaustive or detailed but encompass some of the broad variations we have found. It is worth noting that these categories have no phylogenetic meaning.

(1) trilobed aedeagus (Fig. 3.13A–E)**:** parameres separated from each other for most of their length; parameres and median lobe simple (without subdivisions); basal piece of variable length; gonopore usually well differentiated; e.g., *Agraphydrus* and *Tobochares*-group *sensu* Short et al. (in prep.).

(2) spiked aedeagus (Fig. 3.13F–J)**:** main component of median lobe strongly sclerotized, slender and apically acute, usually accompanied by additional shorter slender sclerotizations; apical region of parameres usually partly heavily sclerotized and partly membranous, often bifurcated; basal piece strongly reduced; gonopore usually not clearly visible; e.g., *Peltochares*.

(3) tubular aedeagus (Fig. 3.13K–O)**:** parameres fused to each other for most of their length, with apex either simple or bifurcate/bilobate; median lobe with very long basal apodemes (as long or longer than main piece of median lobe), either simple (without subdivisions), or with different kinds of sclerotizations of inner membranes; basal piece usually much shorter than parameres; gonopore of variable development; e.g., *Aulonochares*, *Helochares*.

(4) subdivided aedeagus (Fig. 3.13P–T)**:** parameres usually separated from each other for most of their length; median lobe subdivided in dorsal and ventral plates; dorsal and ventral plates may be further bilaterally subdivided, or otherwise shaped; basal piece shorter than parameres, always noticeable; gonopore usually clearly visible; e.g., *Helobata*, *Novochares*.

Some of these aedeagal categories are further modified in an incredible array of shapes, and clearly deserve detailed morphological and functional studies. The particular configuration and relative proportions of parts is, for the most part, genus specific.

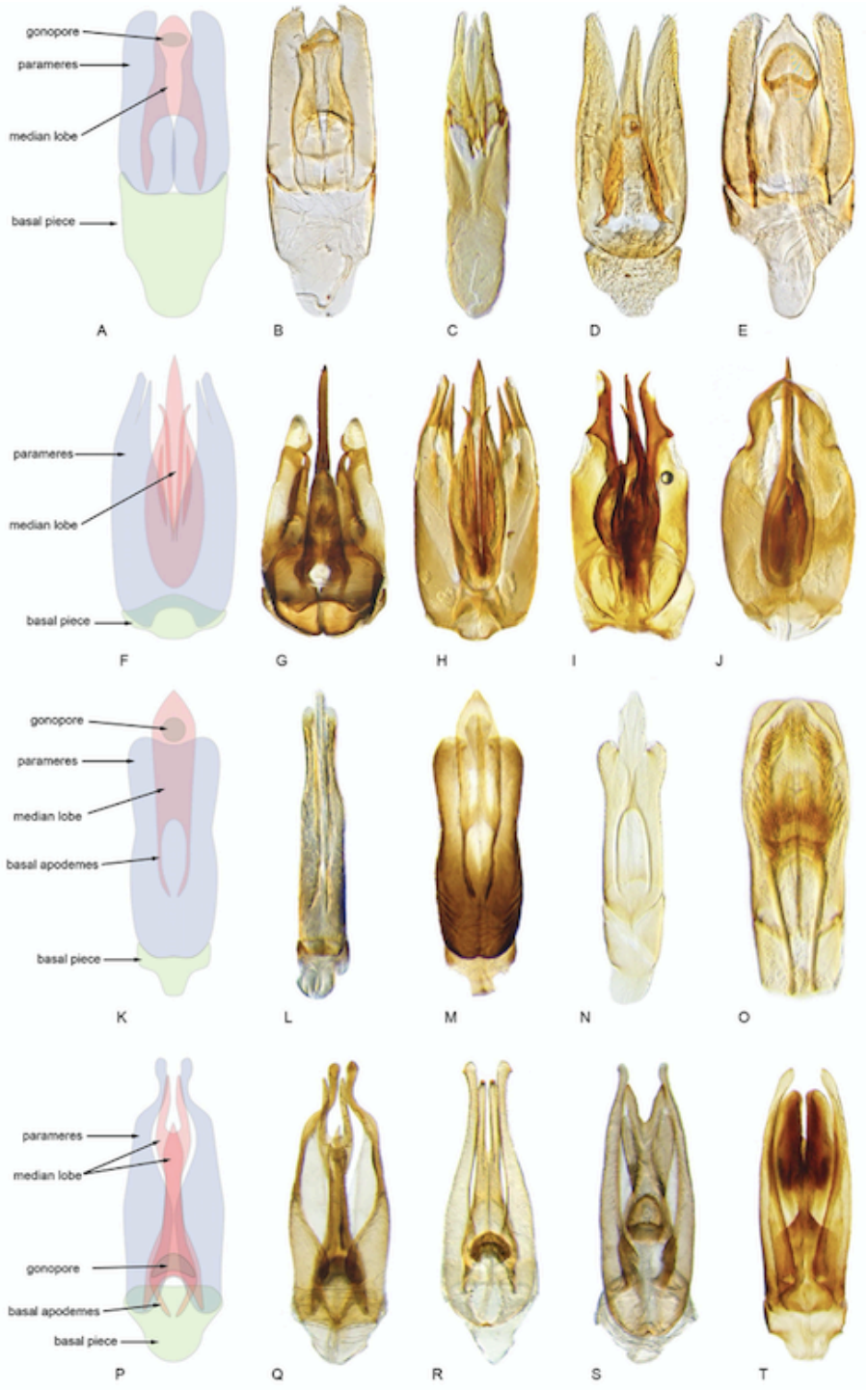


Figure 3.13. Aedeagi: **A–E** trilobed: **A** schematic, **B** *Chasmogenus* sp., **C** *Batochares* sp., **D** *Crucisternum queneyi*, **E** *Ephydrolithus hamadae*, **F–J** spiked: **F** schematic, **G** *Peltochares conspicuus*, **H** *Peltochares foveicollis*, **I** *Peltochares* sp., **J** *Peltochares* sp., **K–O** tubular: **K** schematic, **L** *Aulonochares tubulus*, **M** *Helochares politus*, **N** *Helopeltarium ferrugineum*, **O** *Helochares* sp., **P–T** divided: **P** schematic, **Q** *Novochares pallipes*, **R** *Novochares coya*, **S** *Novochares atratus*, **T** *Helobata* sp. (Ecuador).

Key to genera of Acidocerinae of the World

1 Distributed in the Old World… 2

– Distributed in the New World… 9

2 Labrum concealed by clypeus. Only known from the Indo-Malayan region... *Helopeltarium* (Figs. 3.37I, 3.38)

– Labrum not concealed by clypeus… 3

3 Elytra with distinctly impressed sutural striae… ***Crephelochares*** (Figs. 3.9G, 3.25, 3.26)

– Elytra without sutural striae… 4

4 Labrum with apical region anteriorly flattened, thus bearing a fine transverse carina across anterior margin (see Fig. 3.9D, E); pronotum antero-laterally explanate and bent upwards (marginal areas concave; Fig. 3.20A, B); elytra with margins explanate, especially along anterior third (Fig. 3.20A); body smaller than 5 mm; basal piece of aedeagus nearly 1.5 × longer than parameres (Fig. 3.21A). Only known from the Afrotropical region… ***Batochares*** (Figs. 3.20, 3.21A)

– Labrum with apical region not anteriorly flattened, with even surface (without transverse carina; e.g., Fig. 3.9H, K); pronotum evenly convex, not laterally explanate (e.g., Fig. 3.1A, G); elytra with margins not explanate, at most flared (e.g., Fig. 3.1A, G); if elytra with margins explanate, body approximately 10 mm (e.g., Fig. 3.1C); basal piece of aedeagus variable in

length, usually less than 0.5 × length of parameres (e.g., Fig. 3.13F–O). Afrotropical or elsewhere in the Old World… **5**

5 Head and pronotum with granulate surface (Fig. 3.14); body size small (ca. 3 mm); prosternum with median carina; elytra narrowly explanate laterally, with ten well defined rows of coarse serial punctures impressed into striae (Fig. 3.14A). Only known from the Afrotropical region… ***Acidocerus***

– Head and pronotum shallow to moderately punctate, without granulations (e.g., Fig. 3.1A, E, F); body size variable (2–14 mm); prosternum flat to medially broadly bulging, without median carina; elytra at most flared, with or without impressed serial punctures (e.g., Fig. 3.1A, E, F). Afrotropical or elsewhere in the Old World… **6**

6 Body length 8.5–14.0 mm; body shape broadly oval in dorsal view, strongly and uniformly convex in lateral view (Fig. 3.24); ground punctation extremely fine and shallow; coloration uniformly dark brown (nearly black). Only known from the Afrotropical region… ***Colossochares*** **gen. nov.** (Figs. 3.21B, 3.24)

– Body length 1.4–10.0 mm; body shape broadly oval in dorsal view, weakly to moderately convex in lateral view (Fig. 3.1B, C, E, F); ground punctation from fine and shallow to moderately marked; coloration variable, ranging from yellow to dark brown. Widespread in the Old World… **7**

7 Body length 1.4–4.8 mm; inner margin of maxillary palpomere 2 straight to nearly straight (Fig. 3.10G); metaventrite with posteromedian glabrous patch (e.g., Figs 3.15C, F, 3.16C); antennae with eight or nine antennomeres… ***Agraphydrus*** (Figs 3.15–3.17)

– Body length 2–10 mm; inner margin of maxillary palpomere 2 weakly and evenly curved (e.g., Fig. 3.10H, I), seldom nearly straight; metaventrite without posteromedian glabrous patch (e.g., Figs 3.34C, 3.36F); posterolateral glabrous patches may be present); antennae with nine antennomeres… 8

8 Body length 2–7 mm; dorsal coloration yellow to medium brown (Figs 3.34–3.36); posterior elevation of mesoventrite flat to simply bulging; tibial grooves absent to weakly developed; aedeagus tubular (see Figs 3.13K–O, 3.37)… ***Helochares*** (in part; Figs 3.34–3.37)

– Body length 6–10 mm; dorsal coloration dark brown to black (Fig. 3.44); posterior elevation of mesoventrite longitudinally elevated; tibial grooves sharply marked; aedeagus spiked (see Fig. 3.13F–J)… ***Peltochares*** (Figs 3.44, 3.45)

9 Eyes absent. Known only from a cave in Ecuador… ***Troglochares***

– Eyes present... 10

10 Eyes completely divided into dorsal and ventral sections by a lateral projection of frons (see Fig. 3.9C). Size small (<3 mm). Ranging from Costa Rica to northern South America... ***Quadriops*** (Figs 3.48–3.49)

– Eyes not divided into dorsal and ventral sections by frons (e.g., Fig. 3.9A, B). Size variable. Anywhere in the New World… 11

11 Labrum concealed by clypeus (see Fig. 3.9L), elytral margins broadly explanate (Fig. 3.33A). Body extremely dorsoventrally compressed (Fig. 3.33B). Widespread in the New World… *Helobata* (Figs. 3.21C, 3.33)

– Labrum not concealed by clypeus (e.g., Fig. 3.9H, J), elytral margins not or at most weakly explanate (e.g., Fig. 3.2D, F–J). Body form variable but rarely dorsoventrally compressed (e.g., Fig. 3.2D, F–J). Anywhere in the New World… 12

12 Elytra with distinctly impressed sutural striae (e.g., Fig. 3.2D). Only Neotropical region… 13

– Elytra without sutural striae (e.g., Figs 3.1D, G, K, 3.2G–J). Both Neotropical and Nearctic… 14

13 Posterior elevation of the mesoventrite either flat, broadly elevated or with a longitudinal elevation. Gonopore present and distinct (Fig. 3.23)… *Chasmogenus* (Figs 3.22, 3.23)

– Posterior elevation of the mesoventrite with a transverse curved ridge, either sharp or reduced, or with a sharp, pyramidal (triangular) spine-like projection. Gonopore absent (Fig. 3.47)… *Primocerus* (Figs 3.46, 3.47)

14 Prosternum with strongly elevated median carina... *Crucisternum* (Figs 3.27, 3.28)

– Prosternum not or only very slightly carinate or at most tectiform medially... 15

15 Posterior elevation of mesoventrite with a large, sharp and strongly elevated laminar longitudinal carina; body in lateral view evenly and moderately convex (Fig. 3.52B)… ***Sindolus*** (Figs 3.21D, 3.52)

– Posterior elevation of mesoventrite variable, but never with a large, sharp and strongly elevated laminar longitudinal carina; body in lateral view variable (Fig. 3.2G–J)… 16

16 Elytral systematic punctures very distinct, distinctly larger than surrounding ground punctation, forming five longitudinal rows along each elytron (Figs 3.29, 3.39). Antennae with nine antennomeres… 17

– Elytral systematic punctures indistinct, usually blending with surrounding ground punctation (e.g., Figs 3.31, 3.41, 3.50, 3.53). Antennae with eight or nine antennomeres… 18

17 Metafemora mostly glabrous, with only few scattered setae on anterior surface (Fig. 3.29C, F). Found on eastern Brazil… ***Ephydrolithus*** (Figs 3.29, 3.30)

– Metafemora at most glabrous along apical third (Fig. 3.39C, F). Recorded from the Andean region… ***Katasophistes*** (Figs 3.39, 3.40)

18 Antennae with eight antennomeres. Size small (< 3 mm)… 19

– Antennae with nine antennomeres. Size variable but usually > 4 mm… 21

19 Anterior surfaces of metafemora mostly glabrous (Fig. 3.53C, F)… ***Tobochares*** (Figs 3.53, 3.54)

– Anterior surfaces of metafemora densely covered by hydrofuge pubescence along basal three fourths (e.g., Figs 3.31C, 3.41C, F)… 20

20 Body form circular, rounded (Fig . 3.31A). Size very small (1.9–2.3 mm)… ***Globulosis*** (Figs 3.31, 3.32A)

– Body form ovoid, parallel sided (Fig. 3.41A, D). Size exceedingly small (1.1–1.5 mm)… ***Nanosaphes*** (Figs 3.32B–E, 3.41)

21 Fifth ventrite entire, without apical emargination or truncation. Maxillary palps shorter than the width of the head… ***Radicitus*** (Figs 3.50, 3.51)

– Fifth ventrite with apical emargination. Maxillary palps as long or longer than the width of the head… 22

22 Head subquadrate (Fig. 3.9J); eyes relatively small, separated by a distance nearly 6.5 × the maximum width of an eye; mentum and submentum roughly punctate; pubescence covering abdominal ventrites composed of long golden setae; ventral surface of metatarsomeres 1–4 densely setose… ***Aulonochares*** (Figs 3.18, 3.19)

– Head trapezoid; eyes moderate in size, separated by a distance nearly 4 × the maximum width of an eye; mentum obliquely strigate, submentum smooth to shallowly punctate;

pubescence covering abdominal ventrites composed of short setae; ventral surface of metatarsomeres 1–4 only with paired rows of denticles... **23**

23 Body size 4.2–7.0 mm; maxillary palpi nearly as long as maximum width of the head; internal structural reticulations usually visible along entire dorsal surface of elytra (see Fig. 3.36A–B); metaventrite uniformly covered by hydrofuge pubescence; tibial grooves absent to weakly developed; aedeagus tubular (e.g., Fig. 3.37G). Ranging from southern USA to Venezuela... ***Helochares*** (in part; Figs 3.36A–C, 3.37G)

– Body size 4.5–9.0 mm; maxillary palpi 1.1–1.5 × the maximum width of the head; internal structural reticulations absent (see Fig. 3.42); metaventrite with median glabrous patch, sometimes very narrow and extending along entire length of metaventrite (Fig. 3.32C, F); tibial grooves well-developed, with sharp margins; aedeagus divided (e.g., Fig. 3.13P–S)… ***Novochares*** **gen. nov.** (Figs 3.42, 3.43)

Genus *Acidocerus* Klug, 1855

(Fig. 3.14)

Acidocerus Klug, 1855: 649

Gender. Masculine.

Type species. *Acidocerus aphodioides* Klug, 1855: 649; by monotypy.

Diagnosis. Small beetles, body length nearly 2.8 mm. Body shape elongate oval in dorsal view, moderately convex in lateral view, with dorsal outline nearly straight along anterior two thirds of elytra (Fig. 3.14). Surface of head and pronotum granulate (Fig. 3.14C). Body pale/yellowish brown, with head slightly darker. Eyes with anterior margin straight in lateral view (not emarginate), in dorsal view slightly projecting from outline of head (Fig. 3.14C). Labrum not concealed by clypeus. Antennae with nine antennomeres, with strongly asymmetric cupule, with longer side acute. Maxillary palpi elongate, with palpomere 4 nearly as long as palpomere 3 (see d'Orchymont 1943f: 7, in key). Elytra without sutural striae, narrowly explanate laterally, serial punctures strongly marked, arranged in rows (Fig. 3.14A). Prosternum flat, rather sharply carinate medially, with angulate anteromedian projection. Posterior elevation of mesoventrite only weakly bulging. Metaventrite with hydrofuge pubescence. Metafemora without distinct tibial grooves, mostly pubescent, only glabrous at apex. Metatarsomeres 1–4 similar in length; metatarsomere 5 similar in length to metatarsomeres 1–4 combined. Fifth abdominal ventrite apically emarginate, with stout setae.

Differential diagnosis. The granulate surface of the head and body resembles that of *Helobata*, but the exposed labrum of *Acidocerus* (as opposed to concealed in *Helobata*) allows its recognition. The small size and coarse punctation of the elytra of *Acidocerus* resemble some of the Old World *Helochares* (e.g., Fig. 3.36D–F), except for the lack of scutellary striae (Fig. 3.14; see Hansen 1991).

Taxonomic history. Originally described as related to *Spercheus* with maxillary palpi similar to those of *Hydraena* (Klug 1855). d'Orchymont (1943f: 7) provided a list of diagnostic characters in a key. Redescribed by Hansen (1991: 149) based on syntypes. Short et al. (in prep.) discussion of phylogenetic placement.

Figure 3.14. Habitus of *Acidocerus aphodioides*: **A** dorsal habitus, **B** lateral habitus, **C** head. Scale bar 1 mm.

Distribution. Afrotropical: Mozambique.

Natural history. There is no natural history information available for the genus.

Larvae. Immature stages are not known for the genus.

Remarks. Only one known species. Hansen (1991) studied Klug's syntypes housed at the Museum für Naturkunde der Humboldt-Universität in Berlin, Germany (ZMHB), which are the only known specimens for the genus. The diagnostic features listed above include information from d'Orchymont (1943f), Hansen (1991), and own observations of pictures of the syntypes. Given that specimens are mounted on cards, features of the ventral surface, including head, thorax, and abdomen were not observed. Characters of the ventral features as described above are based on d'Orchymont (1943f) and Hansen (1991).

Species examined. *Acidocerus aphodioides* (pictures of syntypes).

Selected references. Klug 1855: 649: original description; d'Orchymont 1943f: 7; offers diagnostic features in a key; Hansen 1991: 149: redescription; Short and Fikáček 2013: *Acidocerus* listed in Acidocerinae; Short et al. in prep.: phylogenetic position and affinities discussed.

Genus *Agraphydrus* Régimbart, 1903

(Figs 3.2A–C, 3.5, 3.15–3.17)

Agraphydrus Régimbart, 1903a: 33

Type species: *Agraphydrus punctatellus* Régimbart, 1903a: 34; by monotypy.

Pseudohelochares Satô, 1960: 77; synonymy by Satô (1965: 128)

Type species: *Pseudohelochares narusei* Satô, 1960: 77; by original designation and monotypy.

Pseudopelthydrus Jia, 1998: 225

Type species: *Pseudopelthydrus longipalpis* Jia, 1998: 229; by original designation. Synonymy by Komarek (2003: 384).

Megagraphydrus Hansen, 1999a: 137

Type species: *Megagraphydrus siamensis* Hansen, 1999a: 140; by original designation. Synonymy by Minoshima et al. (2015: 7).

Gymnhelochares d'Orchymont, 1932: 692; as subgenus of *Helochares*.

Type species: *Helochares* (*Gymnhelochares*) *geminus* d'Orchymont, 1932: 694; by original designation. Synonymy by Komarek and Hebauer (2018: 17).

Horelophopsis Hansen, 1997: 109.

Type species: *Horelophopsis avita* Hansen, 1997: 109, by original designation; Short et al. (in prep) [synonymy].

Gender. Masculine.

Type species. *Agraphydrus punctatellus* Régimbart, 1903; by monotypy.

Diagnosis. Small beetles, body length 1.4–4.8 mm. Body shape elongate to broadly oval in dorsal view, weakly to moderately convex in lateral view, rarely strongly convex (Figs. 3.15, 3.16). Surface of head and pronotum smooth, with shallow ground punctation. Body ranging from pale/yellowish to dark brown (Figs 3.15, 3.16), either uniform across body regions or with different regions colored differently (e.g., darker head, paler elytra and pronotum). Eyes with anterior margin straight in lateral view (not emarginate), in dorsal view slightly projecting from outline of head. Clypeus moderately convex, with distinct systematic punctures, with anterior margin slightly to clearly emarginate. Labrum not concealed by clypeus. Mentum nearly 1.5 × wider than long, with variable surface, with wide and moderate median anterior depression limited by low transverse carina. Antennae with eight or nine antennomeres, with slightly asymmetric cupule, round in outline. Maxillary palpi elongate, 0.7–1.5 × width of head, with inner margin of palpomere 2 usually straight and palpomere 4 nearly as long to slightly longer than palpomere 3 (see Fig. 3.10G). Pronotum with ground punctation usually moderate. Elytra without sutural striae, not laterally explanate, with serial punctures usually absent; systematic punctures usually rather sparse and aligned in four rows along elytra. Prosternum slightly convex, not carinate medially. Posterior elevation of mesoventrite variable, from simply bulged, to bearing variously shaped elevations; anapleural sutures variable in shape and orientation. Metaventrite with posteromedian glabrous patch. Metafemora without distinct tibial grooves, either mostly pubescent (only glabrous at apex), or with pubescence reduced to small basal area ("*Gymnhelochares*"). Metatarsomere 1 shorter than 2; metatarsomere 2 slightly shorter than 5; metatarsomere 5 similar in length to metatarsomeres 3–4 combined. Fifth abdominal ventrite

apically emarginate, sometimes very slightly, or rounded, with or without fringe of stout setae. Aedeagus generally trilobed in form (see Fig. 3.17); basal piece shorter to longer than parameres; outline of apical region of parameres variable; median lobe triangular, with well-developed lateral basal apodemes, usually rounded at apex; gonopore well developed.

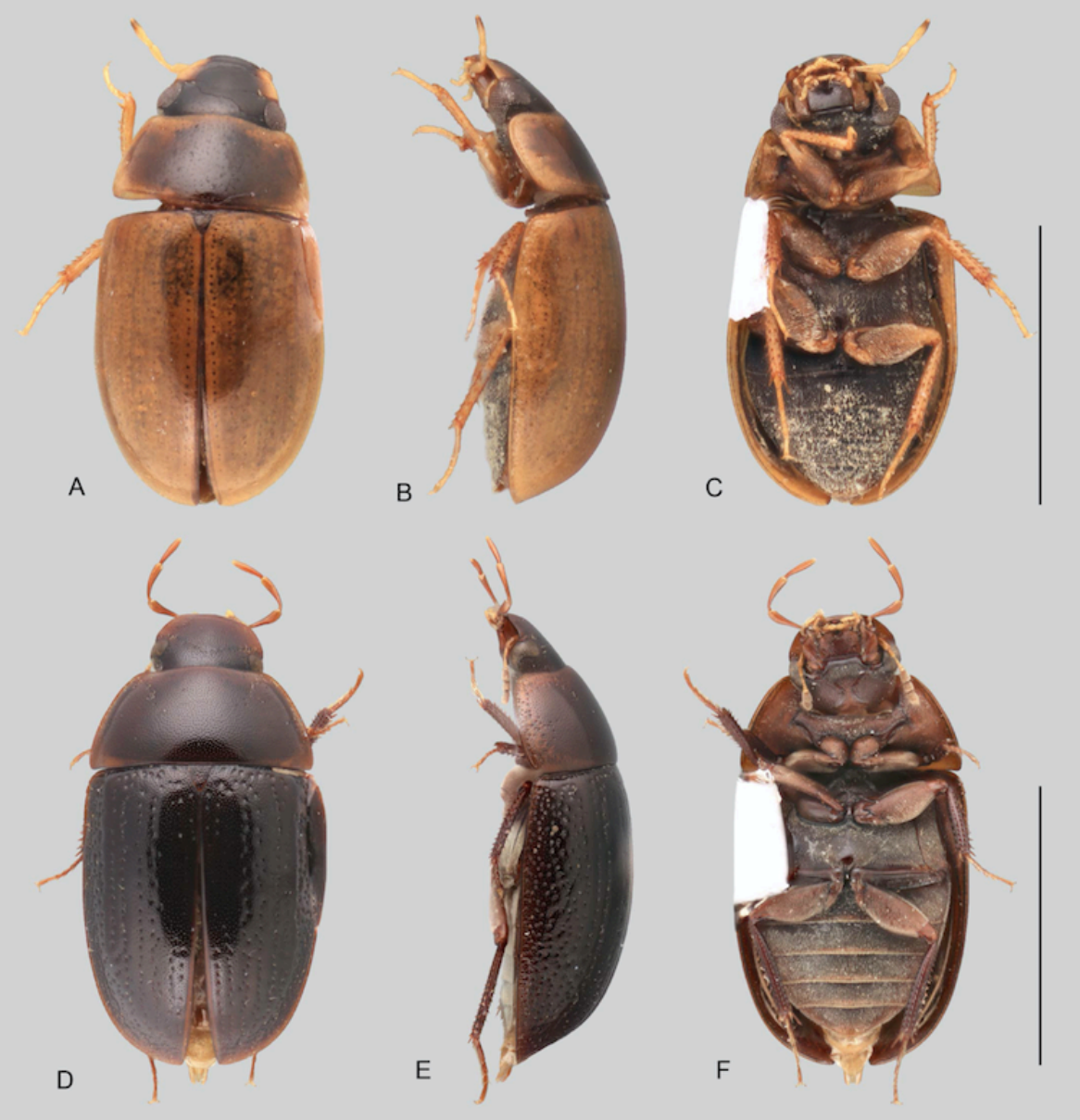


Figure 3.15. Habitus of *Agraphydrus* spp.: **A–C** *A. coomani*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus, **D–F** *A.* cf. *attenuatus*: **D** dorsal habitus, **E** lateral habitus, **F** ventral habitus. Scale bars 1 mm.

Figure 3.16. Habitus of *Agraphydrus* sp.: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus. Scale bar 1 mm.

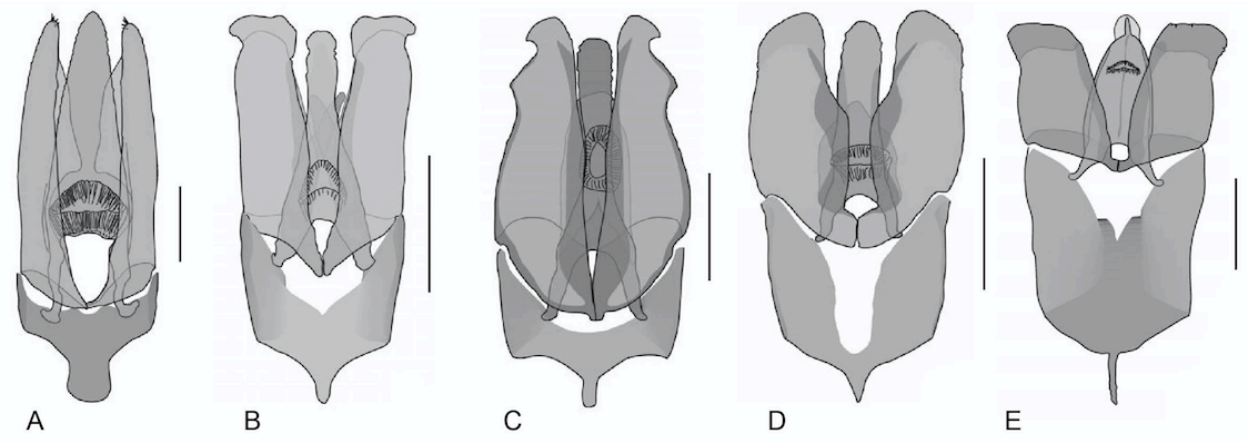


Figure 3.17. Aedeagus of *Agraphydrus* spp.: **A** *A. attenuatus*, **B** *A. gracilipalpis*, **C** *A. masatakai*, **D** *A. chinensis*, **E** *A. puzhelongi*. Scale bars 0.1 mm. Line drawings taken from Komarek (2018).

Differential diagnosis. *Agraphydrus* can be considered highly variable both morphologically and ecologically. Given their usually small to very small size, in the regions where *Agraphydrus* is distributed, they may be confused with smaller species of *Helochares*, from which *Agraphydrus* can be distinguished by the presence of a posteromesal glabrous patch

on the metaventrite (metaventrite uniformly and densely covered by hydrofuge pubescence in *Helochares*); their size allows to differentiate them from the much larger *Colossochares* and *Peltochares*. The lack of sutural stria in *Agraphydrus* allows to recognize the larger *Agraphydrus* from similarly sized *Crephelochares*. The maxillary palpi tend to be shorter in *Agraphydrus*. Most *Agraphydrus* have moderately puncturate head and pronotum, and lack elytral serial punctures; although they may have very coarse systematic punctures somewhat aligned in rows, these rows are not quite uniform as in many Old World *Helochares* or *Acidocerus*. The outer margins of the elytra of *Agraphydrus* are only slightly flared, as opposed to laterally expanded which differentiates them from *Batochares*. The most similar genus to *Agraphydrus* would be the Neotropical genus *Tobochares*, but they do not co-occur; the body shape in *Agraphydrus*, in general, tends to be more elongated (1.1–1.4 × longer than wide), whereas in *Tobochares* it tends to be only slightly longer than wide (1.07–1.15 × longer than wide); in addition, the metafemora in *Tobochares* are always glabrous, and their serial punctures are always well aligned longitudinally.

Taxonomic history. Originally described as genus by Régimbart in 1903; downgraded to subgenus of *Enochrus* by d'Orchymont (1919c: 155); transferred as subgenus to *Helochares* by d'Orchymont (1927a: 250); generic status re-established by Satô (1965: 128). Hansen (1991: 148) placed *Gymnhelochares* as subgenus of *Agraphydrus*; Komarek and Hebauer (2018: 17) placed *Gymnhelochares* as a synonym of *Agraphydrus* given that there are no unique morphological traits that allow to differentiate them. Minoshima et al. (2015: 7) synonymized *Megagraphydrus* with *Agraphydrus* also based on the lack of morphological traits in support of

their separation. Short and Fikáček (2013) recovered *Horelophopsis* and *Agraphydrus* as sister taxa. These affinities were also recognized by Minoshima et al. (2013) based on larval characters. Finally, Short et al. (in prep.), based on their phylogenetic analyses, synonymized *Horelophopsis* with *Agraphydrus*, as *Horelophopsis* was recovered as a lineage within *Agraphydrus*. For more details on the taxonomic history of the genus and its synonyms see Minoshima et al. (2015).

Distribution. Afrotropical: Cameroon, Ethiopia (in doubt), Gabon, Guinea, Ivory Coast, Kenya, Madagascar, Malawi, Mozambique, Namibia, Oman, Saudi Arabia, South Africa (in doubt), Sudan, Tanzania, United Arab Emirates, Yemen, Zimbabwe. **Australasian:** Australia (New South Wales, Northern Territory, Queensland, Western Australia), Indonesia (Java, Papua), Papua New Guinea. **Indo-Malayan:** Bhutan, Brunei, China (Fujian, Guangdong, Guangxi, Guizhou, Hainan, Himachal, Hong Kong, Hunan, Jiangxi, Yünnan, Zhejiang), India (Arunachal Pradesh, Assam, Goa, Himachal Pradesh, Kerala, Karnataka, Madhya Pradesh, Maharashtra, Meghalaya, North Andaman Island, Sikkim, Tamil Nadu, Uttar Pradesh, Uttarakhand), Laos, Malaysia, Myanmar, Nepal, Sri Lanka, Taiwan, Thailand, Vietnam. **Palearctic:** China (Anhui, Gansu, Hubei, Shaanxi, Shandong, Sichuan, Tibet), Japan, Korea, Pakistan, South Korea.

Natural history. *Agraphydrus* can be found in a broad range of habitats, from rivers, streams and forest pools, to hygropetric environments around waterfalls or seepages over rocks; a few species have been collected in terrestrial habitats by sifting moss and leaves from near water bodies, or in the gravel along the bank of a river; in many cases specimens have been

found associated to floating vegetation, mosses and algae (Komarek and Hebauer 2018, Komarek 2018, 2019).

Larvae. Only the larvae of two species of *Agraphydrus* are known until now: *A. narusei* (Satô) (first and third instars; Minoshima and Hayashi 2011), and *A. hanseni* (Satô and Yoshitomi) (third instar; Minoshima et al. 2013). Minoshima (2016) offers a diagnosis for *Agraphydrus* larvae.

Remarks. With 167 described species, *Agraphydrus* is currently the largest genus of Acidocerinae, due to a series of recent revisions and monographs (Minoshima et al. 2015; Komarek 2018, 2019; Komarek and Hebauer 2018). The condition of the maxillary palpomere 2 being straight (with inner margin straight) is not unique to *Agraphydrus* but shared with *Tobochares* and some *Helochares*. Minoshima et al. (2015) proposed the V-shaped male abdominal sternite 9 as a possible synapomorphy of the genus, but the condition is shared with some members of the *Tobochares*-group. Hebauer (2002a) lists several species of *Agraphydrus* as “in press” but those were never formally published.

Species examined. *Agraphydrus anatinus* Komarek, *A. attenuatus* (Hansen), *A. coomani* (d'Orchymont), *A. decipiens** Minoshima, Komarek and Ôhara, *A. insidiator** Minoshima, Komarek and Ôhara, *A. ishiharai* (Matsui), *A. kempi* (d'Orchymont), *A. luteilateralis** (Minoshima and Fujiwara), *A. malayanus** (Hebauer), *A. masatakai** Minoshima, Komarek and Ôhara, *A. minutissimus* (Kuwert), *A. narusei* (Satô), *A. pauculus* (Knisch), *A. politus* (Hansen), *A. pygmaeus*

(Knisch), *A. siamensis* (Hansen), *A. stagnalis* (d'Orchymont), *A. thaiensis* Minoshima, Komarek and Ôhara, and numerous unidentified specimens. For species marked with an asterisk, paratype specimens were studied.

Selected references. Minoshima et al. 2015: character discussion, taxonomic history, synonymization of *Megagraphydrus*, description of seven new species. Komarek and Hebauer (2018: 17) synonymized the subgenus *Gymnhelochares* with *Agraphydrus*; taxonomic revision for China and Taiwan describing 33 new species. Komarek 2018: taxonomic revision for India describing 36 new species. Komarek 2019: taxonomic revision for South East Asia (except Philippines) and Australasian Region, describing 60 new species. Short et al. in prep.: synonymization of *Horelophopsis* with *Agraphydrus*.

Genus *Aulonochares* Girón and Short, 2019

(Figs 3.1D, 3.4, 3.9J, 3.18, 3.19)

Aulonochares Girón and Short, 2019: 112

Gender. Masculine.

Type species. *Aulonochares tubulus* Girón and Short, 2019: 120; by original designation.

Diagnosis. Medium sized beetles, total body length 5.8–7.5 mm. Body shape elongated oval in dorsal view; weakly convex in lateral view (Fig. 3.18). Color orange brown to dark brown;

ventral surface covered with rather long golden setae, especially on abdominal ventrites, and more densely so (with shorter setae) on surface of femora. Head subquadrate in dorsal view, seemingly constricted at anterior margin of eyes (Fig. 3.9J). Eyes relatively small, separated by distance nearly 6.5 × the maximum width of an eye. Clypeus with lateral margins nearly parallel, slightly convex, with anterior margin only slightly narrower than posterior margin. Labrum fully exposed. Mentum and submentum roughly puncturate. Antennae with nine antennomeres, with cupule slightly asymmetrical and round in outline. Maxillary palpi long, nearly 1.5 × longer than maximum width of head, with inner and outer margins of maxillary palpomere 2 evenly curved. Pronotum with ground punctation shallow and uniformly sparse. Elytra without sutural striae, with outer margins slightly flared; serial punctures, ground punctures and systematic punctures similar in size, shallowly impressed. Surface of prosternum flat (slightly carinate only along midline of antero-mesal projection of anterior margin). Posterior elevation of mesoventrite simple, without carinae or ridges; anapleural sutures concave, anteriorly converging, anteriorly separated by distance nearly 0.3 × as wide as anterior margin of mesepisternum. Metaventrite densely and uniformly pubescent. Protibiae with spines of anterior row very small and appressed; apical spurs of protibiae very short (not exceeding the length of the first tarsomere) and stout. Hydrofuge pubescence covering most of surface of metafemora. Ventral face of tarsomeres 1–4 densely covered by stiff setae. Apex of fifth abdominal ventrite strongly emarginate; emargination fringed by stout setae. Aedeagus tubular (Fig. 3.19), somewhat cylindrical, with parameres forming a 5–7 × longer than wide tube; basal piece very short and strongly concave; gonopore reduced, located at apex of median lobe.

Figure 3.18. Habitus of *Aulonochares tubulus*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus. Scale bar 5 mm.

Differential diagnosis. *Aulonochares* can be easily mistaken with *Novochares* in the New World. The subquadrate shape of the head (Fig. 3.9J; as opposed to trapezoid as in Fig. 3.9G), the roughly puncturate mentum, the long setae composing the ventral pubescence of the abdominal ventrites, densely setose tarsomeres, along with the tubular shape of the aedeagus (Fig. 3.19) are very distinctive and uniquely combined in *Aulonochares* among Neotropical acidocerines.

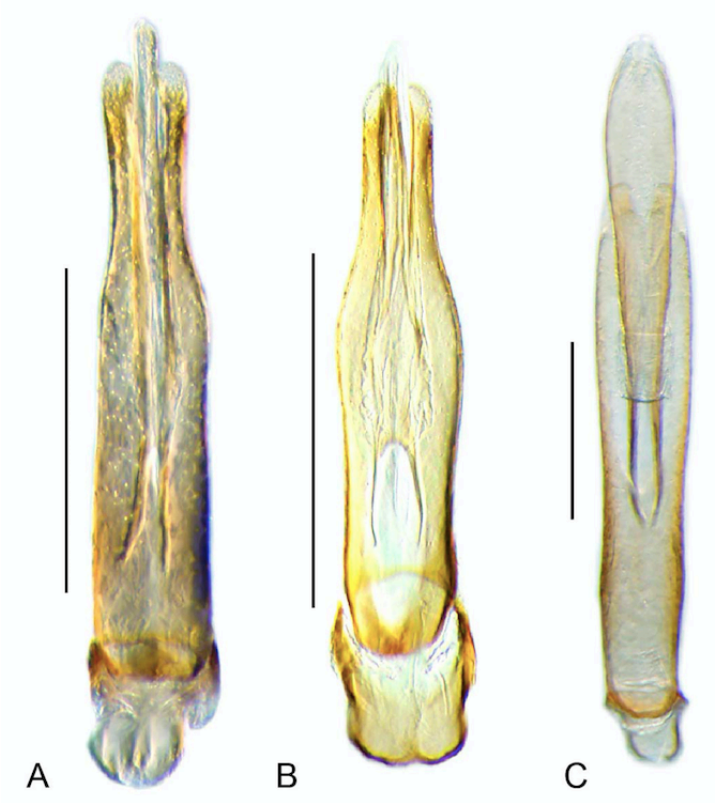


Figure 3.19. Aedeagus of *Aulonochares* spp.: **A** *A. tubulus*, **B** *A. novoairensis*, **C** *A. lingulatus*. Scale bars 0.5 mm.

Taxonomic history. Recently described by Girón and Short (2019).

Distribution. Neotropical: Brazil (Amazonas, Roraima), French Guiana, Guyana, Suriname, Venezuela.

Natural history. Specimens of *Aulonochares* have been collected in densely forested sandy streams and detrital pools in forests along creeks. They seem to prefer habitats with abundant detritus or decaying organic matter. Females of *A. tubulus* have been observed carrying their egg cases underneath their abdomen.

Larvae. Immature stages are not known for the genus.

Remarks. Only three species are known for the genus (see Girón and Short 2019).

Species examined. *Aulonochares lingulatus* Girón and Short, *A. novoairensis* Girón and Short, *A. tubulus* Girón and Short. Holotypes and paratypes of all three species were available for this study.

Selected references. Girón and Short (2019): original description of the genus and all its currently known species.

Genus *Batochares* Hansen, 1991: 292

(Figs. 3.1J, 3.4, 3.9D, E, 3.20, 3.21A)

Batochares d'Orchymont, 1939b: 293 [Described as subgenus; unavailable, ICZN (1999) Art. 13.3: no type species designated].

Fixed as subgenus of *Helochares* by Hansen (1991: 292) [available, granting authorship to Hansen under ICZN (1999) Art. 50.1.]

Elevated to genus by Short et al. (in prep.)

Gender. Masculine.

Type species. *Helochares* (*Batochares*) *burgeoni* d'Orchymont, 1939b: 294 by original designation (Hansen 1991: 292).

Diagnosis. Body length between 3–4 mm. Body shape oval in dorsal view, moderately convex in lateral view, with dorsal outline nearly straight along basal two thirds (Fig. 3.20). Dorsal surfaces smooth, uniformly covered by short setae, brown to pale brown in coloration, either uniform or with yellowish patches along margins of pronotum and elytra, or scattered throughout surface giving spotted appearance; ground punctation fine and shallow; ventral surfaces rather densely covered by rather long and fine golden setae. Head rather oval in dorsal view, clearly constricted at anterior margin of eyes (Fig. 3.9E). Eyes not emarginate, moderate in size, separated by nearly 3.8 × width of eye, strongly projected from outline of head. Clypeus with anterior margin broadly emarginate, with medial region of emargination nearly straight; anterior corners round. Labrum fully exposed, with apical region anteriorly flattened, thus forming fine transverse carina across anterior region (Fig. 3.9D). Mentum rather flat, surface laterally punctate, mesally and anteriorly strigate, with anteromedial region depressed. Submentum finely and shallowly punctate. Antennae with nine antennomeres, with strongly asymmetric and round cupule. Maxillary palpi nearly 1.5 × longer than maximum width of head, with palpomere 4 0.8 × as long as palpomere 3; inner margin of maxillary palpomere 2 nearly straight, outer margin apically slightly curved. Pronotum medially evenly convex, explanate and somewhat bending upwards along antero-lateral areas; posterior margin of pronotum clearly narrower than anterior margin of elytra combined. Elytra without sutural striae, with outer margins explanate, especially along anterior third; serial punctures well developed, forming

longitudinal rows, at least well defined along outer areas, or visible along entire length of elytra; seta bearing systematic punctures irregularly distributed. Surface of prosternum slightly elevated along midline, with anterior margin acutely triangular and slightly projected anteriorly. Posterior elevation of mesoventrite rather flat; intercoxal process of mesoventrite broad (nearly as wide as antennal club), apically truncate; anapleural sutures sinuate, separated at anterior margin by distance slightly shorter than anterior margin of mesepisternum. Metaventrite with medial surface elevated as platform, densely covered by with hydrofuge pubescence, except for posterolateral patches. Protibiae with spines of anterior row very fine and erect; apical spurs of protibiae small (larger spur similar in size and shape to tarsal claws). Metafemora without tibial grooves; metafemora with hydrofuge pubescence covering at least basal two thirds of anterior surface. Metatarsomere 5 1.5 × longer than metatarsomere 2, metatarsomere 2 nearly as long as metatarsomeres 3 and 4 combined; tarsomeres 1 to 4 with sparse long setae on dorsal surface, and spiniform setae on ventral surface; tarsomere 5 with few setae along apical margin. Abdomen with five pubescent ventrites. Fifth abdominal ventrite with apex broadly truncate, without stout setae. Aedeagus trilobed, with basal piece nearly as long as parameres (Fig. 3.21A); parameres somewhat triangular, slender and apically narrowing; median lobe tapering to round apex; gonopore well-developed.

Figure 3.20. Habitus of *Batochares* sp.: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus. Scale bar 1 mm.

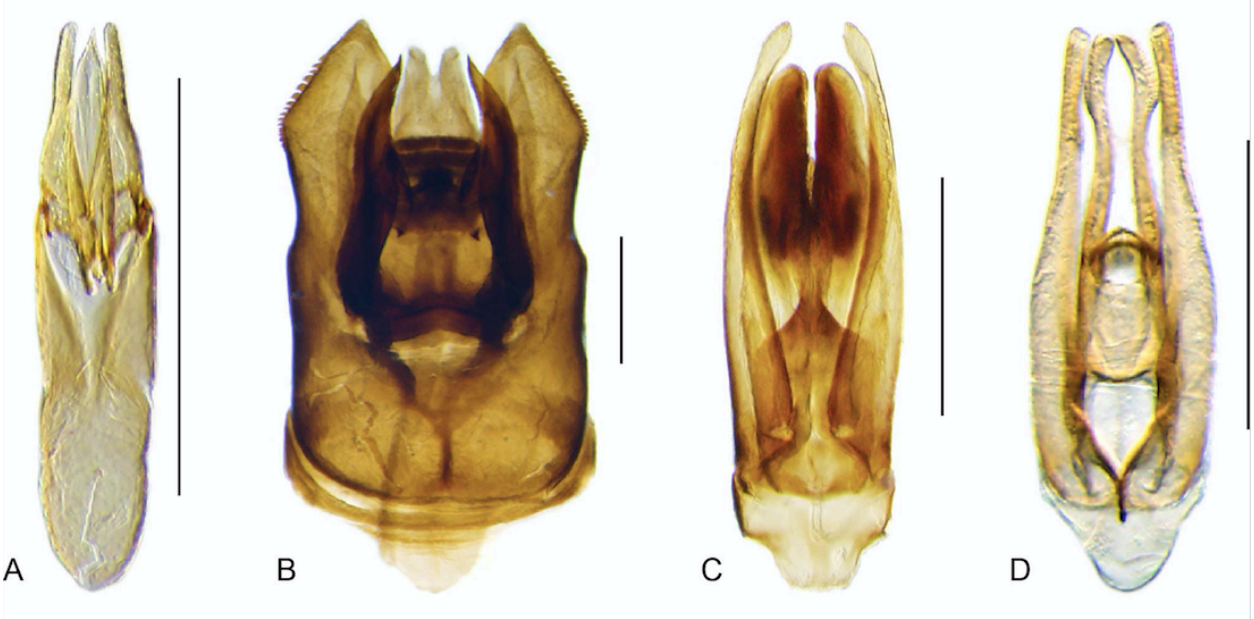


Figure 3.21. Aedeagus of miscellaneous acidocerines in *Helochares*-group: **A** *Batochares* sp. (SLE-1336), **B** *Colossochares ellipticus*, **C** *Helobata* sp. (Ecuador), **D** *Sindolus ventricosus*. Scale bars 0.5 mm.

Differential diagnosis. *Batochares* differs from all other known acidocerines by its unique labrum (with apical region anteriorly flattened, forming a transverse carina across anterior region; see Fig. 3.9D), combined with oval head which is constricted at the anterior margins of the eyes, anterolaterally explanate pronotum, explanate elytra, rows of serial punctures visible at least along outer margins, broadly truncate posterior margin of fifth abdominal ventrite, and unusually large basal piece of the aedeagus (longer than parameres). These features, especially the configuration of the labrum, pronotum and elytra, along with the yellow spots along the surface of the elytra distinguish *Batochares* from all other known acidocerines.

Taxonomic history. *Batochares* was described as a subgenus of *Helochares* by d'Orchymont (1939b) who did not explicitly designate a type species; therefore, the subgenus name was unavailable according to article 13.3 of the ICZN (1999). In 1991, Hansen validated *Batochares* as a subgenus of *Helochares* by fixing the type species for it; therefore, under article 50.1 of the Code (ICZN 1999), Hansen is granted authorship of the subgenus name. *Batochares* was elevated to full generic status based on the phylogenetic analysis presented by Short et al. (in prep.).

Distribution. Afrotropical: Burundi/Rwanda, Central African Republic, Democratic Republic of the Congo, Gabon, Guinea, Kenya, Republic of the Congo, Uganda.

Natural history. There is no natural history information available for the genus.

Larvae. Immature stages for *Batochares* remain unknown.

Remarks. There are three species of *Batochares* described to date. d'Orchymont considered *Batochares* as a subgenus of *Helochares* based for the most part in the number of antennomeres, relatively long maxillary palpi, characters of the mentum and pubescent femora. Although the author recognized the distinctiveness of the shape of the head and the explanate elytra. In his description of *Batochares corrugatus* Balfour-Browne (1958a: 183) pointed out that his record of *B. burgeoni* from Mutsora, Parc National Albert (currently Virunga National Park, Democratic Republic of the Congo; Balfour-Browne 1950b) was not actually *B. burgeoni*, but a larger and likely different species. The author also indicated the existence of a different species from Angola.

Species examined. *Batochares burgeoni* (d'Orchymont) and *B. byrrhus* (d'Orchymont).

Selected references. d'Orchymont (1939b: 293; original description); Balfour-Browne (1958a: 183; description of an additional species); Hansen (1991: 292; type species designated, synonym with *Helochares* (*Batochares*) d'Orchymont, 1939); Short et al. (in prep.; generic status; phylogenetic position and affinities discussed).

Genus *Chasmogenus* Sharp, 1882

(Figs 3.5, 3.9H, 3.22, 3.23)

Chasmogenus Sharp, 1882: 73; Fernández 1986: 189 [generic status reinstated].

Type species: *Chasmogenus fragilis* Sharp, 1882: 73; by monotypy.

Helochares (*Chasmogenus*) Sharp; d'Orchymont 1919c: 149 [as subgenus of *Helochares*]; Knisch 1924: 195 [catalog].

Dieroxenus Spangler, 1979: 753; Girón and Short 2018: 154 [synonymy].

Type species: *Dieroxenus cremnobates* Spangler, 1979: 754; by original designation and monotypy.

Gender. Masculine.

Type species. *Chasmogenus fragilis* Sharp, 1882: 73; by monotypy.

Diagnosis. Body length ranging from 2.5–4.5 mm. Body shape oval in dorsal view, parallel-sided to broader around midlength, dorsoventrally flattened, weakly to moderately convex in lateral view (Fig. 3.22), either evenly convex or flattened along anterior half. Surface of head, pronotum and elytra smooth, with usually shallow ground punctation. Coloration ranging from yellowish orange to dark brown, usually uniform along body, sometimes darker on head or only frons. Shape of head trapezoid (see Fig. 3.9H). Eyes varying in size, usually subquadrate in dorsal view, only very weakly emarginated anteriorly, and usually projected from outline of head. Clypeus trapezoid, with anterior margin mesally weakly to strongly emarginate; membranous preclypeal area visible when clypeus strongly emarginated (see Fig. 3.9H). Labrum fully exposed,

semioval, anteriorly mesally emarginated. Mentum usually rather smooth, with anterior depression often reaching midlength of mentum, sometimes limited by low transverse carina. Antennae with eight antennomeres, with cupule slightly asymmetric and rounded. Maxillary palpi usually slender and slightly longer than width of head, with inner margin slightly and evenly curved, and outer margin curved along apical half. Pronotum evenly convex. Elytra with sutural striae, with outer margins slightly flared; ground punctures usually only shallowly marked, serial punctures absent and at least one median row of systematic punctures clearly visible on each elytron. Surface of prosternum usually flat, only rarely with low medial carina along intercoxal process. Posterior elevation of mesoventrite with an either blunt or sharp longitudinal elevation; anapleural sutures sinuate, separated at anterior margin by distance similar or slightly shorter than anterior margin of mesepisternum. Metaventrite with posteromesal and posterolateral glabrous patches. Protibiae with spines of anterior row semi erect, relatively long, thick and sparse; apical spurs of protibiae moderately long and thick, reaching apex of protarsomere 2. Metafemora with tibial grooves moderately developed, with sharp posterior margin; hydrofuge pubescence covering at least basal three fourths of anterior surface of metafemora. Metatarsomeres 2–4 with two rows of spiniform setae on ventral surface; metatarsomere 5 nearly as long as 3–4 combined; metatarsomere 2 shorter to nearly as long as 5. Apex of fifth abdominal ventrite emarginate, with fringe of flat and stout setae. Aedeagus trilobed (Fig. 3.23); basal piece shorter to nearly as long as parameres; outline of apical region of parameres variable; median lobe triangular, with well-developed lateral basal apodemes and gonopore.

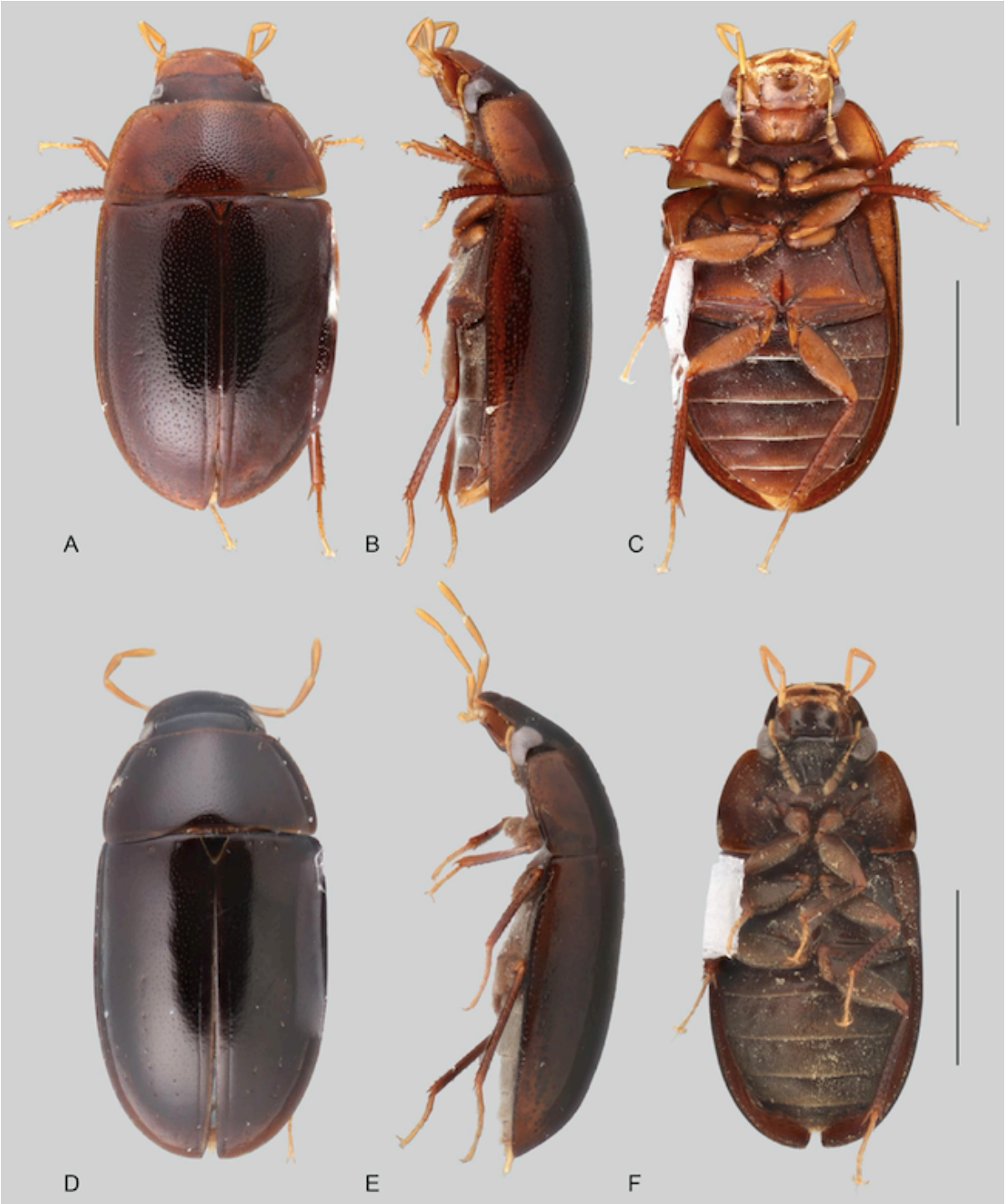


Figure 3.22. Habitus of *Chasmogenus* spp.: **A–C** *Chasmogenus ruidus*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus, **D–F** *Chasmogenus* sp.: **D** dorsal habitus, **E** lateral habitus, **F** ventral habitus. Scale bar 1 mm.

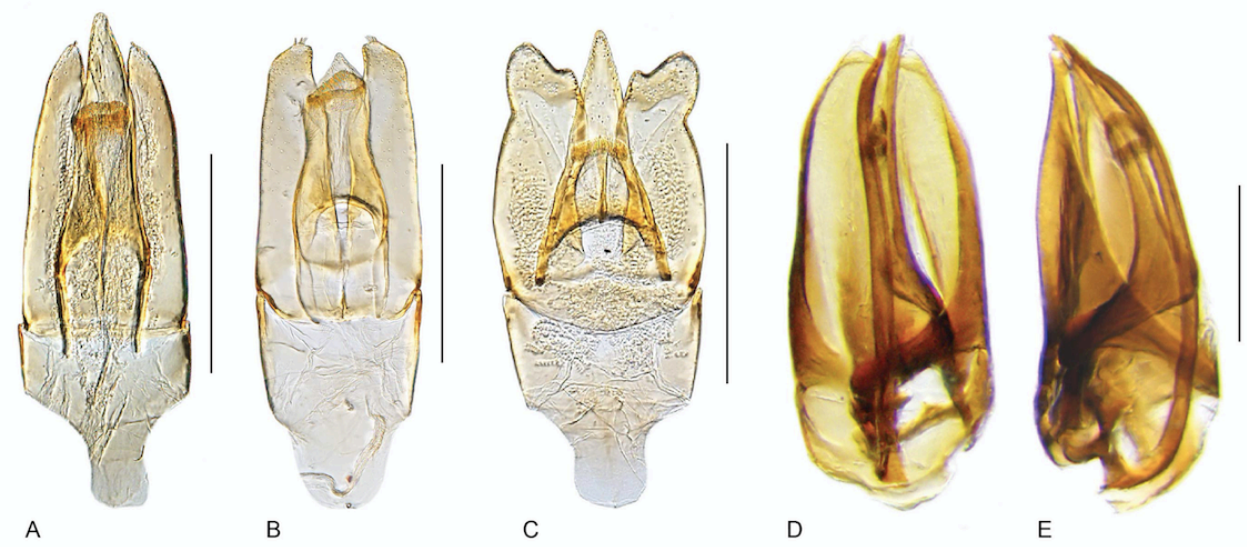


Figure 3.23. Aedeagus of *Chasmogenus* spp.: **A** *C.* sp. (Brazil), **B** *C.* sp. (Suriname), **C** *C.* sp. (Venezuela), **D–E** *C.* sp. (Suriname): **D** dorsal view, **E** lateral view. Scale bars 0.5 mm.

Differential diagnosis. *Chasmogenus* most closely resembles *Crephelochares*, although they do not co-occur in the same biogeographic regions (*Chasmogenus* occurs only in the Neotropical region, whereas *Crephelochares* occurs throughout the Old World). They can be differentiated by the number of antennomeres (8 in *Chasmogenus*, 9 in *Crephelochares*) and by the form of the aedeagus (trilobed in most *Chasmogenus* (see Fig. 3.23), subdivided and further modified in *Crephelochares* (see Fig. 3.26). In the New World *Chasmogenus* can easily be distinguished by the presence of sutural striae, character shared only with *Primocerus*, from which it can be distinguished by the shape of the posterior elevation of the mesoventrite: longitudinally elevated in *Chasmogenus*, transversally elevated in *Primocerus*.

Taxonomic history. *Chasmogenus* was originally described by Sharp (1882) as a genus to accommodate one Neotropical species. d'Orchymont (1919c: 149) synonymized *Chasmogenus*

with *Crephelochares* (from the Old World) and placed it as subgenus of *Helochares*. The generic rank of *Chasmogenus* was re-established by Fernández (1986: 189), with *Crephelochares* still as a junior synonym. The recent phylogeny by Short et al. (in prep.) offered support to consider *Chasmogenus* and *Crephelochares* as separate genera.

Distribution. Neotropical: Argentina, Brazil (Minas Gerais, Pará, Rio de Janeiro, São Paulo), Costa Rica, Ecuador, Guatemala, Panama, Paraguay, Venezuela.

Natural history. Specimens of *Chasmogenus* have been collected on lentic habitats like ponds and marshes, in standing waters, and along margins of rivers. They can also be found among the vegetation and submerged leaf litter. They are also attracted to lights. Only one species (*Chasmogenus cremobates* (Spangler)) has been collected in seepages.

Larvae. The larvae of *Chasmogenus* remain unknown. The only descriptions of immature stages were made for *Chasmogenus nitescens* (from Australia), which is now assigned to *Crephelochares*.

Remarks. There are 16 described species of *Chasmogenus* until now. *Chasmogenus* is a fairly commonly found genus with very little variation on the external morphology. Recent collecting efforts and taxonomic study in the genus is revealing a hidden diversity and interesting biogeographic patterns in South America (Smith and Short in prep.).

Species examined. *Chasmogenus australis** García, *C. bariorum** García, *C. barrae** Short, *C. cremnobates* (Spangler), C. *lorenzo** Short, *C. ruidus** Short. Paratypes of the species marked with an asterisk were available for this study.

Selected references. Sharp (1882), genus description; Spangler (1979), description of *Dieroxenus*; Fernández (1986), notes on the genus and one new species; Hebauer (1992), notes, recognition of two subgenera, emphasis on *Crephelochares*; García (2000), four new species from Venezuela; Short (2005), new species from Costa Rica; Short and Fikáček (2013), inclusion of *Chasmogenus* species in molecular phylogeny; Clarkson and Ferreira-Jr (2014b), four new species from Brazil; Girón and Short (2018), synonymization of *Dieroxenus*.

Genus *Colossochares* Girón and Short, gen. nov.

(Figs. 3.1A, 3.3, 3.9I, 3.21B, 3.24)

Helochares "Clade B", Short et al. (in prep.)

Gender. Masculine.

Type species. *Helochares ellipticus* d'Orchymont, 1933: 306; by present designation.

Etymology. From the Latin word *colossus*, meaning extremely large, in reference to the comparatively large and robust bodies of the members in the genus, combined with the ending *chares*, expressing affinity with *Helochares*. Masculine.

Figure 3.24. Habitus of *Colossochares ellipticus*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus. Scale bar 1 mm.

Diagnosis. Body length 8.5–14.0 mm. Body shape broadly oval in dorsal view, strongly and uniformly convex in lateral view (Fig. 3.24). Dorsal surfaces even and smooth, uniformly dark brown (nearly black) in coloration with reddish antennae, palpi and tarsi; ground punctation extremely fine and shallow; ventral surfaces rather densely covered by rather long and fine golden setae. Eyes not emarginate, moderate in size, subquadrate in dorsal view, separated by nearly 4 × width of eye, projected from outline of head (Fig. 3.9I). Frons with large (and somewhat fused together) systematic punctures along inner margin of eye. Clypeus with anterior margin broadly roundly emarginate. Labrum fully exposed, medially convex. Antennae with nine antennomeres, with strongly asymmetric and round cupule. Maxillary palpi slender, slightly longer than maximum width of head, with palpomere 4 0.7 × as long as palpomere 3. Mentum medially broadly depressed, laterally punctate, mesally and anteriorly strigate;

sculpture of mentum ranging from shallow to strong. Pronotum evenly convex, and very smooth, with ground punctation very fine and shallow; systematic punctures of pronotum reduced to paired depressions near anterior margin and at midlength of lateral margins. Elytra without sutural striae, with margins slightly flared; serial punctures either absent or only visible along outer lateral area and posterior third of elytra; systematic punctures enlarged, broadly separated longitudinally, forming five rows mostly visible along outer lateral area and posterior third of elytra. Surface of prosternum flat to broadly convex, with anterior margin slightly projected anteriorly. Posterior elevation of mesoventrite with broad longitudinal elevation; anapleural sutures concave, anteriorly converging and separated by distance nearly 1/3 of anterior margin of mesepisternum. Metaventrite uniformly densely covered by with hydrofuge pubescence, medial surface elevated as platform. Protibiae with anterior row of spines extremely reduced to tiny and scanty, appressed denticles; apical spurs of protibiae large, outer nearly as thick and reaching apex of protarsomere 2. Metafemora with tibial grooves well-developed; metafemora with hydrofuge pubescence covering basal four fifths of anterior surface. Metatarsomeres laterally compressed, metatarsomere 2 longer than 5, metatarsomere 5 nearly as long as 3 and 4 combined; all tarsomeres with rows spiniform setae covering ventral surface. Fifth abdominal ventrite with apex emarginate, with fringe of flat and stout setae. Aedeagus symmetrical, either trilobed (*C. satoi*; see fig. 1 in Hebauer 2003a) or highly modified (see Fig. 3.21B), with basal piece shorter than parameres; median lobe variable.

Differential diagnosis. *Colossochares* groups some of the largest acidocerines. *Colossochares* species are strongly and uniformly convex and highly polished, with enlarged

systematic punctures on the head and elytra; systematic punctures on the pronotum are reduced to a pair of anterior and a pair of lateral depressions, not forming the usual antero-lateral semicircles that are common in acidocerines. Some members of *Peltochares* may exhibit similar coloration and general highly polished appearance to *Colossochares* (e.g., compare Fig. 3.1A vs. 3.1B); those *Peltochares* are always dorsoventrally flattened, generally slender, and the pronotum has systematic punctures forming antero-lateral semicircles. Other than general appearance, both genera are very similar to each other in details of the external morphology, except by the sculpture of the submentum, which is smooth in *Colossochares* and punctate or otherwise sculptured in *Peltochares*. In addition, the aedeagal form in *Peltochares* (spiked, see Fig. 3.13F–J) is quite different from the forms present in *Colossochares* (trilobed or as in Fig. 3.21B).

Taxonomic history. Régimbart (1907: 47) offers a description for *Helochares ellipticus* but refers it as *Hydrophilus ellipticus* Fabricius. Régimbart expressed his doubts about the affinities of this species, as it exhibits *Helochares* characters, but was described by Fabricius under *Hydrophilus*. Later, d'Orchymont (1933) clarified the situation and confirmed *Helochares ellipticus* as a valid species of *Helochares*, different from *Hydrophilus ellipticus* Fabricius. Hebauer (2003) described *Helochares satoi* Hebauer and discussed its affinities with *Helochares ellipticus*. A specimen of *Helochares ellipticus* was included in the molecular phylogeny by Short et al. (in prep.). Given that it is not nested within *Helochares*, and it is morphologically distinct, the genus *Colossochares* is here established to house the two species: *Colossochares ellipticus*

(d'Orchymont) **comb. nov.** and *Colossochares satoi* (Hebauer) **comb. nov.**, which are among the largest acidocerines.

Distribution. Afrotropical: Benin, Burkina Faso, Cameroon, Democratic Republic of the Congo, Ethiopia, Gabon, Ghana, Guinea, Ivory Coast, Liberia, Malawi, Nigeria, Republic of the Congo, Uganda.

Natural history. No information is known about the biology of species of *Colossochares*, except that *C. ellipticus* has been collected using light traps.

Larvae. The larvae of species of *Colossochares* remain unknown.

Remarks. Despite the great external similarity between the two known species of *Colossochares*, their male genitalia are quite different from each other. This particularity is so far unique in the subfamily given that, in general, each genus has a particular aedeagal type shared by all its species. The genitalia of *C. satoi* can be categorized as trilobed, whereas that of *C. ellipticus* is quite uniquely configured (see Fig. 3.21B).

Species examined. Specimens of *Colossochares ellipticus* (d'Orchymont) and female paratypes of *C. satoi* (Hebauer) were available for study.

Selected references. Régimbart (1907): original description; d'Orchymont (1933) clarification and reaffirmation of species name; Hebauer (2003): new species and discussion of affinities.

Genus *Crephelochares* Kuwert, 1890

(Figs 3.2E, 3.5, 3.9G, 3.25, 3.26)

Helochares (*Crephelochares*) Kuwert, 1890: 38

Helochares (*Crepidelochares*) Ganglbauer, 1904: 248 [unjustified emendation of *Crephelochares* Kuwert, 1890].

Helochares (*Chasmogenus*) Kuwert; d'Orchymont 1919c: 148 [taxonomic treatment]; Knisch 1924a: 195 [catalog].

Crephelochares Kuwert; Fernández 1986: 148 [junior synonym of *Chasmogenus* as genus]; Hansen 1991: 293 [catalog]; Short et al. (in prep.) [elevated to generic rank].

Chasmogenus (*Crephelochares*) Kuwert; Hebauer 1992: 62 [as subgenus of *Chasmogenus*].

Gender. Masculine.

Type species. *Helochares livornicus* Kuwert, 1890: 38; subsequent designation by d'Orchymont (1939a: 154).

Diagnosis. Body length ranging from 2.5–4.8 mm. Body shape oval in dorsal view, dorsoventrally slightly flattened, moderately convex in lateral view, with dorsal outline nearly evenly convex (Fig. 3.25); surface even and smooth, with usually shallow ground punctation. Coloration usually dark brown seldom yellowish, uniform across body regions. Head trapezoid (Fig. 3.9G). Eyes relatively large, at most only slightly emarginated anteriorly, and not or only slightly projected from outline of head. Clypeus trapezoid, with anterior margin mesally emarginate; membranous preclypeal area visible when clypeus strongly emarginated. Labrum fully exposed. Mentum punctate or punctate laterally and medially obliquely strigate; medial surface flat to depressed; anteromedial depression sometimes limited by low transverse carina. Antennae with nine antennomeres, with cupule slightly asymmetric and rounded. Maxillary palpi slender, 1.2–1.5 × longer than width of head; maxillary palpomere 4 nearly 0.7 × length of maxillary palpomere 3; inner margin of maxillary palpomere 2 nearly straight, and outer margin curved along apical half. Pronotum evenly convex. Elytra with sutural striae, with outer margins slightly flared; ground punctures usually only shallowly marked, serial punctures absent and at least one median row of systematic punctures visible on each elytron. Surface of prosternum usually flat, sometimes tectiform. Posterior elevation of mesoventrite with longitudinal carina; anapleural sutures sinuate, separated at anterior margin by distance similar to slightly shorter than anterior margin of mesepisternum. Metaventrite with posteromesal and posterolateral glabrous patches. Protibiae with spines of anterior row semi erect, relatively long, thick and sparse; apical spurs of protibiae relatively short and stout, not reaching apex of protarsomere 2. Metafemora with tibial grooves moderately developed; hydrofuge pubescence covering basal 4/5 of anterior surface of metafemora. Metatarsomeres 2–4 gradually decreasing in size, with

two rows of spines on ventral surface; metatarsomere 2 slightly longer than 5, 5 shorter than 3 and 4 combined. Fifth abdominal ventrite emarginate at apex, with fringe of flat and stout setae. Aedeagus subdivided (Fig. 3.26); parameres at most only fused at base on dorsal surface; median lobe subdivided in dorsal and ventral plates; dorsal plate sclerotized along margins, medially densely membranous, membranes with papillae or denticles along apico-medial region; ventral plate as inverted Y, sometimes accompanied by basal median laminar sclerite; basal piece nearly as long as or longer than ventral length of parameres, always noticeable; gonopore not clearly visible.

Differential diagnosis. Among Old World acidocerines, *Crephelochares* is unique in the presence of sutural stria. *Chasmogenus* (from the New World) is the most similar genus, as they both share this character. They can be differentiated by the number of antennomeres (8 in *Chasmogenus*, 9 in *Crephelochares*) and by the form of the aedeagus (trilobed in *Chasmogenus* (see Fig. 3.23), subdivided and further modified in *Crephelochares* (see Fig. 3.26). The aedeagus of *Crephelochares* is quite unique in Acidocerinae, especially because of the configuration of the median lobe and its inner membranes.

Figure 3.25. Habitus of *Crephelochares nitescens*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus. Scale bar 1 mm.

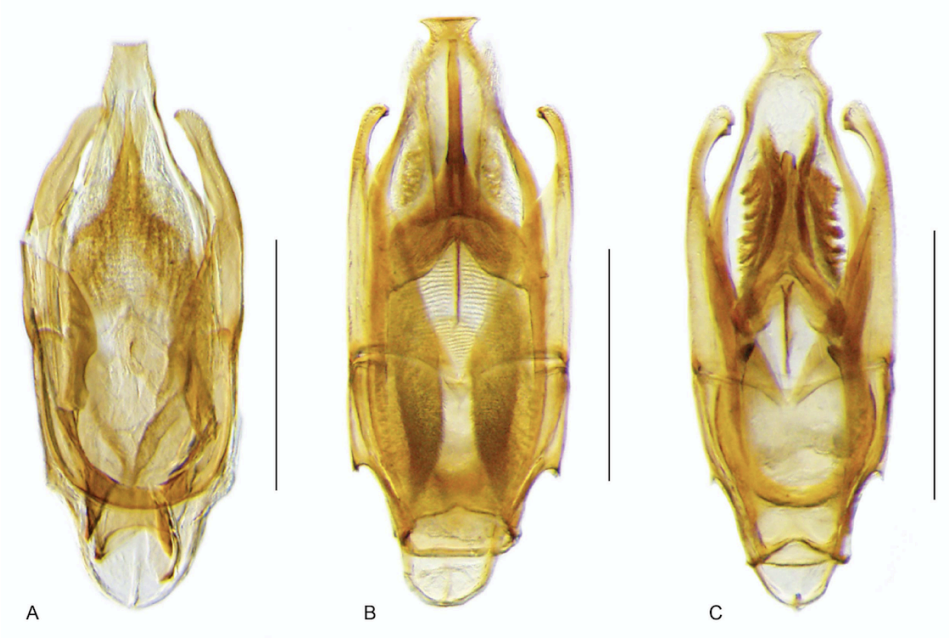


Figure 3.26. Aedeagus of *Crephelochares* spp.: **A** *C. szeli*, **B** *C.* sp. SLE-1332, **C** *C.* sp. SLE-1300. Scale bars 0.5 mm.

Taxonomic history. *Crephelochares* was originally described as a subgenus of *Helochares* by Kuwert (1890: 38). In 1904, Ganglbauer established *Crepidelochares* without justification or explanation. Later, d'Orchymont (1919c: 148) synonymized *Crephelochares* with *Chasmogenus* keeping *Chasmogenus* as a subgenus of *Helochares*. In 1986, Fernández reinstated *Chasmogenus* as genus, with *Crephelochares* as a junior synonym. Hebauer in 1992 removed *Crephelochares* from synonymy with *Chasmogenus*, and established it as a subgenus of *Chasmogenus*, discussing morphological features in support of this view, although these subgenera were not recognized by Hansen (1999b). The phylogenetic analysis by Short et al. (in prep), together with the morphological evidence offered by Hebauer, resulted in the recognition of the generic status of *Crephelochares*.

Distribution. Afrotropical: Angola, Benin, Botswana, Burundi, Cameroon, Democratic Republic of the Congo, Gabon, Gambia, Ghana, Guinea, Kenya, Liberia, Madagascar, Mauritius, Mozambique, Namibia, Niger, Nigeria, Rwanda, Senegal, Seychelles (Aldabra), Sierra Leone, Somalia, South Africa, Sudan, Tanzania, Uganda, Zambia, Zimbabwe. **Australasian:** Australia (New South Wales, Northern Territory, Queensland), Fiji (Vanua Levu, Viti Levu), New Caledonia, Papua New Guinea. **Indo-Malayan:** Cambodia, China (Guangdong, Hong Kong, Yünnan), Indonesia (Borneo, Java, Papua, Sulawesi, Sumatra), Laos, Malaysia, Sri Lanka, Taiwan, Thailand, Vietnam. **Palearctic:** Bosnia, Croatia, Greece, Israel, Italy, Japan, Serbia and Montenegro, Spain, Tunisia, Turkey.

Natural history. Archangelsky (1997: 55) reproduced the larval descriptions by Anderson (1976), who reared larvae from adults of *Crephelochares nitescens* (as *Helochares nitescens*) in laboratory conditions. According to Anderson (1976: 223), females lay between 18 and 25 eggs, "located below the surface of damp soil, in a mossy hollow constructed by the adult; the hollow was always of the same size and shape and lined inside with loose silk. Eggs were deposited at right angles to base of nest, each covered by strands of fine silk attached to floor, walls and adjacent eggs". The larvae hatch in 5–7 days and are predaceous (Archangelsky 1997: 55). "The larvae would not pupate in damp tissue paper, but only in moss. […]. The larvae pupated naked in the upper moss or in curled decaying leaves" (Anderson 1976: 223). Complete development lasted 24–33 days. Fikáček (2003) provided a diagnosis, pointed out the incompleteness of the descriptions and drawings offered by Anderson (1976), and commented on the unusualness of the habit of laying eggs on the ground by hydrophilid standards.

As for the adults, ecological information is very scarce. According to Hebauer (1992), *C. livornicus* (Kuwert) was collected in stagnant water with decaying plants and *C. orbus* (Watanabe) was collected in a rice field. The recently described *C. parorbus* (Jia and Tang) was also recorded from stagnant waters.

Larvae. The only species for which immature stages are known is *Crephelochares nitescens* (from Australia; immature stages were originally described as *Helochares nitescens* (Anderson 1976)). Anderson (1976) described the breeding method he used, the eggs and egg case, first and third instar larvae and pupa, as well as the entire life cycle. Archangelsky (1997: 55) reproduced Anderson's (1976) findings.

Remarks. There are 29 species of *Chephelochares* described to date; some of the older species have long lists of synonyms. The most comprehensive treatment for the genus was by Hebauer (1992); the genus was then considered as a subgenus of *Chasmogenus*.

Species examined. *Crephelochares abnormalis* (Sharp), *C. africanus* (d'Orchymont), *C. balkei** (Short), *C. irianus** (Hebauer), *C. livornicus* (Kuwert), *C. mauritiensis* (Balfour-Browne), *C. molinai** (Hebauer), *C. nitescens* (Fauvel), *C. orbus* (Watanabe), *C. paramollis** (Hebauer), *C. patrizii* (Balfour-Browne), *C. punctulatus** (Short), *C. ruandanus* (Balfour-Browne), *C. rubellus** (Hebauer), *C. rusticus* (d'Orchymont), *C. rutiloides* (d'Orchymont), *C. rutilus* (d'Orchymont), *C. szeli** (Hebauer). For species marked with an asterisk, paratypes were available.

Selected references. Hebauer (1992): diagnosis, key to species, diagnoses, descriptions for 22 species, and genitalia drawings for 19. Watts (1995) revised the Australian species of the genus. Short (2010) revised the species from the Southwest Pacific islands, describing a new species and newly recording *C. nitescens* (Fauvel) for New Caledonia. Devi et al. (2016): redescription and lectotype designation for *C. abnormalis* (Sharp) with a discussion on its distribution and morphological variation.

Genus *Crucisternum* Girón and Short, 2018

(Figs 3.6, 3.11C, 3.27, 3.28)

Crucisternum Girón and Short, 2018: 116

Gender. Masculine.

Type species. *Crucisternum ouboteri* Girón and Short, 2018: 121; by original designation.

Diagnosis. Small beetles, body length 2.0–2.5 mm. Body shape elongated oval in dorsal view; moderately convex in lateral view (Fig. 3.27). Color orange brown to dark brown. Head trapezoid. Eyes moderate to small, projected from outline of head. Clypeus trapezoid, with anterior margin from broadly and roundly emarginate. Labrum fully exposed. Mentum with lateral oblique ridges; anterior median depression marked transverse carina. Antennae with nine antennomeres, with cupule only slightly asymmetrical and rounded. Maxillary palpi moderately long, only slightly longer than width of head. Elytra without sutural striae, with outer margins of elytra slightly flared; serial punctures, ground punctures and systematic punctures similar in size and degree of impression, either shallow or rather sharply marked; all punctures seemingly arranged in rows. Prosternum with well-developed median, longitudinal, laminar carina. Posterior elevation of mesoventrite with a strongly produced, anteriorly pointed transverse ridge, longitudinally carinate (Fig. 3.11C); anapleural sutures sinuate, separated by distance nearly 0.6 × width of anterior margin of mesepisternum. Metaventrite densely pubescent, except for median and postero-lateral glabrous areas. Protibiae with spines of anterior row long and thick; apical spurs of protibiae short and stout, almost reaching apex of protarsomere 2.

Metafemora glabrous at most along apical fifth. Metatarsomeres 2–4 gradually slightly decreasing in size; metatarsomere 5 slightly longer than 2; ventral coverage of tarsomeres composed of fine and spiniform setae. Fifth abdominal ventrite apically rounded, truncate or slightly emarginate, without stout setae. Aedeagus trilobate (Fig. 3.28); basal piece 0.2–0.25 × the length of parameres; median lobe with well-developed lateral basal apodemes, and acute to narrowly rounded apex; parameres nearly as long as median lobe, with outer margins usually sinuate; gonopore situated distad of mid length of median lobe.

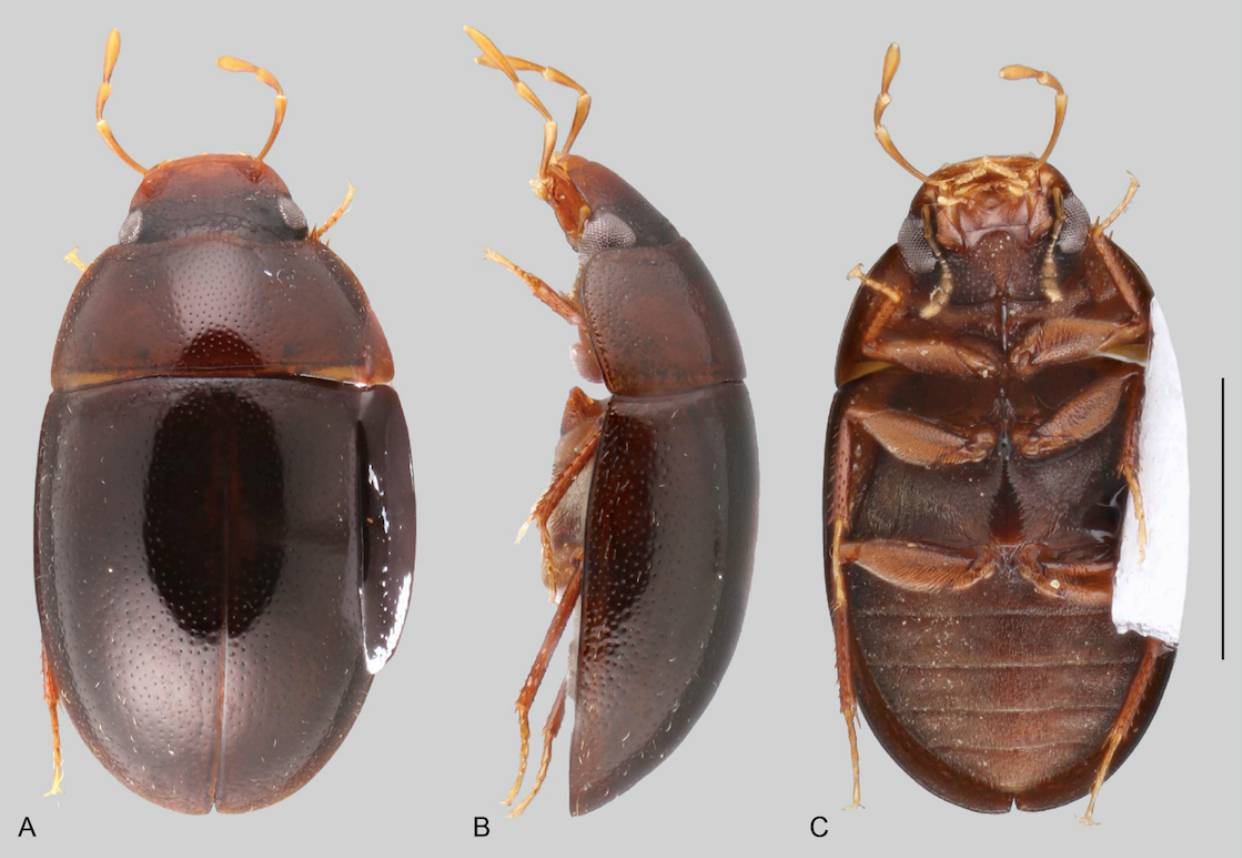


Figure 3.27. Habitus of *Crucisternum ouboteri*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus. Scale bar 1 mm.

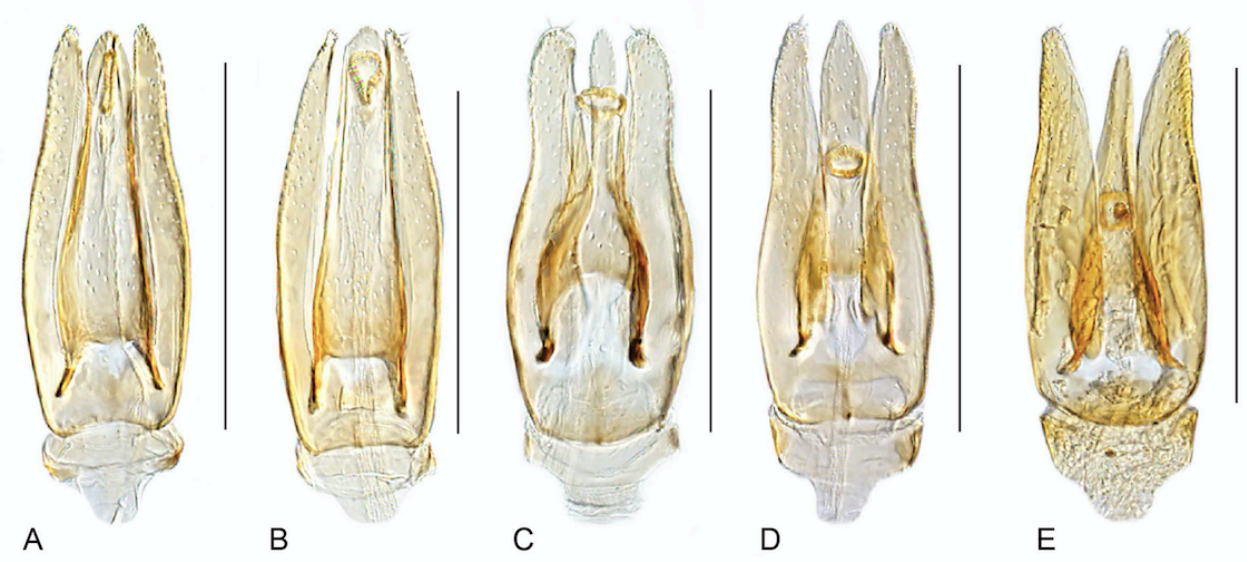


Figure 3.28. Aedeagus of *Crucisternum* spp.: **A** *C. ouboteri*, **B** *C. tobogaensis*, **C** *C. sinuatus*, **D** *C. vanessae*, **E** *C. queneyi*. Scale bars 0.25 mm.

Differential diagnosis. Although *Crucisternum* is generally unremarkable dorsally from other small bodied Neotropical acidocerines, several sternal features easily separate the genus from all others. The strongly developed prosternal carina found in the genus, combined with the cruciform shape of the posterior elevation of the mesoventrite (formed by the fusion of both transverse and longitudinal ridges), is unique for this genus in the subfamily. *Crucisternum* is most likely to be confused in samples as a small *Chasmogenus* but can also easily be distinguished from that genus by the lack of sutural striae.

Taxonomic history. The genus was only recently described.

Distribution. Neotropical: Brazil (Pará), French Guiana, Guyana, Suriname, Venezuela.

Natural history. All species of the genus are associated with forested streams, usually along margins that contain ample detritus. A single specimen of *C. ouboteri* was collected at a black light trap.

Larvae. Immature stages are not known for the genus.

Remarks. There are seven species currently known.

Species examined. Holotypes and paratypes of all the known species were examined for this study.

Selected references. Girón and Short (2018): original description of the genus and all its known species.

Genus *Ephydrolithus* Girón and Short, 2019

(Figs 3.6, 3.29, 3.30)

Ephydrolithus Girón and Short, 2019: 122

Gender. Masculine.

Type species. *Ephydrolithus hamadae* Girón and Short, 2019: 130; by original designation.

Diagnosis. Small beetles, body length 1.8–3.3 mm. Body shape oval in dorsal view, moderate to strongly convex in lateral view (Fig. 3.29); with ground punctation usually moderately marked. Color yellowish brown to dark brown, usually uniform across body regions. Shape of head trapezoid. Eyes relatively small, at most only slightly emarginated anteriorly, usually moderately projected from outline of head. Clypeus trapezoid, with anterior margin from broadly and only slightly emarginate. Labrum fully exposed. Mentum with strong median anterior depression sometimes limited by low transverse carina; surface of mentum mostly smooth and undulated. Antennae with nine antennomeres; cupule slightly asymmetric, with rounded outline. Maxillary palpi short, nearly two thirds width of head, and stout; inner margin of maxillary palpomere 2 nearly straight, outer margin strongly curved along apical half. Elytra without sutural striae, and only rarely with impressed striae; ground punctures moderate to sharply marked, uniformly and rather densely distributed; systematic punctures slightly larger and deeper than remainder punctures; serial punctures usually not clearly differentiated; outer margins of elytra only slightly flared. Prosternum flat, sometimes only slightly elevated along longitudinal midline. Posterior elevation of mesoventrite either with transverse ridge, or with well-developed tooth that extends anteriorly as longitudinal carina; anapleural sutures concave, separated at anterior margin by distance nearly 0.3 × anterior margin of mesepisternum. Metaventrite densely pubescent, except for large median teardrop-shaped glabrous patch; anteromedian area of metaventrite with a deep and narrow transverse depression before anterior intercoxal process. Protibiae with spines of anterior row hair-like, semi erect, relatively long and thick. All tarsomeres bearing long apical hair-like setae on dorsal face, and two lateral rows of hair-like spines on ventral face of tarsomeres 2–4. Posterior femora mostly glabrous,

with few scattered setae along basal half to basal two thirds, with hydrofuge pubescence along anterodorsal margin; tibial grooves well-developed, sometimes covered by hydrofuge pubescence. Fifth abdominal ventrite apically truncate, with stout setae. Aedeagus trilobed (Fig. 3.30), with outer margins convex, straight or sinuate, with basal piece 0.45– 0.9 × length of parameres; median lobe somewhat triangular in shape, with well-developed lateral basal apodemes; apex of median lobe widely to narrowly acute, sometimes "pinched"; parameres nearly as long as median lobe; well-developed gonopore, preapically situated.

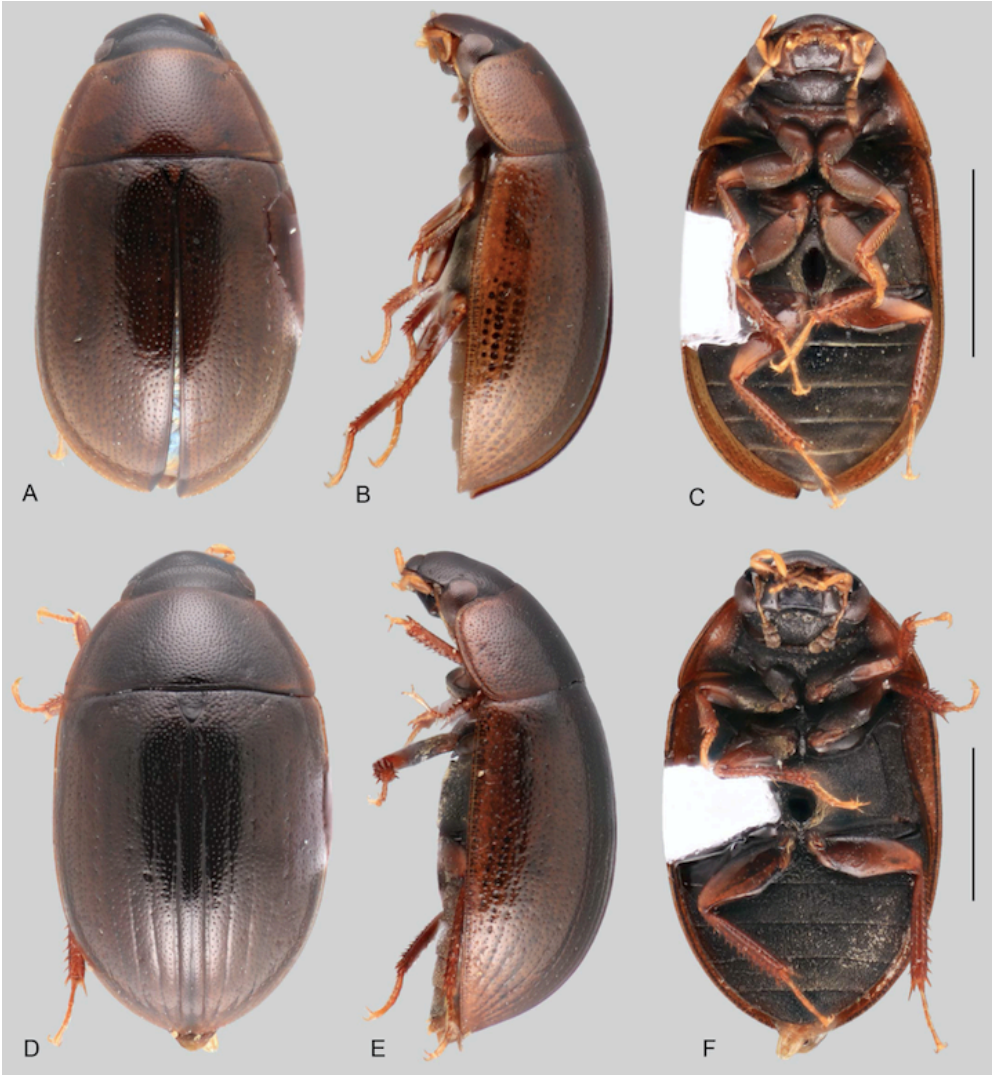


Figure 3.29. Habitus of *Ephydrolithus* spp.: **A–C** *E. hamadae*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus, **D–F** *E. ogmos:* **D** dorsal habitus, **E** lateral habitus, **F** ventral habitus. Scale bars 1 mm.

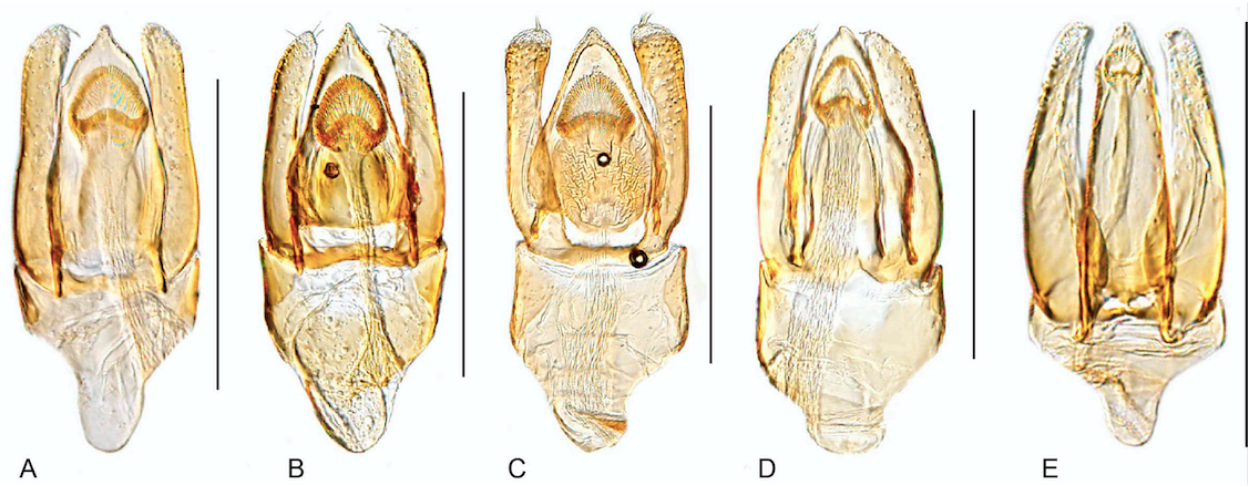


Figure 3.30. Aedeagus of *Ephydrolithus* spp.: **A** *E. hamadae*, **B** *E. teli*, **C** *E. spiculatus*, **D** *E. ogmos*, **E** *E. minor*. Scale bars 0.25 mm.

Differential diagnosis. *Ephydrolithus* can be distinguished from most Neotropical acidocerines by their mostly glabrous metafemora. From other genera exhibiting the same condition, such as *Quadriops* (see Girón and Short 2017), *Ephydrolithus* can be distinguished by the entire (as opposed to divided; see Fig. 3.9C) eyes; from *Tobochares* (see Kohlenberg and Short 2017) *Ephydrolithus* can be differentiated by the number of antennomeres (nine in *Ephydrolithus*, eight in *Tobochares*).

Taxonomic history. *Ephydrolithus* was only recently described.

Distribution. Neotropical: Brazil (Bahía, Minas Gerais).

Natural history. All known species are exclusively associated with rock seepages (Girón and Short 2019).

Larvae. Immature stages are not known for the genus.

Remarks. In the etymology section of the original publication, Girón and Short (2019) indicate that the genus name is neuter, which is erroneous. The name is masculine, which is the gender for the Greek word *lithos*, the last component of the genus name. Four species of *Ephydrolithus* have been described until now, all of them from southeastern Brazil.

Species examined. Holotypes and paratypes of all known species were examined for this study.

Selected references. Girón and Short (2018): original description of the genus and all its known species.

Genus *Globulosis* García, 2001

(Figs. 3.2G, 3.6, 3.31, 3.32)

Globulosis García, 2001: 153

Gender. Masculine.

Type species. *Globulosis hemisphericus* García, 2001: 153; by original designation.

Diagnosis. Small beetles, body length 1.9–2.3 mm. Body shape rounded in dorsal view, strongly convex in lateral view (Fig. 3.31). Surface of head, pronotum and elytra smooth, with moderate to shallow ground punctation. Coloration yellow to dark brown, uniform along body, with paler mouthparts and tarsi. Shape of head relatively oval. Eyes relatively small, anteriorly emarginated, not projected from outline of head. Clypeus trapezoid, with anterior margin mesally broadly emarginate. Labrum fully exposed. Mentum with anterior depression limited by low transverse carina; surface of mentum only slightly strigate. Antennae with eight antennomeres, with cupule only slightly asymmetric and rounded in outline. Maxillary palpi slender, slightly shorter than width of head. Pronotum evenly convex. Elytra without sutural or other distinct striae, with outer margins slightly flared; elytral ground punctation shallow to moderate, uniformly distributed. Surface of prosternum flat. Mesoventrite with transverse ridge, usually elevated medially into acute tooth; anapleural sutures concave, separated at anterior margin by distance nearly as width of anterior margin of mesepisternum. Metaventrite uniformly covered by hydrofuge pubescence, with small, longitudinal posteromesal glabrous patch, and reduced posterolateral glabrous patches. Protibiae with spines of anterior row long, thick, semi erect and sparse; apical spurs of protibiae short and of moderate thickness. Metafemora with moderate tibial grooves; hydrofuge pubescence covering basal 4/5 of anterior surface. Tarsomeres 1–4 ventrally with rows of long and thick setae. Metatarsomeres 2–4 gradually decreasing in size, 5 nearly as long as 2–4 combined. Fifth abdominal ventrite with small truncation at apex, with fringe of flat and stout setae. Aedeagus trilobed (Fig. 3.30A); with short basal piece, less than one-third length of parameres. Median lobe wide, wider than width of parameres; gonopore well differentiated.

Differential diagnosis. *Globulosis* is among the smallest acidocerines. Its small size along with very round and convex body shape, sets it apart from all other acidocerines known to date.

Taxonomic history. García described the genus with one species, and placed it in its own tribe (Globulosina, now synonymized with Acidocerinae) in 2001. The genus was revised in 2017 by Short et al., who described one new species and added new material expanding the range of the previously known species.

Figure 3.31. Habitus of *Globulosis flavus*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus. Scale bar 1 mm.

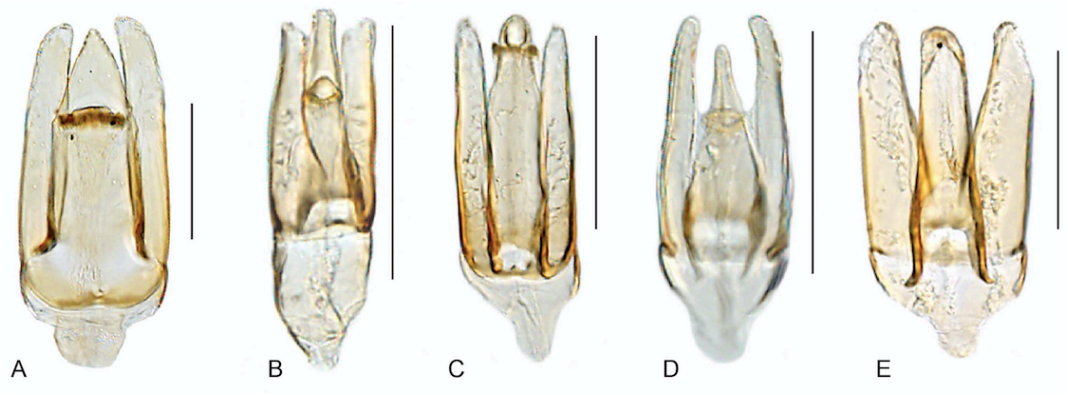


Figure 3.32. Aedeagus: **A** *Globulosis flavus*, **B–E** *Nanosaphes* spp.: **B** *N. tricolor*, **B** *N. hesperus*, **D** *N. castaneus*, **E** *N. punctatus*. Scale bars 0.1 mm.

Distribution. Neotropical: Brazil (Amazonas, Pará), Colombia, Guyana, Suriname, Venezuela.

Natural history. According to Short et al. (2017: 274), the genus has been "primarily found in moving waters, particularly stream margins with detritus. It has been found at elevations from near sea level to 600 m".

Larvae. The immature stages of *Globulosis* remain unknown.

Remarks. There are two described species of *Globulosis*. One female specimen from Colombia has been left undescribed as it could not be reliably identified to species. Because of the extremely uniform external morphology in the genus, the male genitalia is the most reliable feature for species recognition.

Species examined. The holotype, along with several additional specimens of *Globulosis hemisphericus* García, and the holotype and paratypes of *G. flavus* Short, García and Girón were examined in this study.

Selected references. García (2001), genus description, monotypic; Short et al. (2017) description of one new species from Venezuela, range expansion for type species.

Genus *Helobata* Bergroth, 1888

(Figs. 3.1J, 3.4, 3.9L, 3.21C, 3.33)

Helopeltis Horn, 1873: 137

Type species: *Helopeltis larvalis* Horn, 1873: 137; by monotypy.

Helobata Bergroth, 1888: 221 - Replacement name for *Helopeltis* Horn.

Helopeltina Cockerell, 1906: 240 - Replacement name for *Helopeltis* Horn, 1873

Type species: *Helopeltis larvalis* Horn.

Gender. Feminine.

Type species. *Helopeltis larvalis* Horn, 1873: 137; by monotypy.

Diagnosis. Medium sized beetles, body length 4–7 mm. Body shape oval in dorsal view, dorsoventrally flattened, with dorsal outline nearly straight along medial third in lateral view (Fig. 3.33); surface even and granulate. From yellowish, orange brown to dark brown in coloration,

usually with alternating patterns along elytra, with different areas of head and pronotum darkened. Shape of head somewhat trapezoid (Fig. 3.9L). Anterior corners of frons extended laterally and posteriorly, emarginating anterior margin of eyes. Eyes of moderate size, somewhat oval, anteriorly deeply emarginated, not projected from outline of head. Clypeus somewhat pentagonal, laterally explanate, with anterior margin usually straight. Labrum concealed by clypeus. Mentum with surface variably sculptured, usually with oblique and transverse strigae. Antennae with eight antennomeres, with cupule strongly asymmetric and oval in outline. Maxillary palpi slender, slightly longer than greatest width of head; inner margin of maxillary palpomere 2 weakly and evenly curved, and outer margin weakly curved along apical third. Pronotum with surface of lateral areas flat. Elytra without sutural striae, with outer margins laterally explanate; serial punctures clearly aligned in longitudinal rows. Scutellar shield U-shaped. Surface of prosternum flat, to medially bulging, smooth to irregularly sculptured. Posterior elevation of mesoventrite only weakly bulging, with pair of lateral, longitudinal, low ridges; anapleural sutures nearly parallel along anterior section, separated anteriorly by distance slightly shorter than anterior margin of mesepisternum. Metaventrite uniformly covered by hydrofuge pubescence, with medial, narrow and slightly carinate glabrous patch; posterolateral glabrous patches reduced. Protibiae with spines of anterior row short and semi erect; apical spurs of protibiae reduced, much shorter than protarsomere 1. Metafemora with tibial grooves moderately developed; hydrofuge pubescence covering 5/6 of anterior surface. Tarsomeres 1–4 ventrally densely covered by setae; metatarsomere 2 longer than 3–4 combined, 1 nearly as long as 3 and 5 nearly as long as 2–4 combined. Fifth abdominal ventrite apically emarginate, with fringe of flat and stout setae. Aedeagus subdivided (see Fig. 3.21C), parameres separated from

each other for most of length; median lobe subdivided in dorsal and ventral plates; dorsal plate usually strongly sclerotized; ventral plate bilaterally bifurcated, forming thick lateral lobes along apical region; basal piece nearly 0.2 × the length of parameres, always noticeable; gonopore not clearly visible.

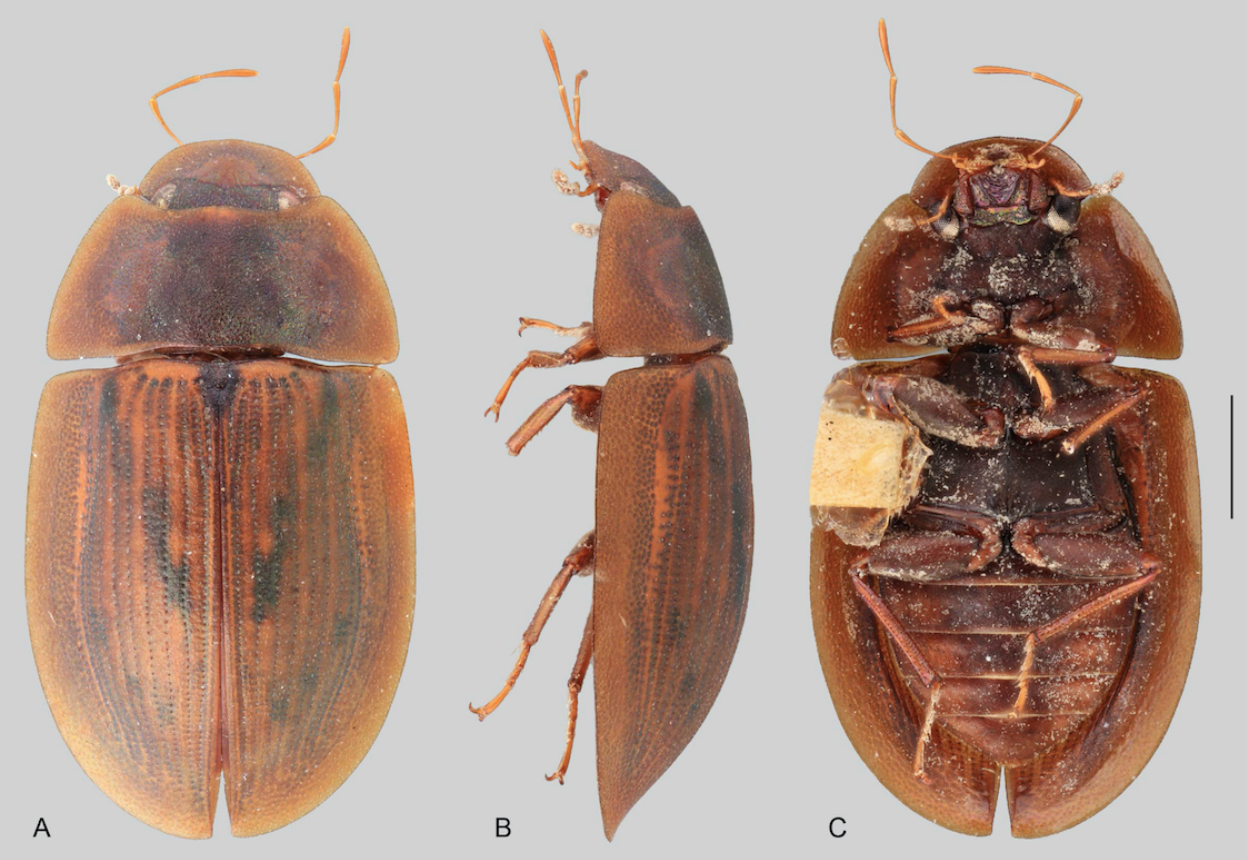


Figure 3.33. Habitus of *Helobata larvalis*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus. Scale bar 1 mm.

Differential diagnosis. *Helobata* is one of the most conspicuous genera of acidocerines, especially in the New World. The flattened and broadly explanate body shape and concealed labrum, accompanied by granulose surface, long and slender maxillary palpi and well-defined elytral serial punctures, are quite unique in the subfamily. The only genus that shares some of these features is *Helopeltarium*, except that the latter has short maxillary palpi, smooth surface

and lacks serial punctures along the elytra. The configuration of the aedeagus (see Fig. 3.21C), in particular the thickness of the lateral lobes of the ventral plate of the median lobe, is also unique among acidocerines.

Taxonomic history. This genus was described by Horn (1873) under the name *Helopeltis*, which was preoccupied by *Helopeltis* Signoret, 1858 (Hemiptera). Bergroth (1888) proposed the name *Helobata* as a replacement name for *Helopeltis* Horn, whereas Cockerell (1906a) proposed the name *Helopeltina*. *Helobata* has priority, so it is the currently valid name for the genus, which was revised by Fernández and Bachmann (1987).

Distribution. Nearctic: United States (California, Florida, Louisiana, Mississippi, North Carolina, South Carolina, Texas). **Neotropical:** Argentina, Bolivia, Brazil (Amazonas, Ceará, Corumbá, Mato Grosso, Pará, Rio de Janeiro), Cuba, Guatemala, Mexico, Paraguay, Suriname, Venezuela.

Natural history. According to Clarkson et al. (2016), specimens of *Helobata* are rare and occur in marshes, swamps and ponds, usually in small numbers. According to Archangelsky (1997), they can be found in slow moving creeks or rivers, living among the littoral vegetation or on floating plants. Females have been observed carrying their egg cases attached to the ventral side of their abdominal ventrites (Archangelsky 1997).

Larvae. The larva (first instar) and egg case is only known for *Helobata larvalis*; the immature stages were described by Spangler and Cross (1972). A differential diagnosis of the first instar larva was provided by Fikáček (2003).

Remarks. There are 13 species of *Helobata* described to date. The type species, *Helobata larvalis* (Horn), has generally been known under the name *striata* (originally published as *Hydrophilus striatus* Brullé, 1841: 58, which is a primary homonym of *Hydrophilus striatus* Say, 1825 (now *Berosus striatus* (Say)); therefore unavailable. The name *Helobata larvalis* (Horn) was then reinstated by Hansen (1991: 293). Photos of a syntype of *Helopeltis larvalis* (Horn) are available at https://mczbase.mcz.harvard.edu/guid/MCZ:Ent:101 (accessed April 27 2019). The external morphology of members of *Helobata* is very homogeneous. Some variation can be observed in the shape of the clypeus. *Helobata* is the only Neotropical genus truly widespread in the New World, as it ranges from southern North America, all the way to Argentina and Southern Brazil.

Species examined. *Helobata cuivaum* García (paratype), *H. larvalis* (Horn), and *H. lilianae* García (paratype).

Selected references. Horn (1873), original description of the genus and the type species. Spangler and Cross (1972), description of egg case and first instar larva. Fernández and Bachmann (1987), review of the genus, description of four new species from Argentina, Brazil and Paraguay; García (2000), three new species from Venezuela; Makhan (2007), two new

species from Suriname; Clarkson et al. (2016), two new species from Brazil, review and new country records of Brazilian species.

Genus *Helochares* Mulsant, 1844

(Figs. 3.1E, 3.F, 3.3, 3.9F, 3.34–3.37)

Helophilus Mulsant, 1844a: 132 [rejected name no. 1707 (ICZN, Opinion 710)].

Helochares Mulsant, 1844a: 197; replacement name for *Helophilus* Mulsant, 1844a: 132; official name no. 1601 (Opinion 710).

Enhydrus Dahl 1823: 34 [nomen nudum; rejected name no. 1705 (ICZN, Opinion 710)].

Enhydrus MacLeay, 1825: 35 [rejected name no. 1704 (ICZN, Opinion 710)].

Pylophilus Motschulsky, 1845: 32.

Type species: *Hydrophilus griseus* Fabricius, 1787: 189; fixed by monotypy = *Dytiscus lividus* Forster, 1771.

Peloxenus Motschulsky, 1845: 549; replacement name for *Pylophilus* Motschulsky, 1845.

Helophygas Motschulsky, 1853: 11 [rejected name no. 1708 (Opinion 710)].

Helocharis Thomson, 1859: 18 [incorrect subsequent spelling].

Hydrobaticus MacLeay, 1871: 131 **syn. n.**

Type species: *Hydrobaticus tristis* MacLeay, 1871: 131; by subsequent designation by d'Orchymont (1943a: 2); originally described as genus; downgraded to subgenus of *Helochares* by d'Orchymont (1919c: 148).

Helocharimorphus Kuwert, 1890: 306 **syn. n.**

Type species: *Helocharimorphus sharpi* Kuwert, 1890: 307; by monotypy; originally described as genus; downgraded to subgenus of *Helochares* by d'Orchymont (1919c: 148).

Graphelochares Kuwert, 1890: 38.

Type species: *Helophilus melanophthalmus* Mulsant, 1844a: 137; by monotypy.

Grapidelochares Ganglbauer, 1904: 248; [unjustified emendation of *Graphelochares* Kuwert, 1890].

Gender. Masculine.

Type species. *Dytiscus lividus* Forster, 1771: 52; by subsequent designation (Thomson 1859: 18).

Diagnosis. Small to medium sized beetles, body length 2–7 mm. Body shape oval in dorsal view; slightly to moderately convex in lateral view, with dorsal outline nearly flat along anterior half of elytra, or somewhat evenly curved (Figs 3.34–3.36). Coloration usually yellowish brown, sometimes orange brown, pale brown to medium brown; ground punctation shallow to strongly marked. Shape of head trapezoid to oval (Fig. 3.9F). Eyes medium sized to large, not or moderately emarginated anteriorly, usually projected from outline of head. Clypeus trapezoid, with anterior margin broadly and roundly emarginate; sometimes lateral margins of clypeus slightly bent upwards. Labrum fully exposed. Mentum rather flat, sparsely punctate, coarsely to shallowly, rarely strigate; median anterior depression of mentum relatively shallow; submentum shallowly punctate to smooth. Antennae with nine antennomeres; cupule strongly asymmetric,

with rounded outline; antennomere 9 slightly, to 3 × longer than antennomere 7. Maxillary palpi slender, moderately long, 0.6–1.2 × the width of head; inner margin of maxillary palpomere 2 weakly and evenly curved to nearly straight, outer margin evenly curved to curved along apical 2/3; maxillary palpomere 3 slightly longer than 4. Prosternum flat to medially bulging to tectiform. Elytra without sutural striae, with ground punctures usually moderately marked; usually serial punctures forming ten longitudinal rows along elytra. Posterior elevation of mesoventrite, flat to simply bulging; bulge usually with long fine setae; anapleural sutures strongly concave, nearly parallel along anterior section, separated anteriorly by distance 0.6–1.0 × anterior margin of mesepisternum. Metaventrite densely covered by hydrofuge pubescence, without glabrous patches. Protibiae with spines of anterior row either nearly absent or as long thick semi-erect setae. Metafemora with tibial grooves weakly developed to absent; hydrofuge pubescence covering basal 6/7 of anterior surface. Tarsomeres 1–4 with pair of lateral rows of long fine spines on ventral face, sometimes ventral face densely covered by hair-like spines; tarsomere 5 with medial row of long fine spines; metatarsomeres variable in proportions (2–4 gradually decreasing in size with 5 nearly as long as 3–4 combined; 2 and 5 similar in length, each slightly longer than 3–4 combined). Fifth abdominal ventrite apically emarginate, with fringe of stout setae. Aedeagus tubular (Fig. 3.37); parameres fused to each other for most of length, with apex either simple or bifurcate/bilobate; median lobe with very long basal apodemes (as long or longer than main piece of median lobe), often extending beyond base of parameres in repose; median lobe either simple (without subdivisions), or with multiple and different kinds of sclerotizations of inner membranes; basal piece usually much shorter than parameres; gonopore of variable development, usually visible when median lobe is simple.

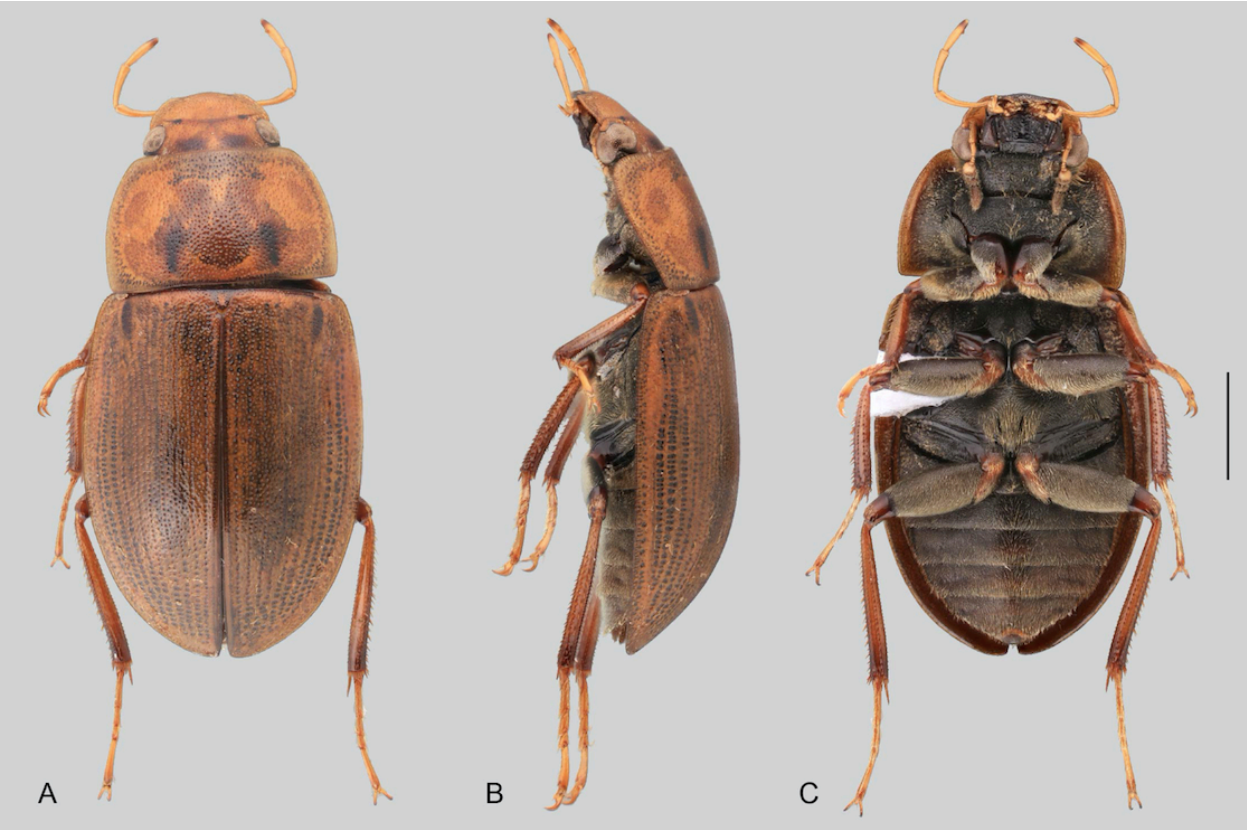


Figure 3.34. Habitus of *Helochares tristis*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus, **D–F** *H. sharpi*: **D** dorsal habitus, **E** lateral habitus, **F** ventral habitus. Scale bar 1 mm.

Differential diagnosis. In the present definition, most species of *Helochares* are yellowish to brown in coloration, ranging in size from 2–7 mm, usually moderately punctate throughout the dorsal surface, and most diverse in the Old World. Smaller members of the genus may be confused with *Agraphydrus*, from which *Helochares* can be distinguished by its uniformly pubescent metaventrite (*Agraphydrus* bears a distinct posteromedian glabrous patch on the metaventrite). From *Peltochares*, and *Novochares*, members of *Helochares* can be distinguished by their shorter and relatively stout maxillary palps (0.6–1.2 × the width of the head in *Helochares*, as opposed to slender, 1.3–1.8 × in *Peltochares*, 1.1–1.5 × in *Novochares*); and by the development of the tibial grooves (weakly developed to absent in *Helochares*, well developed in

both *Novochares* and *Peltochares*). The most problematic species would be those that are dark brown, relatively flattened, highly polished, and 4–5 mm long. In those cases, the most reliable feature for identification would be the male genitalia: *Helochares* has tubular aedeagi, *Peltochares* has spiked aedeagi, and *Novochares* has divided aedeagi (see explanation under the aedeagus section of Morphological variation in Acidocerinae and its taxonomic importance).

Figure 3.35. Habitus of *Helochares sharpi*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus. Scale bar 1 mm.

Taxonomic history. The genus was originally described under the name of *Helophilus*, which was preoccupied by *Helophilus* Leach, 1817 (Diptera), therefore *Helochares* was proposed by Mulsant (1944) as a replacement name. Thomson, in 1859, designated the type species for the genus. Through time, *Helochares* as well as some of its species have accumulated multiple synonyms. In 1919, d'Orchymont recognized five subgenera within *Helochares*: *Helochares*,

Chasmogenus, *Helocharimorphus*, *Hydrobaticus*, and *Sindolus*. *Chasmogenus* was recognized as a separate genus by Fernández (1986). Hansen (1991) added *Batochares* as a subgenus of *Helochares* and commented on the possibility that the recognized subgenera of *Helochares* at the time, represented actually distinct genera. Short et al. (in prep.) elevated *Batochares* and *Sindolus* to generic status based on their molecular phylogeny, in which *Helochares lividus* (Forster), type species of *Helochares* from the Palearctic region, and *Helochares tristis* (MacLeay), type species of *Hydrobaticus* from the Australasian region, belong in the same clade (clade A3 in Short et al. in prep.; see Fig. 3.3). Furthermore, both species share morphological details of the male genitalia, which grants their synonymy at this point. Conversely, the morphological variation under the new concept of *Helochares* encompasses the features that were used for recognizing *Helocharimorphus*: lack of elytral striae, short maxillary palpi, mesoventrite only slightly elevated in front of the mesocoxae, metatibiae slightly curved (see d'Orchymont 1919c: 149, in key). In contrast, more distinct and divergent morphotypes (e.g., small size (nearly 3 mm); strongly punctate surface; emarginated eyes; clypeus laterally bent upwards; see Fig. 3.36D–F) are nested within the main *Helochares* clade. In consequence, despite not knowing the configuration of the aedeagus in *Helocharimorphus*, we consider it a synonym of *Helochares*.

In the new concept of *Helochares* and taking into account the distinct aedeagal forms found within the genus, it is likely appropriate to consider subgenera; the issue at this point is that none of the previous subgeneric concepts remains adequate in the light of the phylogenetic analyses of Short et al. (in prep.). In addition, further studies are needed, including clearing of

the male genitalia (otherwise internal membranes and sclerotizations may not be visible), in order to start making sense of the tremendous morphological diversity within *Helochares*.

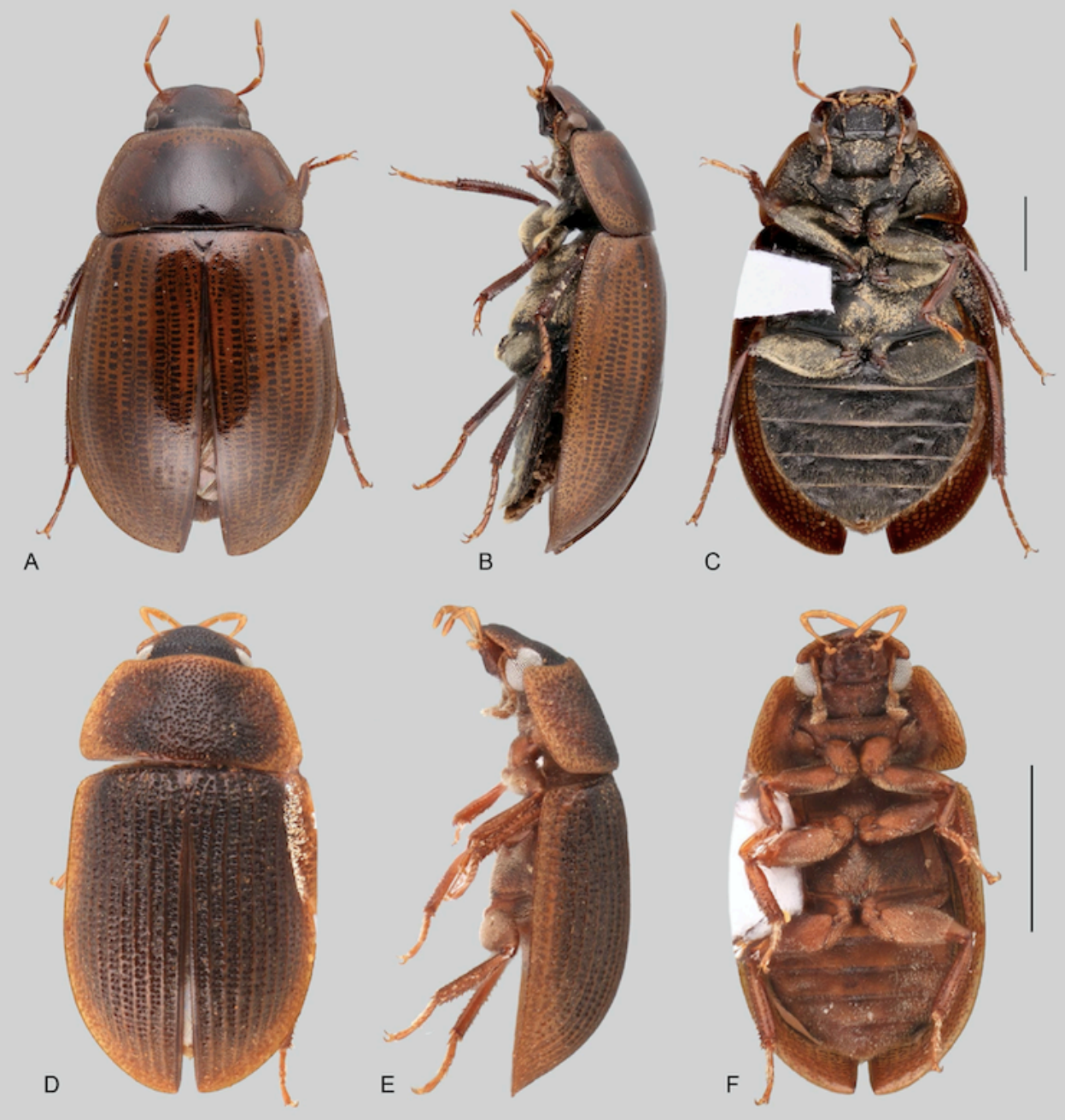


Figure 3.36. Habitus of *Helochares* spp.: **A–C** *H. laevis*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus, **D–F** *H.* sp.: **D** dorsal habitus, **E** lateral habitus, **F** ventral habitus. Scale bar 1 mm.

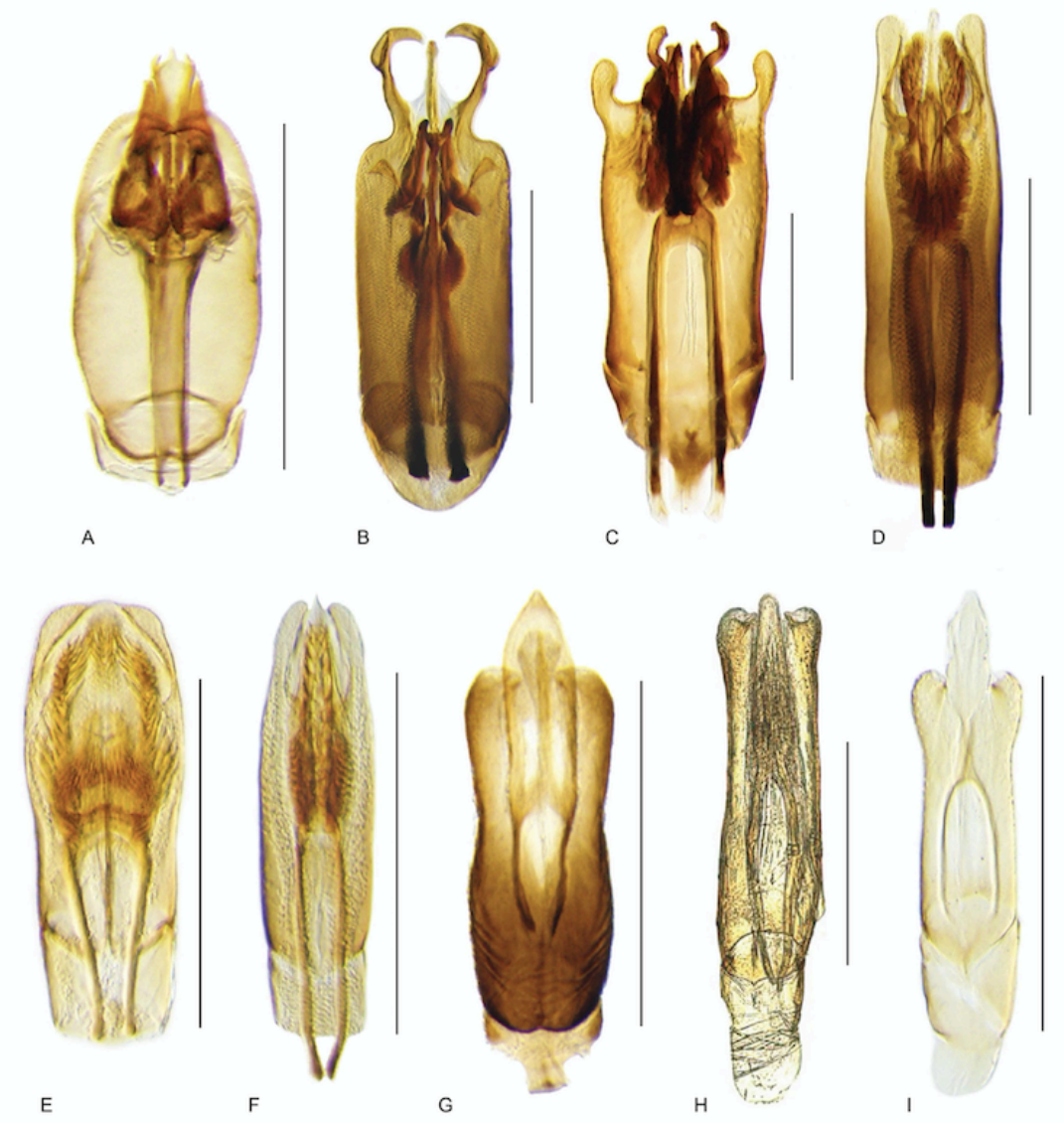


Figure 3.37. Aedeagus: **A–H** *Helochares* spp.: **A** *H.* sp. (Guinea), **B** *H. tristis*, **C** *H.* nr. *cresphontes*, **D** *H.* nr. *tatei*, **E** *H.* sp. (India, Goa), **F** *H*. sp. (Vietnam), **G** *H*. *politus*, **H** *H*. *songi* (from Jia and Tang 2018, fig. 48), **I** *Helopeltarium ferrugineum*. Scale bars 0.5 mm.

Distribution. Afrotropical: Angola, Benin, Botswana, Burkina Faso, Burundi, Cameroon, Chad, Democratic Republic of the Congo, Eritrea, Ethiopia, Gabon, Gambia, Ghana, Guinea, Guinea Bissau, Ivory Coast, Kenya, Liberia, Madagascar, Malawi, Mali, Mauritania, Mauritius (incl. Mascarene Is., Rodrigues), Morocco [in doubt], Mozambique, Namibia, Niger, Nigeria, Oman, Republic of the Congo, Réunion, Rwanda, São Tomé and Príncipe, Saudi Arabia, Senegal,

Seychelles (incl. Aldabra), Sierra Leone, South Africa, South Sudan, Sudan, Tanzania, Togo, Uganda, United Arab Emirates, Yemen (incl. Socotra), Zambia, Zimbabwe. **Australasian:** Australia (Australian Capital Territory, New South Wales, Northern Territory, Queensland, South Australia, Tasmania, Victoria, Western Australia), Fiji, Papua New Guinea (incl. Duke of York), Vanuatu. **Indo-Malayan:** Bangladesh, Burma, Cambodia, China (Fujian, Guangdong, Guangxi, Guizhou, Hainan, Hong Kong, Hunan, Jiangxi, Macao, Yünnan, Zhejiang), India (Andaman Is., Assam, Bihar, Karnataka, Madhya Pradesh, Nicobar Is., Uttarakhand, Uttar Pradesh, Tamil Nadu, West Bengal), Indonesia (Bali, Borneo, Java, Lombok, Papua, Sumatra), Laos, Malaysia (Peninsula, Sabah), Nepal, Philippines (Manila), Singapore, Sri Lanka, Taiwan, Thailand, Vietnam. **Nearctic:** U.S.A. (Alabama, Arkansas, Arizona, California, Delaware, District of Columbia, Florida, Georgia, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maryland, Mississippi, Missouri, Nevada, North Carolina, North Carolina, Ohio, Oklahoma, Oregon, Pennsylvania, South Carolina, Tennessee, Texas, Virginia). **Neotropical:** Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Venezuela. **Oceanian:** Samoa, Tonga. **Palearctic:** Algeria, Austria, Azerbaijan, Belarus, Bosnia Herzegovina, Bulgaria, Canary Islands, China (Chongqing, Hubei, Shaanxi, Sichuan, Xinjiang, Xizang [Tibet]), Croatia, Czech Republic, Denmark, Egypt, Estonia, Finland, France, Germany, Georgia, Great Britain, Greece, Hungary, Iran, Iraq, Ireland, Israel, Italy, Japan, Latvia, Lebanon, Lithuania, Luxembourg, Macedonia, Morocco, Netherlands, Norway, Pakistan, Poland, Portugal, Russia, Serbia and Montenegro, Slovakia, Slovenia, South Korea, Spain, Sweden, Switzerland, Syria, Tunisia, Turkey, Ukraine.

Natural history. Most of the older descriptions have no associated ecological information. Species of *Helochares* are aquatic (see Hansen 1991) with a preference for quiet bodies of water (see Archangelsky 1997); some species have been collected in rivers, streams, ponds, stagnant water, along sides of rivers, forest pool margins, usually associated with live or decomposing floating vegetation. They can be occasionally collected at light, sometimes in large numbers (see Jia and Tang 2018). Females have been observed carrying their egg cases attached to the ventral side of their abdomen.

Larvae. Anderson (1976) described the immature stages of *Helochares tristis* (MacLeay) along with the breeding method he used; the author described the eggs, egg case (25–50 eggs per case), first, second, and third instar larvae and pupa, as well as the entire life cycle. Anderson (1976) recorded observations of the emergence of larvae and adults. As the females carry their eggs attached to the ventral side of their bodies, Anderson (1976: 222) noted: "When hatching from an attached bag, larvae appeared to emerge into the ventral bubble of air. Larvae then rose to the surface of the water and swam away with an alternate head-to-tail movement. They were observed to have bubbles of air in the abdomen. No doubt this was taken from the ventral air bubble and enabled the larvae to become buoyant.". According to Archangelsky (1997) the larvae are predatory and also cannibalistic.

A diagnosis for larvae of *Helochares* as well as a list of the described immatures are provided in Fikáček (2003), at the time considering *Helochares sensu* Hansen (1991), including species of *Novochares* and *Peltochares*; the known larvae of the redefined *Helochares* are *H.*

lividus (Forster) (unknown stage larva in d'Orchymont 1913b; first, second and third instar larvae in Panzera 1932), *H. maculicollis* Mulsant (eggs, first and third instar larvae and pupa in Richmond 1920), *H. obscurus* (Müller) (first, second and third instar larvae in Panzera 1932, as *H. griseus*], *H. tristis* (MacLeay) (eggs, first, second and third instar larvae, and pupa in Anderson 1976), *H. clypeatus* (Blackburn) (third instar larva in Watts 2002), *H. luridus* (MacLeay) (third instar larva in Watts 2002), *H. tenuistriatus* Régimbart (third instar larva in Watts 2002). Minoshima and Hayashi (2011) described *H. anchoralis* Sharp (first instar larva), *H. nipponicus* Hebauer (first, second and third instar larvae), and *H. pallens* (MacLeay) (first, second and third instar larvae).

Remarks. *Helochares* has been generally considered the most diverse, most widespread, and most taxonomically challenging genus of acidocerines. To date, there are 153 described species of *Helochares*. Efforts have been made to try to make sense of such diversity, by studying local faunas (Hansen 1982, Watts 1995, Hebauer 1996, Short and Girón 2017, Jia and Tang 2018), but traditional character systems used for classification have shown inadequate for distinguishing monophyletic groups. Only now, after the phylogenetic study by Short et al. (in prep.), there is some clarity regarding morphological trends in the genus. Most of the representative specimens available for this study are card-mounted, therefore characters of the ventral surfaces in the diagnosis offered here, are based on observations made on a sample of pin-mounted specimens.

Species examined. *Helochares aethiopicus* d'Orchymont, *H. anchoralis**** Sharp, *H. alberti* d'Orchymont, *H. andreinii* d'Orchymont, *H. anthonyae* Watts, *H. balfourbrownei* Hansen, *H. bohemani**** d'Orchymont, *H. camerunensis* d'Orchymont, *H. cancellatus** Hebauer, *H. championi**** Sharp, *H. clypeatus* Blackburn, *H. conformis** Hebauer, *H. congruens* d'Orchymont, *H. crenatostriatus* Régimbart, *H. crenatuloides**** d'Orchymont, *H. crepitus* Balfour-Browne, *H. crispus* d'Orchymont, *H. densepunctus* Régimbart, *H. densus* Sharp, *H. depactus* d'Orchymont, *H. didymus* d'Orchymont, *H. difficilis* d'Orchymont, *H. dilutus**** Erichson, *H. dimorphus* d'Orchymont, *H. dollmani* Balfour-Browne, *H. dolus* d'Orchymont, *H. egregius* Balfour-Browne, *H. endroedyi** Hebauer, *H. fratris** Hebauer, *H. fuliginosus* d'Orchymont, *H. insolitus* d'Orchymont, *H. itylus* Balfour-Browne, *H. ivani** Hebauer, *H. laevis*** Short and Girón, *H. lentus* Sharp, *H. lepidus* d'Orchymont, *H. leptinus* d'Orchymont, *H. lividoides* Hansen and Hebauer, *H. lividus* (Forster), *H. loticus** Hebauer, *H. luridus* (MacLeay), *H. maculicollis* Mulsant, *H. mecarus* d'Orchymont, *H. mediastinus* d'Orchymont, *H. melanophthalmus* (Mulsant), *H. mentinotus* Kuwert, *H. mersus* d'Orchymont, *H. minax* d'Orchymont, *H. minor* d'Orchymont, *H. minusculus* d'Orchymont, *H. nebridius* d'Orchymont, *H. negatus** Hebauer, *H. neglectus**** (Hope), *H. nexus*** Short and Girón, *H. nigrifrons* Brancsik, *H. nigripalpis** Hebauer and Hendrich, *H. nigroseriatus** Hebauer, *H. nipponicus**** Hebauer, *H. normatus* (LeConte), *H. obscurus**** (Müller), *H. pallens**** (MacLeay), *H. percyi* Watts, *H. perminutus* Hebauer, *H. politus*** Short and Girón, *H. punctatus* Sharp, *H. salvazai* d'Orchymont, *H. schwendingeri* Hebauer, *H. scitulus* Balfour-Browne, *H. sharpi**** (Kuwert), *H. skalei* Hebauer, *H. steffani** Hebauer, *H. stenius* d'Orchymont, *H. striatus* Boheman, *H. strictus* d'Orchymont, *H. strigellus** Hebauer, *H. structus* d'Orchymont, *H. subtilis* d'Orchymont, *H. tatei**** (Blackburn), *H. tenuistriatus* Régimbart, *H.*

*tristis**** (MacLeay), *H. trujillo*** Short and Girón, *H. wagneri** Hebauer, *H. wattsi** Hebauer and Hendrich, *H. yangae** Hebauer, Hendrich and Balke, *H. zamora*** Short and Girón.

For species marked with one asterisk (*) at least one paratype was available. For species marked with two asterisks (**) the holotype, and in some cases paratypes were examined in this study; all these specimens were card-mounted. For species marked with three asterisks (***) some specimens were pin-mounted, allowing to view ventral structures. For *H. championi* Sharp one of the available specimens was previously compared with the holotype by A. Short.

Selected references. d'Orchymont (1939b, 1943a, c, e), miscellaneous taxonomic works focused on *Helochares*, for the most part describing new species; some of those works include aedeagal illustrations. Hansen (1982): notes on European species with morphological clarifications. Hansen (1991): generic diagnosis, synonyms, list of subgenera. Watts (1995): faunistic study for Australia. Hebauer (1996): faunistic study for Africa. Short and Girón (2017): faunistic study for the New World. Jia and Tang (2018): faunistic study for China.

Genus *Helopeltarium* d'Orchymont, 1943

(Figs. 3.37I, 3.38)

Helopeltarium d'Orchymont, 1943f: 9

Gender. Masculine.

Type species. *Helopeltarium ferrugineum* d'Orchymont, 1943f: 10; by original designation and monotypy.

Diagnosis. Small beetles, body length nearly 3.5 mm. Body broadly oval and explanate in dorsal view, rather flat in lateral view, with dorsal outline nearly straight along median region (Fig. 3.38). Surface smooth (without granulations or reticulations), with ground punctation strongly marked. Body orange brown, slightly paler along margins. Shape of head somewhat trapezoid. Anterior corners of frons extended laterally and posteriorly, emarginating anterior margin of eyes. Eyes relatively small, with anterior margin markedly emarginate in lateral view, in dorsal view not projecting from outline of head. Clypeus with angulate lateral expansions in front of eyes; anterior margin of clypeus slightly emarginate. Labrum concealed under clypeus. Mentum with surface obliquely strigate. Antennae with nine antennomeres, cupule strongly asymmetric, with rounded outline. Maxillary palpi short and moderately stout, hardly 3/4 as long as width of head; maxillary palpomere 4 nearly as long as palpomere 3; inner margin of maxillary palpomere 2 nearly straight, outer margin curved along apical half. Elytra without sutural striae, broadly explanate laterally, serial punctures absent, ground punctures sharply marked, densely and uniformly distibuted. Prosternum slightly convex, not carinate medially. Posterior elevation of mesoventrite only bulging; anapleural sutures only slightly concave, separated at anterior margin by distance similar to anterior margin of mesepisternum. Metaventrite uniformly covered by hydrofuge pubescence. Protibiae with spines of anterior row long, thick and semi erect; apical spurs of protibiae stout, extending to apex of protarsomere 2. Metafemora without distinct tibial grooves; hydrofuge pubescence covering basal 3/4 of anterior surface of metafemora.

Tarsomeres 2–4 ventrally densely covered by setae; metatarsomere 1 much shorter than 2; metatarsomere 5 nearly as long as metatarsomere 2 or 3–4 combined. Fifth abdominal ventrite apically emarginate, with fringe of flat and stout setae. Aedeagus tubular (Fig. 3.37I); distal region of each paramere diverging; apex of parameres rounded; basal piece nearly half as long as parameres; median lobe broad, apically tapering to rounded tip; gonopore not clearly visible.

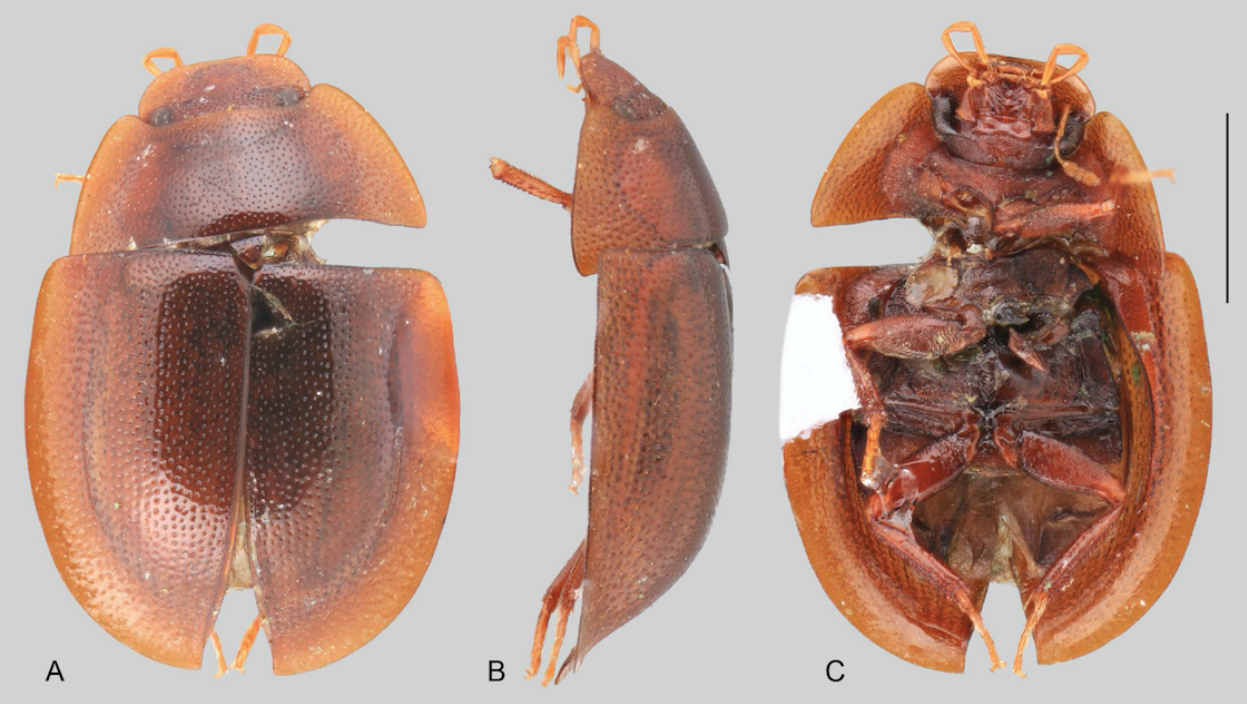


Figure 3.38. Habitus of *Helopeltarium ferrugineum*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus. Scale bar 1 mm.

Differential diagnosis. *Helopeltarium* has a very unique appearance within acidocerines. The flattened and broadly explanate body shape and concealed labrum, accompanied by smooth surface, short and stout maxillary palpi, lacking elytral serial punctures is unique in the subfamily. It may appear like a very small *Helobata*, but the lack of serial punctures, smooth surface and short maxillary palpi sets *Helopeltarium* apart very easily. The configuration of the aedeagus in

Helopeltarium, is very similar to that of some *Helochares*, but the external morphology alone allows for its immediate recognition.

Taxonomic history. Originally described by d'Orchymont (1943f: 9). Redescribed by Hansen (1991: 149).

Distribution. Indo-Malayan: Myanmar (formerly Burma).

Natural history. There is no natural history information available for the genus.

Larvae. Immature stages are not known for *Helopeltarium*.

Remarks. In the original description, d'Orchymont (1943f) compared *Helopeltarium* with *Helobata*. As far as we know, the genus is only known from two lectotype specimens of the only known species.

Species examined. Lectotypes of *Helopeltarium ferrugineum* d'Orchymont.

Selected references. d'Orchymont (1943f: 9, original description); Hansen (1991: 149, redescription).

Genus *Katasophistes* Girón and Short, 2018

(Figs 3.6, 3.39, 3.40)

Katasophistes Girón and Short, 2018: 132

Gender. Masculine.

Type species. *Katasophistes merida* Girón and Short, 2018: 136; by original designation.

Diagnosis. Medium to small beetles, body length 2.7–4.5 mm. Body shape oval to elongated in dorsal view; moderately and evenly convex in lateral view (Fig. 3.39). Color orange brown to dark brown, rather uniform along body regions. Shape of head trapezoid. Eyes relatively small, subquadrate, at most only slightly emarginated anteriorly, moderately projected from outline of head. Clypeus trapezoid, with anterior margin broadly emarginate. Labrum fully exposed. Mentum with strong median anterior depression sometimes limited by low transverse carina; surface of mentum with lateral oblique ridges. Antennae with nine antennomeres; cupule slightly asymmetric, with rounded outline. Maxillary palpi moderately long, 0.7 × to nearly as long as width of head; inner margin of maxillary palpomere 2 slightly curved near apex, outer margin curved, sometimes strongly, along apical half. Each elytron with five rows of deep/large systematic punctures; elytra without sutural striae, with outer margins slightly flared; serial punctures absent. Prosternum slightly convex to tectiform. Posterior elevation of mesoventrite, with a well-defined, curved transverse ridge; anapleural sutures forming an obtuse angle, separated at anterior margin by distance 0.2–0.3 × the width of anterior margin of mesepisternum. Metaventrite densely pubescent, except for large median rhomboid glabrous

patch. Protibiae with spines of anterior row hair-like, semi erect, relatively long and thick. All tarsomeres bearing long apical hair-like setae on dorsal face, and hair-like spines on ventral face of tarsomeres 2–4. Posterior femora glabrous at most along apical third. Fifth abdominal ventrite apically truncate to slightly emarginate, with fringe of stout setae. Aedeagus trilobed (Fig. 3.40), nearly parallel sided, with basal piece between 0.5 and 1.1 × length of parameres; median lobe wider than each paramere, gradually narrowing apically, with conspicuous median longitudinal sclerotization, and well-developed lateral basal apodemes; apex of median lobe acute; parameres nearly as long as median lobe, with apical setae; gonopore preapically situated.

Differential diagnosis. At first glance *Katasophistes* may appear similar to some species of *Chasmogenus*, however the lack of sutural striae easily separates the two. The enlargement of the rows of elytral systematic punctures is also rare within the Acidocerinae (found in some *Chasmogenus* and *Agraphydrus*) and will separate it from New World *Helochares*, with which it may also be confused.

Taxonomic history. *Katasophistes* was only recently described.

Distribution. Neotropical: Ecuador, Peru, Venezuela.

Natural history. Species in this genus can be found in seepage habitats as well as in forested stream pools with abundant detritus.

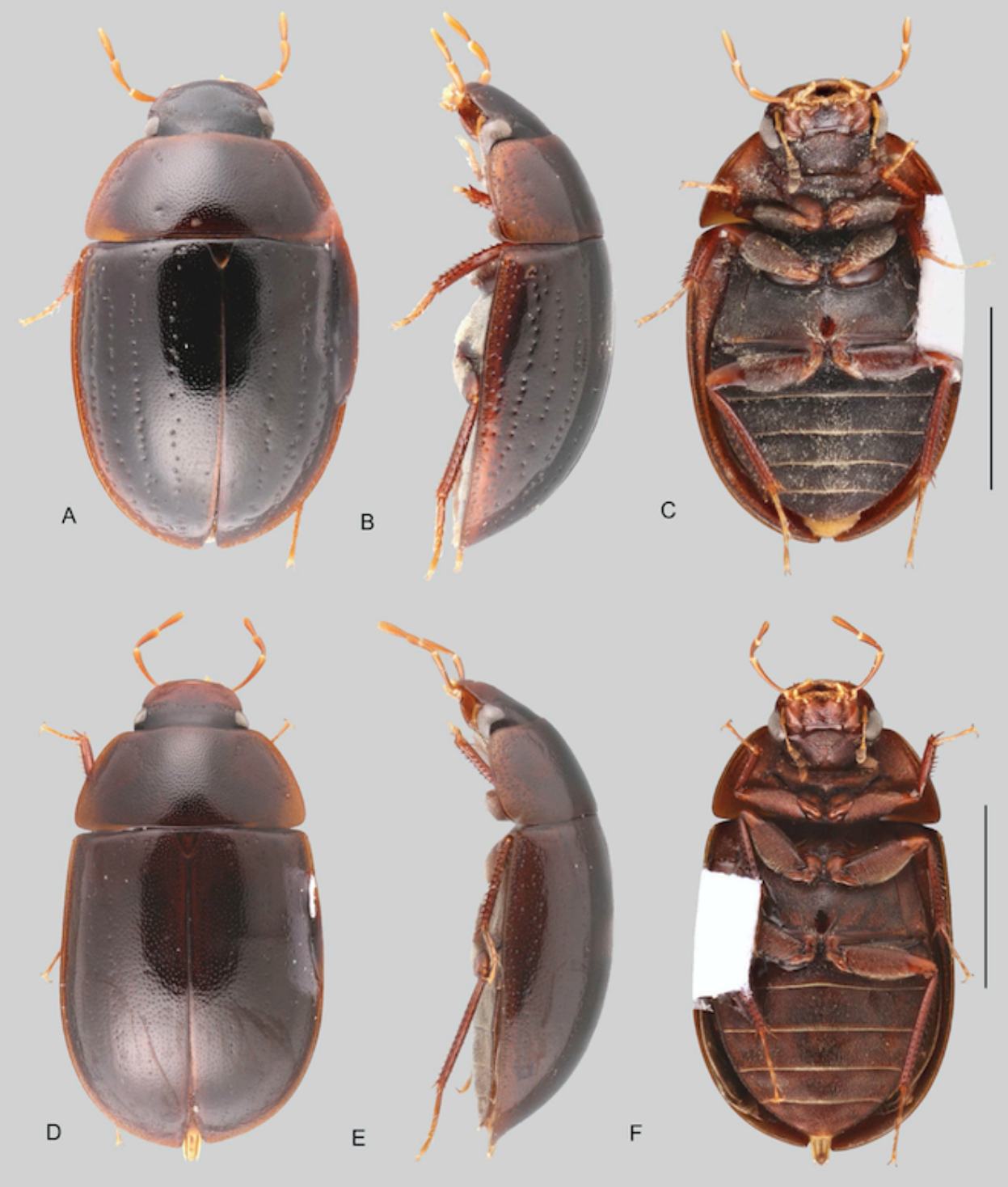


Figure 3.39. Habitus of *Katasophistes* spp.: **A–C** *K. merida*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus, **D–F** *K. superficialis*: **D** dorsal habitus, **E** lateral habitus, **F** ventral habitus. Scale bars 1 mm.

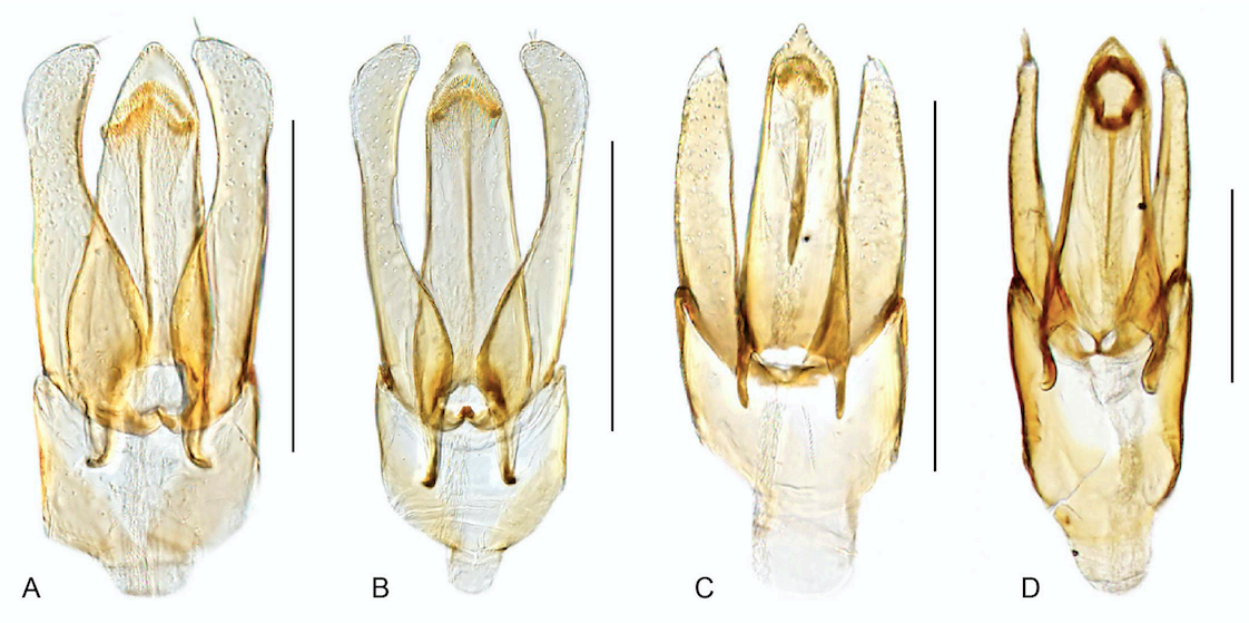


Figure 3.40. Aedeagus of *Katasophistes* spp.: **A** *K. carynae*, **B** *K. cuzco*, **C** *K. merida*, **D** *K. superficialis*. Scale bars 0.3 mm.

Larvae. Immature stages are not known for the genus.

Remarks. There are four known species of *Katasophistes*, all of them from Andean localities.

Species examined. Holotypes and paratypes of all known species were available for this study.

Selected references. Girón and Short (2018): original description of the genus and all its known species.

Genus *Nanosaphes* Girón and Short, 2018

(Figs. 3.6, 3.32B–E, 3.41)

Nanosaphes Girón and Short, 2018: 143

Gender. Masculine.

Type species. *Nanosaphes tricolor* Girón and Short, 2018: 151; by original designation.

Diagnosis. Very small beetles, body length 1.15–1.45 mm. Body shape oval in dorsal view; slightly to moderately, and evenly convex in lateral view (Fig. 3.41). Coloration uniformly brown, to variable along the body; ground punctation shallow to moderately marked. Shape of head trapezoid and relatively wide. Eyes moderate in size, slightly emarginated anteriorly, not projected from outline of head. Clypeus trapezoid, with anterior margin broadly emarginate. Labrum fully exposed. Mentum with lateral oblique ridges. Antennae with eight antennomeres; cupule slightly asymmetric, with rounded outline. Maxillary palpi slender, moderately long nearly 0.7 × the width of head; inner margin of maxillary palpomere 2 nearly straight, outer margin curved along apical half. Each elytron with ground punctures usually only shallowly marked, seemingly forming longitudinal rows, with irregularly distributed systematic punctures bearing rather long setae, denser along lateral and posterior regions; elytra without sutural striae. Prosternum flat, at most only weakly convex. Posterior elevation of mesoventrite, usually projected as low and short longitudinal carina between mesocoxae; anapleural sutures only weakly curved, separated at anterior margin by distance nearly 0.9 × width of anterior margin of

mesepisternum. Metaventrite with posterolateral and mesal glabrous patches. Protibiae with spines of anterior row hair-like, semi erect, relatively long, thick and sparse. Metafemora mostly densely covered by hydrofuge pubescence. All tarsomeres with long and thick spines on ventral face of tarsomeres 2–4; metatarsomeres 2–4 gradually decreasing in size, metatarsomere 5 as long as 3–4 combined, 2 slightly shorter. Fifth abdominal ventrite apically emarginate, with fringe of stout setae. Aedeagus trilobed (Fig. 3.32B–E), nearly parallel sided, with basal piece between 0.3 and 0.6 × length of parameres; median lobe with well-developed lateral basal apodemes, wider at base than base of each paramere, usually narrower at apex than preapical width of parameres; apex of median lobe rounded; parameres from slightly shorter to longer than median lobe, and only narrowing at apex; gonopore situated beyond midpoint of median lobe.

Differential diagnosis. The minute size of *Nanosaphes* make them smaller than any other Acidocerinae in the New World, and about equal in size to the smallest species of *Agraphydrus* in the Old World. They are among the smallest water scavenger beetles worldwide. The lack of elytral serial or sutural striae and the antennae with eight antennomeres also separate *Nanosaphes* from all other Neotropical Acidocerinae genera except the co-occurring *Globulosis*. *Nanosaphes* can be easily separated from *Globulosis* by its smaller size and narrower, more parallel sided body form (broader and almost rotund in *Globulosis*, see Fig. 3.31).

Taxonomic history. *Nanosaphes* was only recently described.

Distribution. Neotropical: Brazil (Pará), Guyana, Suriname.

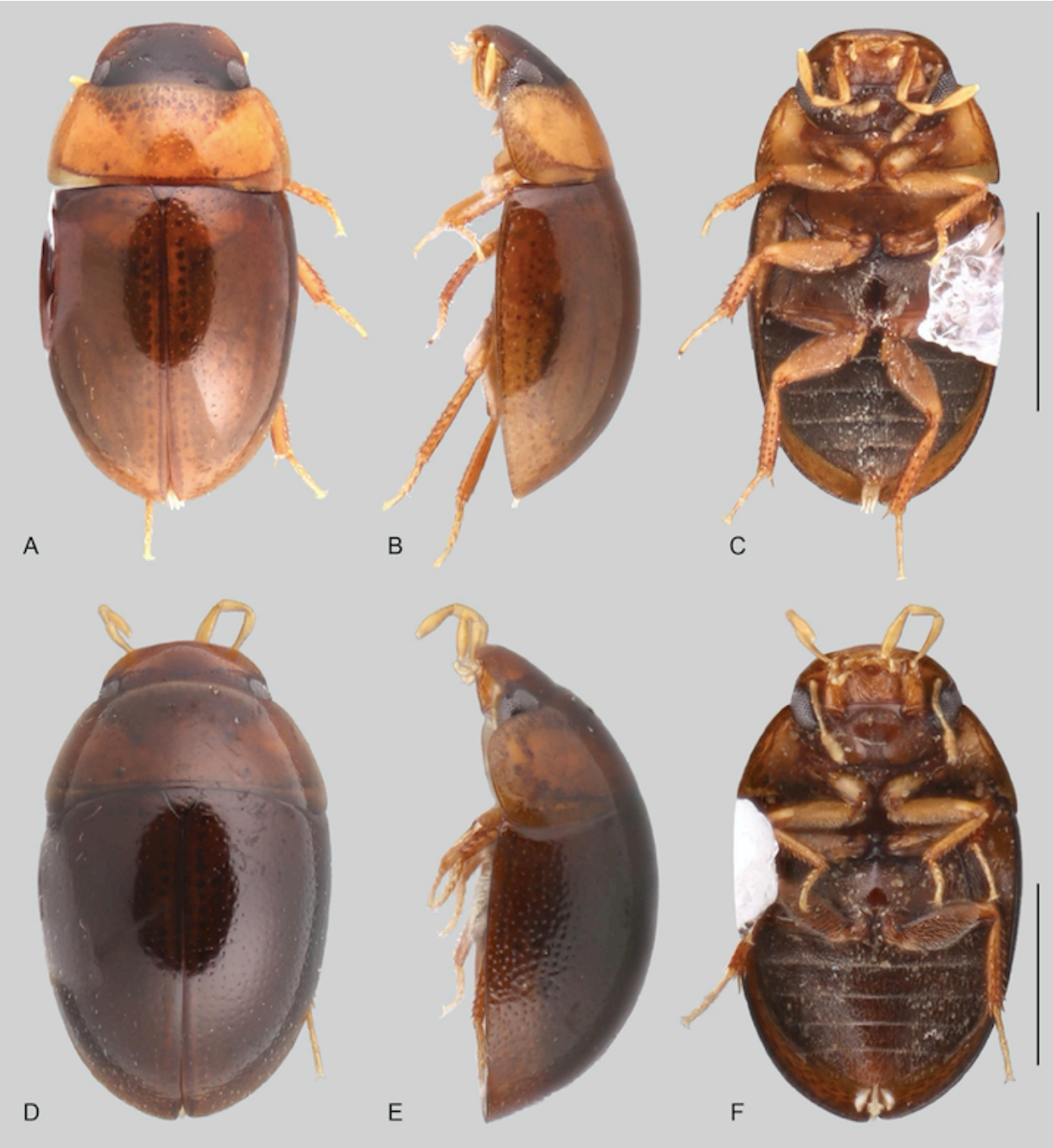


Figure 3.41. Habitus of *Nanosaphes* spp.: **A–C** *N. tricolor*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus, **D–F** *N. punctatus*: **D** dorsal habitus, **E** lateral habitus, **F** ventral habitus. Scale bars 0.5 mm.

Natural history. Species are associated with stream margins, particularly where there are banks for margins of sand and roots.

Larvae. Immature stages are not known for *Nanosaphes*.

Remarks. There are four known species of *Nanosaphes*, which can be differentiated from each other by external morphological features, which is somewhat unusual for acidocerine standards.

Species examined. Holotypes and paratypes of all known species were available for this study.

Selected references. Girón and Short (2018): original description of the genus and all its known species.

Genus *Novochares* gen. n.

(Figs. 3.1G, 3.4, 3.42, 3.43)

Helochares "Clade D", Short et al. (in prep.)

Gender. Masculine.

Type species. *Helochares tectiformis* Fernández, 1982; by present designation.

Etymology. From the Latin word *novus*, meaning new, in reference to the genus being restricted to the New World, combined with the ending *chares*, expressing affinity with *Helochares*. Masculine.

Diagnosis. Medium sized beetles, body length 4.5–9.0 mm. Body shape oval in dorsal view; slightly to moderately convex in lateral view, with dorsal outline nearly flat along anterior half of elytra, or somewhat evenly curved (Fig. 3.43). Coloration usually uniformly dark brown, sometimes orange or pale brown; ground punctation shallow to moderately marked. Shape of head trapezoid. Eyes relatively large, not emarginated anteriorly, usually projected from outline of head. Clypeus trapezoid, with anterior margin broadly and roundly emarginate. Labrum fully exposed. Mentum with lateral longitudinal crenulations, lateral oblique ridges, and transverse crenulations along antero-medial area. Antennae with nine antennomeres; cupule strongly asymmetric, with rounded outline; antennomere 9 slightly to 2 × longer than antennomere 7. Maxillary palpi slender, moderately long, 1.1–1.5 × the width of head; inner margin of maxillary palpomere 2 weakly and evenly curved to nearly straight, outer margin evenly curved or curved along apical half; maxillary palpomere 3 slightly longer than 4. Prosternum flat to weakly convex. Elytra without sutural striae, with ground punctures usually shallowly marked; usually at least one row of systematic punctures visible along midline of each elytron; serial punctures sometimes visible along posterior half of elytra. Posterior elevation of mesoventrite, usually simply bulging, sometimes bulge impressed posteriorly, sometimes bulge extends anteriorly as low, shiny and glabrous longitudinal ridge; anapleural sutures concave, separated at anterior margin by distance 0.6–0.9 × the width of anterior margin of mesepisternum. Metaventrite with

medial glabrous patch, sometimes very narrow and extending along entire length of metaventrite. Protibiae with spines of anterior row extremely reduced to tiny appressed denticles. Metafemora with tibial grooves well developed; hydrofuge pubescence covering basal six sevenths of anterior surface. Tarsomeres 1–4 with long, thick and rather dense setae on ventral face, sometimes with only rows of short spines on metatarsomeres 2–4; metatarsomere 2 as long or slightly longer than 5 and as 3–4 combined. Fifth abdominal ventrite apically emarginate, with fringe of stout setae. Aedeagus subdivided (Fig. 3.43); parameres separated from each other for most of their length; median lobe subdivided in dorsal and ventral plates; dorsal plate usually strongly sclerotized and elongated, often bifurcated or otherwise shaped along apical region; ventral plate sometimes reduced, usually simple and of variable length; basal piece 0.3 × or less than length of parameres, usually clearly noticeable; gonopore usually clearly visible.

Differential diagnosis. *Novochares* includes medium sized, pale to dark brown species that are somewhat dorsoventrally compressed and highly polished (smooth, and often shiny) to the naked eye. In the New World the most similar genus is *Aulonochares*, from which it can be differentiated by the shape of the head (trapezoid in *Novochares*, subquadrate in *Aulonochares* (see Fig. 3.9J)), and the sculpture of the mentum (variously strigate in *Novochares*, punctate in *Aulonochares*). Some members of the New World *Helochares* may resemble *Novochares* in their external features, but the aedeagal form is completely different (tubular in *Helochares* (see Fig. 3.37), subdivided in *Novochares* (see Fig.3. 43).

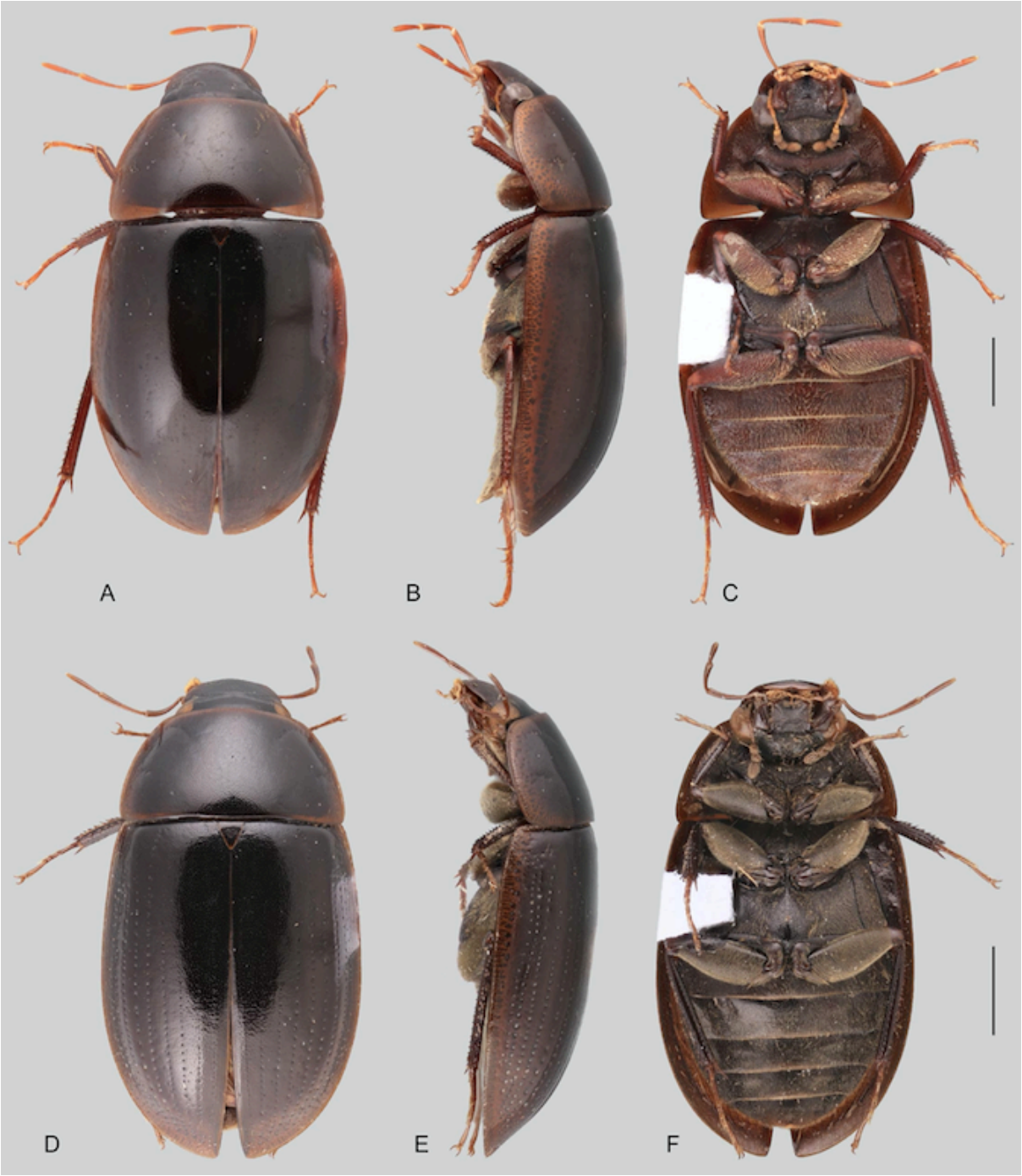


Figure 3.42. Habitus of *Novochares* spp.: **A–C** *N. sallaei*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus, **D–F** *N.* sp.: **D** dorsal habitus, **E** lateral habitus, **F** ventral habitus. Scale bars 1 mm.

From the rest of acidocerines, *Novochares* externally is strikingly similar to the dark and highly polished members of the Old World genus *Peltochares* (compare Fig. 3.1B vs 3.1G), from

which *Novochares* can be distinguished by the shape of the posterior elevation of the mesoventrite (simply and broadly bulging, often with additional anterior low longitudinal ridge in *Novochares*, longitudinally elevated in *Peltochares*), in addition to characteristics of the male genitalia (subdivided aedeagus in *Novochares* (see Fig. 3.43), spiked aedeagus in *Peltochares* (see Fig. 3.45); see also explanation under the aedeagus section of Morphological variation in Acidocerinae and its taxonomic importance).

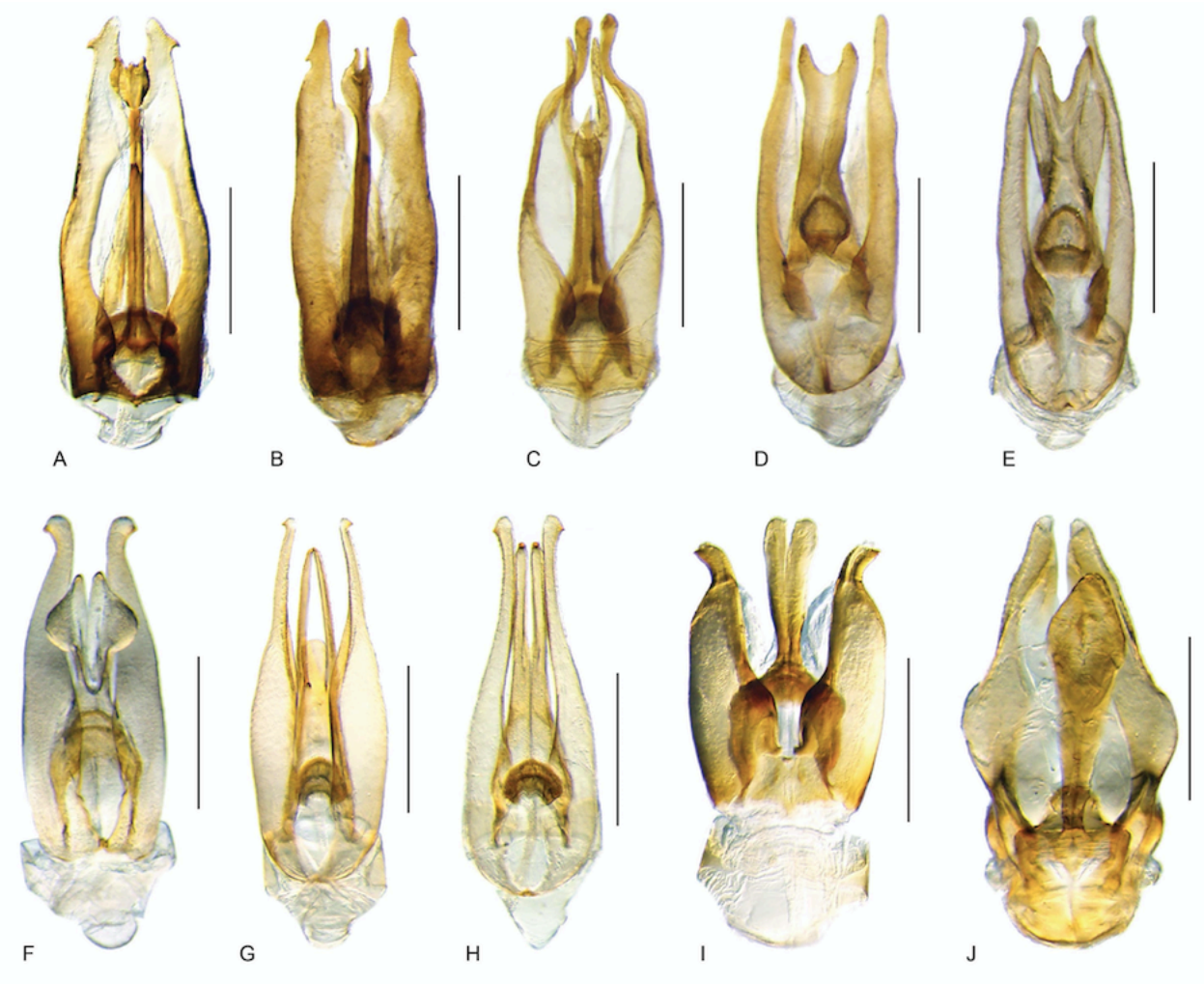


Figure 3.43. Aedeagus of *Novochares* spp.: **A** *N. abbreviatus*, **B** *N. oculatus*, **C** *N. pallipes*, **D** *N. chaquensis*, **E** *N. atratus*, **F** *N. pichilingue*, **G** *N. tectiformis*, **H** *N. coya*, **I** *N. guadelupensis*, **J** *N. cochearis*. Scale bars 0.5 mm.

To differentiate *Novochares* from dark brown, relatively flattened, highly polished, and 4–5 mm long species of *Helochares*, the most reliable feature for identification would be the male genitalia: *Novochares* always exhibit subdivided aedeagi (see Fig. 3.43; parameres separated from each other for most of their length, dorsal plate of the median lobe usually strongly sclerotized, elongated, often bifurcated or otherwise shaped along its apical region), whereas in *Helochares* the aedeagi are always tubular (see Fig. 3.37; parameres fused to each other for most of their length, median lobe with very long basal apodemes) (see also explanation under the aedeagus section of Morphological variation in Acidocerinae and its taxonomic importance).

Taxonomic history. Species of *Novochares* have been described since as early as 1801, but it was only with the investigations of Fernández in the 1980's (Fernández 1981, 1982a, 1982b, 1983, 1989) that the group was studied in a comparative taxonomic framework beyond the description of single species.

Distribution. Nearctic: U.S.A. (Florida; thought to be introduced). **Neotropical:** Argentina, Belize, Bolivia, Brazil (Amazonas, Espírito Santo, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Paraíba, Pernambuco, São Paulo), Colombia, Costa Rica, Cuba, Ecuador, French Guiana, Guatemala, Lesser Antilles (Grenada, Guadeloupe, St. Vincent), Mexico, Panama, Paraguay, Suriname, Uruguay, Venezuela.

Natural history. Information about the ecological habits of *Novocares* species is rather scarce. It is known that *N. abbreviatus* (Fabricius) is found in lentic habitats including marshes,

swamps, and pond margins (Short 2005). *Novochares atlanticus* (Clarkson and Ferreira-Jr.) was collected at temporary ponds with leaf litter and aquatic vegetation, either covered and shaded in the border of the forest (Clarkson and Ferreira-Jr. 2014), or in open areas. *Novochares carmona* (Short) was collected at a mercury vapor light by a drying lowland marsh (Short 2005). Fernández, in describing the immature stages of *N*. *pallipes* (Brullé), indicated that the species was found on coastal zones, associated with swamp plants (*Spirodela intermedia*; Araceae) (Fernández 1983).

Larvae. The immature stages are only known for *Novochares pallipes* (Brullé) (described as *Helochares* (s. str.) *pallipes* Brullé in Fernández 1983: 444); egg sac, first, second and third instar larvae, and pupa are described and illustrated. From each egg sac, between 80 and 103 larvae emerged (Fernández 1983).

Remarks. There are 15 species of *Novochares* described to date. Species of *Novochares* tend to have moderate to shallow punctation and the serial punctures are usually absent. There is a group of species with serial punctures visible along the posterior half to third of the elytra.

Species examined. *Novochares abbreviatus* (Fabricius), *N. carmona* (Short), *N. chaquensis* (Fernández), *N. cochlearis* (Fernández), *N. coya* (Fernández), *N. guadelupensis* (d'Orchymont), *N. pallipes* (Brullé), *N. sallaei* (Sharp), *N. tectiformis* (Fernández). Paratypes of *N. carmona* were examined for this study.

Selected references. Fernández (1982a), notes on the taxonomic status of some of the previously described species; Fernández (1982b), description of four new species; Fernández (1983), description of immature stages for *Novochares pallipes* (Brullé); Fernández (1989), one new species and identification key.

Genus *Peltochares* Régimbart, 1907

(Figs 3.1B, C, 3.4, 3.9K, 3.44, 3.45)

Peltochares Régimbart, 1907: 49

Type species. *Peltochares conspicuus* Régimbart, 1907: 49; by monotypy.

Stagnicola Montrouzier, 1860: 246 [preoccupied name by *Stagnicola* Gray, 1840 (Mollusca)]

Type species: *Stagnicola foveicollis* Montrouzier, 1860: 246; by monotypy; Bedel 1880: CXLVIII [synonymy].

Neohydrobius Blackburn, 1888: 221

Type species: *Philhydrus burrundiensis* Blackburn, 1890: 221; by monotypy; d'Orchymont 1919b: 228 [synonymy].

Helochares "Clade C" in Short et al. in prep.

Gender. Masculine.

Type species. *Peltochares conspicuus* Régimbart, 1907: 49; by monotypy.

Diagnosis. Body length 6–10 mm. Body shape oval in dorsal view, weakly to moderately convex in lateral view (Fig. 3.44). Dorsal surfaces even and smooth, either uniformly covered by short setae (Fig. 3.44A), or with scarce long setae along particular areas of surface (associated with systematic punctures; Fig. 3.44D), dark brown in coloration, usually uniform; ground punctation fine and shallow to moderate; ventral surfaces densely covered by fine golden setae. Head subquadrate (Fig. 3.9K). Eyes not emarginate, moderate in size, subquadrate, separated by 4.5–5.5 × width of eye, strongly projected from outline of head. Clypeus with anterior margin broadly emarginate, either roundly or acutely, sometimes further medially notched; membranous preclypeal area visible when clypeus strongly emarginated. Labrum fully exposed, often medially convex. Antennae with nine antennomeres, with moderately asymmetric and round cupule; antennomere 9 slightly to 2 × longer than antennomere 7. Maxillary palpi slender, 1.3–1.8 × longer than maximum width of head, with palpomere 4 nearly 0.8 × as long as palpomere 3; maxillary palpomere 2 with inner margin slightly and evenly curved, and outer margin curved along apical half. Mentum slightly depressed mesally, surface laterally punctate, mesally and anteriorly strigate, with anteromedial region depressed. Submentum punctate to crenulate. Pronotum evenly convex, usually with systematic punctures forming distinct anterolateral semicircles. Elytra without sutural striae, with margins usually only slightly flared (explanate in *P. conspicuus*; see Fig. 3.44A); serial punctures usually absent (visible along entire length of elytra in *P. conspicuus*; see Fig. 3.44A); ground punctation usually shallow (moderate to strongly marked in *P. foveicollis*). Surface of prosternum flat to broadly convex, with anterior margin roundly projected anteriorly. Posterior elevation of mesoventrite usually with longitudinal or somewhat longitudinal elevation, sometimes forming acute posterior point; apical

region of elevation usually with long fine setae; anapleural sutures forming obtuse angle, nearly parallel along anterior section, separated anteriorly by distance 0.3–0.7 × anterior margin of mesepisternum. Metaventrite densely covered by hydrofuge pubescence, except for posterolateral patches. Protibiae with anterior row of spines reduced to extremely reduced; apical spurs of protibiae stout, ranging from very large (larger spur considerably larger and thicker than tarsal claws, e.g., *P. foveicollis*), or very short (barely reaching apex of protarsomere 1, e.g., *P. conspicuus*); pro- and mesotarsal claws are sexually dimorphic in some species (e.g., *P. foveicollis*). Metafemora with tibial grooves sharply marked; metafemora with hydrofuge pubescence covering at least basal three fourths of anterior surface. Metatarsomeres 5 and 2 similar in length or 2 slightly longer, metatarsomere 2 slightly longer than metatarsomeres 3 and 4 combined; all tarsomeres with ventral surface rather densely covered by long spiniform setae on ventral surface (sparser on tarsomere 5). Abdomen with five pubescent ventrites. Fifth abdominal ventrite with apex emarginate, fringed by stout setae. Aedeagus spiked (Fig. 3.45); main component of median lobe strongly sclerotized, slender and apically acute, usually accompanied by additional shorter slender sclerotizations; apical region of parameres usually partly heavily sclerotized and partly membranous, often bifurcated; basal piece strongly reduced; gonopore usually not clearly visible.

Differential diagnosis. The type species of *Peltochares* is easily recognized by its external morphology alone: laterally explanate pronotum and elytra, well defined serial punctures along elytra, which somewhat resembles *Helobata*, from which *P. conspicuus* can be distinguished by the exposed labrum of *Peltochares* (see Fig 9K; concealed labrum in *Helobata* (see Fig. 3.9L)). The

most common forms of *Peltochares* more closely resemble *Novochares* and some *Helochares*, because of their darkly colored and highly polished bodies. Besides being distributed (although widespread) in the Old World, *Peltochares* species can be distinguished from the New World *Novochares* by the shape of the posterior elevation of the mesoventrite (longitudinally elevated in *Peltochares*, simply and broadly bulging, often with additional anterior low longitudinal ridge in *Novochares*), in addition to characteristics of the male genitalia (spiked aedeagus in *Peltochares* (see Fig. 3.45), subdivided aedeagus in *Novochares* (see Fig. 3.43); see also explanation under the aedeagus section of Morphological variation in Acidocerinae and its taxonomic importance). From dark brown, highly polished, and relatively large species of *Helochares*, *Peltochares* can be distinguished by their slender maxillary palpi, that are 1.3–1.8 × longer than the width of the head, as opposed to shorter (0.6–1.2 × the width of the head) and relatively stout maxillary palpi in *Helochares*, in addition to the aedeagal form (spiked in *Peltochares* (see Fig. 3.45), tubular in *Helochares* (see Fig. 3.37); see also explanation under the aedeagus section of Morphological variation in Acidocerinae and its taxonomic importance).

Taxonomic history. *Peltochares* was described as a monotypic genus by Régimbart in 1907, from specimens collected in Gabon. The group of species previously assigned to *Helochares* (s. str.), hereby transferred to *Peltochares*, was first recognized by Hebauer (2001b) as a discrete unit in morphological terms within *Helochares*. There are currently eight described species of *Peltochares*.

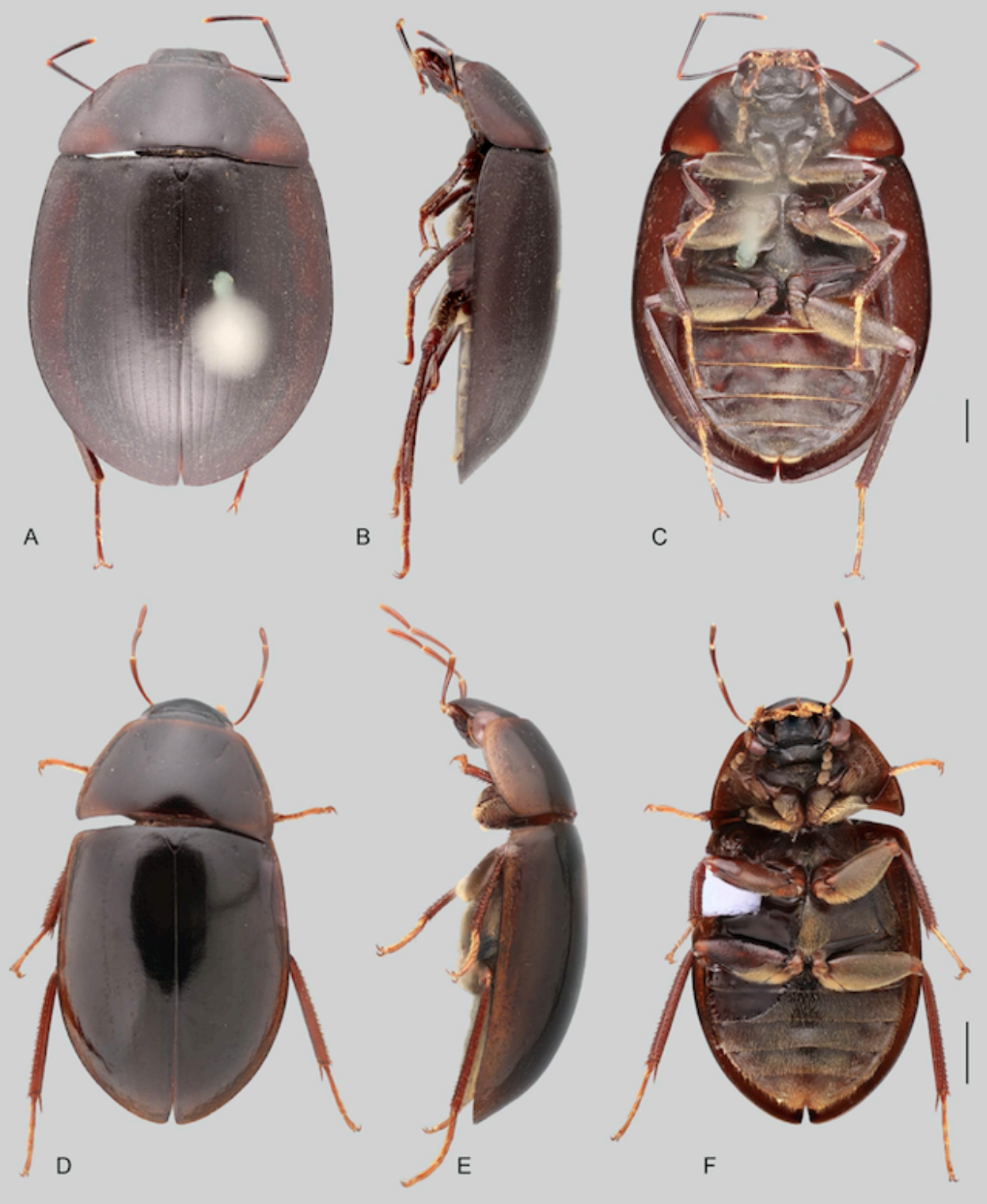


Figure 3.44. Habitus of *Peltochares* spp.: **A–C** *P. conspicuus*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus, **D–F** *P.* sp. (Tanzania): **D** dorsal habitus, **E** lateral habitus, **F** ventral habitus. Scale bars 1 mm.

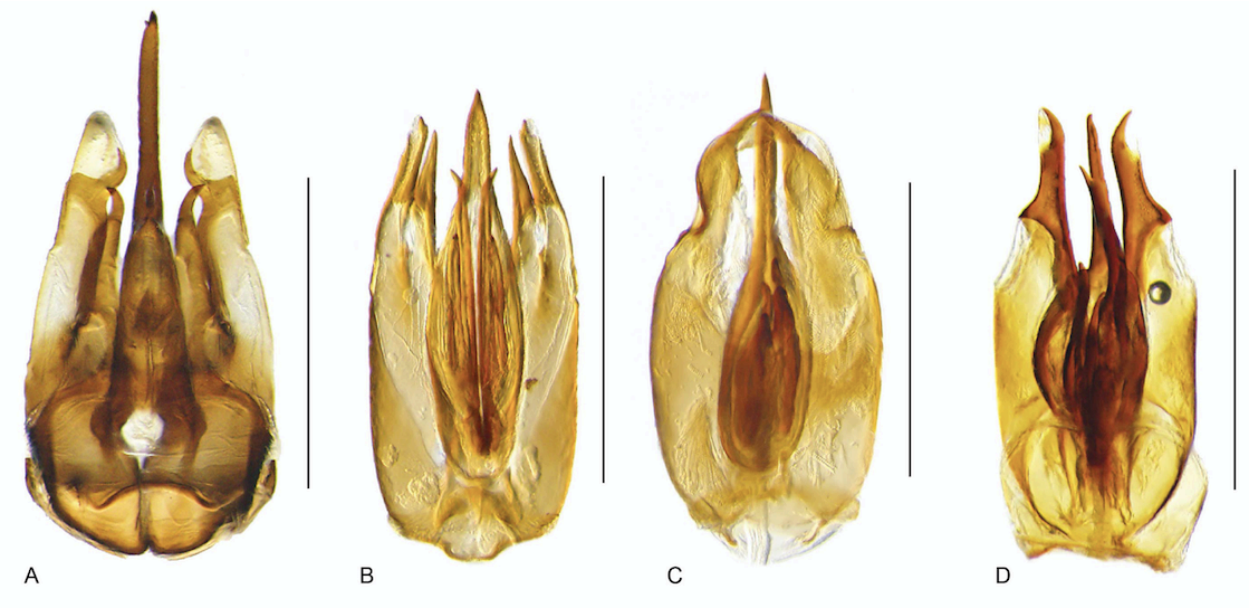


Figure 3.45. Aedeagus of *Peltochares* spp.: **A** *P. conspicuus*, **B** *P. foveicollis*, **C** *P.* sp. (Australia), **D** *P.* sp. SLE-450. Scale bars 1 mm.

Distribution. Afrotropical: Angola, Benin, Botswana, Burkina Faso, Burundi, Cameroon, Central African Republic, Chad, Democratic Republic of the Congo, Ethiopia, Gabon, Gambia, Ghana, Guinea, Ivory Coast, Kenya, Liberia, Madagascar, Malawi, Mozambique, Namibia, Niger, Nigeria, Republic of the Congo, Rwanda, Senegal, Sierra Leone, Somalia, South Africa, South Sudan, Tanzania, Togo, Uganda, Western Sahara, Zambia, Zimbabwe. **Australasian:** Australia (Australian Capital Territory, New South Wales, Northern Territory, Queensland, Western Australia), Indonesia (Papua), New Caledonia, Papua New Guinea. **Indo-Malayan:** Bangladesh, Cambodia, China (Guangdong, Guangxi, Guizhou, Hong Kong, Jiangxi, Macao), Indonesia (Borneo, Sumatra), Laos, Malaysia, Nepal, Sri Lanka, Thailand, Vietnam. **Palearctic:** Canary Islands, Egypt, Israel, Japan (Iriomote-jima).

Natural history. Even though species currently placed in *Peltochares* have been treated in faunistic and taxonomic studies (e.g., Watts 1995, Hebauer 2001b), little is known about their ecology. Jia and Tang (2018) recently reported that *P. atropiceus* (Régimbart) was living in natural ponds with leaf litter or water grass, sometimes collected on wet ground with plenty of grass; it can be collected at light in May and June in South China, and has never been collected from the edges of rivers and streams. The female carries the egg case under the abdominal ventrites (Jia and Tang 2018).

Larvae. Larval stages of *Peltochares conspicuus* Régimbart, were described by Bertrand (1962) from larvae collected along with adults on the surface of rocks in Madagascar. Fikáček (2003) provides a diagnosis of the larvae described by Bertrand (1962), but questions their identification, given that *P. conspicuus* has been never recorded from Madagascar.

Remarks. Since its description, *Peltochares* has been considered unique because of its external appearance (large beetles with explanate pronotum and elytra, with well-defined serial punctures). Short et al. (in prep.) included one unidentified species of *Peltochares* from Indonesia in their phylogenetic analysis, which clusters with a group of species traditionally placed in *Helochares* (s. str.) and is denominated as "*Helochares* clade C" by Short et al. (in prep.). This group of species was the focus of Hebauer (2001b), including *P. atropiceus* (Régimbart) **comb. nov.**, *P. ciniensis* (Hebauer, Hendrich, and Balke) **comb. nov.**, *P. discus* (Hebauer, Hendrich, and Balke) **comb. nov.**, *P. foveicollis* (Montrouzier) **comb. nov.**, *P. longipalpis* (Murray) **comb. nov.**, *P. papuensis* (Hebauer) **comb. nov.**, and *P. taprobanicus* (Sharp) **comb.**

nov.). Hebauer (2001) indicated the striking external similarity among members of the group, accompanied by a specific configuration of the male genitalia. Examination of the male genitalia of one of the syntypes of *P. conspicuus* and members of "*Helochares* clade B" in Short et al. (in prep.) revealed that they share the quite unique conformation of the male genitalia (spiked genitalia, see Fig. 3.13F–J; see also under the aedeagus section of Morphological variation in Acidocerinae and its taxonomic importance), even though they do not look so similar externally.

Species examined. *Peltochares atropiceus*, *P. ciniensis* (including a paratype), *P. conspicuus* (including lectotypes), *P. foveicollis*, *P. longipalpis*, and *P. taprobanicus*.

Selected references. Régimbart (1907): original description of the genus; Hebauer (2001b): taxonomic treatment of *P. taprobanicus* (as *Helochares taprobanicus*) and allied species; Jia and Tang (2018): faunistic review of Chinese species including a redescription and some biological notes on *P. atropiceus* (Régimbart).

Genus *Primocerus* Girón and Short, 2019

(Figs 3.2D, 3.3, 3.46, 3.47)

Primocerus Girón and Short, 2019: 133

Gender. Masculine.

Type species. *Primocerus neutrum* Girón and Short, 2019: 147; by original designation.

Diagnosis. Small to medium sized beetles, body length 2.4–4.9 mm. Body shape elongated oval in dorsal view; moderate to strongly convex in lateral view; dorsal outline uniformly convex or nearly straight and anteriorly inclined along anterior half (Fig. 3.46). Color brown, dark brown, reddish brown, or rather orange, usually uniform along body regions, but sometimes with slightly paler margins, pronotum or ventral surfaces and appendages; ground punctation shallow to moderately marked. Shape of head trapezoid. Eyes small to moderate, seldom very small, not emarginated anteriorly, usually projected from outline of head. Clypeus trapezoid, with anterior margin broadly and roundly emarginate. Labrum fully exposed. Mentum rather flat and smooth, sometimes with lateral oblique ridges, and few crenulations; median anterior depression sometimes marked by a transverse carina. Antennae with eight antennomeres; cupule slightly asymmetric, with rounded outline. Maxillary palpi moderately stout, shorter to nearly as long as width of head; inner margin of maxillary palpomere 2 nearly straight, outer margin curved along apical two thirds; maxillary palpomeres 3 and 4 similar in length. Prosternum flat to mesally only slightly produced. Elytra with sutural striae; elytral punctures from shallow to sharply marked; ground punctures rather uniformly distributed; some species with serial punctures; outer margins of elytra slightly flared. Posterior elevation of mesoventrite usually with curved transverse ridge, rather sharp and low, or bearing sharp, pyramidal (triangular) projection; anapleural sutures concave to forming obtuse angle, separated at anterior margin by distance 0.3–0.4 × width of anterior margin of mesepisternum. Metaventrite with posteromesal glabrous patch nearly as wide as long. Protibiae with spines of anterior row as thick, long semi-erect setae; apical spurs of protibiae moderately stout, reaching

midlength of protarsomere 3. Metafemora with tibial grooves moderately developed; hydrofuge pubescence coverage ranging from sparse (nearly glabrous metafemora) to dense along basal three fourths. Tarsomeres 1–4 with long spiniform setae on ventral face; metatarsomere 2 nearly as long as 5 and as 3–4 combined. Fifth abdominal ventrite apically rounded, truncate or slightly emarginate, usually with fringe of stout setae. Aedeagus trilobed (Fig. 3.47); basal piece as long or longer than parameres; median lobe triangular, nearly as wide at base as basal width of parameres, with apical projection; gonopore absent.

Differential diagnosis. At first sight, the smoother members of *Primocerus* can be mistaken for *Chasmogenus*, given that both genera exhibit sutural striae. The presence of a transverse curved ridge (sometimes very low) on the posterior elevation of the mesoventrite distinguishes *Primocerus* from *Chasmogenus*, in which the mesoventrite is either flat, broadly elevated or with a longitudinal elevation; maxillary palpi of most *Chasmogenus* species are nearly 1.5 × longer than the maximum width of the head, whereas in *Primocerus* the maxillary palpi are shorter, nearly as long as the width of the head.

Punctate members of *Primocerus* (e.g., Fig. 3.46D–F) may resemble some species of *Tobochares* (see Kohlenberg and Short 2017, Girón and Short in prep.); striate *Primocerus* (e.g., Fig. 3.46G–I) may resemble *Radicitus* (see Short and García 2014). In those cases, *Primocerus* can be easily recognized by the presence of sutural striae. Some species of *Primocerus* may also superficially resemble certain New World cylomine genera, such as *Andotypus* (see Fikáček et al. 2014), from which it may be distinguished by the fully exposed labrum of *Primocerus*.

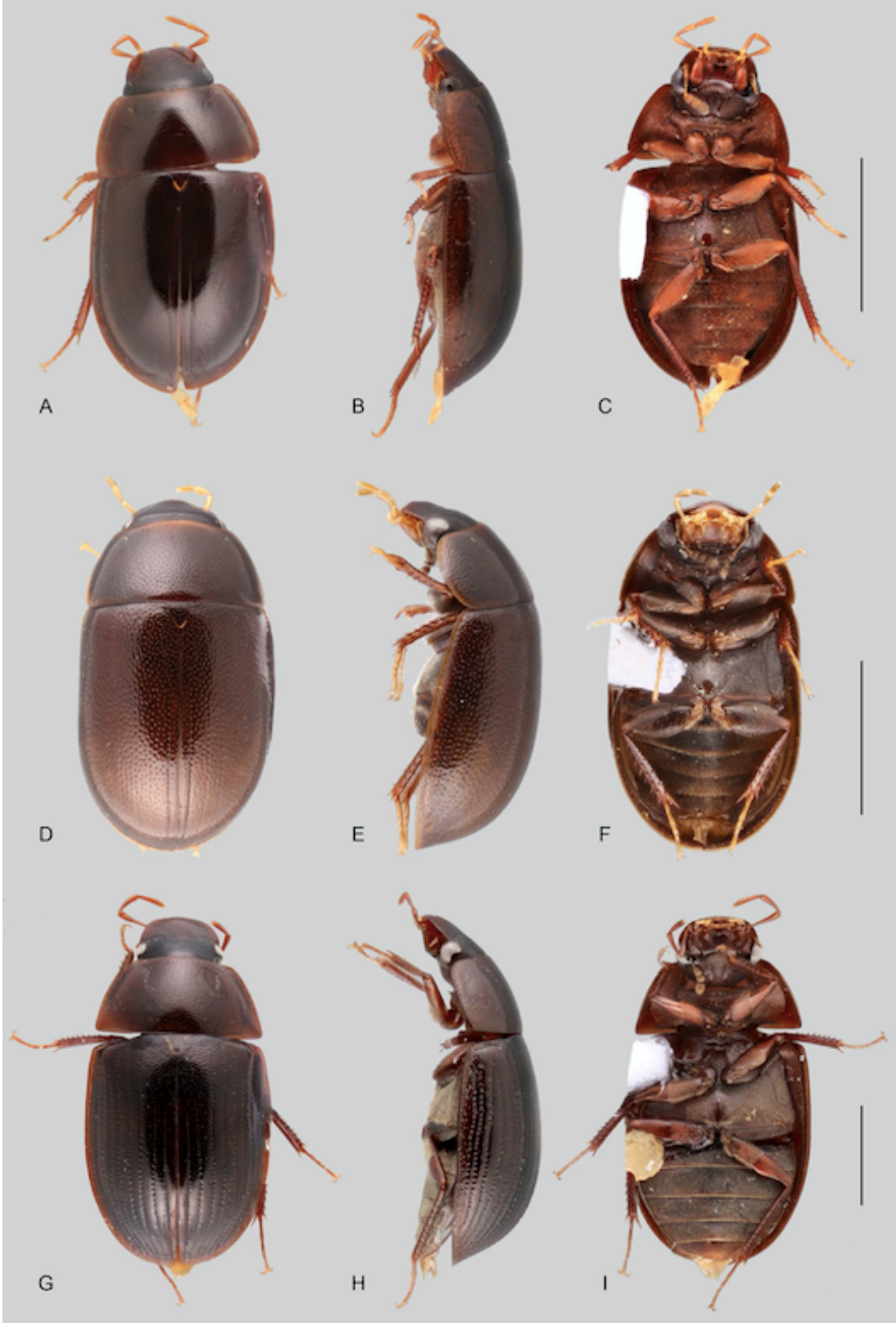


Figure 3.46. Habitus of *Primocerus* spp.: **A–C** *P. neutrum*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus, **D–F** *P. maipure*: **D** dorsal habitus, **E** lateral habitus, **F** ventral habitus, **G–I** *P. semipubescens*: **G** dorsal habitus, **H** lateral habitus, **I** ventral habitus. Scale bars 1 mm.

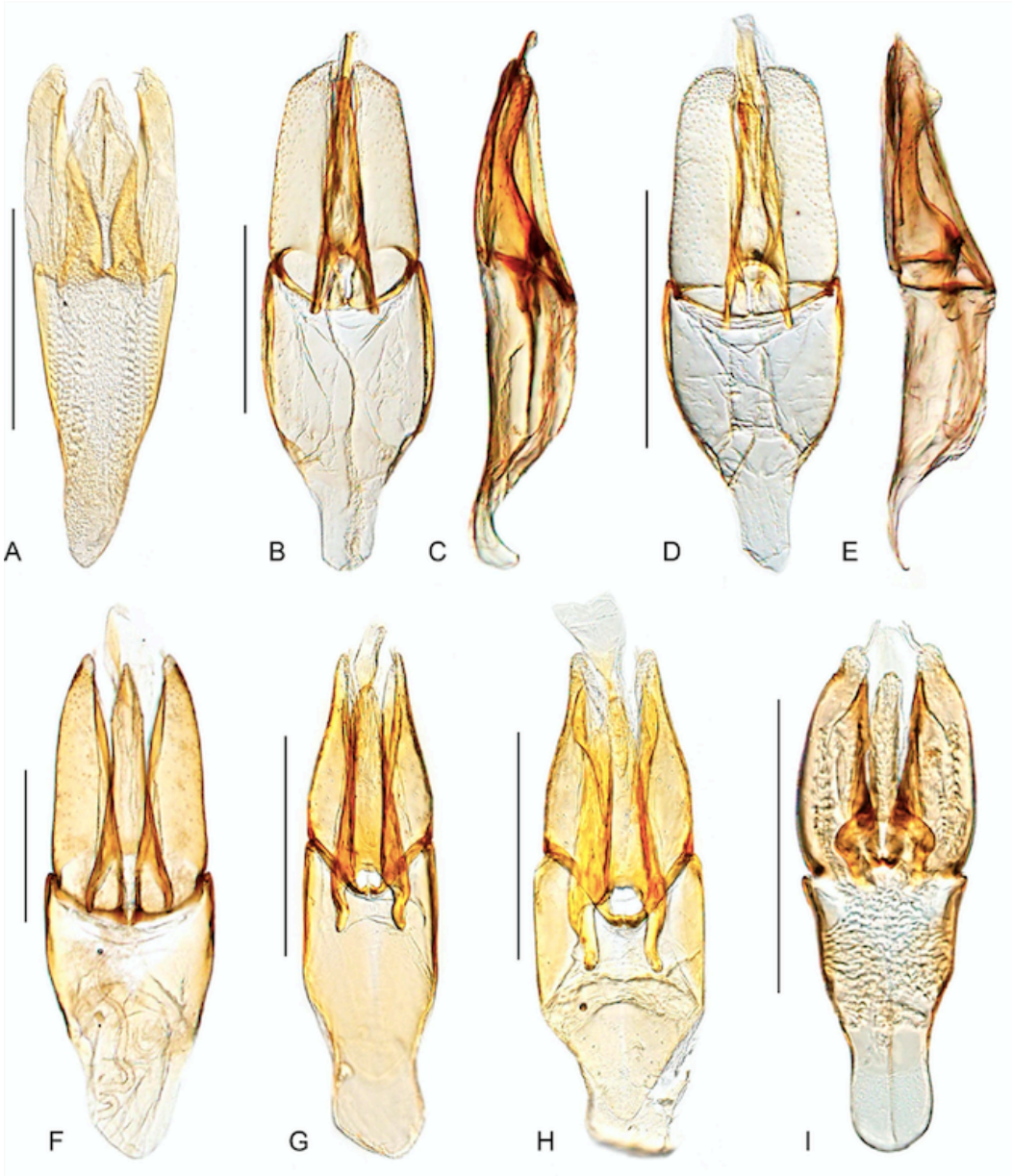


Figure 3.47. Aedeagus of *Primocerus* spp.: **A** *P. neutrum*, **B, C** *P. maipure*: **B** dorsal view **C** lateral view, **D, E** *P. pijiguaense*: **D** dorsal view, **E** lateral view, **F** *P. gigas*, **G** *P. petilus*, **H** *P. striatolatus*, **I** *P. cuspidis*. Scale bars 0.25 mm.

Taxonomic history. *Primocerus* was only recently described.

Distribution. Neotropical: Brazil (Pará), Guyana, Suriname, and Venezuela.

Natural history. The habitats occupied by members of *Primocerus* range from forested pools to seepages. Only one specimen has been collected with a flight intercept trap. Specimens of *Primocerus* are relatively rare, given that so far have only been found in low numbers of specimens per collecting event (Girón and Short 2019).

Larvae. Immature stages are not known for *Primocerus*.

Remarks. *Primocerus* is one of the most variable genera of New World acidocerines in terms of their external morphology. There are nine known species in the genus.

Species examined. Holotypes and paratypes of all known species were examined for this study.

Selected references. Girón and Short (2019): original description of the genus and all its known species.

Genus *Quadriops* Hansen, 1999

(Figs 3.2F, 3.6, 3.9C, 3.48, 3.49)

Quadriops Hansen, 1999a: 131

Gender. Masculine.

Type species. *Quadriops depressus* Hansen, 1999a: 136; by original designation.

Diagnosis. Small to very small beetles, body length 1.6–2.6 mm. Body shape oval in dorsal view; moderate to strongly convex in lateral view, dorsal outline evenly convex or nearly straight along median region (Fig. 3.48). Color orange brown to dark brown, uniform along body regions; ground punctation shallow to moderately marked. Shape of head somewhat rectangular. Frons lateral and posteriorly expanded, forming canthus completely dividing eyes in dorsal and ventral portions (see Fig. 3.9C). Eyes very small in dorsal view. Clypeus laterally expanded in front and around outer margin of eyes; anterior margin of clypeus straight. Labrum partly exposed. Mentum rather smooth and medially depressed; median anterior depression marked by a transverse carina. Antennae with nine antennomeres, cupule slightly asymmetric with rounded outline. Maxillary palpi rather short and stout, nearly half as long as width of head; maxillary palpomere 4 slightly longer than palpomere 3; inner margin of maxillary palpomere 2 straight to convex, outer margin strongly curved along apical two thirds. Elytra without sutural striae, with punctures either irregularly distributed or forming well defined longitudinal rows; elytra narrowly explanate anteriorly, explanation gradually broader towards apex. Posterior elevation of mesoventrite, usually with well-defined transverse ridge, seldom with acute tooth; anapleural sutures concave, separated at anterior margin by distance nearly 0.7 × width of anterior margin of mesepisternum. Metaventrite uniformly densely pubescent. Protibiae with spines of anterior row hair-like, semi erect, relatively long and thick; apical spurs of protibia moderately stout, reaching apex of protarsomere 3. All tarsomeres with thick hair-like spines on ventral face of tarsomeres 2–4; metatarsomeres 1–4 similar in length, 5 nearly as long as 3–4 combined.

Metafemora with tibial grooves moderately developed; anterior surface of metafemora mostly glabrous, with few very scattered small setae. Fifth abdominal ventrite apically rounded and without fringe of stout setae. Aedeagus trilobed (Fig. 3.49), with basal piece about half length of parameres; median lobe wider than base of each paramere, with narrow, triangular, longitudinal sclerite, usually extending along apical third; parameres as long as, to longer than median lobe, and nearly half as wide; gonopore preapically situated; basal piece with lateral margins straight to sinuate, apically slightly diverging.

Differential diagnosis. *Quadriops* is the only known acidocerine with fully divided eyes. Species with uniformly distributed punctures along the elytra may resemble *Globulosis*, but the moderate punctation of *Quadriops* is very evident (punctation only shallowly marked in *Globulosis*; see Fig. 3.31). Some species of *Tobochares* have nearly divided eyes, and lack impressed striae along the elytra, resembling species of *Quadriops* with uniformly distributed punctures along the elytra, but they differ in the shape of the posterior elevation of the mesoventrite (sharply elevated as a tooth or a blunt transverse carina in *Quadriops*, medially bulging in *T. canthus* Kohlenberg and Short).

Taxonomic history. Hansen (1999a) described the genus with five species, differentiated mostly in the presence and degree of impression of reticulation on the head and clypeus. García (2000b) described an additional species from Venezuela. The genus was revised by Girón and Short (2017): two species were synonymized with *Quadriops depressus* Hansen; two new species were described.

Figure 3.48. Habitus of *Quadriops* spp.: **A–C** *Q. acroreius*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus, **D–F** *Q. clusia*: **D** dorsal habitus, **E** lateral habitus, **F** ventral habitus. Scale bars 1 mm.

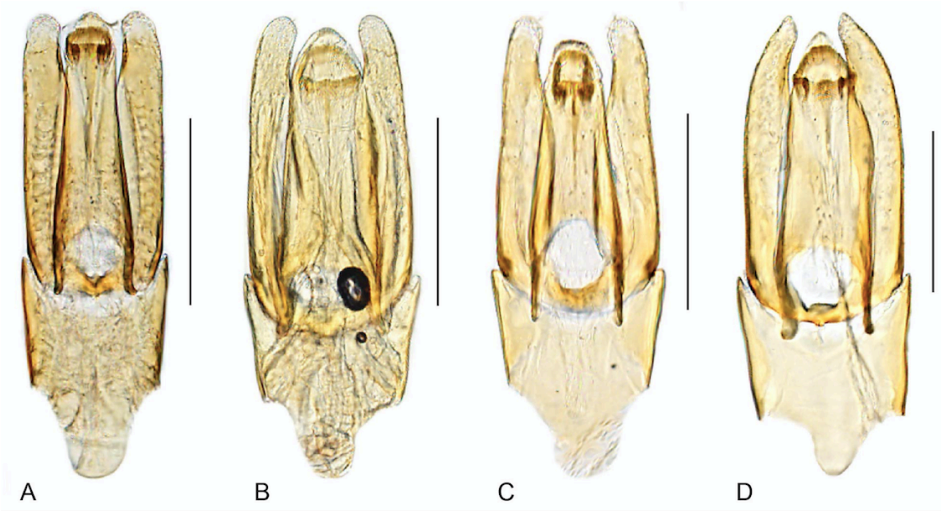


Figure 3.49. Aedeagus of *Quadriops* spp.: **A** *Q. clusia*, **B** *Q. depressus*, **C** *Q. reticulatus*, **D** *Q. similaris*. Scale bars 0.1 mm.

Distribution. Neotropical: Brazil (Amazonas), Costa Rica, Ecuador, French Guiana, Guyana, Panama, Peru, Suriname, Venezuela.

Natural history. Specimens have been caught using flight intercept traps, many long series have been collected on decaying *Clusia* fruits, which can be somewhat used as bait. Additional specimens have been collected in rotten logs, sap flows on freshly cut trees, and in the refuse piles of leafcutter ants (Girón and Short 2017).

Larvae. The immature stages of *Quadriops* remain unknown.

Remarks. *Quadriops* is the only fully terrestrial genus of Acidocerines in the New World. There are six described species within the genus.

Species examined. *Quadriops acroreius* Girón and Short (holotype and paratype), *Q. clusia* Girón and Short (holotype, paratypes and additional specimens), *Q. dentatus* Hansen (holotype and additional specimens), *Q. depressus* Hansen (holotype and additional specimens), *Q. reticulatus* Hansen (holotype and additional specimens), *Q. similaris* Hansen (holotype and additional specimens).

Selected references. Hansen (1999a): original description. García (2000b): description of one additional species from Venezuela. Girón and Short (2017): generic revision including two synonimies and two new species.

Genus *Radicitus* Short and García, 2014

(Figs 3.1K, 3.4, 3.50, 3.51)

Radicitus Short and García, 2014: 252

Gender. Masculine.

Type species. *Radicitus ayacucho* Short and García, 2014: 252; by original designation.

Diagnosis. Medium sized beetles, body length 4.5–6.2 mm. Body shape oval in dorsal view; moderate to strongly convex in lateral view; dorsal outline nearly straight and anteriorly inclined along anterior half (Fig. 3.50). Color dark brown, usually uniform along body regions, sometimes margins of pronotum and elytra slightly paler; ground punctation fine, moderately

marked. Shape of head trapezoid and rather wide. Eyes moderate in size, not emarginated anteriorly, slightly projected from outline of head. Clypeus trapezoid, with anterior margin broadly, roundly and weakly emarginate. Labrum fully exposed. Mentum rather medially broadly depressed, laterally longitudinally elevated; median anterior depression marked by transverse nearly straight carina. Antennae with nine antennomeres; cupule slightly asymmetric, with rounded outline. Maxillary palpi short and stout, nearly as long as half width of head; inner margin of maxillary palpomere 2 nearly straight, outer margin strongly curved along apical 2/3; maxillary palpomere 4 slightly shorter than 3. Prosternum flat, only slightly carinate along midline of anterior projection. Elytra without sutural striae; elytral punctures shallow to moderately marked; ground punctures rather uniformly distributed; some species with serial punctures clearly visible along posterior third of elytra; outer margins of elytra slightly flared. Posterior elevation of mesoventrite with median longitudinal carina elevated and forming posteriorly pointing process; anapleural sutures strongly concave, separated at anterior margin by distance nearly half width of anterior margin of mesepisternum. Metaventrite sometimes with posteromesal glabrous patch. Protibiae with anterior row of spines completely reduced; apical spurs of protibiae stout, reaching apex of protarsomere 3. Metafemora with tibial grooves very sharply marked and covered by hydrofuge pubescence; hydrofuge pubescence along dorsal half on basal three-quarters of anterior surface. Tarsomeres 1–4 with long spiniform setae on ventral face; metatarsomere 2 nearly as long as 5 and as 3–4 combined. Fifth abdominal ventrite evenly rounded, without apical emargination or fringe of stout setae. Aedeagus either trilobed (Fig. 3.51E–H) or divided (Fig. 3.51A–D), with basal piece short and rather simple parameres separated from each other for most of their length; gonopore well developed.

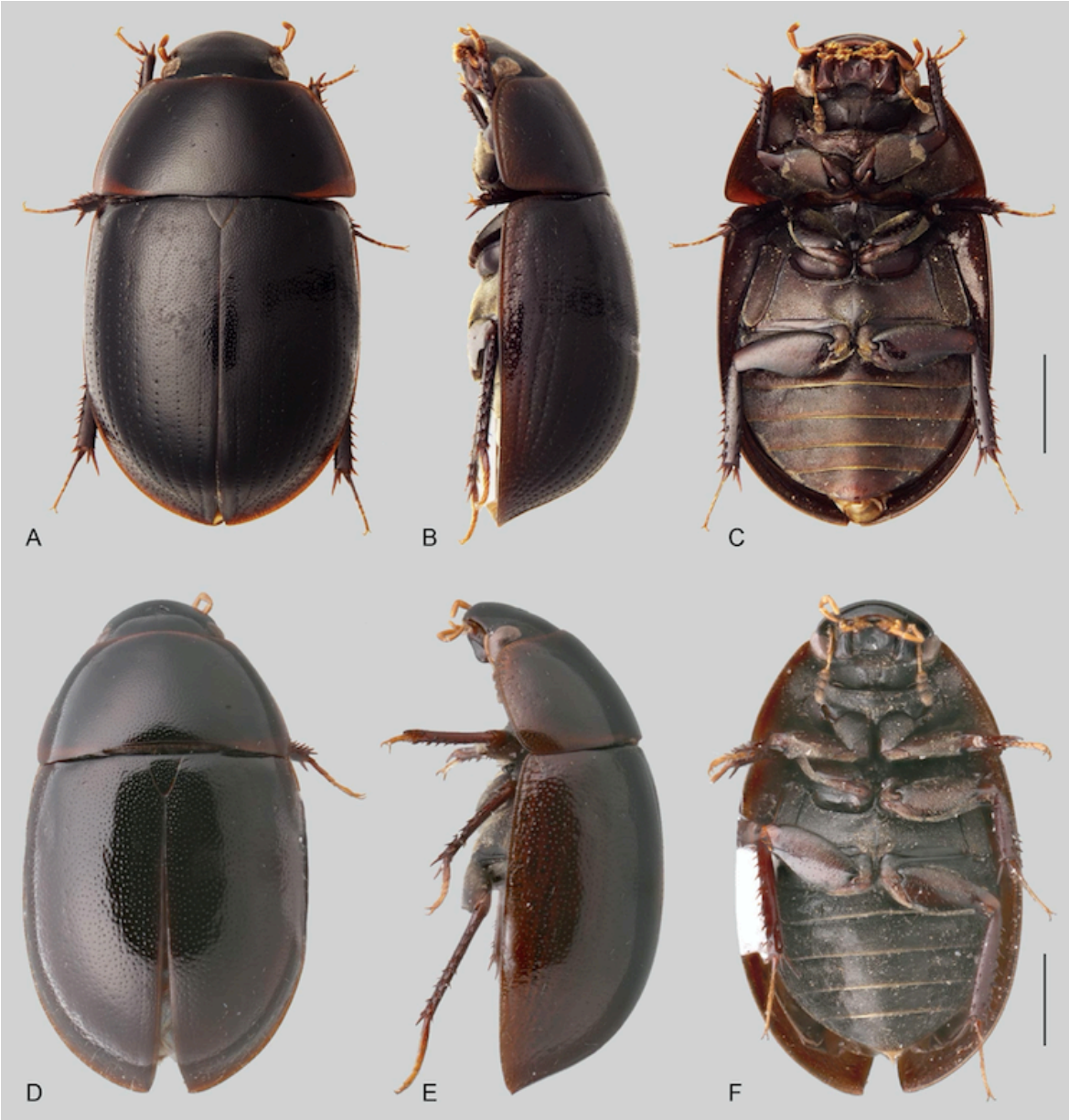


Figure 3.50. Habitus of *Radicitus* spp.: A–C *R. ayacucho*: A dorsal habitus, B lateral habitus, C ventral habitus, D–F *R. granitum*: D dorsal habitus, E lateral habitus, F ventral habitus. Scale bars 1 mm.

Differential diagnosis. *Radicitus* may resemble some punctate *Novochares* but can be recognized by the short and stout maxillary palpi along with only partly covered metafemora (long and slender maxillary palpi with mostly covered metafemora in *Novochares*).

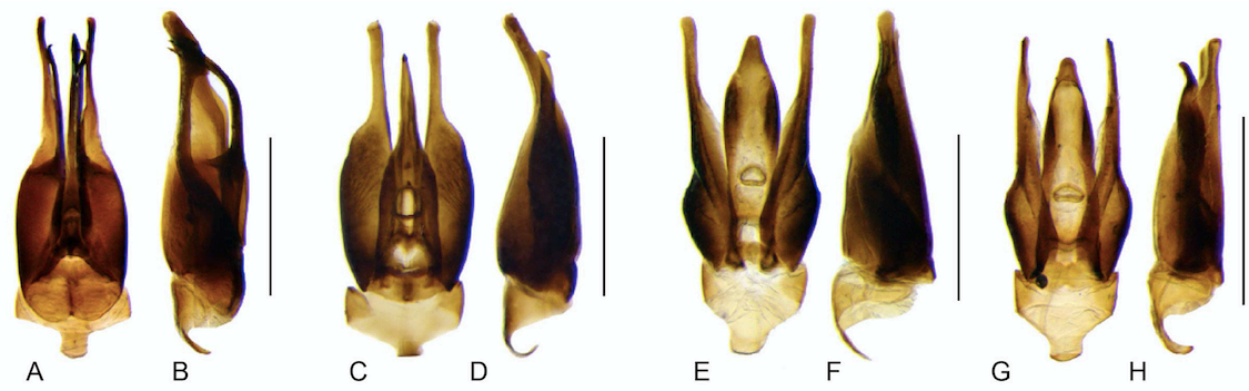


Figure 3.51. Aedeagus of *Radicitus* spp.: **A, B** *R. ayacucho*: **A** dorsal view, **B** lateral view, **C, D** *R. surinamensis*: **C** dorsal view, **D** lateral view, **E, F** *R.* cf. *granitum* (Suriname): **E** dorsal view, **F** lateral view, **G, H** *R. granitum* (Venezuela): **G** dorsal view, **H** lateral view. Scale bars 0.5 mm.

Taxonomic history. *Radicitus* was only recently described.

Distribution. Neotropical: Suriname, Venezuela.

Natural history. Species of *Radicitus* have been found on a variety of habitats associated with streams and seeps on rock outcrops. Some have been collected by submerging root mats found along streams, and in the roots of vegetation growing on seepage areas on granite outcrops (Short and García 2014).

Larvae. The immature stages of *Radicitus* remain unknown.

Remarks. There are three known species of *Radicitus*, all currently endemic to the Guiana Shield.

Selected references. Short and García (2014): original description of the genus and all known species.

Genus *Sindolus* Sharp, 1882

(Figs 3.4, 3.21D, 3.52)

Sindolus Sharp, 1882: 72

Helochares (*Sindolus*) Sharp; d'Orchymont 1919c: 148; Knisch 1924: 199; Hansen 1999b: 158.

Gender. Masculine.

Type species. *Sindolus optatus* 1882: 72; by subsequent designation (Hansen 1991: 292).

Diagnosis. Small to medium sized beetles, body length 2.5–5.0 mm. Body shape oval in dorsal view, moderately to strongly convex in lateral view (Fig. 3.52); dorsal outline usually evenly curved. Dorsal surfaces even and smooth, yellowish, orange brown to brown and rather uniform in coloration; ground punctation fine and extremely shallow. Shape of head trapezoid. Eyes not emarginate, moderate to relatively large in size, subquadrate, separated by nearly 5 × width of eye, only slightly projected from outline of head. Clypeus trapezoid, with anterior margin broadly and slightly emarginate. Labrum fully exposed, convex and anteriorly emarginate. Mentum rather flat, with few shallow transverse crenulations on anterior region; median anterior depression relatively shallow, sometimes marked by transverse carina. Submentum

smooth to very shallowly sculptured. Antennae with nine antennomeres, with strongly asymmetric and round cupule; antennomere 9 nearly 3 × longer than antennomere 8. Maxillary palpi slender, 1.2–1.5 × longer than maximum width of head; inner margin of maxillary palpomere 2 usually evenly weakly curved, outer margin curved along apical third; palpomere 4 nearly 0.8 × as long as palpomere 3. Pronotum evenly convex, usually with systematic punctures forming distinct anterolateral semicircles. Elytra without sutural striae, with margins only slightly flared; serial punctures absent; scarce systematic punctures, bearing moderately long setae. Surface of prosternum somewhat longitudinally elevated, sometimes with low and blunt longitudinal carina; anterior margin acutely to roundly projected anteriorly. Posterior elevation of mesoventrite with sharp and strongly elevated (laminar) longitudinal carina, extending at full height along its entire length; anapleural sutures concave, separated at anterior margin by distance nearly half width of anterior margin of mesepisternum. Metaventrite densely and uniformly covered by hydrofuge pubescence. Protibiae with anterior row of spines reduced (short appressed spines) to extremely reduced (tiny denticles); apical spurs of protibiae moderate, broad and reaching apex of protarsomere 2. Metafemora with tibial grooves sharply marked, and hydrofuge pubescence covering at least basal four fifths of anterior surface. Metatarsomere 2 slightly shorter or similar in length to metatarsomere 5, metatarsomere 2 similar in length to metatarsomeres 3 and 4 combined; ventral surface of all tarsomeres with long setiform setae on ventral surface (tarsomeres 1 and 2 with small stout spines). Abdomen with five pubescent ventrites. Fifth abdominal ventrite emarginate at apex; emargination fringed by stout setae. Aedeagus subdivided (Fig. 3.21D), somewhat pear-shaped, with basal piece nearly 0.3 × length of parameres; parameres slender, narrowing apically, with outer margins at

least slightly sinuated, usually apically rounded; median lobe divided into dorsal and ventral plates; dorsal plate of median lobe medially bifurcate, with narrow, slender and apically rounded lobes; ventral lobe of median lobe varying in width and length, usually very lightly sclerotized; gonopore well-developed, usually positioned at midlength of aedeagus.

Differential diagnosis. *Sindolus* is the only known genus of acidocerines that bears a sharp and strongly elevated (laminar) longitudinal carina.

Figure 3.52. Habitus of *Sindolus optatus*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus. Scale bar 1 mm.

Taxonomic history. Originally described as a genus by Sharp (1882) to accommodate two species from Central America; downgraded to subgenus of *Helochares* by d'Orchymont (1919c: 148); Hansen (1991): designates type species.

Distribution. Neotropical: Argentina, Bolivia, Brazil (Amazonas, Mato Grosso do Sul, Rio de Janeiro, Rio Grande do Sul), Colombia [in doubt; see d'Orchymont, 1943d: 56], French Guiana [in doubt; see d'Orchymont, 1943d: 56], Guatemala, Lesser Antilles (Antigua), Mexico, Nicaragua, Paraguay, Uruguay.

Natural history. *Sindolus mundus* Sharp and *S. optatus* Sharp have been collected in stagnant waters at low elevations in dry areas; both species have been collected at mercury vapor lights in a drying lowland marsh where *S. optatus* Sharp was extremely abundant (Short 2005). The annual life cycle and the spatial and temporal distribution of a population of *S. femoratus* in Argentina were studied by Fernández and Kehr (1994, 1995, respectively).

Larvae. Immature stages are known for *Sindolus talarum* (Fernández) (as *Helochares* (*Sindolus*) *talarum*); egg case, first, second and third instar larvae and pupae were all described and illustrated by Fernández (1983). From each egg case between 25 and 40 larvae emerged; some larvae perforated and entered the aerenchyma of *Spirodella intermedia* (Araceae) and spent some time in there, apparently breathing the air stored in the plant tissues (Fernández 1983). In Argentina (Buenos Aires Province) first instar larvae start appearing in September, become abundant in October, and in November and the first two months of the summer all

larval stages are abundant; at the end of March third instar larvae are the most common. Fernández (2004) also described the egg case and third instar larva of *Sindolus femoratus* (Brullé) (as *Helochares* (*Sindolus*) *femoratus*).

Remarks. There are eight Species of *Sindolus* described. The genus is among the most easily recognized acidocerines in the New World.

Species examined. *Sindolus femoratus* (Brullé), *S. mundus* Sharp, *S. optatus* Sharp. One of the available specimens of *S. mundus* had been previously compared with the holotype by A. Short.

Selected references. Sharp (1882): original description of the genus and two species. Fernández (1981): description of two new species. Fernández (1983): description of immature stages for *Sindolus talarum* (Fernández). Fernández (2004): description of immature stages for *Sindolus femoratus* (Brullé).

Genus *Tobochares* Short and García, 2007: 2

(Figs 3.2H, 3.I, 3.6, 3.9A, 3.B, 3.53, 3.54)

Subgenus *Tobochares* Short and García, 2007: 2

Type species: *Tobochares sulcatus* Short and García, 2007: 4; by original designation.

Subgenus *Araiokris* Girón and Short (in prep.)

Type species: *Tobochares* (*Araiokris*) *luteomargo* Girón and Short (in prep.); by original designation.

Subgenus *Tobocharoides* Girón and Short (in prep.)

Type species: *Tobochares* (*Tobocharoides*) *communis* Girón and Short (in prep.); by original designation.

Gender. Masculine.

Type species. *Tobochares sulcatus* Short and García, 2007: 4; by original designation.

Diagnosis. Small beetles, total body length 1.5–2.6 mm. Body shape oval in dorsal view; moderately to strongly convex in lateral view (see Fig. 3.53); dorsal outline usually evenly curved. Color yellowish brown, orange brown to dark brown, sometimes with paler spots on head, or paler margins of pronotum and elytra; ground punctation moderate to shallow. Shape of head somewhat oval. Eyes not emarginate to strongly emarginate, moderate to small in size, somewhat oval, slightly to strongly projected from outline of head. Clypeus trapezoid, with anterior margin broadly emarginate; membranous preclypeal area often visible. Labrum fully exposed, convex and anteriorly emarginate. Mentum rather smooth, often medially depressed, or anteriorly shallowly crenulated; median anterior depression marked by transverse carina. Submentum anteriorly smooth and shiny. Antennae with eight antennomeres, cupule slightly asymmetric with rounded outline. Maxillary palpi from short and slender (slightly shorter than the width of the head) to very short and stout (nearly half the width of the head); maxillary palpomere 4 similar in length to slightly longer than palpomere 3; inner margin of maxillary

palpomere 2 straight, outer margin strongly curved along apical two thirds. Elytra without sutural striae (in some species, stria 1 more strongly impressed along posterior half of elytra); elytral punctures seemingly arranged in rows, in some species more pronounced; interserial punctures occasionally longitudinally aligned; serial punctures sometimes impressed into distinct grooves. Prosternum flat. Posterior elevation of mesoventrite either flat, bulging or with transverse or longitudinal ridge (Fig. 3.11F, G); anapleural sutures concave, separated at anterior margin by distance nearly 0.3–0.5 × width of anterior margin of mesepisternum. Metaventrite densely pubescent, except for median glabrous patch, either ovoid and broad or longitudinal and narrow. Protibiae with spines of anterior row hair-like, semi erect, relatively long and thick; apical spurs of protibia from very short and stout, to enlarged to reach apex of protarsomere 3. Tarsomeres 2–4 densely covered by hair-like spines on ventral face; metatarsomeres 1–4 similar in length, 5 nearly as long as 3–4 combined, or metatarsomere 2 similar in length to 5. Metafemora mostly glabrous, with only few scattered setae, sometimes with hydrofuge pubescence along basal half of anterodorsal margin. Fifth abdominal ventrite apically evenly rounded, without fringe of stout setae. Aedeagus trilobed (Fig. 3.54), with basal piece usually very short (nearly one third length of parameres); median lobe usually broader than each paramere; median lobe and parameres apically rounded to truncate; gonopore well developed.

Differential diagnosis. *Tobochares* are among the smaller acidocerines. Some members of the group are unique in the presence of impressed elytral striae. *Tobochares* without elytral striae may resemble some *Agraphydrus* (with eight antennomeres and mostly glabrous femora), and other than their distributions (*Tobochares* in the New World, *Agraphydrus* in the Old World)

and slight differences in overall body shape, they can only be differentiated by the shape of the aedeagus (slender in *Tobochares* (see Fig. 3.54); overall broader in *Agraphydrus* (see Fig. 3.17)).

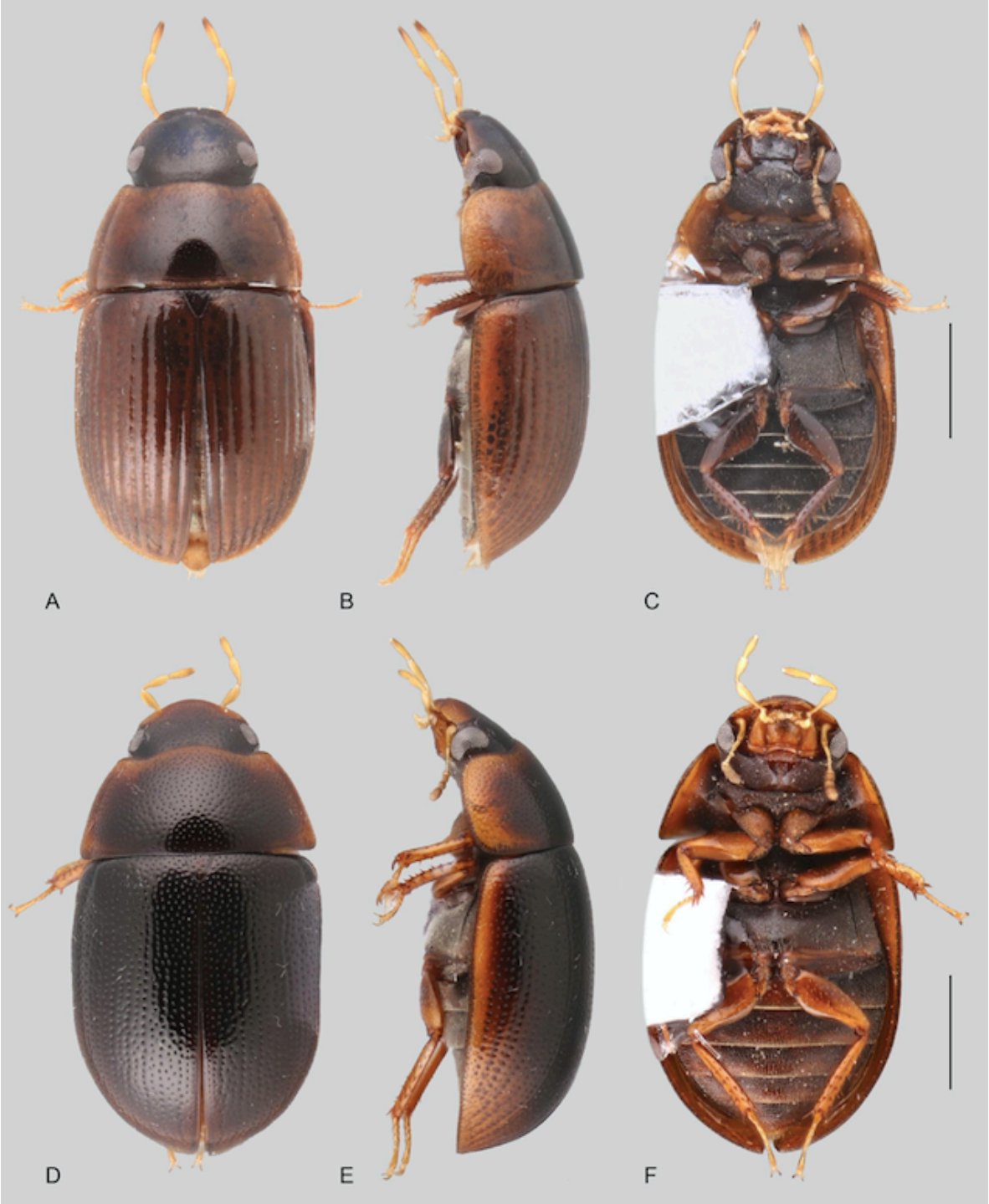


Figure 3.53. Habitus of *Tobochares* spp.: **A–C** *T. sulcatus*: **A** dorsal habitus, **B** lateral habitus, **C** ventral habitus, **D–F** *T.* sp.: **D** dorsal habitus, **E** lateral habitus, **F** ventral habitus. Scale bars 0.5 mm.

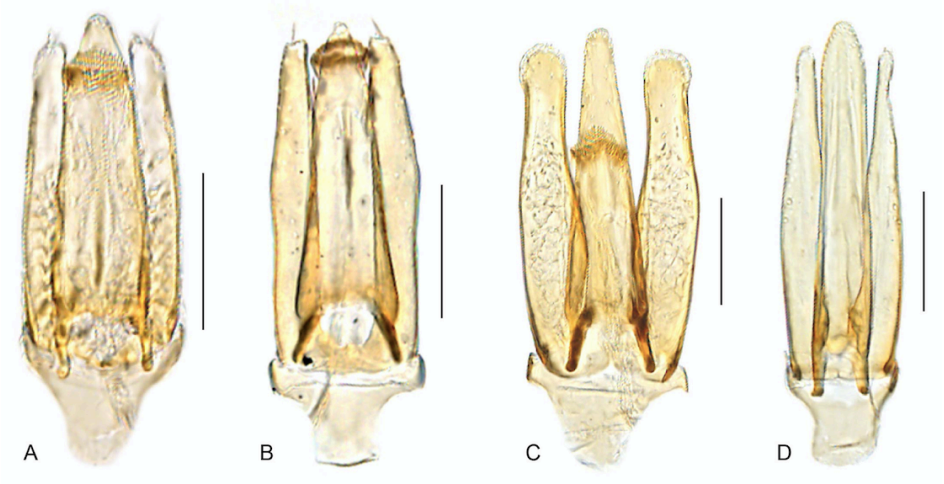


Figure 3.54. Aedeagus of *Tobochares* spp.: **A** *T. canthus*, **B** *T. emarginatus*, **C** *T. kusad*, **D** *T. kasikasima*. Scale bars 0.1 mm.

Taxonomic history. Short and García (2007) described the genus and one species from Venezuela. Additional species were described from Suriname, one by Short and Kadosoe (2011) and two more by Short (2013). The genus was revised by Kohlenberg and Short (2017), including the description of five new species and the characterization of one specimen from Tobogán de la Selva (Venezuela) left undescribed until additional material can be studied.

Distribution. Neotropical: Brazil (Amazonas, Goiás, Roraima), Guyana, Suriname, Venezuela.

Natural history. Most *Tobochares* specimens have been collected at hygropetric habitats (see Kohlenberg and Short 2017).

Larvae. The immature stages of *Tobochares* remain unknown.

Remarks. There are eight described species of *Tobochares*. The genus is rather highly variable in its external morphology: there is variation in coloration, the degree of emargination of the eyes and the degree of development and extension of the elytral striae.

Species examined. Holotypes, paratypes, and additional specimens of all the species were examined for this study.

Selected references. Short and García (2007): original description of the genus and its type species; Short and Kadosoe (2011): description of one additional species; Short (2013): description of two additional species; Kohlenberg and Short (2017): revision of the genus and description of five new species.

Genus *Troglochares* Spangler, 1981

Troglochares Spangler, 1981a: 316

Gender. Masculine.

Type species. *Troglochares ashmolei* Spangler, 1981a: 318; by original designation and monotypy.

Diagnosis. Small beetles, body length 1.9 mm. Body shape oval in dorsal view; moderately convex in lateral view (see fig. 39 in Hansen 1991). Color yellowish light brown; ground punctation extremely shallowly marked. Shape of head trapezoid. Eyes absent. Clypeus trapezoidal, with anterior margin broadly emarginate, with medial region of emargination nearly straight. Labrum fully exposed, convex. Mentum rather smooth and antero-medially depressed; median anterior depression broad. Antennae with nine antennomeres (see fig. 3 in Spangler 1981a); cupule slightly asymmetric, with rounded outline. Maxillary palpi slender, nearly as long as width of head; inner margin of maxillary palpomere 2 nearly straight, outer margin curved along apical third; maxillary palpomere 3 slightly shorter than 4. Prosternum non carinate, slightly convex. Elytra without sutural striae; ground punctation fine shallow; outer margins slightly flared. Posterior elevation of mesoventrite with curved, transverse ridge (see fig. 8 in Spangler 1981a); anapleural sutures concave, separated at anterior margin by distance 0.7 × width of anterior margin of mesepisternum. Metaventrite densely pubescent except for median short and narrow posterior glabrous patch; metaventrite short (nearly as long as first abdominal ventrite; see fig. 8 in Spangler 1981a). Protibiae with spines of anterior row long; apical spurs of protibiae moderately slender, reaching apex of protarsomere 2; metatarsomeres 2–4 slightly decreasing in size; metatarsomere 5 nearly as long as 2–4 combined. Posterior femora densely covered by hydrofuge pubescence along basal two thirds (see fig. 8 in Spangler 1981a). Fifth abdominal ventrite apically truncate, without stout setae (see fig. 9 in Spangler 1981a).

Differential diagnosis. *Troglochares* is the only genus of acidocerines (and Hydrophilids) lacking eyes.

Taxonomic history. The genus and its only known species were described by Spangler (1981a).

Distribution. Neotropical: Ecuador.

Natural history. The only known specimen was collected in a cave on calcite formations and is presumably aquatic (Spangler 1981a).

Larvae. The immature stages are unknown for *Troglochares*.

Remarks. The genus is only known from a single female specimen, which is pin-mounted in pieces.

Species examined. The holotype specimen of *Troglochares ashmolei* Spangler was examined.

Selected references. Original description by Spangler (1981a).

Catalog of the subfamily Acidocerinae

The following species list is based for the most part on Hansen (1999b), and therefore follows its format. Species described between 1999 and November 2019 have been added to the present catalog. Generic synonyms are omitted here as those are listed for each genus above. For each species the currently valid name is provided, followed by the original name with a reference to the original description, including page number and full type locality as provided in the original publication. For countries which current names are different from those indicated in the original description the name of the country has been updated, leaving in square brackets the country names that have been previously cited (e.g., Sri Lanka [Ceylon]).

For each name that has been used, a list of references including page number and details on the nature/content of the reference in square brackets (e.g., [catalog], [checklist], [new record], etc.) is also provided. 'Catalog' refers to publications listing synonyms and references, whereas 'checklist' only presents the name of a species for a particular region. 'Faunistic treatment' is used for works revising the fauna of a particular country or region, which sometimes include discussions on taxonomic status of certain species, whereas 'taxonomic treatment' is used when the reference includes a taxonomic revision for a particular group. 'New record' is used for new country records, as opposed to new localities from a previously recorded country. The currently known distribution (extracted from the literature) is summarized for each valid name.

Acidocerus Klug, 1855

Acidocerus aphodioides Klug, 1855

Acidocerus aphodioides Klug, 1855: 649 - Mozambique, Tete ["Mossambique: Tette"]; Knisch 1924: 222 [catalog]; Hansen 1999b: 158 [catalogue]; Hebauer 2006a: 25 [checklist].

DISTRIBUTION. Afrotropical: Mozambique.

Agraphydrus Régimbart, 1903

Agraphydrus activus Komarek and Hebauer, 2018

Agraphydrus activus Komarek and Hebauer, 2018: 18 - China, Hong Kong Admin. Reg., New Territories, Tai Mo Shan Country Park, SW Tai Po New Town, Lam Tsuen River; Komarek 2019: 157 [new record].

DISTRIBUTION: Indo-Malayan: China (Fujian, Hong Kong, Guangdong, Jiangxi). Palearctic: China (Anhui), Thailand.

Agraphydrus agilis Komarek and Hebauer, 2018

Agraphydrus agilis Komarek and Hebauer, 2018: 20 - China, Guangxi Province, Liuzhou Prefecture, 10 km N Liuzhou City, ca. 2 km E Shanmenjiang Forest Station; Komarek 2019: 158 [taxonomic treatment].

DISTRIBUTION: Indo-Malayan: China (Guangxi, Yünnan), Vietnam.

Agraphydrus albescens (Régimbart, 1903)

Helochares albescens Régimbart, 1903a: 27 - Madagascar, "Centre-Sud".

Helochares (s. str.) *albescens* Régimbart; Knisch 1924a: 196 [catalog].

Helochares (*Agraphydrus*) *albescens* Régimbart; d'Orchymont 1939c: 198 [taxonomic discussion; new record].

Agraphydrus (*Agraphydrus*) *albescens* (Régimbart); Hansen 1999b: 156 [new combination; catalog]; Hebauer 2006a: 27 [checklist, new records].

DISTRIBUTION: Afrotropical: Madagascar, Malawi, Namibia, Sudan, Tanzania [Zanzibar], Zimbabwe.

Agraphydrus anacaenoides Komarek, 2019

Agraphydrus anacaenoides Komarek, 2019: 158 - Malaysia, Penang, Southwest Penang Island District, Pantai Aceh Forest Reserve (= Penang N.P.).

DISTRIBUTION: Indo-Malayan: Malaysia.

Agraphydrus anatinus Komarek, 2018

Agraphydrus anatinus Komarek, 2018: 107 - India, Goa, South Goa District, Salcete (= Salcette or Saxti) Subdivision.

DISTRIBUTION: Indo-Malayan: India (Goa, Kerala, Maharashtra).

Agraphydrus andamanicus Komarek, 2018

Agraphydrus andamanicus Komarek, 2018: 108 - India, North Andaman Island, Diglipur.

DISTRIBUTION: Indo-Malayan: India (North Andaman Island).

Agraphydrus angulatus Komarek, 2019

Agraphydrus angulatus Komarek, 2019: 159 - Laos, Khammouan Province, Nakai District, Nakai, 17°43'N 105°09'E.

DISTRIBUTION: Indo-Malayan: Laos.

Agraphydrus angustipenis Komarek, 2018

Agraphydrus angustipenis Komarek, 2018: 109 - Sri Lanka, “Dambuwa Estate”.

DISTRIBUTION: Indo-Malayan: Sri Lanka.

Agraphydrus anhuianus (Hebauer, 2000)

Megagraphydrus anhuianus Hebauer, 2000: 15 - China, Anhui, Huang Shan 30 km W Tunxi. Hansen 2004: 52 [catalog]; Short and Hebauer 2006: 337 [catalog]; Fikáček et al. 2015: 62 [catalog].

Agraphydrus (*Agraphydrus*) *anhuianus* (Hebauer); Minoshima et al. 2015: 12 [new combination; redescription; new record].

Agraphydrus anhuianus (Hebauer); Komarek and Hebauer 2018: 21 [excludes only known specimen from Hong Kong].

DISTRIBUTION: Indo-Malayan: Thailand. Palearctic: China (Anhui).

Agraphydrus annapurnensis Komarek, 2018

Agraphydrus annapurnensis Komarek, 2018: 110 - Nepal, Western Region, Gandaki Zone, Kaski District, Annapurna Mountains, ca. 10 km ENE Pokhara, tributary of Madi Khola River below Kwinkal (village), ca. 28°13'55"N 84°5'16"E.

DISTRIBUTION: Indo-Malayan: Nepal.

Agraphydrus arduus Komarek and Hebauer, 2018

Agraphydrus arduus Komarek and Hebauer, 2018: 22 - China Yünnan Prov., Xishuangbanna Dai Autonomous Prefecture, Mengla County, Wushiwu He River, ca. 10 km NW Menglun Town; Komarek 2019: 160 [new record].

DISTRIBUTION: Indo-Malayan: China (Guangdong, Yünnan), Laos. Palearctic: China (Hubei).

Agraphydrus ater Komarek, 2018

Agraphydrus ater Komarek, 2018: 111 - Nepal, Western Region, Gandaki Zone, Annapurna, N Pokhara, Kali Khola, below Garlang, ca. 28°17'10"N 83°59'39"E.

DISTRIBUTION: Indo-Malayan: Nepal.

Agraphydrus attenuatus (Hansen, 1999)

Megagraphydrus attenuatus Hansen, 1999a: 141 - Vietnam, Vĩnh Phúc Province (N Viertnam), Tam Dao. Hansen 1999b: 157 [catalog]; Hebauer 2000: 15 [taxonomic treatment].

Agraphydrus (*Agraphydrus*) *attenuatus* (Hansen); Minoshima et al. 2015: 16 [new combination; redescription; new records].

Agraphydrus attenuatus (Hansen); Komarek and Hebauer 2018: 23 [redescription]; Komarek 2019: 161 [taxonomic treatment].

DISTRIBUTION: Indo-Malayan: China (Yünnan), Laos, Vietnam.

Agraphydrus audax Komarek and Hebauer, 2018

Agraphydrus audax Komarek and Hebauer, 2018: 24 - China Hunan Prov., Xiangxi Prefecture; Dayong County; Zhangjiajie Forest National Park, Suoxiyü Nature Reserve, Wulingyüan section, 30 km N Dayong City.

DISTRIBUTION: Indo-Malayan: China (Guizhou, Hunan). Palearctic: China (Hubei, Shaanxi, Sichuan).

Agraphydrus avita (Hansen, 1997) **comb. n.**

Horelophopsis avita Hansen, 1997: 109 - Indonesia, Papua [New Guinea; Irian Jaya], Japen Island, SSE Sumberbaba, Dawai R. Hansen 1999b: 68 [catalog].

DISTRIBUTION: Australasian: Indonesia (Papua (Yapen Island)).

Agraphydrus bacchusi Komarek, 2019

Agraphydrus bacchusi Komarek, 2019: 162 - Papua New Guinea, Central Province, road between Port Moresby and Brown River.

DISTRIBUTION: Australasian: Papua New Guinea (Central Province).

Agraphydrus balkeorum Komarek, 2019

Agraphydrus balkeorum Komarek, 2019: 163 - West Sumatra Province, Solok Regency, Solok – Alahan Panjang road, ca. 0°56'20''S 100°46'24''E.

DISTRIBUTION: Indo-Malayan: Indonesia (Sumatra).

Agraphydrus bhutanensis Komarek, 2018

Agraphydrus bhutanensis Komarek, 2018: 113 - Bhutan, Sarpang Province, 11 km NW Sarpang, Bhur Khola, 26°55'23''N 90°23'51''E.

DISTRIBUTION: Indo-Malayan: Bhutan.

Agraphydrus biprojectus Minoshima, Komarek, and Ôhara, 2015

Agraphydrus (*Agraphydrus*) *biprojectus* Minoshima, Komarek, and Ôhara, 2015: 36 - Vietnam, Lào Cai Province, Sa Pa, Ô Quy Hồ; Komarek 2019: 164 [taxonomic treatment].

DISTRIBUTION: Indo-Malayan: Laos, Vietnam.

Agraphydrus borneensis Komarek, 2019

Agraphydrus borneensis Komarek, 2019: 165 - Malaysia, Sabah, West Coast Division, Kota Kinabalu District, Crocker Range, km 56 of road Kota Kinabalu – Tambunan, near Sunsuron Waterfall.

DISTRIBUTION: Indo-Malayan: Malaysia (Borneo).

Agraphydrus boukali Komarek, 2018

Agraphydrus boukali Komarek, 2018: 114 - India, Kerala, Thiruvananthapuram District, Cardamom Hills, 50 km NW Pathanamthitta, near Pambaiyar River, ca. 9°25'N 77°05'E.

DISTRIBUTION: Indo-Malayan: India (Kerala, Karnataka, Tamil Nadu).

Agraphydrus brevipenis Komarek, 2019

Agraphydrus brevipenis Komarek, 2019: 167 - Malaysia, Pahang, Cameron Highlands District, Mt. Jasar.

DISTRIBUTION: Indo-Malayan: Malaysia.

Agraphydrus burmensis Komarek, 2019

Agraphydrus burmensis Komarek, 2019: 168 - Myanmar, Mandalay Region, Pyin Oo Lwin District, Mogok Township, NW Mogok, S Panlin village, west slope of Mt. Taung Mae, 22°57'57"N 96°27'29"E.

DISTRIBUTION: Indo-Malayan: Myanmar.

Agraphydrus calvus Komarek and Hebauer, 2018

Agraphydrus calvus Komarek and Hebauer, 2018: 25 - China, Hong Kong Admin. Reg., New Territories, Tai Mo Shan Country Park, SW Tai Po New Town, Lam Tsuen River.

DISTRIBUTION: Indo-Malayan: China (Guangdong, Guangxi, Hong Kong, Jiangxi).

Agraphydrus cantonensis Komarek and Hebauer, 2018

Agraphydrus cantonensis Komarek and Hebauer, 2018: 27 - China, Guangdong Prov., Zhaoqing Pref., Fengkai County, ca. 50 km E of Fengkai, ca. 5 km W of Qixing, Heishiding Nature Reserve, 23°27'04"N 111°53'53"E.

DISTRIBUTION: Indo-Malayan: China (Guangdong).

Agraphydrus carinatulus Komarek, 2019

Agraphydrus carinatulus Komarek, 2019: 169 - Indonesia, East Kalimantan Province, Kutai Kartanegara Regency, Tabang District, ca. 200 km NW of Samarinda City near Ritan Baru village.

DISTRIBUTION: Indo-Malayan: Indonesia.

Agraphydrus cervus Komarek, 2019

Agraphydrus cervus Komarek, 2019: 170 - Malaysia, Sarawak, Kapit Division, Kapit District, ca. 25 km E of Kapit.

DISTRIBUTION: Indo-Malayan: Malaysia (Borneo).

Agraphydrus ceylonensis Komarek, 2018

Agraphydrus ceylonensis Komarek, 2018: 115 - Sri Lanka [Ceylon], Sabaragamuwa Province, Kegalle District, a few km E Kitulgala.

Helochares sp.: Jäch 1984: 243.

DISTRIBUTION: Indo-Malayan: Sri Lanka.

Agraphydrus chinensis Komarek and Hebauer, 2018

Agraphydrus chinensis Komarek and Hebauer, 2018: 27 - China, Fujian Prov., Jianyuan Prefecture, Chong'an City Region, Chong'an Wuyi Shan.

DISTRIBUTION: Indo-Malayan: China (Fujian, Zhejiang). Palearctic: China (Anhui).

Agraphydrus cinnamum Komarek, 2018

Agraphydrus cinnamum Komarek, 2018: 117 - India, Kerala, Thiruvananthapuram District, Cardamom Hills, 50 km NW Pathanamthitta, near Pambaiyar River, ca. 9°25'N 77°05'E.

DISTRIBUTION: Indo-Malayan: India (Kerala).

Agraphydrus clarus Komarek, 2019

Agraphydrus clarus Komarek, 2019: 171 - Malaysia, Sabah, West Coast Division, Kota Kinabalu District, Crocker Range, km 56 of road between Kota Kinabalu and Tambunan, near Sunsuron Waterfall.

DISTRIBUTION: Indo-Malayan: Malaysia (Borneo).

Agraphydrus comes Komarek and Hebauer, 2018

Agraphydrus comes Komarek and Hebauer, 2018: 28 - China, Hainan Prov., Ledong County, foot of Jianfeng Mountain, ca. 4 km E Jianfeng Town.

DISTRIBUTION: Indo-Malayan: China (Hainan).

Agraphydrus communis Komarek, 2018

Agraphydrus communis Komarek, 2018: 118 - Nepal, Central Region, Sindhupalchok District, torrent above Tatobani near Kodari.

DISTRIBUTION: Indo-Malayan: Bhutan, Nepal, India (Uttarakhand).

Agraphydrus confusus Komarek and Hebauer, 2018

Agraphydrus confusus Komarek and Hebauer, 2018: 29 - China, Hong Kong Admin. Reg., Tai Po Kau Nature Reserve; Komarek 2019: 173 [new record].

DISTRIBUTION: Indo-Malayan: China (Guizhou, Hong Kong, Yünnan), Laos, Vietnam.

Agraphydrus conicus Komarek and Hebauer, 2018

Agraphydrus conicus Komarek and Hebauer, 2018: 30 - ChinaJiangxi Prov., Jinggangshan Mountains, Jingzhushan, 26°31.0'N 114°05.9'E.

DISTRIBUTION: Indo-Malayan: China (Hunan, Jiangxi). Palearctic: China (Anhui).

Agraphydrus connexus Komarek and Hebauer, 2018

Agraphydrus connexus Komarek and Hebauer, 2018: 31 - Malaysia, Pahang, Kuala Lipis [Town] surround. Komarek 2018: 120 [new records]; Komarek 2019: 173 [taxonomic treatment].

DISTRIBUTION: Indo-Malayan: Bhutan, China (Hainan), India (Madhya Pradesh), Laos, Malaysia, Myanmar, Nepal, Thailand, Vietnam.

Agraphydrus constrictus Komarek, 2018

Agraphydrus constrictus Komarek, 2018: 121 - India, Uttarakhand, Chamoli District, Nandakini River, below Sedoli, ca. 10 km E Nandaprayag, 30°15'50''N 79°26'32''E.

DISTRIBUTION: Indo-Malayan: India (Assam, Uttarakhand), Nepal.

Agraphydrus contractus Komarek and Hebauer, 2018

Agraphydrus contractus Komarek and Hebauer, 2018: 33 - China, Fujian Prov., Jianyuan Prefecture; Yong'an City Region; ca. 20 km SE Yong'an City, 5 km SW Xiyang Village, Ziyungdong Shan.

DISTRIBUTION: Indo-Malayan: China (Fujian, Guangdong).

Agraphydrus coomani (d'Orchymont, 1927)

Helochares (*Agraphydrus*) *coomani* d'Orchymont, 1927a: 248 - Vietnam, [Tonkin], Lac Tho, nr. Hoa Binh Province; d'Orchymont 1928: 108 [faunistic treatment].

Agraphydrus coomani (d'Orchymont); Watts 1995: 115 [new records]; Komarek and Hebauer 2018: 34 [new records; redescription]; Komarek 2018: 122 [new records]; Komarek 2019: 174 [new records].

Agraphydrus (*Agraphydrus*) *coomani* (d'Orchymont); Hansen 1999b: 156 [catalog].

Enochrus ryukyuensis Matsui 1994: 217 - Japan, Amami-shoio (Kagoshima Pref.), Tokuno-shima Is., Tokunoshima Town, Kamize Dam.

Agraphydrus ryukyuensis (Matsui); Gentili et al. 1995: 208 [checklist]; Komarek and Hebauer 2018: 34 [synonym of *A. coomani* (d'Orchymont)].

Agraphydrus (*Agraphydrus*) *ryukyuensis* (Matsui); Hansen 1999b: 157 [catalog]; Hansen 2004: 49 [checklist]; Fikáček et al. 2015: 61 [catalog]; Minoshima 2016: 361 [redescription].

DISTRIBUTION: Indo-Malayan: Brunei, China (Fujian, Guangdong, Hainan), Indonesia, Laos, Malaysia (Peninsula), Myanmar, Sri Lanka, Taiwan, Thailand, Vietnam. Palearctic: Japan. Australasian: Australia (New South Wales, Northern Territory, Queensland, Western Australia), Papua New Guinea.

Agraphydrus coronarius Minoshima, Komarek, and Ôhara, 2015

Agraphydrus (*Agraphydrus*) *coronarius* Minoshima, Komarek, and Ôhara, 2015: 41 - Laos, Bolikhamsai Province, Lak Sao; Komarek 2019: 179 [taxonomic treatment].

DISTRIBUTION: Indo-Malayan: Laos.

Agraphydrus crassipenis Komarek, 2018

Agraphydrus crassipenis Komarek, 2018: 123 - Nepal, Eastern Region, Kosi (= Koshi) Zone, Sunsari District, Dharan (city) environment.

DISTRIBUTION: Indo-Malayan: Bhutan, Nepal.

Agraphydrus decipiens Minoshima, Komarek, and Ôhara, 2015

Agraphydrus (*Agraphydrus*) *decipiens* Minoshima, Komarek, and Ôhara, 2015: 44 - Taiwan, Taichung City, Heping District, Basian-shan National Forest Recreation Area, N24°11.55′, E121°00.83′.

Agraphydrus decipiens Minoshima, Komarek, and Ôhara; Komarek and Hebauer 2018: 36 [redescription].

DISTRIBUTION: Indo-Malayan: Taiwan.

Agraphydrus delineatus Komarek, 2019

Agraphydrus delineatus Komarek, 2019: 180 - Malaysia, Sarawak, Kuching Division, Mt. Serapi, ca. 19 km W Kuching.

DISTRIBUTION: Indo-Malayan: Malaysia (Borneo).

Agraphydrus elongatus Ribera, Hernando, and Cieslak 2019

Agraphydrus elongatus Ribera, Hernando, and Cieslak 2019: 264 - Oman, Murri, Wadi Bani Ghafir, N23 29 46.2 E56 53 34.8.

DISTRIBUTION: Afrotropical: Oman, United Arab Emirates.

Agraphydrus engkari Komarek, 2019

Agraphydrus engkari Komarek, 2019: 181 - Malaysia, Sarawak, Sri Aman Division, Lubok Antu District, Batang Ai N.P., E of Bandar Sri Aman, Engkari River.

DISTRIBUTION: Indo-Malayan: Malaysia (Borneo).

Agraphydrus excisus Komarek, 2019

Agraphydrus excisus Komarek, 2019: 182 - Malaysia, Sarawak, Kapit Division, Kapit District, ca. 25 km of E Kapit.

DISTRIBUTION: Indo-Malayan: Malaysia (Borneo).

Agraphydrus exedis (d'Orchymont, 1937)

Helochares (*Agraphydrus*) *exedis* d'Orchymont, 1937a: 29 - India, Maharashtra [Bombay Presidency], Pune distr. ["Poona distr."], Khandala.

Agraphydrus (*Agraphydrus*) *exedis* (d'Orchymont); Hansen 1999b: 156 [new combination].

Agraphydrus exedis (d'Orchymont); Komarek 2018: 124 [new records].

DISTRIBUTION: Indo-Malayan: India (Madhya Pradesh, Maharashtra).

Agraphydrus exiguus Komarek, 2019

Agraphydrus exiguus Komarek, 2019: 183 - Malaysia, Pahang, Cameron Highlands District, Tanah Rata (town), Sungai Ruil near village of Orang Asli.

DISTRIBUTION: Indo-Malayan: Malaysia (Peninsula).

Agraphydrus falcatus Komarek, 2018

Agraphydrus falcatus Komarek, 2018: 125 - India, Tamil Nadu, Dindigul District, Palni Hills, Kodaikanal, Pallangi, ca. 10°15'N 77°30'E.

DISTRIBUTION: Indo-Malayan: India (Kerala, Tamil Nadu).

Agraphydrus fasciatus Komarek and Hebauer, 2018

Agraphydrus fasciatus Komarek and Hebauer, 2018: 37 - China, Hong Kong Admin. Reg., New Territories, Plover Cove Reservoir.

DISTRIBUTION: Indo-Malayan: China (Guangdong, Hong Kong, Jiangxi).

Agraphydrus fikaceki Komarek and Hebauer, 2018

Agraphydrus fikaceki Komarek and Hebauer, 2018: 38 - China, Jiangxi Prov., Jinggangshan Mts., Pingshui Shan, 26°30.4'N 114°06.9'E.

DISTRIBUTION: Indo-Malayan: China (Hong Kong, Jiangxi).

Agraphydrus flavonotus Komarek, 2018

Agraphydrus flavonotus Komarek, 2018: 127 - Bhutan, Sarpang Province, Geylephug – Shemgang road, 26°56'43''N 90°31'29''E.

DISTRIBUTION: Indo-Malayan: Bhutan.

Agraphydrus floresinus Komarek, 2019

Agraphydrus floresinus Komarek, 2019: 185 - Indonesia, East Nusa Tenggara Province, East Manggarai Regency, Borong District, Flores Island, Lake Ranamese, between Ruteng and Borong.

DISTRIBUTION: Indo-Malayan: Indonesia (Flores).

Agraphydrus forcipatus Komarek and Hebauer, 2018

Agraphydrus forcipatus Komarek and Hebauer, 2018: 39 - China, Anhui Prov., Weizhou Prefecture; Huang Shan NP; 60 km NNW Huang Shan City (= Tunxi), near Tang Kou.

DISTRIBUTION: Indo-Malayan: (Fujian, Guangdong, Guizhou, Hunan, Jiangxi, Zhejiang). Palearctic: China (Anhui, Hubei).

Agraphydrus fortis Komarek, 2018

Agraphydrus fortis Komarek, 2018: 128 - Sri Lanka [Ceylon], Uva Province, Monaragala District, Gowinda Hela (a giant rock mountain known also as Westminster Abbey).

DISTRIBUTION: Indo-Malayan: Sri Lanka.

Agraphydrus fujianensis Komarek and Hebauer, 2018

Agraphydrus fujianensis Komarek and Hebauer, 2018: 41 - China, Fujian Prov., Jianyuan Prefecture, Chong'an City Region, Wuyi Shan, 3 km SW Wuyi Gong Village (= Shanqian).

DISTRIBUTION: Indo-Malayan: China (Fujian).

Agraphydrus geminus (d'Orchymont, 1932)

Helochares (*Gymnhelochares*) *geminus* d'Orchymont, 1932: 694 - Indonesia, W. Java, "Tjibodas-Bach".

Agraphydrus (*Gymnhelochares*) *geminus* (d'Orchymont); Hansen 1991: 292 [subgenus transferred from *Helochares* to *Agraphydrus*]; Hansen 1999b: 157 [catalog].

Agraphydrus geminus (d'Orchymont); Komarek 2019: 186 [taxonomic treatment].

DISTRIBUTION: Indo-Malayan: Indonesia (Java, Sumatra).

Agraphydrus gilvus Komarek, 2018

Agraphydrus gilvus Komarek, 2018: 129 - India, Kerala, Kallar Valley, 10 km WSW Munnar, 10°3'N 76°59'E.

DISTRIBUTION: Indo-Malayan: India (Kerala).

Agraphydrus glaber Komarek, 2018

Agraphydrus glaber Komarek, 2018: 130 - India, Madhya Pradesh, Hoshangabad District, ca. 5 km NE Hoshangabad, ca. 60 km SSE Bhopal, Bandrabhan, Narmada River, 22°48'1''N 77°46'45''E.

DISTRIBUTION: Indo-Malayan: India (Madhya Pradesh).

Agraphydrus globipenis Komarek and Hebauer, 2018

Agraphydrus globipenis Komarek and Hebauer, 2018: 41 - China, Hunan Prov., Huaihua Pref., Huitong County, Jinlong Shan, ca. 30 km NE Huitong City.

DISTRIBUTION: Indo-Malayan: China (Guangxi, Hunan).

Agraphydrus gracilipalpis Komarek and Hebauer, 2018

Agraphydrus gracilipalpis Komarek and Hebauer, 2018: 42 - China, Guangdong Prov., Zhaoqing Prefecture, Dinghu Nature Reserve, 23°11'03"N 112°33'06"E.

DISTRIBUTION: Indo-Malayan: China (Fujian, Guangdong).

Agraphydrus hamatus Komarek, 2019

Agraphydrus hamatus Komarek, 2019: 187 - Vietnam, Hòa Binh Province, Lac Tho.

DISTRIBUTION: Indo-Malayan: Vietnam.

Agraphydrus hanseni (Satô and Yoshitomi, 2004) **comb. n.**

Horelophopsis hanseni Satô and Yoshitomi, 2004: 42 - Japan, Ôura-gawa Kakou, Okinawa-jima, Ryukyus. Yoshitomi and Nakajima 2005: 376 [new record]; Short and Hebauer 2006: 321 [catalog]; Minoshima et al. 2013 [description of larva; phylogenetic placement]; Short and Fikáček 2013: 731 [phylogenetic placement]; Fikáček et al. 2015: 62 [catalog]; Short et al. in prep. [phylogenetic placement].

DISTRIBUTION: Palearctic: Japan.

Agraphydrus heinrichi Komarek, 2018

Agraphydrus heinrichi Komarek, 2018: 131 - India, Kerala, Thiruvananthapuram District, Cardamom Hills, 50 km NW Pathanamthitta, near Pambaiyar River, ca. 9°25'N 77°5'E

DISTRIBUTION: Indo-Malayan: India (Kerala).

Agraphydrus helicopter Komarek, 2019

Agraphydrus helicopter Komarek, 2019: 188 - Malaysia, Johor, Gunung Ledang N.P., Gunung Ledang (= Mt. Ophir), Hutan (= forest) Lipur.

DISTRIBUTION: Indo-Malayan: Malaysia (Peninsula).

Agraphydrus hendrichi Komarek, 2019

Agraphydrus hendrichi Komarek, 2019: 189 - Malaysia, Pahang, Taman Negara N.P., surroundings of Nusa Camp.

DISTRIBUTION: Indo-Malayan: Malaysia (Peninsula).

Agraphydrus heterochromatus Komarek, 2019

Agraphydrus heterochromatus Komarek, 2019: 190 - Malaysia, Penang, George Town City, Botanic Gardens (= Waterfall Gardens).

DISTRIBUTION: Indo-Malayan: Malaysia (Peninsula), Thailand.

Agraphydrus hortensis Komarek, 2019

Agraphydrus hortensis Komarek, 2019: 192 - Malaysia, Penang, George Town City, Botanic Garden.

DISTRIBUTION: Indo-Malayan: Malaysia (Peninsula)

Agraphydrus hygropetricus Komarek, 2018

Agraphydrus hygropetricus Komarek, 2018: 132 - Sri Lanka [Ceylon], Western Province, 24miles ESE Colombo, Labugama (village).

DISTRIBUTION: Indo-Malayan: Sri Lanka.

Agraphydrus igneus Komarek and Hebauer, 2018

Agraphydrus igneus Komarek and Hebauer, 2018: 43 - China, Hong Kong, Lantau Island, Ngong Ping village, Po Lin Monastery environment, 22°15.2–5'N 113°54.6''E; Komarek 2019: 193 [taxonomic treatment].

DISTRIBUTION: Indo-Malayan: China (Guangdong, Hong Kong), Laos.

Agraphydrus imitans Komarek, 2019

Agraphydrus imitans Komarek, 2019: 193 - Myanmar, Mandalay Region, ca. 50 km NW Kalaw, Myitsone River, 20°48'27.42''N 96°21'36.6''E.

DISTRIBUTION: Indo-Malayan: Laos, Myanmar, Thailand, Vietnam.

Agraphydrus indicus (d'Orchymont, 1932)

Helochares (*Gymnhelochares*) *indicus* d'Orchymont, 1932a: 694 - India, Uttar Pradesh, Kumaon, Haldwani distr.

Agraphydrus (*Gymnhelochares*) *indicus* (d'Orchymont); Hansen 1999b: 157 [new combination]; Hebauer 2002a: 20 [new records]; Hansen 2004: 49 [checklist]; Fikáček et al. 2015: 61 [catalog].

Agraphydrus indicus (d'Orchymont); Komarek 2018: 133 [new records; redescription].

DISTRIBUTION: Indo-Malayan: Bhutan, India (Arunachal Pradesh, Himachal Pradesh, Meghalaya, Uttarakhand, Uttar Pradesh), Nepal.

Agraphydrus inflatus Komarek, 2018

Agraphydrus inflatus Komarek, 2018: 136 - India, Kerala, Idukki District, Cardamom Hills, Kallar Valley, 15 km SW Munnar, ca. 10°02'N 76°58'E.

DISTRIBUTION: Indo-Malayan: India (Kerala, Tamil Nadu).

Agraphydrus infuscatus Komarek, 2019

Agraphydrus infuscatus Komarek, 2019: 195 - Thailand, Phang Nga Province, Khuraburi District, Baan Tumnang, west of Si Phang Nga N.P.

DISTRIBUTION: Indo-Malayan: Thailand.

Agraphydrus insidiator Minoshima, Komarek, and Ôhara, 2015

Agraphydrus (*Agraphydrus*) *insidiator* Minoshima, Komarek, and Ôhara, 2015: 48 - Taiwan: Taichung City, Heping District, Basian-shan National Forest Recreation Area, N24°11.55′, E121°00.83′.

Agraphydrus insidiator Minoshima, Komarek, and Ôhara; Komarek and Hebauer 2018: 44 [redescription].

DISTRIBUTION: Indo-Malayan: Taiwan.

Agraphydrus ishiharai (Matsui, 1994)

Enochrus ishiharai Matsui, 1994: 215 - Japan, Kyushu, Kumamoto Pref., Ue Village, Menda River.

Agraphydrus (*Agraphydrus*) *ishiharai* (Matsui); Hansen 1999b: 156 [new combination]; Hansen 2004: 49 [checklist]; Fikáček et al. 2015: 60 [catalog]; Minoshima 2016: 353 [redescription]; Lee and Ahn 2017: 39.

DISTRIBUTION: Palearctic: Japan, Korea.

Agraphydrus jaechi (Hansen, 1999)

Megagraphydrus jaechi Hansen, 1999a: 140 - Malaysia, Penang Aceh Forest Reserve 2 km W Telok Bahang; Hansen 1999b: 157 [catalog].

Agraphydrus (*Agraphydrus*) *jaechi* (Hansen); Minoshima et al. 2015: 18 [new combination; redescription].

Agraphydrus jaechi (Hansen); Komarek 2019: 196 [taxonomic treatment].

Megagraphydrus superans Hebauer, 2000: 16 - Malaysia, Pahang, Taman Negara National Park, Nusa Camp; Short and Hebauer 2006: 337 [catalog]; Komarek 2019 [synonymy].

Agraphydrus (*Agraphydrus*) *superans* (Hebauer); Minoshima et al. 2015: 35 [new combination].

DISTRIBUTION: Indo-Malayan: Malaysia (Peninsula).

Agraphydrus jankodadai Komarek, 2019

Agraphydrus jankodadai Komarek, 2019: 197 - Malaysia, Sabah, Interior Division, Nabawan District, near Batu Punggul Resort.

DISTRIBUTION: Indo-Malayan: Malaysia (Borneo).

Agraphydrus jilanzhui Komarek and Hebauer, 2018

Agraphydrus jilanzhui Komarek and Hebauer, 2018: 45 - China, Shaanxi Prov., Qin Ling Shan, 33°55'N 108°49'E.

DISTRIBUTION: Palearctic: China (Gansu, Hubei, Shaanxi, Sichuan).

Agraphydrus kallar Komarek, 2018

Agraphydrus kallar Komarek, 2018: 137 - India, Kerala, Thiruvananthapuram District, 30 km NNE Thiruvananthapuram, Kallar, ca. 8°45'N 77°5'E.

DISTRIBUTION: Indo-Malayan: India (Kerala).

Agraphydrus kathapa Komarek, 2019

Agraphydrus kathapa Komarek, 2019: 198 - Myanmar, Sagaing Region, Alaungdaw Kathapa N.P., 22°19'5.64''N 94°28'49.38''E.

DISTRIBUTION: Indo-Malayan: Myanmar.

Agraphydrus kempi (d'Orchymont, 1922)

Helochares (s. str.) *kempi* d'Orchymont, 1922b: 626 - India, Arunachal Pradesh, Abors, "Yembung".

Helochares (*Agraphydrus*) *kempi* (d'Orchymont); d'Orchymont 1927a: 5 [transferred from subgenus (s. str.) to subgenus (*Agraphydrus*)]; d'Orchymont 1928: 108 [faunistic treatment].

Agraphydrus (*Agraphydrus*) *kempi* (d'Orchymont); Hansen 1999b: 156 [new combination]; Hebauer 2002a: 21 [new record]; Hansen 2004: 60 [checklist]; Fikáček et al. 2015: 60 [catalog].

Agraphydrus kempi (d'Orchymont); Komarek 2018: 138 [new records; redescription].

DISTRIBUTION: Indo-Malayan: Bhutan, India (Arunachal Pradesh, Meghalaya, Uttar Pradesh, Uttarakhand), Nepal.

Agraphydrus khasiensis Komarek, 2018

Agraphydrus khasiensis Komarek, 2018: 141 - India, Meghalaya, Khasi Hills District, Shillong Peak, 25°32.8'N 91°52.5'E.

DISTRIBUTION: Indo-Malayan: India (Meghalaya).

Agraphydrus kodaguensis Komarek, 2018

Agraphydrus kodaguensis Komarek, 2018: 142 - India, Karnataka, Kodagu District, Tadiyendamol Mountain, ca. 12°14'N 75°36'E.

DISTRIBUTION: Indo-Malayan: India (Karnataka).

Agraphydrus laocaiensis Komarek, 2019

Agraphydrus laocaiensis Komarek, 2019: 200 - Vietnam, Lào Cai Province, Sa Pa District, near Sa Pa (District capital), Cát Cát (village), 22°19'N 103°50'E.

DISTRIBUTION: Indo-Malayan: Vietnam.

Agraphydrus latus Komarek, 2019

Agraphydrus latus Komarek, 2019: 201 - Malaysia, Perak, Manjung District, Pangkor Island, Teluk Nipah (village).

DISTRIBUTION: Indo-Malayan: Malaysia (Peninsula).

Agraphydrus longipalpus (Jia, 1998)

Pseudopelthydrus longipalpus Jia, 1998: 229 - China, Hainan, Jianfengling, Tianchi; Hansen 1999b: 126 [catalog].

Agraphydrus longipalpis (Jia) [incorrect subsequent spelling]; Komarek 2003: 384 [new combination]; Short and Hebauer 2006: 330 [catalog].

Agraphydrus (*Gymnhelochares*) *longipalpis* (Jia) [incorrect subsequent spelling]; Hansen 2004: 49 [checklist].

Agraphydrus (*Agraphydrus*) *longipalpus* (Jia); Fikáček et al. 2015: 60 [catalog].

Agraphydrus longipalpus (Jia); Komarek and Hebauer 2018: 46 [redescription].

DISTRIBUTION: Indo-Malayan: China (Hainan).

Agraphydrus longipenis Komarek and Hebauer, 2018

Agraphydrus longipenis Komarek and Hebauer, 2018: 47 - Laos, Luang Nam Tha Prov., Luang Nam Tha [City] environment; Komarek 2019: 202 [taxonomic treatment].

DISTRIBUTION: Indo-Malayan: China (Yünnan), Laos.

Agraphydrus lunaris Komarek, 2019

Agraphydrus lunaris Komarek, 2019: 202 - Laos, Khammouan Province, Khoun Ngeun (village), 18°07'N 104°29'E.

DISTRIBUTION: Indo-Malayan: Laos.

Agraphydrus luteilateralis (Minoshima and Fujiwara, 2009)

Megagraphydrus luteilateralis Minoshima and Fujiwara, 2009: 55 - Japan, Okinawa Prefecture, Iriomote-jima Island, Shirahama, N24°21'59", E123°45’22"; Short and Fikáček 2011: 91 [checklist].

Agraphydrus (*Agraphydrus*) *luteilateralis* (Minoshima and Fujiwara); Minoshima et al. 2015: 22 [new combination]; Minoshima 2016: 355 [taxonomic treatment].

Agraphydrus (*Agraphydrus*) *luteimarginalis* (Minoshima and Fujiwara) [incorrect subsequent spelling]; Fikáček et al. 2015: 62 [catalog].

DISTRIBUTION: Palearctic: Japan.

Agraphydrus maehongsonensis Komarek, 2019

Agraphydrus maehongsonensis Komarek, 2019: 203 - Thailand, Mae Hong Son Province.

DISTRIBUTION: Indo-Malayan: Thailand.

Agraphydrus malayanus (Hebauer, 2000)

Megagraphydrus malayanus Hebauer, 2000: 15 - Malaysia, Kedah, SW Langkawi, Telaga Tujuh; Short and Hebauer 2006: 337 [catalog].

Agraphydrus (*Agraphydrus*) *malayanus* (Hebauer); Minoshima et al. 2015: 22 [new combination; record from Thailand in doubt].

Agraphydrus malayanus (Hebauer); Komarek 2019: 158 [taxonomic treatment; excluded from Thailand].

DISTRIBUTION: Indo-Malayan: Malaysia.

Agraphydrus manfredjaechi Komarek, 2019

Agraphydrus manfredjaechi Komarek, 2019: 206 - Indonesia, North Sulawesi Province, Dua Saudara N.P., E of Manado (capital city).

DISTRIBUTION: Indo-Malayan: Indonesia (Seram, Sulawesi).

Agraphydrus masatakai Minoshima, Komarek, and Ôhara, 2015

Agraphydrus (*Agraphydrus*) *masatakai* Minoshima, Komarek, and Ôhara, 2015: 49 - Houaphanh Province, Xam Neua, Ban Saleui.

Agraphydrus masatakai Minoshima, Komarek, and Ôhara; Komarek and Hebauer 2018: 48 [redescription]; Komarek 2019: 207 [new records].

DISTRIBUTION: Indo-Malayan: China (Guangdong, Hainan, Hong Kong, Yünnan), Laos, Malaysia, Myanmar, Thailand, Vietnam.

Agraphydrus mazzoldii Komarek, 2019

Agraphydrus mazzoldii Komarek, 2019: 209 - Thailand, Mukdahan Province, Phu Pha Thoep N.P.

DISTRIBUTION: Indo-Malayan: Thailand.

Agraphydrus meghalayanus Komarek, 2018

Agraphydrus meghalayanus Komarek, 2018: 143 - India, Meghalaya, East Khasi Hills District, 11 km SW Cherrapunjee, Laitkynsew, 25°12'N 91°40'E.

DISTRIBUTION: Indo-Malayan: India (Meghalaya).

Agraphydrus microphthalmus Komarek, 2019

Agraphydrus microphthalmus Komarek, 2019: 210 - Malaysia, Sarawak, Kapit Division, Kapit District, ca. 25 km E of Kapit.

DISTRIBUTION: Indo-Malayan: Malaysia (Borneo).

Agraphydrus minutissimus (Kuwert, 1890)

Helochares (s. str.) *minutissimus* Kuwert, 1890: 304 - Syria; d'Orchymont 1923a: 9 [faunistic treatment]; Hebauer 1994: 112 [faunistic treatment; identification doubtful].

Helochares minutissimus Kuwert; d'Orchymont 1926a: 379 [as synonym of *H. pallens*]

Helochares (*Agraphydrus*) *minutissimus* Kuwert; d'Orchymont 1939c: 197 [not synonym of *Helochares pallens* (MacLeay) as in d'Orchymont 1926a: 379); Balfour-Browne 1951: 213 [new record].

Agraphydrus minutissimus (Kuwert); Hebauer 1995a: 265 [new combination; new record]; Hebauer 1997: 264 [new record]; Fikáček et al. 2010: 149 [faunistic treatment].

Agraphydrus (*Agraphydrus*) *minutissimus* (Kuwert, 1890); Hansen 1999b: 156 [catalog]; Hansen 2004: 49 [checklist]; Hebauer 2006a: 27 [checklist]; Fikáček et al. 2015: 60 [catalog]; Ribera et al. 2019: 264 [checklist].

DISTRIBUTION: Palearctic: Syria. Afrotropical: Ethiopia (in doubt), Kenya, Madagascar, Oman, Saudi Arabia, South Africa (in doubt), Sudan, Yemen.

Agraphydrus mirabilis Komarek, 2019

Agraphydrus mirabilis Komarek, 2019: 212 - Thailand, Chiang Mai Province, Doi (= mountain) Suthep N.P., Huai Sa Lad, 18°48'18.6''N 98°54'31.2''E.

DISTRIBUTION: Indo-Malayan: Thailand.

Agraphydrus montanus Minoshima, Komarek, and Ôhara, 2015

Agraphydrus (*Agraphydrus*) *montanus* Minoshima, Komarek, and Ôhara, 2015: 54 - India, West Sikkim, Sikkim State, Yuksom.

Agraphydrus montanus Minoshima, Komarek, and Ôhara; Komarek 2018: 144 [redescription].

DISTRIBUTION: Indo-Malayan: India (Sikkim).

Agraphydrus muluensis Komarek, 2019

Agraphydrus muluensis Komarek, 2019: 213 - Malaysia, Sarawak, Miri Division, Gunung Mulu National Park.

DISTRIBUTION: Indo-Malayan: Malaysia (Borneo).

Agraphydrus musculus Komarek, 2019

Agraphydrus musculus Komarek, 2019: 214 - Malaysia, Sarawak, Kapit Division, Kapit District, ca. 25 km E of Kapit.

DISTRIBUTION: Indo-Malayan: Malaysia (Borneo).

Agraphydrus namthaensis Komarek, 2019

Agraphydrus namthaensis Komarek, 2019: 215 - Laos, Luang Nam Tha Province, Muang Sing District, ca. 20 km SE Muang Sing (town).

DISTRIBUTION: Indo-Malayan: Laos.

Agraphydrus nanus Komarek, 2018

Agraphydrus nanus Komarek, 2018: 145 - India, Kerala, Thiruvananthapuram District, Cardamom Hills, 50 km NW Pathanamthitta, Pambaiyar River, 9°25'N 77°05'E.

DISTRIBUTION: Indo-Malayan: India (Karnataka, Kerala, Madhya Pradesh).

Agraphydrus narusei (Satô, 1960)

Pseudohelochares narusei Satô, 1960: 77 - Japan, Shikoku, Kôchi Pref., Kurosongawa River.

Agraphydrus narusei (Satô); Satô, 1965: 128 [new combination]; Hansen 1999b: 156 [checklist]; Hansen 2004: 49 [checklist]; Lee and Ahn 2009: 317 [redescription; new record]; Minoshima and Hayashi 2011: 17 [description of larva]; Fikáček et al. 2015: 60 [catalog]; Minoshima 2016: 356 [redescription].

DISTRIBUTION: Palearctic: Japan, South Korea.

Agraphydrus nemorosus Komarek, 2019

Agraphydrus nemorosus Komarek, 2019: 216 - Laos, Houaphan Province, 25 km SE (by road) of Vieng Xai City, Kangpabong (village), 20°19'N 104°25'E.

DISTRIBUTION: Indo-Malayan: Laos.

Agraphydrus nepalensis Komarek, 2018

Agraphydrus nepalensis Komarek, 2018: 146 - Nepal, Eastern Region, Koshi Zone, 2 km E Mangsingma.

DISTRIBUTION: Indo-Malayan: Nepal.

Agraphydrus niger Komarek and Hebauer, 2018

Agraphydrus niger Komarek and Hebauer, 2018: 50 - China, Fujian Prov., Jianyuan Prefecture, Chong'an City Region, ca. 1 km W Wuyi Gong Village (=Shanqian, ca. 10 km S Chong'an City).

DISTRIBUTION: Indo-Malayan: China (Fujian, Zheijang).

Agraphydrus nigroflavus Komarek, 2019

Agraphydrus nigroflavus Komarek, 2019: 217 - Indonesia, North Kalimantan Province [formerly part of East Kalimantan Province], Malinau Regency, Kayan Selatan District, Apokayan Highlands, Sungai Barang (village), Lalut Wai.

DISTRIBUTION: Indo-Malayan: Indonesia (Borneo).

Agraphydrus obesus Komarek, 2019

Agraphydrus obesus Komarek, 2019:218 - Vietnam, Central Highlands, Lâm Đồng Province, 12 km N Đà Lạt, Lang Bian.

DISTRIBUTION: Indo-Malayan: Vietnam.

Agraphydrus obscuratus Komarek, 2018

Agraphydrus obscuratus Komarek, 2018: 148 - India, Kerala, Thiruvananthapuram District, Cardamom Hills, 50 km NW Pathanamthitta, near Pambaiyar River, ca. 9°25'N 77°5'E.

DISTRIBUTION: Indo-Malayan: India (Karnataka, Kerala, Maharashtra).

Agraphydrus obsoletus Komarek, 2018

Agraphydrus obsoletus Komarek, 2018: 149 - India, Kerala, Idukki District, 10 km WSW Munnar, Kallar Valley, ca. 10°3'N 76°58'E.

DISTRIBUTION: Indo-Malayan: India (Karnataka, Kerala, Tamil Nadu).

Agraphydrus ogatai Minoshima, 2016

Agraphydrus (*Agraphydrus*) *ogatai* Minoshima, 2016: 359 - Japan, Fukuoka Pref., Koga-shi, Taniyama, Taniyamagawa River [about 33°42'N, 130°30'E].

Agraphydrus sp. Inoue et al. 2009: 76 [photo, as an undescribed species similar to *A. narusei*; in Japanese].

DISTRIBUTION: Palearctic: Japan.

Agraphydrus orbicularis Komarek, 2019

Agraphydrus orbicularis Komarek, 2019: 219 - Malaysia, Sarawak, Kuching Division, Semengoh, 30 km S Kuching, Semengoh Nature Reserve.

DISTRIBUTION: Indo-Malayan: Malaysia (Borneo).

Agraphydrus orientalis (d'Orchymont, 1932)

Helochares (*Agraphydrus*) *orientalis* d'Orchymont, 1932: 690 - Indonesia, E. Java, "Ranu Bedali".

Agraphydrus orientalis (d'Orchymont); Satô 1965: 128 [*Agraphydrus* re-established as genus]; Gentili et al. 1995: 208 [checklist]; Komarek and Hebauer 2018: 65 [taxonomic treatment]; Komarek 2019: 220 [taxonomic treatment].

Agraphydrus (*Agraphydrus*) *orientalis* (d'Orchymont); Hansen 1999b: 156 [catalog]; Hansen 2004: 49 [checklist]; Fikáček et al. 2015: 60 [catalog].

DISTRIBUTION: Indo-Malayan: China (Yünnan) (in doubt, see Komarek and Hebauer 2018: 65–66), Indonesia (Bali, Java, Lombok, Siberut, Sumatra), Taiwan (in doubt, see Komarek and Hebauer 2018: 65–66).

Agraphydrus pallidus Komarek, 2019

Agraphydrus pallidus Komarek, 2019:222 - Vietnam, Vĩnh Phúc Province, Tam Đảo.

DISTRIBUTION: Indo-Malayan: Vietnam.

Agraphydrus papuanus Komarek, 2019

Agraphydrus papuanus Komarek, 2019: 223 - Indonesia, West Papua, Pegunungan Bintang Regency, Central Range, Kali Takime, 4°24'S 140°25'E.

DISTRIBUTION: Australasian: Indonesia (New Guinea), Papua New Guinea.

Agraphydrus pauculus (Knisch, 1924)

Helochares (Helocharimorphus) pauculus Knisch, 1924b: 36 - India, Uttar Pradesh, Kumaun, W. Almora.

Helochares panculus Knisch [incorrect subsequent spelling]; d'Orchymont 1927a: 5 [taxonomic treatment].

Helochares (*Agraphydrus*) *pauculus* Knisch; d'Orchymont 1928: 108 [faunistic treatment].

Agraphydrus pauculus (Knisch); Hansen 1991: 148 [examined species]; Komarek 2018: 151 [new record; redescription].

Agraphilydrus pauculus Knisch; Chiesa 1967: 275 [incorrect identification, see Komarek 2018: 153]

Agraphydrus (*Agraphydrus*) *pauculus* (Knisch); Hansen 1999b: 156 [catalog]; Hebauer 2002a: 22 [new records]; Hansen 2004: 49 [checklist]; Fikáček et al. 2015: 60 [checklist].

DISTRIBUTION: Palearctic: China (Tibet, see Komarek 2018: 153). Indo-Malayan: India (Uttarakhand), Nepal.

Agraphydrus penangensis Komarek, 2019

Agraphydrus penangensis Komarek, 2019: 225 - Malaysia, Penang, Southwest Penang Island, Pantai Aceh Forest Reserve (= Penang National Park).

DISTRIBUTION: Indo-Malayan: Malaysia (Peninsula).

Agraphydrus piceus Komarek, 2019

Agraphydrus piceus Komarek, 2019: 226 - Malaysia, Sabah, West Coast Division, Ranau District, Ranau (town), Liwagu River.

DISTRIBUTION: Indo-Malayan: Malaysia (Borneo).

Agraphydrus politus (Hansen, 1999)

Megagraphydrus politus Hansen, 1999a: 138 - Taiwan, Taipei Wulai; Hansen 1999b: 158 [checklist]; Hebauer 2000: 18 [checklist]; Hansen 2004: 52 [checklist]; Fikáček et al. 2015: 62 [catalog].

Agraphydrus (*Agraphydrus*) *politus* (Hansen); Minoshima et al. 2015: 24 [new combination; redescription].

Agraphydrus politus (Hansen); Komarek and Hebauer 2018: 51 [redescription].

Megagraphydrus wangi Hebauer, 2000: 17 - Taiwan, Taipei Hsien, Sanhsia, 24°51'21"N 121°24'33"E; Hansen 2004: 52 [checklist]; Short and Hebauer 2006: 337 [catalog]; Fikáček et al. 2015: 63 [catalog]; Minoshima et al. 2015: 25 [synonym with *A. politus*].

DISTRIBUTION: Indo-Malayan: Taiwan.

Agraphydrus praecipuus (d'Orchymont, 1937)

Helochares (*Agraphydrus*) *praecipuus* d'Orchymont, 1937b: 252 - Madagascar (south), "Pays Androy Nord".

Agraphydrus (*Agraphydrus*) *praecipuus* (d'Orchymont); Hansen 1999b: 157 [new combination; catalog]; Hebauer 2006a: 27 [checklist].

DISTRIBUTION: Afrotropical: Madagascar.

Agraphydrus protentus Komarek, 2018

Agraphydrus protentus Komarek, 2018: 153 - India, Uttarakhand, Nainital.

DISTRIBUTION: Indo-Malayan: India (Uttarakhand), Nepal.

Agraphydrus pullus Komarek, 2018

Agraphydrus pullus Komarek, 2018: 154 - Nepal, Eastern Region, Koshi Zone, Sunsari District, Dharan (city) environment.

DISTRIBUTION: Indo-Malayan: Nepal.

Agraphydrus punctatellus Régimbart, 1903

Agraphydrus punctatellus Régimbart, 1903a: 34 - Madagascar ["Diégo-Suarez; forêt de la côte Est de Madagascar".

Enochrus (*Agraphydrus*) *punctatellus* Régimbart; Knisch 1924a: 219 [catalog].

Agraphydrus (*Agraphydrus*) *punctatellus* Régimbart; Satô, 1965: 128 [subgenus transferred from *Enochrus* to *Agraphydrus*]; Hansen 1999b: 157 [catalog]; Hebauer 2006a: 27 [checklist; new records].

DISTRIBUTION: Afrotropical: Madagascar, Mozambique, South Africa, Tanzania.

Agraphydrus punctulatus Komarek, 2018

Agraphydrus punctulatus Komarek, 2018: 155 - India, Madhya Pradesh, Hoshangabad District, Pachmarhi Wildlife Sanctuary, Satpura Mountain Range, Apsara Vihar (stream), ca. 3 km SSE Pachmarhi, 22°27'7''N 78°26'39''E.

DISTRIBUTION: Indo-Malayan: India (Madhya Pradesh).

Agraphydrus puzhelongi (Jia, 2010)

Megagraphydrus puzhelongi Jia, 2010: 65 - China, Jiangxi Province, Shangrao, Sanqingshan mount, Upper Xinjiang river; Short and Fikáček 2011: 91 [catalog]; Fikáček et al. 2015: 63 [catalog].

Agraphydrus (*Agraphydrus*) *puzhelongi* (Jia); Minoshima et al. 2015: 30 [new combination].

Agraphydrus puzhelongi (Jia); Komarek and Hebauer 2018: 52 [redescription].

DISTRIBUTION: Indo-Malayan: China (Guizhou, Jiangxi).

Agraphydrus pygmaeus (Knisch, 1924)

Helochares (Helocharimorphus) pygmaeus Knisch, 1924b: 38 - India, Kumaon, W Almora. d'Orchymont 1927a: 5 [taxonomic treatment].

Helochares (*Agraphydrus*) *pygmaeus* Knisch; d'Orchymont 1928: 108 [checklist].

Agraphydrus (*Agraphydrus*) *pygmaeus* Knisch; Hansen 1999b: 157 [new combination]; Hebauer 2002a: 22 [new record]; Hansen 2004: 49 [checklist]; Fikáček et al. 2015: 60 [catalog].

Agraphydrus pygmaeus (Knisch); Komarek 2018: 156 [new record].

DISTRIBUTION: Indo-Malayan: Bhutan, India (Meghalaya, Uttarakhand), Nepal. Palearctic: China (Tibet, see Komarek 2018: 158).

Agraphydrus raucus Komarek, 2019

Agraphydrus raucus Komarek, 2019: 227 - Indonesia, West Sumatra Province, Lima Puluh Kota Regency, Lembah Harau Nature Reserve, 15 km NE of Payakumbu City.

DISTRIBUTION: Indo-Malayan: Indonesia (Sumatra).

Agraphydrus reductus Komarek and Hebauer 2018

Agraphydrus reductus Komarek and Hebauer 2018: 53 - China, Yünnan Prov., Xishuangbanna Dai Autonomous Prefecture, Mengla County, Menglun Town, ca. 10 km NW Menglun, Wushiwu He River.

DISTRIBUTION: Indo-Malayan: China (Yünnan).

Agraphydrus regularis (Hansen, 1999)

Megagraphydrus regularis Hansen, 1999a: 140 - Thailand, Phetchabun, 36 km SE Sila, Ban Pala Yai; Hansen 1999b: 158 [catalog].

Agraphydrus (*Agraphydrus*) *regularis* (Hansen); Minoshima et al. 2015: 30 [new combination; redescription].

Agraphydrus regularis (Hansen); Komarek 2019: 228 [taxonomic treatment].

DISTRIBUTION: Indo-Malayan: Thailand.

Agraphydrus reticulatus Komarek, 2019

Agraphydrus reticulatus Komarek, 2019: 230 - Thailand, Surat Thani Province, Khao Sok N.P.

DISTRIBUTION: Indo-Malayan: Thailand.

Agraphydrus reticuliceps Komarek and Hebauer, 2018

Agraphydrus reticuliceps Komarek and Hebauer, 2018: 53 - China, Hunan Prov., Zhangjiajie Pref., Wulingyuan, N Dayong City, Suoxiyu Nature Reserve.

DISTRIBUTION: Indo-Malayan: China (Guizhou, Hunan). Palearctic: China (Hubei).

Agraphydrus rhomboideus Komarek, 2019

Agraphydrus rhomboideus Komarek, 2019: 231 - Malaysia, Sarawak, Miri Division, Kelabit Highlands, 5 km E Bario (village community), Pa'Ukat (village).

DISTRIBUTION: Indo-Malayan: Brunei, Indonesia (Borneo), Malaysia (Borneo).

Agraphydrus robustus Komarek and Hebauer, 2018

Agraphydrus robustus Komarek and Hebauer, 2018: 55 - China, Yünnan Prov., Simao Pref., 54 km SW Simao, Jian Shan River.

DISTRIBUTION: Indo-Malayan: China (Guangdong, Yünnan).

Agraphydrus rostratus Komarek, 2018

Agraphydrus rostratus Komarek, 2018: 158 - India, Tamil Nadu, Nilgiris District, Nilgiri Hills, Kotagiri (town) environment, Honnatti, ca. 11°25'N 76°55'E.

DISTRIBUTION: Indo-Malayan: India (Kerala, Tamil Nadu).

Agraphydrus rugosus Komarek, 2018

Agraphydrus rugosus Komarek, 2018: 160 - India, Tamil Nadu, Nilgiris District, Nilgiri Hills, 15 km SE Kotagiri (town), Kunjapanai (village), ca. 11°22'N 76°56'E.

DISTRIBUTION: Indo-Malayan: India (Kerala, Tamil Nadu).

Agraphydrus sarawakensis Komarek, 2019

Agraphydrus sarawakensis Komarek, 2019: 232 - Malaysia, Sarawak, Kapit Division, Kapit District, 25 km E of Kapit.

DISTRIBUTION: Indo-Malayan: Malaysia (Borneo).

Agraphydrus schoedli Komarek, 2019

Agraphydrus schoedli Komarek, 2019: 233 - Indonesia, North Sumatra Province, Toba Samosir Regency, Lumban Julu.

DISTRIBUTION: Indo-Malayan: Indonesia (Sumatra).

Agraphydrus schoenmanni Komarek and Hebauer, 2018

Agraphydrus schoenmanni Komarek and Hebauer, 2018: 56 - China, Yünnan Prov., Xishuangbanna Dai Autonomous Prefecture, Mengla County, Menglun Town, near Mangmo Village, road Menglun–Ganlanba, ca. 15 km W Menglun.

DISTRIBUTION: Indo-Malayan: China (Yünnan).

Agraphydrus scintillans Komarek, 2019

Agraphydrus scintillans Komarek, 2019: 235 - Vietnam, Vĩnh Phúc Province, Tam Đảo.

DISTRIBUTION: Indo-Malayan: Vietnam.

Agraphydrus setifer Komarek and Hebauer, 2018

Agraphydrus setifer Komarek and Hebauer, 2018: 57 - Vietnam, Lào Cai Prov., Cat Cat, near Sa Pa, 22°19'43"N 103°50'E; Komarek 2019: 236 [taxonomic treatment].

DISTRIBUTION: Indo-Malayan: China (Yünnan), Vietnam.

Agraphydrus shaverdoae Komarek, 2019

Agraphydrus shaverdoae Komarek, 2019: 236 - Myanmar, Shan State, Taunggyi District, NW Kalaw (town), km 23 on road between Kalaw and Thazi, 20°42'22.68''N 96°30'13.08''E.

DISTRIBUTION: Indo-Malayan: Myanmar, Thailand.

Agraphydrus siamensis (Hansen, 1999)

Megagraphydrus siamensis Hansen, 1999a: 140 - Thailand, “Prae Siam”; Hansen 1999b: 158 [checklist]; Hebauer 2000: 18 [checklist].

Agraphydrus (*Agraphydrus*) *siamensis* (Hansen); Minoshima et al. 2015: 33 [new combination; redescription].

Agraphydrus siamensis (Hansen); Komarek 2019: 238 [taxonomic treatment].

DISTRIBUTION: Indo-Malayan: Thailand.

Agraphydrus sipekorum Komarek, 2018

Agraphydrus sipekorum Komarek, 2018: 161 - India, Meghalaya, East Khasi Hills District, 11 km SW Cherrapunjee, Laitkynsew, 25°12'48''N 91°39'48''E.

DISTRIBUTION: Indo-Malayan: India (Meghalaya).

Agraphydrus skalei Komarek, 2019

Agraphydrus skalei Komarek, 2019: 239 - Indonesia, West Papua Province, Raja Ampat Regency, Waigeo Island, Lopintol, Rowery River, ca. 0°7'S 130°53'E.

DISTRIBUTION: Australasian: Indonesia (Waigeo Island).

Agraphydrus spadix Komarek, 2019

Agraphydrus spadix Komarek, 2019: 240 - Thailand, Kanchanaburi Province, Sangkhla Buri District, Thung Yai Naresuan Wildlife Sanctuary.

DISTRIBUTION: Indo-Malayan: Thailand.

Agraphydrus splendens Komarek and Hebauer, 2018

Agraphydrus splendens Komarek and Hebauer, 2018: 58 - Laos, Saisombun Special Zone, Mount Phu Bia.

DISTRIBUTION: Indo-Malayan: China (Yünnan), Laos.

Agraphydrus spinosus Komarek, 2019

Agraphydrus spinosus Komarek, 2019: 241 - Malaysia, Selangor, Gombak District, Rawang Subdistrict, Templer Park.

DISTRIBUTION: Indo-Malayan: Malaysia (Peninsula).

Agraphydrus stagnalis (d'Orchymont, 1937)

Helochares (*Agraphydrus*) *stagnalis* d'Orchymont, 1937c: 37 - Pakistan, Punjab, Salt Range, Khewra Gorge.

Agraphydrus (*Agraphydrus*) *stagnalis* d'Orchymont; Hansen 1999b: 157 [new combination]; Hebauer 2002a: 22 [new record]; Hansen 2004: 49 [checklist]; Fikáček et al. 2015: 60 [catalog].

Agraphydrus stagnalis (d'Orchymont); Komarek 2018: 162 [new records].

DISTRIBUTION: Indo-Malayan: Bhutan, India (Himachal, Uttar, Uttarakhand), Nepal. Palearctic: Pakistan.

Agraphydrus stramineus Komarek, 2019

Agraphydrus stramineus Komarek, 2019: 242 - Malaysia, Sarawak, Miri Division, 30 km S Miri, Lambir Hills National Park.

DISTRIBUTION: Indo-Malayan: Malaysia (Borneo).

Agraphydrus sucineus Komarek, 2019

Agraphydrus sucineus Komarek, 2019: 244 - Malaysia, Pahang, Taman Negara N.P., surroundings of Nusa Camp.

DISTRIBUTION: Indo-Malayan: Malaysia (Peninsula).

Agraphydrus sundaicus Komarek, 2019

Agraphydrus sundaicus Komarek, 2019: 245 - Indonesia, West Sumatra Province, Padang City, 25 km E Padang, Taman Raya Bung Hatta Nature Reserve.

DISTRIBUTION: Indo-Malayan: Indonesia (Java, Sumatra).

Agraphydrus tamdao Komarek, 2019

Agraphydrus tamdao Komarek, 2019: 246 - Vietnam, Vĩnh Phúc Province, Tam Đảo.

DISTRIBUTION: Indo-Malayan: Vietnam.

Agraphydrus taprobanensis Komarek, 2018

Agraphydrus taprobanensis Komarek, 2018: 164 - Sri Lanka, Sabaragamuwa Province, Ratnapura District, Ratnapura (city).

DISTRIBUTION: Indo-Malayan: Sri Lanka.

Agraphydrus thaiensis Minoshima, Komarek, and Ôhara, 2015

Agraphydrus (*Agraphydrus*) *thaiensis* Minoshima, Komarek, and Ôhara, 2015: 56 - Thailand, Songkhla Province, Ton Nga Chang Wildlife Sanctuary.

Agraphydrus thaiensis Minoshima, Komarek, and Ôhara; Komarek 2019: 247 [taxonomic treatment].

DISTRIBUTION: Indo-Malayan: Thailand.

Agraphydrus tristis Komarek, 2019

Agraphydrus tristis Komarek, 2019: 248 - Myanmar, Mandalay Region, Pyin Oo Lwin District, Mogok Township, S Panlin village, west slope of Mt. Taung Mae, ca. 22°58'9''N 96°27'11''E.

DISTRIBUTION: Indo-Malayan: Myanmar.

Agraphydrus tulipa Komarek, 2019

Agraphydrus tulipa Komarek, 2019: 250 - Thailand, Chiang Mai Province, Chiang Dao District, Doi (Luang) Chiang Dao (mountain).

DISTRIBUTION: Indo-Malayan: Thailand.

Agraphydrus tumulosus Komarek, 2018

Agraphydrus tumulosus Komarek, 2018: 165 - India, Kerala, Pathanamthitta District, Cardamom Hills, 50 km NW Pathanamthitta, Pambaiyar River, 77°5'E 9°25'N.

DISTRIBUTION: Indo-Malayan: India (Kerala).

Agraphydrus umbrosus Komarek and Hebauer, 2018

Agraphydrus umbrosus Komarek and Hebauer, 2018: 59- China, Fujian Prov., Jianyuan Prefecture, Yong'an City Region, ca. 20 km SE Yong'an City, 5 km SW Xiyang Village, Ziyungdong Shan.

DISTRIBUTION: Indo-Malayan: China (Fujian, Guangdong).

Agraphydrus uncinatus Komarek and Hebauer, 2018

Agraphydrus uncinatus Komarek and Hebauer, 2018: 60 - China, Yünnan Prov., Xishuangbanna Dai Autonomous Prefecture, Mengla County, along Mengla–Mengyüan road, ca. 6 km NW Mengla.

DISTRIBUTION: Indo-Malayan: China (Yünnan).

Agraphydrus uvaensis (Hebauer, 2000)

Megagraphydrus uvaensis Hebauer, 2000: 17 - Sri Lanka [Ceylon], Prov. of Uva, Gampaha Estate, 9 miles W Badulla; Short and Hebauer 2006: 337 [catalog].

Agraphydrus (*Agraphydrus*) *uvaensis* (Hebauer); Minoshima et al. 2015: 36 [new combination; redescription].

Agraphydrus uvaensis (Hebauer); Komarek 2018: 166 [redescription].

DISTRIBUTION: Indo-Malayan: Sri Lanka.

Agraphydrus variabilis Komarek and Hebauer, 2018

Agraphydrus variabilis Komarek and Hebauer, 2018: 61 - China, Hong Kong, Lantau Island, Pak Kung Au, NW Cheung Sha.

DISTRIBUTION: Indo-Malayan: China (Fujian, Guangdong, Guangxi, Guizhou, Hong Kong, Hunan, Jiangxi, Yünnan, Zhejiang). Palearctic: China (Anhui, Gansu, Hubei, Shaanxi, Shandong, Sichuan), Taiwan.

Agraphydrus vietnamensis Komarek, 2019

Agraphydrus vietnamensis Komarek, 2019: 251 - Vietnam, Lâm Đồng Province, 14 km SW Bao Loc.

DISTRIBUTION: Indo-Malayan: Vietnam.

Agraphydrus villiersi (Balfour-Browne, 1958)

Helochares (*Gymnhelochares*) *villiersi* Balfour-Browne, 1958a: 184 - Ivory Coast, Tonkoui.

Agraphydrus (*Gymnhelochares*) *villiersi* (Balfour-Browne); Hansen 1999b: 157 [new combination]; Hebauer 2006a: 27 [checklist; new records].

DISTRIBUTION: Afrotropical: Cameroon, Gabon, Guinea [French Guinea], Ivory Coast.

Agraphydrus wangmiaoi Komarek and Hebauer, 2018

Agraphydrus wangmiaoi Komarek and Hebauer, 2018: 63 - China, Hainan Prov., Ledong County, Jianfeng Mountains, ca. 5 km E Tian Chi Village.

DISTRIBUTION: Indo-Malayan: China (Hainan).

Agraphydrus yunnanensis Komarek and Hebauer, 2018

Agraphydrus yunnanensis Komarek and Hebauer, 2018: 64 - China, Yünnan Prov., Xishuangbanna Dai Autonomous Prefecture, Mengla County, ca. 50 km SSE Menglun, Mengyüan.

DISTRIBUTION: Indo-Malayan: China (Yünnan).

Aulonochares Girón and Short, 2019

Aulonochares lingulatus Girón and Short, 2019

Aulonochares lingulatus Girón and Short, 2019: 119 - Suriname, Sipaliwini District; 2.97731N, 55.38500W; Camp 4 (low), Kasikasima; sandy stream on trail to METS camp.

DISTRIBUTION: Neotropical: French Guiana, Suriname.

Aulonochares novoairensis Girón and Short, 2019

Aulonochares novoairensis Girón and Short, 2019: 119 - Brazil, Amazonas: Novo Airão; 2°41'2.2878"S, 60°56'18.24"W.

DISTRIBUTION: Neotropical: Brazil (Amazonas).

Aulonochares tubulus Girón and Short, 2019

Aulonochares tubulus Girón and Short, 2019: 120 - Suriname, Sipaliwini District; 2°00.342'N, 55°58.149'W; 337 m; Sipaliwini Savanna nature Res., 4-Brothers Mts.

DISTRIBUTION: Neotropical: Brazil (Roraima), Guyana, Suriname, Venezuela.

Batochares Hansen, 1991

Batochares burgeoni (d'Orchymont, 1939) comb. n.

Helochares (*Batochares*) *burgeoni* d'Orchymont, 1939b: 293 - Democratic Republic of the Congo [Congo belge], Haut Uélé, Moto; Balfour-Browne 1950b: 54 [faunistic treatment]; Hebauer 1996: 10 [taxonomic treatment]; Hansen 1999b: 172 [catalog]; Hebauer 2006a: 27 [checklist, new records].

DISTRIBUTION: Afrotropical: Burundi/Rwanda, Democratic Republic of the Congo [Congo belge; Zaire], Guinea, Kenya, Republic of the Congo [Congo/Brazzaville], Uganda.

Batochares byrrhus (d'Orchymont, 1939) comb. n.

Helochares (*Batochares*) *byrrhus* d'Orchymont, 1939b: 294 - Democratic Republic of the Congo [Congo belge], Mayumbe, Sanzulu; Hebauer 1996: 10 [taxonomic treatment]; Hansen 1999b: 172 [catalog]; Hebauer 2006a: 27 [checklist, new records].

DISTRIBUTION: Afrotropical: Central African Republic, Democratic Republic of the Congo [Congo belge; Zaire], Gabon, Republic of the Congo [Congo/Brazzaville].

Batochares corrugatus (Balfour-Browne, 1958) comb. n.

Helochares (*Batochares*) *corrugatus* Balfour-Browne, 1958a: 183 - Guinea, Mount Nimba, "Camp de Ya"; Hebauer 1996: 10 [taxonomic treatment]; Hansen 1999b: 172 [catalog]; Hebauer 2006a: 27 [checklist].

DISTRIBUTION: Afrotropical: Guinea.

Chasmogenus Sharp, 1882

Chasmogenus australis García, 2000

Chasmogenus australis García, 2000a: 52 - Venezuela, Apure, Samán de Apure, Achaguas, 50 km NW of San Fernando de Apure; Short and Hebauer 2006: 331 [catalog].

DISTRIBUTION: Neotropical: Venezuela.

Chasmogenus bariorum García, 2000

Chasmogenus bariorum García, 2000a: 49 - Venezuela, Zulia, Machiques de Perijá, Misión Angeles de Tukuko, El Manantial, 36 km SW of Machiques; Short and Hebauer 2006: 331 [catalog].

DISTRIBUTION: Neotropical: Venezuela.

Chasmogenus barrae Short, 2005

Chasmogenus barrae Short, 2005: 194 - Costa Rica, Guanacaste Prov. road to Barra Honda National Park, 6.6 km after junction with route 13; Short and Hebauer 2006: 331 [catalog].

DISTRIBUTION: Neotropical: Costa Rica.

Chasmogenus cremnobates (Spangler, 1979)

Dieroxenus cremnobates Spangler, 1979: 754 - Ecuador, Napo, Baeza, 72 km E; Hansen 1999: 173 [catalog].

Chasmogenus cremnobates (Spangler); Girón and Short 2018: 155 [new combination].

DISTRIBUTION: Neotropical: Ecuador.

Chasmogenus fluminensis Clarkson and Ferreira-Jr, 2014

Chasmogenus fluminensis Clarkson and Ferreira-Jr, 2014b: 484 - Brazil Rio de Janeiro, Rio de Janeiro, Parque Nacional da Tijuca, 22°58'13''S, 43°15'25'' W.

DISTRIBUTION: Neotropical: Brazil (Rio de Janeiro).

Chasmogenus fragilis Sharp, 1882

Chasmogenus fragilis Sharp, 1882: 73 - Guatemala, San Gerónimo; Fernández, 1986: 190 [lectotype designation; redescription]; Hansen 1999b: 174 [catalog]; Short 2005: 195 [taxonomic treatment].

Helochares (*Chasmogenus*) *fragilis* (Sharp); Knisch 1924a: 195 [catalog].

Chasmogenus (*Chasmogenus*) *fragilis* (Sharp); Hebauer 1992: 84 [taxonomic treatment].

DISTRIBUTION: Neotropical: Guatemala, Panama.

Chasmogenus itatiaia Clarkson and Ferreira-Jr, 2014

Chasmogenus itatiaia Clarkson and Ferreira-Jr, 2014b: 487 - Brazil - Rio de Janeiro, Itatiaia, Parque Nacional de Itatiaia, Poça no caminho das Agulhas Negras, 22°23'05.4"S 44°40'41.7"W.

DISTRIBUTION: Neotropical: Brazil (Minas Gerais, Rio de Janeiro).

Chasmogenus lilianae Clarkson and Ferreira-Jr, 2014

Chasmogenus lilianae Clarkson and Ferreira-Jr, 2014b: 489 - Brazil, Rio de Janeiro, Nova Friburgo, Macaé de Cima, Tributário de 1a Ordem do Rio Macaé, Casa amarela, campo das hortênsias.

DISTRIBUTION: Neotropical: Brazil (Rio de Janeiro).

Chasmogenus lorenzo Short, 2005

Chasmogenus lorenzo Short, 2005: 195; Costa Rica - Alajuela Province, small stream near Rio San Lorenzo, 6km from Los Lagos; Short and Hebauer 2006: 331 [catalog].

DISTRIBUTION: Neotropical: Costa Rica.

Chasmogenus occidentalis García, 2000

Chasmogenus occidentalis García, 2000a: 49; Venezuela, Zulia, Machiques de Perijá, Misión Angeles de Tukuko, El Manantial, 35 km SW of Machiques; Short and Hebauer 2006: 331 [catalog].

DISTRIBUTION: Neotropical: Venezuela.

Chasmogenus rufinasus (Knisch, 1924)

Helochares (*Chasmogenus*) *rufinasus* Knisch, 1924c: 124 - Ecuador (Guayaquil).

Chasmogenus rufinasus (Knisch); Fernández 1986: 193 [new combination; taxonomic treatment]; Hansen 1999b: 175 [catalog].

DISTRIBUTION: Neotropical: Ecuador.

Chasmogenus ruidus Short, 2005

Chasmogenus ruidus Short, 2005: 196 - Costa Rica, Limón Province, Sector Cerro Cocori, Farm of Elias Rojas, A. C. Tortuguero; Short and Hebauer 2006: 331 [catalog].

DISTRIBUTION: Neotropical: Costa Rica.

Chasmogenus sapucay Fernández, 1986

Chasmogenus sapucay Fernández, 1986: 192 - Paraguay, Sapucay; Hansen 1999b: 176 [checklist]; Clarkson and Ferreira-Jr 2014b: 492 [new record].

DISTRIBUTION: Neotropical: Argentina, Brazil (Pará, Rio de Janeiro), Paraguay.

Chasmogenus schoedli Short, 2005

Chasmogenus schoedli Short, 2005: 197 - Costa Rica, Guanacaste, 9 km S Santa Cecilia, Pitilla Station; Short and Hebauer 2006: 331 [catalog].

DISTRIBUTION: Neotropical: Costa Rica.

Chasmogenus ubatuba Clarkson and Ferreira-Jr, 2014

Chasmogenus ubatuba Clarkson and Ferreira-Jr, 2014b: 491 - Brasil, São Paulo, Ubatuba, Parque Estadual da Serra do Mar, Núcleo Picinguaba.

DISTRIBUTION: Neotropical: Brazil (São Paulo).

Chasmogenus yukparum García, 2000

Chasmogenus yukparum García, 2000a: 50 - Venezuela, Zulia, Machiques de Perijá, Misión Angeles de Tukuko, El Manantial, 35 km SW of Machiques; Short and Hebauer 2006: 331 [catalog].

DISTRIBUTION: Neotropical: Venezuela.

Colossochares Short and Girón, gen. nov.

Colossochares ellipticus (d'Orchymont, 1933) comb. nov.

Helochares ellipticus Régimbart, 1907: 47 - Gabon, Lambarené, Cape Lopez, Rembo Nkomi; [misinterpretation of *Hydrophilus ellipticus* Fabricius].

Helochares ellipticus Régimbart; d'Orchymont 1933: 306 [new name]; Hebauer 2003: 129.

Helochares (s. str.) *ellipticus* d'Orchymont; Hansen 1999b: 160 [catalog].

Helochares (s. str.) *ellipticus* Régimbart; Balfour-Browne 1950b: 59 [faunistic treatment]; Hebauer 1996: 6 [taxonomic treatment]; Hebauer 2006a: 25 [checklist].

DISTRIBUTION: Afrotropical: Benin, Burkina Faso, Cameroon, Democratic Republic of the Congo, Ethiopia, Gabon, Ghana, Guinea, Ivory Coast, Liberia, Nigeria, Republic of the Congo, Uganda.

Colossochares satoi (Hebauer, 2003) comb. nov.

Helochares (s. str.) *satoi* Hebauer 2003a: 129 - Malawi: "Balaka env."; Hebauer 2005: 39; Hebauer 2006a: 25 [checklist]; Short and Hebauer 2006: 336 [catalog].

DISTRIBUTION: Afrotropical: Malawi.

Crephelochares Kuwert, 1890

Crephelochares abnormalis (Sharp, 1890) **comb. nov.**

Philydrus abnormalis Sharp, 1890: 351 - Sri Lanka, Colombo ["Ceylon: Colombo"]; [specific rank confirmed by d'Orchymont 1937d: 7; not syn. of *livornicus* Kuwert, as in d'Orchymont 1925: 70].

Helochares (*Chasmogenus*) *abnormalis* (Sharp); Knisch 1921: 68 [catalog].

Helochares (*Crephelochares*) *abnormalis* (Sharp); d'Orchymont 1937d: 7 [checklist]; d'Orchymont 1939a: 159 [taxonomic treatment].

Chasmogenus (*Crephelochares*) *abnormalis* (Sharp); Hebauer 1992: 68 [taxonomic treatment].

Enochrus (*Lumetus*) *abnormicollis* (Sharp); Zaitzev 1908: 385 [catalog - error for *abnormalis* Sharp].

Phylhydrus ferrugatus Régimbart, 1903b: 57 - Vietnam ["Cochinchine"] (My Tho); Indonesia (Sumatra); d'Orchymont 1939a: 159 [synonymy; not syn. of *livornicus* Kuwert, as in d'Orchymont 1925: 70).

Enochrus (*Lumetus*) *ferrugatus* Régimbart; Zaitzev 1908: 386 [catalog].

Helochares (*Chasmogenus*) *ferrugatus* Régimbart; Knisch 1924a: 195 [catalog].

Philhydrus nigritulus Régimbart, 1903b: 57 - Vietnam (Ho Chi Minh ["Saigon"], My Tho); Cambodia (Phnom Penh); Indonesia (Sumatra); Knisch 1924a: 195 [transferred to *Helochares*, thereby becoming a junior secondary homonym of *Helochares nigritulus* Kuwert, 1889]. Permanently invalid: replaced before 1961 (ICZN Code Art. 59b); d'Orchymont 1939a: 159 [synonymy].

Enochrus (*Lumetus*) *nigritulus* Régimbart; Zaitzev 1908a: 388 [catalog].

Helochares (*Chasmogenus*) *regimbarti* Knisch, 1924a: 195 (replacement name for *nigritulus* Régimbart); d'Orchymont 1939a: 159 [synonymy].

Chasmogenus abnormalis (Sharp); Gentili et al. 1995: 210 [checklist]; Hansen 1999b: 173 [catalog]; Hansen 2004: 49 [checklist]; Hebauer and Ryndevich 2005: 46 [new record]; Fikáček et al. 2015: 61 [catalog]; Devi et al. (2016) [redescription; lectotype designation]; Jia and Tang 2018a: 63 [new record].

DISTRIBUTION: Indo-Malayan: Cambodia, China (Guangdong), Indonesia (Borneo, Java, Sulawesi, Sumatra), Laos, Sri Lanka, Taiwan, Thailand, Vietnam. Palearctic: Japan.

Crephelochares africanus (d'Orchymont, 1937) **comb. nov.**

Helochares (*Crephelochares*) *africanus* d'Orchymont, 1937: 7 - Zambia; d'Orchymont 1939a: 163 [taxonomic treatment]; Balfour-Browne 1950b: 58 [faunistic treatment].

Chasmogenus (*Crephelochares*) *africanus* (d'Orchymont); Hebauer 1992: 69 [taxonomic treatment]; Hebauer 1995a: 265 [faunistic treatment]; Hebauer 2006a: 27 [checklist].

Chasmogenus africanus (d'Orchymont, 1937); Hansen 1999b: 174 [catalog].

DISTRIBUTION: Afrotropical: Botswana, Cameroon, Democratic Republic of the Congo, Gambia, Ghana, Guinea, Mozambique, Namibia, Niger, Nigeria, Senegal, South Africa, Sudan, Uganda, Zimbabwe.

Crephelochares balkei (Short, 2010) **comb. nov.**

Chasmogenus balkei Short, 2010: 301 - Fiji (Vanua Levu); Short and Fikáček 2011: 89 [catalog].

DISTRIBUTION: Australasian: Fiji (Vanua Levu).

Crephelochares cattienus (Hebauer, 2002) **comb. nov.**

Chasmogenus cattienus Hebauer, 2002b: 9 - Vietnam, S Cát Tiên, 120 km NNE Ho Chi Minh, Cát Tiên National Park.

DISTRIBUTION: Indo-Malayan: Vietnam.

Crephelochares irianus (Hebauer, 2001) **comb. nov.**

Chasmogenus irianus Hebauer, 2001: 15 - Indonesia, Papua [West New Guinea], Fak-Fak, IR 27, Kali Mati 4 km N of Fak-Fak.

DISTRIBUTION: Indo-Malayan: Indonesia (Papua).

Crephelochares larsi (Hebauer, 1995) **comb. nov.**

Chasmogenus (*Crephelochares*) *larsi* Hebauer, 1995: 8 - Malaysia, Cameron Highlands, Tanah Rata, G. Jasar track 11.

Chasmogenus larsi Hebauer; Hansen 1999b: 174 [catalog].

DISTRIBUTION: Indo-Malayan: Malaysia (Peninsula).

Crephelochares livornicus (Kuwert, 1890) **comb. nov.**

Helochares (*Crephelochares*) *livornicus* Kuwert, 1890a: 38 - Italy, Livorno; Heyden 1891: 67 [catalog]; d'Orchymont 1939a: 158 [taxonomic treatment].

Crephelochares livornicus (Kuwert); Kuwert 1890b: 327 (also as "n. sp.").

Helochares (Crepidelochares) livornicus Kuwert; Ganglbauer 1904: 248 [faunistic treatment].

Helochares (*Chasmogenus*) *livornicus* Kuwert; Knisch 1924a: 195 [catalog]; d'Orchymont 1925: 70 [taxonomic treatment]; d'Orchymont 1928: 106 [faunistic treatment].

Chasmogenus (*Crephelochares*) *livornicus* (Kuwert); Hebauer 1992: 70 [taxonomic treatment]

Chasmogenus livornicus (Kuwert); Hebauer 1994: 111 [faunistic treatment]; Hansen 1999b: 174 [catalog]; Hansen 2004: 49 [checklist]; Fikáček et al. 2015: 61 [catalog].

DISTRIBUTION: Palearctic: Bosnia, Croatia, Greece, Israel, Italy, Serbia and Montenegro, Spain, Tunisia, Turkey.

Crephelochares luctuosus (d'Orchymont, 1939) comb. nov.

Helochares (*Crephelochares*) *luctuosus* d'Orchymont, 1939a: 164 - Gabon; Hebauer 1988: 157 [faunistic treatment].

Chasmogenus (*Crephelochares*) *luctuosus* (d'Orchymont); Hebauer 1992: 71 [taxonomic treatment]; Hebauer 2006a: 27 [checklist].

Chasmogenus luctuosus (d'Orchymont, 1939); Hansen 1999: 174 [catalog].

DISTRIBUTION: Afrotropical: Cameroon, Democratic Republic of the Congo (in doubt, see Hebauer 2006a: 27), Gabon, Ghana (in doubt, see Hebauer 2006a: 27), Guinea, Namibia, Senegal.

Crephelochares lycetus (d'Orchymont, 1939) comb. nov.

Helochares (*Crephelochares*) *lycetus* d'Orchymont, 1939a: 163; Kenya ["Afrique orientale anglaise"], Taveta.

Chasmogenus (*Crephelochares*) *lycetus* (d'Orchymont); Hebauer 1992: 72 [taxonomic treatment]; Hebauer 1995a: 266 [faunistic treatment]; Hebauer 2006a: 27 [checklist].

Chasmogenus lycetus (d'Orchymont); Hansen 1999: 174 [catalog].

DISTRIBUTION: Afrotropical: Angola, Benin, Botswana, Kenya, Namibia, South Africa, Tanzania, Zambia, Zimbabwe.

Crephelochares mauritiensis (Balfour-Browne, 1958) **comb. nov.**

Helochares (*Crephelochares*) *mauritiensis* Balfour-Browne, 1958b: 143 - Mauritius, Les Mares.

Chasmogenus (*Crephelochares*) *mauritiensis* (Balfour-Browne); Hebauer 1992: 72 [taxonomic treatment]; Hebauer 2006a: 27 [checklist].

Chasmogenus mauritiensis (Balfour-Browne); Hansen 1999: 174 [catalog].

DISTRIBUTION: Afrotropical: Mauritius.

Crephelochares molinai (Hebauer, 1992) **comb. nov.**

Chasmogenus (*Crephelochares*) *molinai* Hebauer, 1992: 73 - Congo, Loudima; Hebauer 1995a: 266 [faunistic treatment]; Hebauer 2006a: 27 [checklist].

Chasmogenus molinai Hebauer; Hansen 1999: 174 [catalog].

DISTRIBUTION: Afrotropical: Democratic Republic of the Congo, Namibia.

Crephelochares mollis (Régimbart, 1903) **comb. nov.**

Philhydrus mollis Régimbart, 1903a: 32 - Madagascar, "Baie d'Antongil; pays Androy";

(specific rank confirmed by d'Orchymont, 1937d: 7; not syn. of *abnormalis* Sharp, as in Scott 1913: 205; not syn. of *livornicus* Kuwert, as in d'Orchymont 1925: 70)

Enochrus (*Lumetus*) *mollis* (Régimbart); Zaitzev, 1908: 387 [catalog].

Helochares (*Crephelochares*) *mollis* (Régimbart); d'Orchymont, 1937d: 7; d'Orchymont 1939a: 161 [taxonomic treatment]; Hebauer 1988: 157 [faunistic treatment].

Philydrus abnormalis; Scott 1913: 205 [misinterpret. of *Philydrus abnormalis* Sharp]; d'Orchymont 1939a: 161 [synonymy].

Chasmogenus (*Crephelochares*) *mollis* (Régimbart); Hebauer, 1992: 74 [taxonomic treatment]; Hebauer 2006a: 27 [checklist].

Chasmogenus mollis (Régimbart); Hansen 1999: 174 [catalog].

DISTRIBUTION: Afrotropical: Madagascar, Seychelles (Aldabra).

Crephelochares molluscus (Hebauer, 1992) comb. nov.

Chasmogenus (*Crephelochares*) *molluscus* Hebauer, 1992: 75 - Tanzania (Lake Manyara); Hebauer 2006a: 27 [checklist].

Chasmogenus molluscus Hebauer; Hansen 1999: 175 [catalog].

DISTRIBUTION: Afrotropical: Tanzania.

Crephelochares nitescens (Fauvel, 1883) comb. nov.

Philydrus nitescens Fauvel, 1883: 354 - New Caledonia (Anse Vata).

Enochrus (*Lumetus*) *nitescens* Fauvel; Zaitzev 1908: 388.

Helochares (*Crephelochares*) *nitescens* (Fauvel); d'Orchymont 1939a: 157 [taxonomic treatment].

Helochares (*Chasmogenus*) *nitescens* (Fauvel); Balfour-Browne 1945: 117 [checklist].

Chasmogenus nitescens (Fauvel); Hansen 1991: 156 [examined species]; Watts 1995: 116 [lectotype designated; redescription]; Hansen 1999: 175 [catalog]; Short (2010) [new record].

Chasmogenus (*Crephelochares*) *nitescens* (Fauvel); Hebauer 1992: 75 [taxonomic treatment].

DISTRIBUTION: Australasian: Australia (New South Wales, Northern Territory, Queensland), Fiji (Viti Levu), New Caledonia, Papua New Guinea.

Crephelochares omissus (Hebauer, 1995) comb. nov.

Chasmogenus (Crephelochares) omissus Hebauer, 1995: 266 - Namibia, East Caprivi, Mudumu National Park, Nakatwa, 18°10' S, 23°26' E; Hebauer 1995a: 266 [faunistic treatment]; Hebauer 2006a: 27 [checklist].

Chasmogenus omissus Hebauer; Hansen 1999: 175 [catalog].

DISTRIBUTION: Afrotropical: Namibia.

Crephelochares orbus (Watanabe, 1987) comb. nov.

Helochares (Crephelochares) orbus Watanabe, 1987: 12; Japan, Honshu, Gumma-ken, Tatebayashi-shi, Hanetsuku.

Chasmogenus (Crephelochares) orbus (Watanabe); Hebauer, 1992: 76 [taxonomic treatment].

Chasmogenus orbus (Watanabe); Hansen 1999: 175 [catalog]; Hansen 2004: 49 [checklist]; Fikáček et al. 2015: 61 [catalog]; Jia and Tang 2018a: 63 [new record].

DISTRIBUTION: Indo-Malayan: China (Hong Kong). Palearctic: Japan.

Crephelochares paramollis (Hebauer, 1992) **comb. nov.**

Chasmogenus (Crephelochares) paramollis Hebauer, 1992: 76 - Tanzania, Usa river; Hebauer 1995a: 266 [faunistic treatment; new records]; Hebauer 2006a: 27 [checklist; new records].

Chasmogenus paramollis Hebauer; Hansen 1999: 175 [catalog].

DISTRIBUTION: Afrotropical: Cameroon, Democratic Republic of the Congo, Gabon, Ghana, Guinea, Kenya, Namibia, South Africa [Transvaal], Zambia, Zimbabwe.

Crephelochares parorbus (Jia and Tang, 2018) **comb. nov.**

Chasmogenus parorbus Jia and Tang, 2018a: 61 - China, Yünnan Prov., Yingjiang, Tongbiguan, Kaibangyahu, 24.58°N, 97.67°E.

DISTRIBUTION: Indo-Malayan: China (Yünnan).

Crephelochares patrizii (Balfour-Browne, 1948) **comb. nov.**

Helochares (Crephelochares) patrizii Balfour-Browne, 1948: 830 - Somalia [Italian Somaliland], Giuba, Belet Amin.

Chasmogenus (Crephelochares) patrizii (Balfour-Browne); Hebauer 1992: 77 [taxonomic treatment]; Hebauer 2006a: 27 [checklist].

Chasmogenus patrizii (Balfour-Browne); Hansen 1999: 175 [catalog].

DISTRIBUTION: Afrotropical: Cameroon, Kenya, Mozambique, Somalia, South Africa, Sudan, Tanzania, Uganda, Zambia, Zimbabwe.

Crephelochares punctulatus (Short, 2010) **comb. nov.**

Chasmogenus punctulatus Short, 2010: 303 - Fiji, Viti Levu, Nadarivatu; Short and Fikáček 2011: 89 [checklist].

DISTRIBUTION: Australasian: Fiji (Viti Levu).

Crephelochares rhodesiensis (Hebauer, 2006) **comb. nov.**

Chasmogenus (Crephelochares) rhodesiensis Hebauer, 2006b: 18 - Zambia, Copperbelt, W of Kapiri Mposhi.

Chasmogenus rhodesiensis Hebauer; Short and Fikáček 2011: 89 [checklist].

DISTRIBUTION: Afrotropical: Zambia.

Crephelochares ruandanus (Balfour-Browne, 1957) **comb. nov.**

Helochares (Crephelochares) ruandanus Balfour-Browne, 1957: 22 - Rwanda, Kibuye.

Chasmogenus (Crephelochares) ruandanus (Balfour-Browne); Hebauer 1992: 78 [taxonomic treatment]; Hebauer 2006a: 27 [checklist].

Chasmogenus ruandanus (Balfour-Browne, 1957); Hansen 1999: 175 [catalog].

DISTRIBUTION: Afrotropical: Burundi, Kenya, Rwanda.

Crephelochares rubellus (Hebauer, 1992) **comb. nov.**

Chasmogenus (Crephelochares) rubellus Hebauer, 1992: 79 - Senegal, village Sare Sara, 21 km ESE Kolda; Hebauer 2006: 27 [checklist].

Chasmogenus rubellus Hebauer; Hansen 1999: 175 [catalog].

DISTRIBUTION: Afrotropical: Gambia, Senegal.

Crephelochares rubricollis (Régimbart, 1903) **comb. nov.**

Philhydrus rubricollis Régimbart, 1903b: 58 - Indonesia, Sumatra, Palembang; (specific rank confirmed by d'Orchymont, 1925: 71; not syn. of *abnormalis* Kuwert, as in Knisch 1921: 68).

Enochrus (*Lumetus*) *rubricollis* (Régimbart); Zaitzev 1908: 389.

Helochares (*Chasmogenus*) *rubricollis* (Régimbart); d'Orchymont 1925: 71 [taxonomic treatment].

Helochares (Crephelochares) rubricollis (Régimbart); d'Orchymont 1939a: 162 [taxonomic treatment].

Chasmogenus (Crephelochares) rubricollis (Régimbart); Hebauer 1992: 79 [taxonomic treatment].

Helochares (*Chasmogenus*) *abnormalis*; Knisch 1921: 68; misinterpret. of *Philydrus abnormalis* Sharp; d'Orchymont, 1939a: 162 [synonymy].

Chasmogenus rubricollis (Régimbart); Hansen 1999: 175 [catalog].

DISTRIBUTION: Indo-Malayan: Indonesia (Borneo, Sumatra).

Crephelochares rudis (Hebauer, 1992) **comb. nov.**

Chasmogenus (Crephelochares) rudis Hebauer, 1992: 80 - Congo, Kindamba, Meya, Bangou forest; Hebauer 2006a: 27 [checklist].

Chasmogenus rudis Hebauer; Hansen 1999: 175 [catalog].

DISTRIBUTION: Afrotropical: Congo [Kindamba locality in both Democratic Republic of the Congo and Republic of the Congo].

Crephelochares rusticus (d'Orchymont, 1939) **comb. nov.**

Helochares (Crephelochares) rusticus d'Orchymont, 1939a: 165 - Gabon.

Chasmogenus (Crephelochares) rusticus (d'Orchymont); Hebauer 1992: 81 [taxonomic treatment]; Hebauer 2006: 27 [checklist].

Chasmogenus rusticus (d'Orchymont); Hansen 1999: 175 [catalog].

DISTRIBUTION: Afrotropical: Gabon, Ghana.

Crephelochares rutiloides (d'Orchymont, 1939) **comb. nov.**

Helochares (Crephelochares) rutiloides d'Orchymont, 1939a: 323 - Gabon.

Chasmogenus (Crephelochares) rutiloides (d'Orchymont); Hebauer 1992: 82 [taxonomic treatment]; Hebauer 1995a: 266 [faunistic treatment]; Hebauer 2006: 27 [checklist].

Chasmogenus rutiloides (d'Orchymont); Hansen 1999: 175 [catalog].

DISTRIBUTION: Afrotropical: Botswana, Cameroon, Democratic Republic of the Congo, Gabon, Gambia, Ghana, Namibia, Zambia.

Crephelochares rutilus (d'Orchymont, 1925) **comb. nov.**

Helochares (*Chasmogenus*) *rutilus* d'Orchymont, 1925: 71. - Gabon; d'Orchymont 1939a: 163 [taxonomic treatment].

Helochares (Crephelochares) rutilus d'Orchymont; d'Orchymont 1928: 107 [faunistic treatment]; d'Orchymont 1937d: 7 [checklist].

Chasmogenus (Crephelochares) rutilus (d'Orchymont); Hebauer 1992: 82 [new combination; taxonomic treatment]; Hebauer 2006: 27 [checklist; new records].

Chasmogenus rutilus (d'Orchymont); Hansen 1991: 156 [examined species]; Hansen 1999: 176 [catalog].

Helochares (*Chasmogenus*) *abnormalis* Sharp; Knisch 1921a: 68 [misinterpretation of *Philydrus abnormalis* Sharp]; d'Orchymont, 1939a: 163 [synonymy].

DISTRIBUTION: Afrotropical: Cameroon, Democratic Republic of the Congo, Gabon, Ghana, Nigeria, South Africa.

Crephelochares szeli (Hebauer, 1992) **comb. nov.**

Chasmogenus (Crephelochares) szeli Hebauer, 1992: 84 - Ghana, Ashanti region, Kumashi, Nhiasu, 6°43'N, 1°36'W; Hebauer 2006: 27 [checklist; new records].

Chasmogenus szeli Hebauer; Hansen 1999: 176 [catalog].

DISTRIBUTION: Afrotropical: Democratic Republic of the Congo, Ghana, Liberia, Nigeria, Sierra Leone, Uganda.

Crucisternum Girón and Short, 2018

Crucisternum escalera Girón and Short 2018

Crucisternum escalera Girón and Short 2018: 120 - Venezuela, Bolívar State, along La Escalera, 6°2'10.5"N, 61°23'57.8"W.

DISTRIBUTION: Neotropical: Venezuela.

Crucisternum ouboteri Girón and Short 2018

Crucisternum ouboteri Girón and Short 2018: 121 - Suriname, Sipaliwini District, Brownsberg Nature Park, 04°56.871'N, 55°10.911'W.

DISTRIBUTION: Neotropical: French Guiana, Guyana, Suriname, Venezuela.

Crucisternum queneyi Girón and Short 2018

Crucisternum queneyi Girón and Short 2018: 123 - French Guiana, Sinnamary.

DISTRIBUTION: Neotropical: French Guiana.

Crucisternum sinuatus Girón and Short 2018

Crucisternum sinuatus Girón and Short 2018: 124 - Brazil, Minas Gerais, Lassance, Cachoeira da Palmeira, -17.83384, -44.50515.

DISTRIBUTION: Neotropical: Brazil (Minas Gerais, Pará).

Crucisternum toboganensis Girón and Short 2018

Crucisternum toboganensis Girón and Short 2018: 126 - Venezuela, Amazonas, Puerto Ayacucho (40 km S), El Tobogán, Caño Coromoto.

DISTRIBUTION: Neotropical: Venezuela.

Crucisternum vanessae Girón and Short 2018

Crucisternum vanessae Girón and Short 2018: 127 - Suriname, Sipaliwini District, Central Suriname Nature Reseserve: Tafelberg Summit, near Caiman Creek Camp, N3°53.942' W56°10.849'.

DISTRIBUTION: Neotropical: Suriname.

Crucisternum xingu Girón and Short 2018

Crucisternum xingu Girón and Short 2018: 131 - Brazil, Pará, Rio Xingu Camp, ca 60km S Altamira, 52°22'W, 3°39'S.

DISTRIBUTION: Neotropical: Brazil (Pará).

Ephydrolithus Girón and Short, 2019

Ephydrolithus hamadae Girón and Short, 2019

Ephydrolithus hamadae Girón and Short, 2019: 130 - Brazil, Minas Gerais, Lassance, Cachoeira da Palmeira; 17.83384S, 44.50515W.

DISTRIBUTION: Neotropical: Brazil (Minas Gerais).

Ephydrolithus minor Girón and Short, 2019

Ephydrolithus minor Girón and Short, 2019: 130 - Brazil, Bahia, Abaíra, Pico do Barbado W of Catolés, 13.29053S, 41.90489W.

DISTRIBUTION: Neotropical: Brazil (Bahia).

Ephydrolithus ogmos Girón and Short, 2019

Ephydrolithus ogmos Girón and Short, 2019: 131- Brazil, Brazil, Bahia, Abaíra, Pico do Barbado W of Catolés, 13.29053S, 41.90489W.

DISTRIBUTION: Neotropical: Brazil (Bahia).

Ephydrolithus spiculatus Girón and Short, 2019

Ephydrolithus spiculatus Girón and Short, 2019: 132 - Brazil, Minas Gerais, Lassance, Cachoeira da Palmeira, 17.83384S, 44.50515W.

DISTRIBUTION: Neotropical: Brazil (Minas Gerais).

Ephydrolithus teli Girón and Short, 2019

Ephydrolithus teli Girón and Short, 2019: 132 - Brazil, Bahia, Abaíra, Pico do Barbado, W of Catolés; 13.29053S, 41.90489W.

DISTRIBUTION: Neotropical: Brazil (Bahia, Minas Gerais).

Globulosis García, 2001

Globulosis hemisphericus García, 2001

Globulosis hemisphericus García, 2001: 156 - Venezuela, Bolívar, Municipio Sifontes, Tierra Blanca Pantano; Short et al. 2017: 275 [new records].

Globulosis hemisphaericus García [incorrect subsequent spelling]; Short and Hebauer 2006: 338 [catalog].

Globulosis sp. 1 Short and Kadosoe 2011: 89 [checklist]; Short 2013: 87 [checklist].

DISTRIBUTION: Neotropical: Venezuela, Guyana, Suriname, Brazil (Amazonas, Pará).

Globulosis flavus Short, García, and Girón, 2017

Globulosis flavus Short, García, and Girón, 2017: 277 - Venezuela, Amazonas State, nr. Iboruwa: "Tobogancito", 5 48.141'N, 67 26.313'W

DISTRIBUTION: Neotropical: Venezuela.

Helobata Bergroth, 1888

Helobata amazonensis Clarkson, Dias Dos Santos, and Ferreira-Jr, 2016

Helobata amazonensis Clarkson, Dias Dos Santos, and Ferreira-Jr, 2016: 550 - Brazil, Amazonas, Itacoatiara, Ilha da Trinidade.

DISTRIBUTION: Neotropical: Brazil (Amazonas).

Helobata aschnakiranae Makhan, 2007

Helobata aschnakiranae Makhan, 2007: 1 - Suriname (Niew Amsterdam); Short and Fikáček 2011: 90 [catalog].

DISTRIBUTION: Neotropical: Suriname.

Helobata bitriangulata García, 2000

Helobata bitriangulata García, 2000c: 244 - Venezuela, Apure State, Achaguas, Samán de Apure; Short and Hebauer 2006: 335 [catalog].

DISTRIBUTION: Neotropical: Venezuela.

Helobata confusa Fernández and Bachmann, 1987

Helobata confusa Fernández and Bachmann, 1987: 155 - Paraguay (Asunción); Hansen 1999b: 173 [catalog].

DISTRIBUTION: Neotropical: Argentina, Paraguay.

Helobata corumbaensis Fernández and Bachmann, 1987

Helobata corumbaensis Fernández and Bachmann, 1987: 155 - Brazil (Mato Grosso, Corumbá); Hansen 1999b: 173 [catalog]; Clarkson et al. 2016: 555 [taxonomic treatment].

DISTRIBUTION: Neotropical: Brazil (Mato Grosso, Mato Grosso do Sul).

Helobata cossyphoides (Bruch, 1915)

Helopeltis cossyphoides Bruch, 1915: 458 - Argentina, Buenos Aires Province, La Plata, "Tiro Federal"; Fernández and Bachmann 1987: 153 [lectotype designation].

Helobata cossyphoides (Bruch, 1915); Fernández and Bachmann 1987: 151 (specific rank confirmed; not synonym of *striata* Brullé (= *larvalis* Horn), as in Knisch, 1924a: 223); Hansen 1999b: 173 [catalog].

DISTRIBUTION: Neotropical: Argentina.

Helobata cuivaum García, 2000

Helobata cuivaum García, 2000c: 242 - Venezuela (Apure State, Achaguas, Samán de Apure); Short and Hebauer 2006: 335 [catalog].

DISTRIBUTION: Neotropical: Venezuela.

Helobata larvalis (Horn, 1873)

Helopeltis larvalis Horn, 1873: 137 - U.S.A. (Louisiana, California (Sonora)).

Helopeltina larvalis (Horn); Cockerell 1906a: 240.

Helobata larvalis (Horn); Cockerell, 1906b: 349; Hansen 1991: 293 [reinstated as valid name]; Jasper and Vogtsberger 1996: 56 [checklist]; Clarkson et al. 2016: 557 [taxonomic treatment].

Hydrophilus (*Philydrus*) *striatus* Brullé, 1841: 58 (primary homonym of *Hydrophilus striatus* Turton, 1802 and *Hydrophilus striatus* Say, 1825).

Helopeltis striatus (Brullé); Bedel 1881b: XCIV [new combination].

Enochrus (*Lumetus*) *striatus* (Brullé); Zaitzev 1908: 389 [checklist].

Helobata striata (Brullé); Knisch, 1924a: 223 [catalog]; Fernández and Bachmann 1987: 53 [taxonomic treatment].

DISTRIBUTION: Neotropical: Argentina, Bolivia, Brazil (Amazonas, Ceará, Corumbá, Mato Grosso, Mato Grosso do Sul), Cuba, Guatemala, Mexico, Paraguay, Venezuela. Nearctic: U.S.A. (California, Florida, Louisiana, Mississippi, North Carolina, South Carolina, Texas, Virginia).

Helobata lilianae García, 2000

Helobata lilianae García, 2000c: 239 - Venezuela, Apure State, Achaguas, Saman de Apure; Short and Hebauer 2006: 335 [catalog].

DISTRIBUTION: Neotropical: Venezuela.

Helobata pantaneira Clarkson, Dias Dos Santos, and Ferreira-Jr, 2016

Helobata pantaneira Clarkson, Dias Dos Santos, and Ferreira-Jr, 2016: 553 - Brazil, Mato Grosso, Poconé.

DISTRIBUTION: Neotropical: Brazil (Mato Grosso).

Helobata perpunctata Fernández and Bachmann, 1987

Helobata perpunctata Fernández and Bachmann, 1987: 156 - Argentina (Chaco Province, San Bernardo); Hansen 1999b: 173.

DISTRIBUTION: Neotropical: Argentina.

Helobata quatipuru Fernández and Bachmann, 1987

Helobata quatipuru Fernández and Bachmann, 1987: 158 - Brazil, Pará State, Quatipurú; Hansen 1999b: 173 [catalog]; Clarkson et al. 2016: 558 [taxonomic treatment].

DISTRIBUTION: Neotropical: Brazil (Pará, Rio de Janeiro).

Helobata soesilae Makhan, 2007

Helobata soesilae Makhan, 2007: 3 - Suriname, Niew Amsterdam; Short and Fikáček 2011: 90 [catalog].

DISTRIBUTION: Neotropical: Suriname.

Helochares Mulsant, 1844

Helochares aeacus Balfour-Browne, 1952

Helochares aeacus Balfour-Browne, 1952b: 515 - Mauritania, “Hamdoun”.

Helochares (*Hydrobaticus*) *aeacus* Balfour-Browne; Hebauer 1996: 11 [listed]; Hansen 1999b: 164 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Mauritania.

Helochares aethiopicus d’Orchymont, 1939

Helochares (*Hydrobaticus*) *aethiopicus* d’Orchymont, 1939c: 309 - Ethiopia [“Abyssinie”]; Hebauer 1996: 11 [taxonomic treatment]; Hansen 1999b: 164 [catalog]; Hebauer 2006: 26 [checklist]; Salah and Régil Cueto 2017: 270 [excluded from Egypt checklist].

DISTRIBUTION: Afrotropical: Ethiopia.

Helochares alberti d’Orchymont, 1943

Helochares (*Hydrobaticus*) *alberti* d’Orchymont, 1943a: 10 - Zaire [Congo belge], Madimba; Hebauer 1996: 11 [taxonomic treatment]; Hansen 1999b: 164 [catalog]; Hebauer 2006a: 26 [checklist].

DISTRIBUTION: Afrotropical: Democratic Republic of the Congo [Zaire], Gabon, Republic of the Congo, "West Africa (Uelleburg)".

Helochares alcimus d'Orchymont, 1943

Helochares (*Hydrobaticus*) *alcimus* d'Orchymont, 1943a: 12 - Democratic Republic of the Congo [Zaire; Congo belge], Haut Uélé, Yebo (Moto); Hebauer 1996: 11 [listed]; Hansen 1999b: 164 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Democratic Republic of the Congo [Zaire].

Remarks: Based on the general description and the male genitalia drawing presented by d'Orchymont (1943a: 11), this species likely belongs in *Agraphydrus*.

Helochares alcinous Balfour-Browne, 1948: 831

Helochares (*Hydrobaticus*) *alcinöus* Balfour-Browne, 1948b: 831 - Kenya, Mombasa; Hebauer 1996: 11 [listed]; Hansen 1999b: 164 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Kenya, Tanzania.

Helochares altus d'Orchymont, 1943

Helochares (*Hydrobaticus*) *altus* d'Orchymont, 1943f: 5 - India, Tamil Nadu, Nilgiri, southern border of Lake Oatacamund; Hansen 1999b: 164 [catalog].

DISTRIBUTION: Indo-Malayan: India (Tamil Nadu).

Helochares anchoralis Sharp, 1890

Helochares anchoralis Sharp, 1890: 352 - Sri Lanka [Ceylon], Colombo; Gentili et al. 1995: 211 [checklist].

Helochares (Grapidelochares) anchoralis Sharp; Zaitzev 1908: 381 [catalog].

Helochares (*Hydrobaticus*) *anchoralis* Sharp; d'Orchymont 1923a: 9 [faunistic treatment]; d'Orchymont 1928: 105 [faunistic treatment]; d'Orchymont 1943a: 6 [faunistic treatment]; Hebauer 1995b: 4 [faunistic treatment]; Hansen 1999b: 164 [catalog]; Hebauer 2002a: 23 [new record]; Hebauer and Ryndevich 2005: 45 [new record].

Helochares (Hydrovaticus) anchoralis Sharp; Matsui 1995: 320 [new record; misspelled subgenus name; year in error].

DISTRIBUTION: Indo-Malayan: Bangladesh, Cambodia, China (Fujian, Hainan, Yünnan), India, Indonesia (Sumatra), Laos, Philippines, Sri Lanka, Taiwan, Thailand, Vietnam. Palearctic: China (Hubei), Japan.

Helochares anchoralis* ssp. *expansus Knisch, 1921

Helochares (*Hydrobaticus*) *crenatus* ssp. *expansus* Knisch, 1921: 67 - New Guinea.

Helochares (*Hydrobaticus*) *anchoralis* ssp. *expansus* Knisch; d'Orchymont 1943a: 6 [taxonomic treatment]; Hansen 1999b: 164 [catalog]; Hansen 2004: 52 [checklist]; Fikáček et al. 2015: 62 [catalog].

Helochares (*Hydrobaticus*) *anchoralis* Sharp; Watts 1995: 119 [faunistic treatment].

DISTRIBUTION: Australasian: Papua New Guinea.

Helochares ancoroides Hebauer, 2001

Helochares (*Hydrobaticus*) *ancoroides* Hebauer 2001a: 13 - Indonesia, Papua, [W. Neuguinea], Paniai Province, Wanggar-Kali Bumi, IR 14; Short and Hebauer 2006: 335 [catalog].

DISTRIBUTION: Indo-Malayan: Indonesia (Papua).

Helochares andreinii d'Orchymont, 1939

Helochares (*Hydrobaticus*) *andreinii* d'Orchymont, 1939f: 320 - Eritrea, Sabarguma; Balfour-Browne 1951: 212 [new records]; Hebauer 1997: 263 [new record]; Hansen 1999b: 165 [catalog]; Hansen 2004: 52 [checklist]; Fikáček et al. 2015: 62 [catalog].

Helochares (*Hydrobaticus*) *andreini* d'Orchymont; Hebauer 1996: 11 [listed; misspelled]; Hebauer 2006: 26 [checklist; new record; misspelled].

DISTRIBUTION: Afrotropical: Eritrea, Oman, Saudi Arabia, Yemen, Zimbabwe.

Helochares androgynus Hebauer, 1996

Helochares (*Hydrobaticus*) *androgynus* Hebauer, 1996: 11 - Tanzania ["Tanganyika"], 2 mi to Lake Manyara, SE shore; Hansen 1999b: 165 [catalog]; Hebauer 2006: 26 [new records].

DISTRIBUTION: Afrotropical: South Africa, Tanzania, Zambia.

Helochares anthonyae Watts, 1995

Helochares (*Hydrobaticus*) *anthonyae* Watts, 1995: 120 - Papua New Guinea, Morobe District, 11 km Lae-Bulolo Rd.; Hansen 1999b: 165 [catalog].

DISTRIBUTION: Australasian: Australia (Northern Territory), Papua New Guinea.

Helochares balfourbrownei Hansen, 1999: 165

Helochares (*Hydrobaticus*) *balfourbrownei* Hansen, 1999b: 165 [nomen novum]; Hebauer 2006: 26 [checklist].

Helochares (*Hydrobaticus*) *rusticus* Balfour-Browne, 1952a: 132 - Ivory Coast, River Lerabara; (primary homonym of *Helochares rusticus* d'Orchymont, 1939 - currently in *Crephelochares*); Balfour-Browne 1959: 311 [faunistic treatment]; Hebauer 1996: 21 [new records].

DISTRIBUTION: Afrotropical: Benin, Burkina Faso, Ghana, Guinea, Ivory Coast, Liberia, Nigeria, Senegal, Sierra Leone.

Helochares basilewskyi Balfour-Browne, 1957

Helochares (*Hydrobaticus*) *basilewskyi* Balfour-Browne, 1957: 23 - Rwanda, Rutovu, forêt du Rugege; Hebauer 1996: 12 [faunistic treatment]; Hansen 1999b: 165 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Rwanda.

Helochares bilardoi Hebauer, 2009

Helochares (*Hydrobaticus*) *bilardoi* Hebauer, 2009: 4 - Gabon, Monts de Cristal National Park, Andok Village, Foula; Short and Fikáček 2011: 90 [catalog].

DISTRIBUTION: Afrotropical: Gabon.

Helochares blaesus d'Orchymont, 1936

Helochares (*Hydrobaticus*) *blaesus* d'Orchymont, 1936b: 111 (112) - Botswana [Kalahari], Tsotsoroga Pan; Hebauer 1995a: 262 [faunistic treatment]; Hebauer 1996: 12 [faunistic treatment]; Hansen 1999b: 165 [catalog]; Hebauer 2005: 39 [checklist], 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Botswana [Kalahari], Democratic Republic of the Congo, Ethiopia, Kenya, Malawi, Mozambique, Namibia, South Africa.

Helochares bohemani d'Orchymont, 1936

Helochares (*Hydrobaticus*) *bohemani* d'Orchymont, 1936b: 111 - Namibia ["South-West Africa"], Eenfelsbach 25 km SSE Okahandja; Hebauer 1995a: 262 [faunistic treatment]; Hebauer 1996: 12 [faunistic treatment; new records]; Hansen 1999b: 165 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Angola, Botswana, Cameroon, Ethiopia, Kenya, Madagascar, Namibia, South Africa, Zambia, Zimbabwe.

Helochares camerunensis d'Orchymont, 1939

Helochares (*Hydrobaticus*) *camerunensis* d'Orchymont, 1939e: 303 - Cameroon, Douala [Duala]; Balfour-Browne 1952a: 130 [faunistic treatment]; Hebauer 1996: 13 [faunistic treatment]; Hansen 1999b: 165 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Benin, Cameroon, Democratic Republic of the Congo, Gabon, Gambia, Ghana, Guinea, Ivory Coast, Nigeria, Republic of the Congo, Senegal.

Helochares cancellatus Hebauer, 1998

Helochares (*Hydrobaticus*) *cancellatus* Hebauer, 1998: 42 - Sri Lanka [Ceylon], Labugama, 24 mi ESE of Colombo; Hansen 1999b: 165 [catalog].

DISTRIBUTION: Indo-Malayan: Sri Lanka.

Helochares championi Sharp, 1882

Helochares (*Hydrobaticus*) *championi* Sharp, 1882: 75 - Guatemala (Guatemala City, Dueñas, San Géronimo) and Nicaragua (Chontales); Balfour-Browne, 1939: 293 [faunistic treatment]; Hansen 1999b: 165; Short 2005: 217 [faunistic treatment]; Short and Girón 2018: 34 [new record; faunistic treatment].

DISTRIBUTION: Neotropical: Costa Rica, Guatemala, Nicaragua.

Helochares chappuisi Balfour-Browne, 1952

Helochares (*Hydrobaticus*) *chappuisi* Balfour-Browne, 1952a: 132; Hansen 1999b: 165 [catalog].

Helochares (*Hydrobaticus*) *chappiusi* Balfour-Browne; Hebauer 1996: 13 [listed; misspelled]; Hebauer 2006: 26 [listed; misspelled].

DISTRIBUTION: Afrotropical: Benin, Mali, Niger.

Helochares clypeatus (Blackburn, 1891)

Hydrobaticus clypeatus Blackburn, 1891a: 305 - Australia, Northern Territory, Burrundie.

Helochares (*Hydrobaticus*) *clypeatus* (Blackburn); Knisch 1924a: 193 [catalog]; d'Orchymont 1943a: 4 [faunistic treatment]; Watts 1995: 120 [redescription]; Hansen 1999b: 165 [catalog].

DISTRIBUTION: Australasian: Australia (New South Wales, Northern Territory, Queensland, Western Australia).

Helochares collarti d'Orchymont, 1939

Helochares (*Hydrobaticus*) *collarti* d'Orchymont, 1939b: 315 - Democratic Republic of the Congo [Congo belge; Zaire], Blukwa; Balfour-Browne 1950b: 56 [faunistic treatment]; Hebauer 1996: 13 [new record]; Hansen 1999: 165 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Democratic Republic of the Congo, Rwanda.

Helochares compactus Hebauer, 2001

Helochares (*Hydrobaticus*) *compactus* Hebauer 2001: 13 - Indonesia, Papua [Irian Jaya], Paniai Province, Nabire - Kali Bobo; Short and Hebauer 2006: 336 [catalog].

DISTRIBUTION: Indo-Malayan: Indonesia (Papua).

Helochares conformis Hebauer, 1995

Helochares (*Hydrobaticus*) *conformis* Hebauer, 1995a: 263 - Namibia, East Caprivi, Katima Mulilo, 17°29'S 24°17'E; Hebauer 1996: 13 [faunistic treatment]; Hansen 1999b: [catalog]; Hebauer 2006: 26 [new records].

DISTRIBUTION: Afrotropical: Namibia, South Africa, Zambia, Zimbabwe.

Helochares congoensis d'Orchymont, 1939

Helochares (*Hydrobaticus*) *congoensis* d'Orchymont, 1939b: 304 - Democratic Republic of the Congo [Congo belge; Zaire], Boma; Hebauer 1996: 13 [faunistic treatment]; Hansen 1999b: 165 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Democratic Republic of the Congo.

Helochares congruens d'Orchymont, 1939

Helochares (*Hydrobaticus*) *congruens* d'Orchymont, 1939b: 304 - Senegal, Thiès; Hebauer 1988: 156 [faunistic treatment]; Hebauer 1996: 13 [faunistic treatment]; Hansen 1999b: 166 [catalog]; Hebauer 2005: 39 [checklist]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Democratic Republic of the Congo, Ghana, Kenya [in doubt], Madagascar, Malawi, Namibia, Senegal, South Africa, Tanzania, Uganda, Zambia [in doubt], Zimbabwe.

Helochares conjectus d'Orchymont, 1939

Helochares (*Hydrobaticus*) *conjectus* d'Orchymont, 1939b: 305 - Tanzania, Lake Victoria, Ukerewe I.; Balfour-Browne 1950a: 394 [faunistic treatment]; Hebauer 1996: 13 [faunistic treatment]; Hebauer 1996: 14 [faunistic treatment]; Hansen 1999b: 166 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Ethiopia, Tanzania, Zambia, Zimbabwe.

Helochares crenatostriatus Régimbart, 1903

Helochares (*Graphelochares*) *melanophthalmus* var. *crenatostriatus* Régimbart, 1903a: 28. - Madagascar; Seychelles (Aldabra).

Helochares (*Hydrobaticus*) *crenatostriatus* Régimbart; d'Orchymont, 1939e: 298; Hebauer 1996: 14 [faunistic treatment]; Hebauer 1996: 14 [faunistic treatment]; Hansen 1999b: 166 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Cameroon, Gabon, Ghana, Kenya [in doubt], Madagascar, Republic of the Congo, Seychelles (Aldabra).

Helochares crenatuloides d'Orchymont, 1943

Helochares (*Hydrobaticus*) *crenatuloides* d'Orchymont, 1943e: 2 - India, "Bengal, Tetara"; Hebauer 1997: 263; Hansen 1999b: 166 [catalog]; Hansen 2004: 52 [checklist]; Fikáček et al. 2010: 151 [new record]; Fikáček et al. 2015: 62 [catalog]; Ribera et al. 2019: 264 [faunistic treatment].

DISTRIBUTION: Afrotropical: Oman, United Arab Emirates. Indo-Malayan: India ("Bengal", Madhya Pradesh, Uttar Pradesh).

Helochares crenatus Régimbart, 1903

Helochares (*Graphelochares*) *crenatus* Régimbart, 1903b: 54 - India, Tamil Nadu, Pondicherry; d'Orchymont 1940: 168 [lectotype designation].

Helochares (*Hydrobaticus*) *crenatus* Régimbart; d'Orchymont, 1923a: 9 [faunistic treatment]; d'Orchymont 1928: 105 [faunistic treatment]; Hebauer, 1995b: 4 [faunistic treatment]; Hansen 1999b: 166 [catalog]; Hansen 2004: 52 [checklist]; Fikáček et al. 2015: 62 [catalog].

Helochares crenatus Régimbart; Gentili et al. 1995: 211 [checklist].

DISTRIBUTION: Indo-Malayan: China (Yünnan), India (Tamil Nadu, West Bengal), Thailand.

Helochares crepitus Balfour-Browne, 1950

Helochares (*Hydrobaticus*) *crepitus* Balfour-Browne, 1950a: 395 - Zambia ["Northern Rhodesia"], "Mwengwa"; Balfour-Browne 1950a: 395 [faunistic treatment]; Hebauer 1996: 14 [faunistic treatment]; Hansen 1999b: 166 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Ghana, Tanzania, Zambia.

Helochares cresphontes d'Orchymont, 1939

Helochares (*Hydrobaticus*) *cresphontes* d'Orchymont, 1939b: 313 - Uganda, Kampala; Balfour-Browne 1957: 23 [faunistic treatment]; Hebauer 1996: 14 [faunistic treatment]; Hansen 1999b: 166 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Ghana, Rwanda, Tanzania, Uganda.

Helochares crespulus d'Orchymont, 1939

Helochares (*Hydrobaticus*) *crespulus* d'Orchymont, 1939b: 313 - Zaire ["Congo belge"], Haut Uélé, Watsa; Hebauer 1996: 14 [listed]; Hansen 1999b: 166 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Democratic Republic of the Congo, Gabon.

Helochares crispus d'Orchymont, 1939

Helochares (*Hydrobaticus*) *crispus* d'Orchymont, 1939b: 311 - "Zanguebar"; Hebauer 1996: 14 [faunistic treatment]; Hansen 1999b: 166 [catalog]; Hebauer 2005: 39 [new record]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Ethiopia, Kenya, Malawi, Namibia, South Africa, Rwanda, Tanzania, Zimbabwe.

Helochares dalhuntyi Watts, 1995

Helochares (*Hydrobaticus*) *dalhuntyi* Watts, 1995: 121 - Australia, Queensland, Dalhunty River.

Helochares (*Hydrobaticus*) *anthonyae* Watts; Hansen 1999b: 166 [synonym in error].

DISTRIBUTION: Australasian: Australia (Northern Territory, Queensland).

Helochares densepunctus Régimbart, 1907

Helochares densepunctus Régimbart, 1907a: 48 - Guinea Bissau [Guinée Portugaise] (Bolama); Madagascar (Helodrano Antongila [Baie d'Antongil]; "Pays Androy".

Helochares (*Hydrobaticus*) *densepunctatus* Régimbart; Knisch 1924: 193 [catalog; misspelled]; Hebauer 1996: 14 [faunistic treatment; misspelled].

Helochares (*Hydrobaticus*) *densepunctus* Régimbart; Hansen 1999: 166 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Cameroon, Gabon, Gambia, Guinea, Guinea Bissau, Ivory Coast, Kenya, Liberia, Madagascar, Senegal, Tanzania, Zambia.

Helochares densus Sharp, 1890

Helochares densus Sharp, 1890: 352 - Sri Lanka [Ceylon]: Kandy; Dikoya; Bogawantalawa; d'Orchymont 1943e: 7 [specific rank confirmed: not syn. of *lentus* Sharp, as in Zaitzev 1908: 381 (as syn. dub.) and d'Orchymont 1913a: 5].

Helochares (*Hydrobaticus*) *densus* Sharp; d'Orchymont 1923a: 9 [faunistic treatment]; d'Orchymont 1943e: 7 [faunistic treatment]; Hebauer 1995b: 4 [faunistic treatment]; Hansen 1999b: 166 [catalog]; Hebauer 2002a: 23 [new record]; Hansen 2004: 52 [checklist]; Fikáček et al. 2015: 62 [catalog].

DISTRIBUTION: Indo-Malayan: China (Guangdong, Hainan), India (Andaman Is., "Bengal", Madhya Pradesh, Nicobar Is., Tamil Nadu, Uttarakhand, Uttar Pradesh), Nepal, Thailand, Vietnam.

Helochares dentalus d'Orchymont, 1943

Helochares (*Hydrobaticus*) *dentalus* d'Orchymont, 1943e: 8 - Malaysia, Sabah ["Borneo septentrional"], Bettotan nr Sandakan; Hansen 1999b: 166 [catalog].

DISTRIBUTION: Indo-Malayan: Malaysia (Sabah).

Helochares denudatus d'Orchymont, 1943

Helochares (*Hydrobaticus*) *denudatus* d'Orchymont, 1943e: 9 - Indonesia, Sumatra, Bedagei NE of Tebingtinggi; Hansen 1999b: 166 [catalog].

DISTRIBUTION: Indo-Malayan: Indonesia (Sumatra), Malaysia (Peninsula).

Helochares depactus d'Orchymont, 1939

Helochares (*Hydrobaticus*) *depactus* d'Orchymont, 1939e: 302 - Kenya, Aberdare Ra. (eastside), Kigangop; Hebauer 1996: 15 [faunistic treatment]; Hansen 1999b: 167 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Kenya.

Helochares diductus d'Orchymont, 1939

Helochares (*Hydrobaticus*) *diductus* d'Orchymont, 1939e: 318 - Gabon, Cape Lopez; Hebauer 1996: 15 [faunistic treatment]; Hansen 1999b: 167 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Gabon.

Remarks: Based on original description, probably *Agraphydrus*: small size, pronotal punctures of two different sizes; aedeagus with median lobe spatulate, arched on the sides and truncated in a straight line at apex.

Helochares didymoides Balfour-Browne, 1947

Helochares (*Hydrobaticus*) *didymoides* Balfour-Browne, 1947: 141 - Sudan, Didinga Hills, Nagishot; Hebauer 1996: 15 [faunistic treatment]; Hansen 1999b: 167; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Cameroon, Gabon, Sudan.

Helochares didymus d'Orchymont, 1939

Helochares (*Hydrobaticus*) *didymus* d'Orchymont, 1939b: 318 - Uganda, Kampala; Hebauer 1996: 15 [faunistic treatment]; Hansen 1999b: 167 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Cameroon, Democratic Republic of the Congo, Gabon, Ghana, Guinea, Kenya, Republic of the Congo, Uganda.

Helochares difficilis d'Orchymont, 1939

Helochares (*Hydrobaticus*) *difficilis* d'Orchymont, 1939b: 314 - Uganda (central), "rivière Kizoungou"; Hebauer 1996: 15 [faunistic treatment]; Hansen 1999b: 167 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Democratic Republic of the Congo [Zaire], Kenya, Sudan, Tanzania, Uganda, Zambia.

Helochares dilutus (Erichson, 1843)

Hydrobius dilutus Erichson, 1843: 228 - Angola, Benguela; d'Orchymont, 1943c: 1 [specific rank confirmed: not syn. of *lividus* Forster, as in Bedel 1881a: 330).

Philhydrus dilutus (Erichson); Gemminger and Harold 1868: 481 [catalog].

Helochares dilutus (Erichson); Reiche and Saulcy 1856: 358 [faunistic treatment]; Heyden 1891: 67 [catalog].

Helochares (s. str.) *dilutus* (Erichson); d'Orchymont, 1943c: 1 [taxonomic treatment]; Balfour-Browne 1950a: 393 [faunistic treatment]; Balfour-Browne 1950b: 59 [faunistic treatment]; Balfour-Browne 1957: 21 [faunistic treatment]; Hebauer 1988: 156 [faunistic treatment]; Hebauer 1995a: 264 [faunistic treatment]; Hebauer 1996: 5 [faunistic treatment]; Hansen 1999b: 160 [catalog]; Hebauer 2005: 39 [new record]; Hebauer 2006: 25 [checklist]; Fikáček et al. 2015: 61 [catalog; new record].

Helochares niloticus Sharp, 1903: 7 - Sudan, Jebel Ahmed Agha [Gebel Ahmed Agha]; d'Orchymont, 1943c: 1 [synonymy].

DISTRIBUTION: Afrotropical: Angola, Botswana, Cameroon, Democratic Republic of the Congo, Ethiopia, Gambia, Ghana, Ivory Coast, Kenya, Liberia, Madagascar, Malawi, Mauritius (incl. Rodrigues), Mozambique, Namibia, Republic of the Congo, Réunion, Rwanda, Senegal, South Africa, Sudan, Tanzania, Uganda, Yemen (Socotra), Zambia, Zimbabwe.

Helochares dilutus* ssp. *consputus Boheman, 1851

Hydrobius consputus Boheman, 1851: 598 - South Africa [Caffraria], Orange river reg. [regione fluvii Gariepis]; Hebauer 1988: 156 [as synonym of *dilutus* Erichson]; Hebauer 1996: 5 [as synonym of *dilutus* Erichson].

Helochares consputus (Boheman); Bedel 1880: CXLVIII [new combination].

Enochrus (*Lumetus*) *consputus* (Boheman); Knisch 1924: 208 [catalog].

Helochares (s. str.) *dilutus consputus* (Boheman); d'Orchymont 1943c: 6 [taxonomic treatment]; Hansen 1999b: 160 [catalog]; Salah and Régil Cueto 2017: 269 [excluded from Egypt checklist].

Helochares variabilis Régimbart, 1903a: 25. - Madagascar, pays Androy, Fort-Dauphin, bassin du Mandraré, Centre-Sud, forêts de la côte Est, Tananarive, baie d'Antongil; Mascarene Is., Réunion (Salazie); d'Orchymont, 1926b: 232 [synonymy].

DISTRIBUTION: Afrotropical: Madagascar, Mauritius (Mascarene Is.), Namibia, South Africa.

Helochares dimorphus d'Orchymont, 1939

Helochares (*Hydrobaticus*) *dimorphus* d'Orchymont, 1939e: 322 - Democratic Republic of the Congo [Congo belge; Zaire], Lower Uele, Buta; Balfour-Browne 1950b: 57 [faunistic treatment]; Hebauer 1996: 15 [faunistic treatment]; Hansen 1999b: 167 [catalog]; Hebauer 2006: 26 [checklist; new records].

DISTRIBUTION: Afrotropical: Cameroon [in doubt]; Democratic Republic of the Congo, Ghana, Guinea, Kenya, Liberia, Nigeria, Republic of the Congo, Uganda.

Helochares dollmani Balfour-Browne, 1950

Helochares (s. str.) *dollmani* Balfour-Browne, 1950a: 393 - Zambia [Northern Rhodesia], Namwala, Kafue River; Hebauer 1995a: 265 [faunistic treatment]; Hebauer 1996: 6 [faunistic treatment]; Hansen 1999b: 160 [catalog]; Hebauer 2005: 39 [checklist; new record]; Hebauer 2006: 26 [checklist; new record].

DISTRIBUTION: Afrotropical: Madagascar, Malawi, Namibia, Zambia, Zimbabwe.

Helochares dolus d'Orchymont, 1939

Helochares (*Hydrobaticus*) *dolus* d'Orchymont, 1939b: 319 - Mali [Haut Sénégal; Senegal], Khayes; Balfour-Browne 1952a: 130 [faunistic treatment]; Hebauer 1996: 15 [faunistic treatment]; Hansen 1999b: 167 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Benin, Cameroon, Democratic Republic of the Congo [Zaire], Gambia, Ghana, Ivory Coast, Mali, Nigeria, Republic of the Congo [Congo-Brazzaville], Senegal, Sierra Leone, Sudan, Tanzania.

Helochares egregius Balfour-Browne, 1952

Helochares (*Hydrobaticus*) *egregius* Balfour-Browne, 1952a: 131 - Ivory Coast, Toumodi; Hebauer 1995a: 264 [faunistic treatment]; Hebauer 1996: 16 [new records]; Hansen 1999b: 167 [catalog]; Hebauer 2006: 26 [checklist; new record].

DISTRIBUTION: Afrotropical: Benin, Democratic Republic of the Congo, Ghana, Ivory Coast, Namibia, Nigeria, Republic of the Congo, Senegal.

Helochares endroedyi Hebauer, 1996

Helochares (*Hydrobaticus*) *endroedyi* Hebauer, 1996: 16 - Ghana, Ashanti Region, Bobiri forest res., 6°40'N, 1°15'W; Hansen 1999b: 167 [catalog]; Hebauer 2006: 26

DISTRIBUTION: Afrotropical: Democratic Republic of the Congo, Ghana, Guinea, Zambia.

Helochares fratris Hebauer, 2003

Helochares (*Hydrobaticus*) *fratris* Hebauer, 2003b: 68 - SW Madagascar, Morondave district, Miandrivazo, 246 km W of Antsirabe; Hebauer 2006: 26 [checklist]; Short and Hebauer 2006: 336 [catalog].

DISTRIBUTION: Afrotropical: Madagascar.

Helochares fulgurans Hebauer, 1995

Helochares (s. str.) *fulgurans* Hebauer, 1995: 7 - Thailand, Chantaburi Khao Sabap NP; Hansen 1999b: 160 [catalog].

DISTRIBUTION: Indo-Malayan: Thailand.

Remarks: Described from a single female specimen, as similar (related) to *fuliginosus* and *Agraphydrus*.

Helochares fuliginosus d'Orchymont, 1932

Helochares (s. str.) *fuliginosus* d'Orchymont, 1932a: 689 - Indonesia, West Java, Bogor ["Buitenzorg"]; Hebauer 1995b: 7 [faunistic treatment]; Hansen 1999b 160 [catalog]; Jia and Tang 2018: 6 [redescription; new records].

DISTRIBUTION: Indo-Malayan: China (Fujian, Guangdong, Guangxi, Hong Kong, Macao), Indonesia (Java, Sumatra), Laos, Malaysia (Peninsula).

Helochares goticus Hebauer, 1996

Helochares (*Hydrobaticus*) *goticus* Hebauer, 1996: 16 - Democratic Republic of the Congo [Congo-Brazzaville], Kindamba, Meya settlement; Hansen 1999b: 167 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Democratic Republic of the Congo.

Helochares hiekei Hebauer, 1995

Helochares (*Hydrobaticus*) *hiekei* Hebauer, 1995b: 5 - India, Karnataka, Ablathi; Hansen 1999b: 167 [catalog].

DISTRIBUTION: Indo-Malayan: India (Karnataka).

Helochares insolitus d'Orchymont, 1925

Helochares (s. str.) *pallens-insolitus* d'Orchymont, 1925b: 202 (and 1926a: 380) - Philippines, Manila; Short and Hebauer 2006: 336 [catalog].

Helochares (s. str.) *insolitus* d'Orchymont; Hebauer 2002b: 15 [elevated to species; not subspecies of *Helochares pallens* (MacLeay), as in Hansen 1999b: 163]; Hebauer and Ryndevich 2005: 45 [new record].

DISTRIBUTION: Indo-Malayan: Philippines (Manila), Vietnam.

Helochares interjectus Hebauer, 1998

Helochares (*Hydrobaticus*) *interjectus* Hebauer, 1998: 42 - Madagascar, Morarano, “Chrome-Ambakireni”, 10 km W Maheriara; Hansen 1999b: 167 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Madagascar.

Helochares iteratus Hebauer, 1996

Helochares (*Hydrobaticus*) *iteratus* Hebauer, 1996: 17 - Republic of the Congo, "Uamgebiet Bosum"; Hansen 1999b: 167 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Democratic Republic of the Congo [in doubt], Republic of the Congo, Tanzania [in doubt].

Helochares itylus Balfour-Browne, 1952

Helochares (*Hydrobaticus*) *itylus* Balfour-Browne, 1952a: 131 - Benin ["Dahomey"], Ketou forest; Hebauer 1996: 17 [faunistic treatment]; Hansen 1999b: 167 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Benin, Cameroon, Democratic Republic of the Congo [in doubt], Gambia, Ghana, Ivory Coast, Republic of the Congo [Congo-Brazzaville], Senegal.

Helochares ivani Hebauer, 1996

Helochares (*Hydrobaticus*) *ivani* Hebauer, 1996: 18 - Ghana, Kumasi; Hansen 1999b: 167; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Benin, Cameroon, Ghana, Ivory Coast, Liberia, Nigeria, Republic of the Congo [Congo-Brazzaville], Zambia [in doubt].

Helochares kerstinneumanni Hebauer, 2009

Helochares (*Hydrobaticus*) *kerstinneumanni* Hebauer, 2009: 4 - Gabon, Makokou-Riv. Ivindo Chutes Kongou; Short and Fikáček 2011: 91 [catalog].

DISTRIBUTION: Afrotropical: Gabon.

Helochares knischi d'Orchymont, 1939

Helochares (*Hydrobaticus*) *Knischi* d'Orchymont, 1939b: 320 - Democratic Republic of the Congo [Belg. Congo; Zaire]; Hebauer 1996: 18 [faunistic treatment]; Hansen 1999b: 167; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Democratic Republic of the Congo.

Helochares laevis Short and Girón, 2018

Helochares (*Hydrobaticus*) *laevis* Short and Girón, 2018: 36 - Mexico, Chiapas, San Cristobal de las Casas.

DISTRIBUTION: Neotropical: Mexico.

Helochares lamprus d'Orchymont, 1940

Helochares (*Hydrobaticus*) *lamprus* d'Orchymont, 1940: 169 - Indonesia, [Sumatra], Lampong, "Wai Lima"; Hansen 1999b: 167 [catalog].

DISTRIBUTION: Indo-Malayan: Indonesia (Sumatra).

Remarks: Described as similar to *nebridus* and/or *crenatus*; the aedeagal form as illustrated by d'Orchymont (1940, see fig. 8 - p. 170) is rather unusual among *Helochares*.

Helochares lentus Sharp, 1890

Helochares lentus Sharp, 1890: 352. - Sri Lanka [Ceylon], Dikoya; Gentili et al. 1995: 211 [checklist].

Helochares (Grapidelochares) lentus Sharp; Zaitzev 1908: 381 [catalog].

Helochares (*Hydrobaticus*) *lentus* Sharp; d'Orchymont 1923a: 9 [faunistic treatment]; d'Orchymont 1928: 105 [faunistic treatment]; d'Orchymont, 1943e: 3 [taxonomic treatment]; Hebauer 1995b: 5 [faunistic treatment]; Hansen 1999b: 168 [catalog]; Hebauer 2002a: 23 [faunistic treatment]; Hansen 2004: 52 [checklist]; Hebauer and Ryndevich 2005: 45 [new record]; Fikáček et al. 2015: 62 [catalog].

DISTRIBUTION: Indo-Malayan: Bangladesh, Cambodia, China (Fujian, Guangdong, Yünnan), India, Indonesia (Borneo, Java, Lombok, Sumatra), Laos, Malaysia (Peninsula), Nepal, Sri Lanka, Taiwan, Thailand, Vietnam. Palearctic: China (Tibet).

Helochares lepidus d'Orchymont, 1943

Helochares (*Hydrobaticus*) *lentus lepidus* d'Orchymont, 1943e: 5 - Philippines, Luzon, Montalban.

Helochares (*Hydrobaticus*) *lepidus* d'Orchymont; Hebauer 1995b: 4 [elevated to species; not subspecies of *lentus* as in d'Orchymont, 1943e]; Hansen 1999b: 168 [catalog].

DISTRIBUTION: Indo-Malayan: Philippines.

Helochares leptinus d'Orchymont, 1943

Helochares (*Hydrobaticus*) *lentus leptinus* d'Orchymont, 1943e: 5 - Philippines, Luzon, Balbalan.

Helochares (*Hydrobaticus*) *leptinus* d'Orchymont; Hebauer 1995b: 5 [specific rank confirmed; not subspecies of *lentus* as in d'Orchymont, 1943e]; Hansen 1999b: 168 [catalog]; Hebauer 2002a: 23 [new record].

DISTRIBUTION: Indo-Malayan: Bangladesh, Nepal, Philippines.

Helochares letus d'Orchymont, 1943

Helochares (*Hydrobaticus*) *lentus letus* d'Orchymont, 1943e: 6. - Philippines.

Helochares (*Hydrobaticus*) *letus* d'Orchymont; Hebauer, 1995b: 4 [elevated to species; not subspecies of *lentus* as in d'Orchymont, 1943e]; Hansen 1999: 168 [catalog].

DISTRIBUTION: Indo-Malayan: Philippines.

Helochares livianus d'Orchymont, 1939

Helochares (*Hydrobaticus*) *livianus* d'Orchymont, 1939b: 317 - Uganda, Kampala, Hoima Rd.; Balfour-Browne, 1950b: [faunistic treatment]; Balfour-Browne, 1957: 22 [faunistic treatment]; Hebauer 1996: 18 [faunistic treatment]; Hansen 1999b 168 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Democratic Republic of the Congo, Rwanda, Tanzania, Uganda.

Helochares lividoides Hansen and Hebauer, 1988: 27

Helochares (s. str.) *lividoides* Hansen and Hebauer, 1988: 27 - Israel, Golan, Ein Sha'abanyia; Hebauer 1994: 112 [faunistic treatment]; Hansen 1999b: 160 [catalog]; Hansen 2004: 52 [catalog]; Hebauer and Ryndevich 2005: 45 [new record]; Mart et al. 2010: 298 [faunistic treatment]; Darilmaz and İncekara 2011: 710 [checklist]; Fikáček et al. 2015: 61 [catalog].

DISTRIBUTION: Palearctic: Israel, Turkey.

Helochares lividus (Forster, 1771)

Dytiscus lividus Forster, 1771: 52 (Official Specific Name No. 1992, cf. ICZN, 1964: 242); England and Germany [Anglia; Gallia].

Hydrophilus lividus (Forster); Olivier 1792: 127 [faunistic treatment].

Philydrus lividus (Forster); Solier 1834: 316 [taxonomic treatment].

Helophilus lividus (Forster); Mulsant 1844b: 134 [faunistic treatment].

Helocharis lividus (Forster); Thomson 1859: 18 [faunistic treatment; misspelled].

Helophygas lividus (Forster); Motschulsky 1853: 11 [faunistic treatment].

Philhydrus lividus (Forster); Fairmaire and Laboulbène, 1854: 230 [faunistic treatment].

Hydrophilus fulvus Fourcroy, 1785: 66 - France, Paris [Parisiensis]; Hansen 1982: 203 [synonymy; not synonym of *obscurus* Müller, as in d'Orchymont 1936a: 10].

Hydrophilus griseus Fabricius, 1787: 188 - Germany, Sachsen [Saxonia]; Illiger 1798: 246 [synonym]; Hansen 1982: 203 [not synonym of *obscurus* Müller, as in d'Orchymont, 1933: 304).

Dytiscus griseus (Fabricius); de Villers 1789: 342 [faunistic treatment].

Philydrus griseus (Fabricius); Solier 1834: 316 [faunistic treatment].

Philhydrus griseus (Fabricius); Brullé 1835: 278 [faunistic treatment].

Hydrobius griseus (Fabricius); Erichson 1837: 211 [faunistic treatment].

Phylidrus griseus (Fabricius); Castelnau 1840: 52 [faunistic treatment].

Pylophilus griseus (Fabricius); Motschulsky 1845: 32 [faunistic treatment].

Helochares (s. str.) *griseus* (Fabricius); Ganglbauer 1904: 249 [faunistic treatment].

Hydrophilus pallidus Rossi, 1792: 66 - NW. Italy [Etruria]; Bedel 1881a: 330 [synonymy]; Hansen 1982: 203 [synonym of *griseus* Fabricius: Paykull 1798: 183].

Helophilus lividus var. *pallidus* (Rossi); Mulsant 1844a: 135 [faunistic treatment].

Philhydrus lividus var. *pallidus* (Rossi); Gemminger and Harold 1868a: 481 [catalog].

Helochares dilutus var. *pallidus* (Rossi); Rey 1885b: 287 [faunistic treatment].

? *Hydrophilus chrysomelinus* Herbst, 1797: 313 (primary homonym of *Hydrophilus chrysomelinus* Müller, 1776); Germany; Schönherr, 1808: 7 [synonymy; sub nom. *griseus*); Knisch, 1924: 197 [as syn. dub. of *griseus*].

Hydrophilus lividus Herbst, 1797: 316 (secondary homonym of *Dytiscus lividus* Forster, 1771). - Germany; Schönherr, 1808: 7 [synonymy; sub nom. *griseus*].

Hydrophilus bicolor; Paykull, 1798: 184 [misinterpretation of *Hydrophilus bicolor* Fabricius); Bedel 1878a: CLXXVII [synonymy].

Helochares Ludovici Schaufuss, 1869: 11 - Spain, Ibiza [Ibiza, Llano de Villa]; Heyden 1891: 67 [catalog]; Ganglbauer 1904: 249 [synonymy]; Hansen 1982: 203 [taxonomic treatment].

Helochares lividus v. *pallide-testaceus* Stierlin, 1900: 219 [ascribed to Heer, who merely used "pallide" and "testaceus" as the first two adjectives in a description of an unnamed variety [Heer 1841: 485]] - Switzerland [Helvetiae]; Knisch 1924: 198 [synonymy].

Helochares (s. str.) *lividus* (Forster); Hansen 1982: 203 [taxonomic treatment]; Hebauer 1994: 111 [faunistic treatment; identification doubtful]; Hebauer 1996: 7 [faunistic treatment]; Ribera et al. 1996: 10 [checklist]; Hansen 1999b: 161 [catalog]; Hansen 2004: 52 [catalog]; Hebauer and Ryndevich 2005: 45 [new record]; Darilmaz and Kiyak 2006: 79 [new record]; Hebauer 2006: 25 [checklist]; Mart et al. 2010: 298 [faunistic treatment]; Darilmaz and İncekara 2011: 710 [checklist]; Fikáček et al. 2015: 61 [catalog]; Salah and Régil Cueto 2017: 269 [record from Egypt in doubt]; Gentili et al. 2018: 23 [faunistic treatment].

Helochares lividus (Forster); Reiche 1854: 9 [catalog]; Heyden 1891: 67 [catalog].

DISTRIBUTION: Palearctic: Algeria, Austria, Belarus, Bosnia Herzegovina, Bulgaria, Canary Islands, Croatia, Czech Republic, Egypt [in doubt], France, Germany, Great Britain, Greece, Hungary, Iran, Italy, Luxembourg, Macedonia, Morocco, Netherlands, Poland, Portugal, Serbia and Montenegro, Slovakia, Slovenia, Spain, Switzerland, Syria, Tunisia, Turkey, Ukraine.

Helochares lobatus d'Orchymont, 1948

Helochares (s. str.) *lobatus* d'Orchymont, 1948: 730 - Ethiopia, Abyssinian Highlands, Muger Wenz, "Mulu"; Hebauer 1996: 7 [faunistic treatment]; Hansen 1999b: 161 [catalog]; Hebauer 2006: 25 [checklist].

DISTRIBUTION: Afrotropical: Ethiopia.

Remarks: This species was described as similar to *lividus*, but the aedeagus is remarkably different; it needs to be studied in detail, as the drawing provided by d'Orchymont (1948: fig. 5A) is not entirely clear and does not allow to establish affinities with other *Helochares* groups.

Helochares lollius d'Orchymont, 1939

Helochares (*Hydrobaticus*) *lollius* d'Orchymont, 1939b: 321 - Uganda, Kampala; Hebauer 1996: 18 [faunistic treatment]; Hansen 1999b: 168 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Gabon, Uganda.

Helochares loticus Hebauer, 1998

Helochares (*Hydrobaticus*) *loticus* Hebauer, 1998: 43 - Thailand (north), Lom Sak, 40 km N Phetchabun; Hansen 1999b: 168 [catalog].

DISTRIBUTION: Indo-Malayan: Thailand.

Helochares loweryae Watts, 1995

Helochares (*Hydrobaticus*) *loweryae* Watts, 1995: 122 - Papua New Guinea, Mt. Lamington; Hansen 1999b: 168 [catalog].

DISTRIBUTION: Australasian: Australia (Northern Territory), Papua New Guinea.

Helochares luridus (MacLeay, 1871)

Hydrobaticus luridus MacLeay, 1871: 131 - Australia, Queensland, Gayndah.

Hydrobaticus tristis var. *luridus* MacLeay; Blackburn, 1893: 99 [faunistic treatment].

Helochares (*Hydrobaticus*) *luridus* (MacLeay); Watts, 1995: 122 [valid species, not syn. of *tristis* MacLeay, as in Zaitzev 1908: 390); Hansen 1999b: 168 [catalog].

DISTRIBUTION: Australasian: Australia (New South Wales, Northern Territory, Queensland, Western Australia).

Helochares lutulentus Balfour-Browne, 1952

Helochares (*Hydrobaticus*) *lutulentus* Balfour-Browne, 1952b: 516 - Mauritania, Kédia d'Idjil; Hebauer 1996: 18 [faunistic treatment]; Hansen 1999b: 168 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Benin, Mauritania, Morocco [in doubt].

Helochares maculatus Hebauer, 1988

Helochares (Helocharimorphus) maculatus Hebauer, 1988: 157 - Namibia, Okavango, Nyangana; Hebauer 1995a: 265 [faunistic treatment]; Hebauer 1996: 9 [faunistic treatment]; Hansen 1999b: 164 [catalog]; Hebauer 2006:27 [checklist].

DISTRIBUTION: Afrotropical: Namibia.

Helochares maculicollis Mulsant, 1844

Helochares maculicollis Mulsant, 1844b: 379 - U.S.A., Louisiana [Louisiane].

Philhydrus maculicollis (Mulsant); Lacordaire, 1854: 457 [faunistic treatment].

Philhydrus (s. str.) *maculicollis* (Mulsant); LeConte 1855: 370 [faunistic treatment].

Helochares (Grapidelochares) maculicollis Mulsant; Zaitzev 1908: 381 [catalog].

Helochares (*Hydrobaticus*) *maculicollis* Mulsant; Hansen 1999b: 168 [catalog]; Short 2005: 218 [faunistic treatment]; Short and Girón 2018: 36 [taxonomic review].

? *Helochares bipunctatus* Sharp, 1882: 76. - Mexico (Cordova) and Guatemala (Torola); d'Orchymont 1943b: 3 [synonymy in doubt].

Helochares (Grapidelochares) bipunctatus Sharp; Zaitzev, 1908a: 381.

DISTRIBUTION: Nearctic: U.S.A. (Alabama, Arkansas, Delaware, District of Columbia, Florida, Georgia, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maryland, Mississippi, Missouri, North Carolina, North Carolina, Ohio, Oklahoma, Pennsylvania, South Carolina, Tennessee, Texas, Virginia). Neotropical: Guatemala [in doubt], Mexico.

Helochares madli Hebauer, 2002

Helochares (s. str.) *madli* Hebauer, 2002b: 15 - Madagascar, Mahajanga Katsepi; Hebauer 2006: 25 [checklist]; Short and Hebauer 2006: 336 [catalog].

DISTRIBUTION: Afrotropical: Madagascar.

Remarks: This species was described from a single female specimen. According to Hebauer (2002b) it is similar to a small *H. dilutus*, but with shorter maxillary palpi and different elytral punctation. Given that the male of this species remains unknown, the placement of this species in *Helochares* needs to be confirmed.

Helochares marreensis Watts, 1995

Helochares (*Hydrobaticus*) marreensis Watts, 1995: 123 - Australia, Northern Territory, 7 km NW by N of Cahills Crossing, East Alligator River, 12°23'S, 132°56'E; Hansen 1999b: 168 [catalog].

DISTRIBUTION: Australasian: Australia (New South Wales, Northern Territory, Queensland, South Australia, Victoria, Western Australia).

Helochares mecarus d'Orchymont, 1939

Helochares (*Hydrobaticus*) *mecarus* d'Orchymont, 1939b: 310 - Ethiopia, Arussi Galla, A. Ganale Gudda; Hebauer 1996: 19 [faunistic treatment]; Hansen 1999b: 169 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Benin, Botswana, Ethiopia, Kenya, Namibia, Zambia.

Helochares mediastinus d'Orchymont, 1939

Helochares (*Hydrobaticus*) *mediastinus* d'Orchymont, 1939b: 311 - Ethiopia, Arussi Galla, A. Ganale Gudda; Hebauer 1996: 19 [faunistic treatment]; Hansen 1999b: 169 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Angola, Benin, Ethiopia, Kenya, Madagascar, Namibia, Tanzania.

Helochares melanophthalmus (Mulsant, 1844)

Helophilus melanophthalmus Mulsant, 1844a: 137 (ascribed to Dufour) - Sudan [in doubt: type locality probably Sudan (see d'Orchymont 1936a), not Spain [Espagne] as stated in the original description].

Hydrobius melanophthalmus (ascribed to Dufour); Dejean 1833: 134 [nomen nudum].

Helochares melanophthalmus (Mulsant); Rey 1885b: 288 [specific rank confirmed; not synonym of *dilutus* Erichson, as in Reiche and Saulcy 1856: 358].

Helochares (*Graphelochares*) *melanophthalmus* (Mulsant); Kuwert 1890: 39 [catalog]; Heyden 1891: 67 [catalog].

Helochares (*Hydrobaticus*) *melanophthalmus* (Mulsant); Hebauer 1996: 19 [faunistic treatment]; Hansen 1999b: 169 [catalog]; Hebauer 2006: 26 [checklist]; Salah and Régil Cueto 2017: 270 [excluded from Egypt].

DISTRIBUTION: Afrotropical: Cameroon, Ethiopia, Ghana, Ivory Coast, Nigeria, Senegal, Seychelles, Sudan.

Helochares mendosus Hebauer, 1996

Helochares (*Hydrobaticus*) *mendosus* Hebauer, 1996: 19 - Ghana, Ashanti region, Bobiri forest reserve 6°40'N, 1°15'W; Hansen 1999b: 19 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Ghana.

Helochares mentinotus Kuwert, 1888

Helochares mentinotus Kuwert, 1888: 292 - Egypt [Aegyptus].

Helochares (Crephelochares) mentinotus Kuwert; Kuwert 1890a: 38 [faunistic treatment].

Helochares (*Chasmogenus*) *mentinotus* Kuwert; Knisch 1824a: 195 [checklist].

Helochares (*Hydrobaticus*) *mentinotus* Kuwert; d'Orchymont 1936d: 6 [taxonomic treatment]; Balfour-Browne, 1950b: 57 [faunistic treatment]; Hebauer 1994: 112 [faunistic treatment]; Hebauer 1996: 20 [faunistic treatment]; Hansen 1999b: 169 [catalog]; Hansen 2004: 52 [catalog]; Hebauer 2006: 26 [checklist]; Fikáček et al. 2015: 62 [catalog]; Salah and Régil Cueto 2017: [faunistic treatment].

Helochares squalidus Sharp, 1903: 7 - South Sudan (White Nile River; Jebel Ahmed Agha; north of Jebel Ahmed Agha; north of Kaka; d'Orchymont 1936d: 6 [synonymy].

Helochares (Grapidelochares) squalidus Sharp; Zaitzev 1908: 381 [checklist].

DISTRIBUTION: Afrotropical: Chad, Democratic Republic of the Congo [Zaire; DR Congo], Ethiopia [Abyssinia], Kenya, South Sudan, Uganda. Palearctic: Egypt, Israel.

Helochares menulus d'Orchymont, 1943

Helochares (*Hydrobaticus*) *menulus* d'Orchymont, 1943a: 10 - Democratic Republic of the Congo [Congo belge; Zaire], Nizi-Blukwa; Hebauer 1996: 20 [faunistic treatment]; Hansen 1999b: 169 [catalog]; Hebauer 2006: 26

DISTRIBUTION: Afrotropical: Democratic Republic of the Congo [Zaire; DR Congo], Kenya, Nigeria, Tanzania.

Helochares meracus Balfour-Browne, 1950

Helochares (*Hydrobaticus*) *meracus* Balfour-Browne, 1950a: 395 - Zambia [Northern Rhodesia], Nama-ula; Hebauer 1996: 20 [faunistic treatment]; Hansen 1999b: 169 [catalog]; Hebauer 2005: 39 [checklist]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Ethiopia, Malawi, South Africa [in doubt], Zambia.

Helochares mersus d'Orchymont, 1939

Helochares (*Hydrobaticus*) *mersus* d'Orchymont, 1939c: 307 - Ethiopia [Abyssinie]; Balfour-Browne 1950b: 56 [faunistic treatment]; Hebauer 1988: 156 [faunistic treatment]; Hebauer 1995a: 264 [faunistic treatment]; Hebauer 1996: 20 [faunistic treatment]; Hansen 1999b: 169 [catalog]; Hebauer 2005: 39 [checklist]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Botswana [in doubt; "Kalahari"], Democratic Republic of the Congo [Zaire; DR Congo], Ethiopia, Kenya, Malawi, Namibia, Rwanda, Tanzania, Uganda, Zimbabwe.

Helochares minax d'Orchymont, 1939

Helochares (*Hydrobaticus*) *minax* d'Orchymont, 1939c: 316 - Uganda, Kampala; Balfour-Browne 1950b: 57 [faunistic treatment]; Hebauer 1996: 20 [faunistic treatment]; Hansen 1999b: 169 [catalog]; Hebauer 2006: 26 [checklist]

DISTRIBUTION: Afrotropical: Rwanda, Uganda, Gabon [in doubt], Kenya, Tanzania.

Helochares minor d'Orchymont, 1925

Helochares (*Hydrobaticus*) *minor* d'Orchymont, 1925c: 293 - Vietnam [Indo-Chine], Cha Pa; d'Orchymont 1928: 106 [faunistic treatment]; d'Orchymont 1943e: 9 [faunistic treatment]; Hansen 1999b: 189 [catalog].

DISTRIBUTION: Indo-Malayan: India (Bihar), Vietnam.

Helochares minusculus d'Orchymont, 1943

Helochares (*Hydrobaticus*) *minusculus* d'Orchymont, 1943e: 10 - Indonesia, North Sumatra, Danau Toba region, nr Huta Gindjang; Hansen 1999b: 169 [catalog]; Hebauer and Ryndevich 2005: 46 [new record].

DISTRIBUTION: Indo-Malayan: Burma, Indonesia (Sumatra), Laos.

Helochares namcatensis Hebauer, 2002

Helochares (*Hydrobaticus*) *namcatensis* Hebauer 2002b: 12 - Vietnam, Nam Cat Tien National Park; Hebauer 2002b: 12 [faunistic treatment]; Short and Hebauer 2006: 336 [catalog].

DISTRIBUTION: Indo-Malayan: Vietnam.

Helochares nebridius d'Orchymont, 1940

Helochares (*Hydrobaticus*) *nebridius* d'Orchymont, 1940: 169 - Indonesia, Sumatra, Palembang; Hebauer 1995b: 5 [faunistic treatment]; Hansen 1999b: 169 [catalog].

DISTRIBUTION: Indo-Malayan: Indonesia (Java, Lombok, Sumatra), Singapore.

Helochares negatus Hebauer, 1995

Helochares (*Hydrobaticus*) *negatus* Hebauer, 1995b: 5 - Bangladesh, Dinajpur; Hansen 1999b: 169 [catalog]; Hebauer 2002a: 24 [new record]; Hansen 2004: 52 [catalog]; Hebauer and Ryndevich 2005: 46 [new record]; Fikáček et al. 2015: 62 [catalog].

DISTRIBUTION: Indo-Malayan: Bangladesh, India (Tamil Nadu), Nepal.

Helochares neglectus (Hope, 1845)

Hydrobius neglectus Hope, 1845: 16 - China, Guangdong, Guangzhou, Canton; Gentili et al. 1995: 211 [catalog].

Helochares (*Hydrobaticus*) *neglectus* (Hope); d'Orchymont 1919c: 150 [new combination in doubt]; d'Orchymont 1940b: 166 [new combination confirmed]; Hebauer 1995b: 6 [faunistic treatment]; Hansen 1999b: 169 [catalog]; Hansen 2004: 52 [catalog]; Fikáček et al. 2015: 62 [catalog].

DISTRIBUTION: Indo-Malayan: Cambodia, China (Fujian, Guangdong, Yünnan, Zhejiang), Malaysia (Peninsula), Thailand, Vietnam. Palearctic: China (Hubei).

Helochares nexus Short and Girón, 2018: 39

Helochares (*Hydrobaticus*) *nexus* Short and Girón, 2018: 39 - Panama, Coclé Province, 8°39'05.2"N, 80°35'18.7"W.

DISTRIBUTION: Neotropical: Ecuador, Panama, Venezuela.

Helochares nigrifrons Brancsik, 1893

Helochares melanophthalmus var. *nigrifrons* Brancsik, 1893: 219 - Madagascar, Nosy Bé [Nossibé]; Régimbart 1900: 50 [faunistic treatment].

Helochares (Grapidelochares) nigrifrons Brancsik; Zaitzev 1908: 381 [catalog].

Helochares (*Hydrobaticus*) *melanophthalmus* var. *nigrifrons* Brancsik; Knisch 1924: 194 [catalog].

Helochares (Hydrocaticus) nigrifrons Brancsik; d'Orchymont 1939b: 297 [specific rank confirmed; subgeneric name misspelled].

Helochares (*Hydrobaticus*) *nigrifrons* Brancsik; d'Orchymont 1941: 15 [list]; Hebauer 1996: 20 [new records]; Hansen 1999b: 170 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Madagascar, Seychelles (Aldabra), Tanzania.

Helochares nigripalpis Hebauer and Hendrich, 1999

Helochares (*Hydrobaticus*) *nigripalpis* Hebauer and Hendrich, 1999: 48 - Australia, Northern Territory, Kakadu National Park, Jim Jim Falls Camp Area, S 13°16.218' E 132°49.276'; Short and Hebauer 2006: 336 [catalog].

DISTRIBUTION: Australasian: Australia (Northern Territory).

Helochares nigritulus Kuwert, 1889

Helochares nigritulus Kuwert, 1889: 8 [and 1890a: 34] - Italy, Sicily

Helochares (s. str.) *nigritulus* Kuwert; Heyden 1891: 67 [catalog]; Hansen 1999b: 162 [catalog]; Hansen 2004: 52 [catalog]; Fikáček et al. 2015: 61 [catalog].

DISTRIBUTION: Palearctic: Italy.

Helochares nigroseriatus Hebauer, 1998

Helochares (*Hydrobaticus*) *nigroseriatus* Hebauer, 1998c: 43 - Zimbabwe, vicinity of Kotwa, "Broken Causeway", 17°0'S, 32°45'E; Hansen 1999b: 170 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Zambia, Zimbabwe.

Remarks: Hebauer (2002) indicates that the aedeagus of *nigroseriatus* corresponds to fig. 5 in Hebauer 1998.

Helochares niobelus d'Orchymont, 1939

Helochares (*Hydrobaticus*) *niobelus* d'Orchymont, 1939e: 308 - Democratic Republic of the Congo [Congo belge; Zaire], Haut Uélé, Watsa; Hebauer 1996: 20 [faunistic treatment]; Hansen 1999b: 170 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Cameroon [in doubt], Democratic Republic of the Congo, South Africa, Uganda.

Helochares nipponicus Hebauer, 1995

Helochares striatus Sharp, 1873: 60 [secondary homonym of *Hydrobius striatus* Boheman, 1851: 599]; Hebauer 1995b: 6 [synonymy; not synonym of *lepidus* d'Orchymont, *leptinus* d'Orchymont or *lentus* Sharp, as in d'Orchymont 1943e: 6].

Helochares (*Hydrobaticus*) *nipponicus* Hebauer, 1995b: 6 [replacement name for *striatus* Sharp]; Hansen 1999b: 170 [catalog]; Hansen 2004: 52 [catalog]; Fikáček et al. 2015: 62 [catalog].

DISTRIBUTION: Palearctic: Japan, South Korea.

Helochares normatus (LeConte, 1861)

Philhydrus normatus LeConte, 1861: 341 - U.S.A., California, Bodega.

Helochares normatus (LeConte); Horn 1890: 252 [faunistic treatment].

Chasmogenus normatus (LeConte); Zaitzev 1908: 383 [catalog].

Helochares (*Hydrobaticus*) *normatus* (LeConte); Knisch 1924: 194 [catalog]; Hansen 1999b: 170 [catalog]; Short 2005: 218 [new records]; Short and Girón 2018: 42 [taxonomic treatment].

Helochares seriatus Sharp, 1882: 76. - Guatemala (Guatemala City; Pantaleon; Coatepeque; Rio Naranjo; San Gerónimo); d'Orchymont 1943b: 4 [synonymy].

Helochares (Grapidelochares) seriatus Sharp; Zaitzev 1908: 381 [catalog].

? Helochares regularis Sharp, 1882: 76. - Mexico - d'Orchymont 1943d: 4 [synonymy in doubt].

? *Helochares (Grapidelochares) regularis* Sharp; Zaitzev 1908a: 381 [catalogue].

DISTRIBUTION: Nearctic: USA (Arizona, California, Nevada, Oregon, Texas). Neotropical: Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua.

Helochares notaticollis Régimbart, 1906

Helochares melanophthalmus var. *notaticollis* Régimbart, 1906: 260 - Kenya, Nairobi.

Helochares (*Hydrobaticus*) *notaticollis* Régimbart; Balfour-Browne 1950a: 394 [faunistic treatment]; Balfour-Browne 1950b: 54 [faunistic treatment]; d'Orchymont, 1936b: 111 [specific rank confirmed]; Hebauer 1996: 20 [faunistic treatment]; Hansen 1999b: 170 [catalog]; Hebauer 2005: 39 [checklist]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Kenya, Malawi, Rwanda, Tanzania, Uganda.

Helochares notaticollis* ssp. *curtus Régimbart, 1906

Helochares melanophthalmus var. *curtus* Régimbart, 1906: 260 - Kenya, Bura.

Helochares (*Hydrobaticus*) *notaticollis* var. *curtus* Régimbart; d'Orchymont, 1936a: 111.

Helochares (*Hydrobaticus*) *notaticollis curtus* Régimbart, 1906; Hansen 1999b: 170 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Kenya.

Helochares obliquus Mart, İncekara and Karaca, 2010: 299

Helochares obliquus Mart, İncekara and Karaca, 2010: 299 - Turkey, Ordu province, Mesudiye, Lake Ulugöl, 40°24′N 37°49′E.

Helochares (s. str.) *obliquus* Mart, İncekara and Karaca; Darilmaz and İncekara 2011: 711 [checklist]; Short and Fikáček 2011 [catalog]; Fikáček et al. 2015: 61 [catalog].

DISTRIBUTION: Palearctic: Turkey.

Helochares obscurus (Müller, 1776)

Hydrophilus obscurus Müller, 1776: 69 - Denmark and Norway [Dania et Norvegia].

Helochares (s. str.) *obscurus* (Müller); d'Orchymont 1933: 306 [specific rank confirmed; not syn. of *griseus* Fabricius, as in Illiger 1798: 246; not syn. of *lividus* Forster, as in Mulsant 1844a: 134]; Hebauer 1994: 113 [faunistic treatment]; Hansen 1999b: 162 [catalog]; Hansen 2004: 52 [catalog]; Hebauer and Ryndevich 2005: 45 [new records]; Mart et al. 2010: 299 [faunistic treatment]; Darilmaz and İncekara 2011: 711 [checklist]; Fikáček et al. 2015: 62 [catalog]; Jia and Tang 2018b: 12 [redescription; new record].

Hydrophilus erythrocephalus Fabricius, 1792: 185 - No type locality given; Hansen 1982: 207 [synonymy; not syn. of *griseus* Fabricius, as in Erichson 1837: 211].

Helophilus lividus var. *erythrocephalus* (Fabricius); Mulsant 1844a: 135 [faunistic treatment].

Philhydrus lividus var. *erythrocephalus* (Fabricius); Gemminger and Harold 1868: 481 [catalog].

Helochares (s. str.) *erythrocephalus* (Fabricius); Kuwert 1890a: 37 [taxonomic treatment].

Helochares erythrocephalus (Fabricius); Heyden 1891: 67 [catalog].

Hydrophilus variegatus Herbst, 1797: 304 - Germany [... in hiesigen Gewässern (i.e. German waters)]; Hansen 1982: 207 [synonymy; not syn. of *griseus* Fabricius, as in Illiger 1801a: 60].

Hydrophilus griseus var. *variegatus* Herbst; Gyllenhal, 1808: 122 [faunistic treatment].

Philhydrus lividus var. *variegatus* (Herbst); Gemminger and Harold 1868: 481 [catalog].

Hydrobius lividus; Stephens, 1829: 130 [misinterpretation of *Dytiscus lividus* Forster].

Philhydrus lividus; Stephens, 1839: 91 [misinterpretation of *Dytiscus lividus* Forster].

Helochares subcompressus Rey, 1885a: 14 - France, Lille; Hansen 1982: 207 [synonymy; (Fauvel, 1895: 92 [synonym of *erythrocephalus* Fabricius]); not syn. of *griseus* Fabricius, as in Ganglbauer, 1904: 249)]; Heyden 1891: 67 [catalog].

Helochares erythrocephalus var. *substriatus* Sahlberg, 1903: 20 - Greece, Corfu, Stravopotamos [(Corcyra): prope flumen Stravopotamos]; Hansen 1982: 207 [synonymy].

Helochares (s. str.) *griseus* (?) var. *substriatus* Sahlberg; Zaitzev 1908: 382 [catalog].

Helochares griseus a. Mülleri Reitter, 1909a: 364 [infrasubspecific name; unavailable under ICZN Code Art. 1b (5), 45f)]; Hansen 1982: 207 [synonymy].

? *Hydrophilus chrysomelinus*; Panzer, 1795: 72 [misinterpretation of *Dytiscus chrysomelinus* Fabricius]. Hansen, 1982: 202 [synonymy in doubt; not synonym of *griseus* Fabricius, as in Schönherr 1808: 7 - in doubt; not syn. of *pallidus* Rossi, as in Mulsant 1844a: 135].

? *Philhydrus lividus* var. *chrysomelinus* (Panzer); Gemminger and Harold 1868: 481 [catalog].

DISTRIBUTION: Palearctic: Austria, Azerbaijan, Belarus, China (Xinjiang), Croatia, Czech Republic, Denmark, Estonia, Finland, France, Germany, Georgia, Great Britain, Greece, Hungary, Iran, Israel, Italy, Latvia, Lithuania, Luxembourg, Montenegro, Netherlands, Norway, Poland, Russia, Slovakia, Sweden, Switzerland, Turkey.

Helochares opacus Hebauer, 2009

Helochares (*Hydrobaticus*) *opacus* Hebauer, 2009: 5 - Gabon, Monts de Cristal National Park, Asseng Assala Village; Short and Fikáček 2011: 91 [catalog].

DISTRIBUTION: Afrotropical: Gabon.

Helochares pallens (MacLeay, 1825)

Enhydrus pallens MacLeay, 1825: 35 - Indonesia, Java.

Philhydrus pallens (MacLeay); Gemminger and Harold 1868: 482 [catalog].

Enochrus (*Lumetus*) *pallens* (MacLeay); Zaitzev 1908: 388 [catalog].

Helochares pallens (MacLeay); Gentili et al. 1995: 211 [catalog].

Helochares (s. str.) *pallens* (MacLeay); d'Orchymont 1926b: 232 [new combination]; d'Orchymont 1928: 107 [faunistic treatment]; Balfour-Browne 1950b: 59 [faunistic treatment]; Balfour-Browne 1951: 213 [faunistic treatment]; Balfour-Browne 1952a: 129 [faunistic treatment]; Balfour-Browne 1957: 21 [faunistic treatment]; Hebauer 1988: 156 [faunistic treatment]; Hebauer 1994: 113 [faunistic treatment]; Hebauer 1995a: 265 [faunistic treatment]; Hebauer 1995b: 7 [faunistic treatment]; Hebauer 1996: 8 [faunistic treatment]; Hebauer 1997: 263 [faunistic treatment]; Hansen 1999b: 162 [catalog]; Hebauer 2002a: 24 [new record]; Hansen 2004: 52 [catalog]; Hebauer 2005: 39 [checklist]; Hebauer and Ryndevich 2005: 46 [new record]; Hebauer 2006: 25 [checklist; new records]; Mart et al. 2010: 298 [new record]; Short 2010: 312 [faunistic treatment]; Darilmaz and İncekara 2011: 711 [checklist]; Fikáček et al. 2015: 62 [catalog]; Jia and Tang 2018: 15 [redescription].

Helochares parvulus Reiche and Saulcy [in Reiche 1854: 9 - nomen nudum].

Helochares parvulus Reiche and Saulcy, 1856: 359 - Lebanon, Beirut [Beyrouth]; d'Orchymont 1927b: 6 [synonymy]; d'Orchymont 1932: 688 [faunistic treatment].

Philhydrus parvulus (Reiche and Saulcy); Gemminger and Harold 1868: 482 [catalog].

Enochrus (Methydrus) parvulus (Reiche and Saulcy); Zaitzev 1908: 384 [catalog].

? *Helochares simplex* Wollaston, 1867: 44 [published in synonymy with *dilutus* Erichson; unavailable under ICZN Code Art. 11e]; d'Orchymont 1943e: 8 [synonymy in doubt].

Helochares lewisius Sharp, 1873: 60 - Japan (Kyushu (Nagasaki), and Honshu (Hyogo)) [Nagasaki and Hiogo]; Balfour-Browne 1939: 293 [synonymy].

Helochares (s. str.) *lewisianus* Sharp; Zaitzev 1908: 382 [catalog; misspelled].

? *Philhydrus parvulus* Guillebeau, 1896: 226 - "Le Cuire" [secondary homonym of *Helochares parvulus* Reiche and Saulcy, 1856; possibly synonym of the same, as in Knisch 1924: 219]; Handen 1999b: 162 [synonymy confirmed].

Helochares dispar Sharp, 1903: 7 - Sudan (White Nile River; Jebel Ahmed Agha; north of Jebel Ahmed Agha; north of Kaka); d'Orchymont 1926b: 232 [synonymy].

Helochares laeviusculus Régimbart, 1906: 261 - Kenya, Lake Victoria, Winam Gulf [Baie de Kavirondo]; Hebauer 1996: 8 [synonymy].

Helochares (s. str.) *pallens laeviusculus* Régimbart - Democratic Republic of the Congo, Ishango, Semliki River; Balfour-Browne 1950b: 60 [new combination]; Hebauer 2006: 25 [checklist].

DISTRIBUTION: Afrotropical: Benin, Botswana, Cameroon, Chad, Democratic Republic of the Congo, Ethiopia, Ghana, Guinea, Ivory Coast, Kenya, Liberia, Madagascar, Namibia, Rwanda, South Africa, Sudan, Tanzania, Uganda, Yemen, Zambia, Zimbabwe. Indo-Malayan: Bangladesh, Burma, China (Fujian, Guangdong, Guangxi, Guizhou, Hainan, Hong Kong, Hunan, Jiangxi, Macao, Yünnan), India (Assam, Bihar), Indonesia (Java, Sumatra), Laos, Malaysia (Peninsula), Nepal, Philippines, Sri Lanka, Thailand. Palearctic: China

(Chongqing, Hubei, Shaanxi, Sichuan, Xizang [Tibet]), Egypt, Israel, Japan, Lebanon, Pakistan, Syria, Turkey. Australasian: Papua New Guinea (New Guinea), Vanuatu.

Helochares parallelus Hebauer, 1999

Helochares (*Hydrobaticus*) *parallelus* Hebauer 1999: 11 - Botswana, Kasane Chobe Safari Lodge, Chobe Banks; Hebauer 2006: 26 [checklist]; Short and Hebauer 2006: 336 [catalog].

DISTRIBUTION: Afrotropical: Botswana, South Africa.

Helochares percyi Watts, 1995

Helochares (*Hydrobaticus*) *percyi* Watts, 1995: 125 - Australia, Queensland (N.), Boar Pocket Road; Hansen 1999b: 170 [catalog].

DISTRIBUTION: Australasian: Australia (Australian Capital Territory, New South Wales, Northern Territory, Queensland, Western Australia).

Helochares perminutus Hebauer, 1996

Helochares (*Hydrobaticus*) *perminutus* Hebauer, 1996: 20 - Nigeria [Nig.], Pandam W.P. River Li; Hebauer 1996: 20 [faunistic treatment]; Hansen 1999b: 170 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Benin, Ghana, Nigeria, Sierra Leone.

Helochares phallicus d'Orchymont, 1936

Helochares (*Hydrobaticus*) *phallicus* d'Orchymont, 1936b: 111 - Botswana, Makgadikgadi [Makarikari], Nkate; Hebauer 1995a: 264 [faunistic treatment]; Hebauer 1996: 21 [faunistic treatment]; Hansen 1999b: 170 [checklist]; Hebauer 2005: 39 [checklist]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Angola, Botswana, Malawi, Namibia, South Africa, Zambia, Zimbabwe.

Helochares politus Short and Girón, 2018

Helochares (*Hydrobaticus*) *politus* Short and Girón, 2018: 45 - Guatemala, Departamento de Huehuetenango, 11 km N. Santa Eulalia on road to San Mateo Ixtatán.

DISTRIBUTION: Neotropical: Guatemala.

Helochares punctatus Sharp, 1869

Helochares punctatus Sharp, 1869: 241 - England (Whittlesea, Mere, Cambridge, London and the New Forest); Hansen 1982: 206 [specific rank confirmed; not synonym of *erythrocephalus* Fabricius, as in Heyden, 1891: 67; not synonym of *griseus* Fabricius, as in Ganglbauer 1904: 249].

Helochares punctulatus Sharp [misspelling]; Bedel 1881a: 312 [catalog]; Heyden 1891: 67 [catalog].

Helochares (s. str.) *punctatus* Sharp; Hansen 1999b: 163 [catalog]; Hansen 2004: 52 [catalog]; Hebauer and Ryndevich 2005: 45 [new records]; Darilmaz and İncekara 2011: 711 [checklist]; Fikáček et al. 2015: 62 [catalog].

DISTRIBUTION: Palearctic: Belarus, Denmark, France, Germany, Great Britain, Hungary, Ireland, Lithuania, Luxembourg, Netherlands, Portugal, Russia, Spain, Turkey, Ukraine.

Helochares rugipennis Balfour-Browne, 1958

Helochares (*Hydrobaticus*) *rugipennis* Balfour-Browne, 1958a: 183 - Mali ["French Sudan"], Source Sanga; Hebauer 1996: 21 [faunistic treatment]; Hansen 1999b: 171 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Guinea, Ivory Coast, Mali, Nigeria, Sierra Leone.

Helochares salvazai d'Orchymont, 1919

Helochares (*Hydrobaticus*) *salvazai* d'Orchymont, 1919a: 76 (and 1921: 11) - Cambodia; d'Orchymont 1928: 106 [faunistic treatment]; d'Orchymont 1943e: 10 [faunistic treatment]; Hansen 1999b: 171 [catalog].

DISTRIBUTION: Indo-Malayan: Cambodia.

Helochares sauteri d'Orchymont, 1943

Helochares (*Hydrobaticus*) *sauteri* d'Orchymont, 1943e: 6 - Taiwan [Formose], "Kosempo"; Hansen 1999b: 171 [catalog]; Hansen 2004: 52 [catalog]; Fikáček et al. 2015: 62 [catalog].

Helochares sauteri d'Orchymont; Gentili et al. 1995 [catalog].

DISTRIBUTION: Indo-Malayan: China (Zhejiang), Taiwan.

Helochares schoedli Hebauer, 1996

Helochares (*Hydrobaticus*) *schoedli* Hebauer, 1996: 22 - Democratic Republic of the Congo [Zaire; Haut-Zaire], Dungu; Hansen 1999b: 171 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Democratic Republic of the Congo.

Helochares schwendingeri Hebauer, 1995

Helochares (*Hydrobaticus*) *schwendingeri* Hebauer, 1995b: 7 - Thailand, Chiang Mai; Hansen 1999b: 171 [catalog]; Hebauer and Ryndevich 2005: 46 [new record].

Helochares (*Hydrobaticus*) *ubudensis* Hebauer, 1998: 44 - Indonesia, Bali, Ubud; Hansen 1999b: 171; Hebauer 2002b: 13 [synonymy]; Short and Hebauer 2006: 337 [catalog].

DISTRIBUTION: Indo-Malayan: Indonesia (Bali), Laos, Malaysia (Peninsula), Thailand, Vietnam.

Remarks: Hebauer (2002b) indicates that the aedeagus of *schwendingeri* (as *ubudensis*) corresponds to fig. 4 in Hebauer 1998.

Helochares scitulus Balfour-Browne, 1952

Helochares (*Hydrobaticus*) *scitulus* Balfour-Browne, 1952a: 130 - Benin [Dahomey], Bassila; Hebauer 1996: 22 [faunistic treatment]; Hansen 1999b: 171 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Benin, Gambia, Ghana, Mali, Senegal, Sudan.

Helochares sechellensis Régimbart, 1903

Helochares (*Graphelochares*) *melanophthalmus* var. *sechellensis* Régimbart, 1903a: 27 - Seychelles [Iles Séchelles].

Helochares (*Hydrobaticus*) *sechellensis* Régimbart; d'Orchymont 1939b: 297 [specific rank confirmed]; Hansen 1999b: 171 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: Seychelles.

Helochares serpentinus Hebauer, 1998

Helochares (*Hydrobaticus*) *serpentinus* Hebauer, 1998: 44 - South Africa, Wilderness National Park, Lang Wie, 33°59'0''S, 22°40'6''E); Hansen 1999b: 171 [catalog]; Hebauer 2006: 26 [checklist].

DISTRIBUTION: Afrotropical: South Africa.

Helochares sharpi (Kuwert, 1890)

Helocharimorphus sharpi Kuwert, 1890a: 63 (and 1890b: 306) - Egypt [Aegypten]; Syria, Lebanon or Israel [Syria]; Iraq [Mesopotamien].

Helochares (Helocharimorphus) sharpi (Kuwert); Knisch 1924: 195 [catalog]; Hebauer 1994: 113 [faunistic treatment]; Hansen and Hebauer 1988: 29 [in key]; Hansen 1999b: 164 [catalog]; Hansen 2004: 52 [catalog]; Hebauer 2006: 27 [checklist]; Fikáček et al. 2015: 62 [catalog]; Salah and Régil Cueto 2017: 265 [faunistic treatment].

DISTRIBUTION: Afrotropical: Ghana, Madagascar, Tanzania, Togo, Uganda, Zambia. Palearctic: Egypt, Iraq, Israel.

Helochares silvester Hebauer, 2009

Helochares (*Hydrobaticus*) *silvester* Hebauer, 2009: 5 - Republic of the Congo, Brazzaville, d'Odzala Mboko National Park; Short and Fikáček 2011: 91 [catalog].

DISTRIBUTION: Afrotropical: Republic of the Congo.

Helochares simulator Knisch, 1922

Helochares (*Hydrobaticus*) *simulator* Knisch, 1922: 104 - Papua New Guinea, Bismarck Archipelago, Duke of York [not "Duke of York" (= Atafu) in Polynesia]; d'Orchymont 1943a: 7 [faunistic treatment]; Hansen 1999b: 171 [catalog]; Short 2010: 313 [faunistic treatment].

DISTRIBUTION: Australasian: Fiji, Papua New Guinea (Duke of York). Oceanian: Samoa, Tonga.

Helochares skalei Hebauer, 2002

Helochares (*Hydrobaticus*) *skalei* Hebauer, 2002b: 13; Hebauer 2005: 39 [checklist]; Hebauer 2006: 27 [checklist]; Short and Hebauer 2006: 336 [catalog].

DISTRIBUTION: Afrotropical: Malawi, South Africa, Zimbabwe.

Helochares songi Jia and Tang, 2018

Helochares (s. str.) *songi* Jia and Tang, 2018: 3 - China, Guangxi Province, Shiwandashan, Nalin River.

DISTRIBUTION: Indo-Malayan: China (Guangxi).

Helochares steffani Hebauer, 2002

Helochares (*Hydrobaticus*) *steffani* Hebauer, 2002b: 13 - Namibia, Ongongo falls, 13°49'W 19°08'S, ca 6 km upp. Warmquelle; Hebauer 2006: 27 [catalog]; Short and Hebauer 2006: 336 [catalog].

DISTRIBUTION: Afrotropical: Namibia.

Helochares stenius d'Orchymont, 1943

Helochares (*Hydrobaticus*) *stenius* d'Orchymont, 1943a: 8 - Democratic Republic of the Congo [Congo belge; Zaire], Lubutu nr Kisangani [Stanleyville]; Hebauer 1996: 22 [faunistic treatment]; Hansen 1999b: 171 [catalog]; Hebauer 2006: 27 [checklist].

DISTRIBUTION: Afrotropical: Democratic Republic of the Congo, Gabon, Republic of the Congo.

Helochares striatus (Boheman, 1851)

Hydrobius striatus Boheman, 1851: 599 - South Africa, Natal [terra Natalensi].

Helochares striatus (Boheman); Bedel 1880: CXLVIII [new combination].

Helochares (*Hydrobaticus*) *striatus* (Boheman); d'Orchymont 1919c: 150 [faunistic treatment]; d'Orchymont 1943e: 6 [faunistic treatment]; Balfour-Browne 1950a: 394 [faunistic treatment]; Hebauer 1996: 22 [faunistic treatment]; Hansen 1999b: 171 [catalog]; Hebauer 2006: 27 [checklist].

DISTRIBUTION: Afrotropical: Democratic Republic of the Congo, Gambia, Senegal, Sierra Leone, South Africa, Uganda.

Helochares strictus d'Orchymont, 1939

Helochares (*Hydrobaticus*) *strictus* d'Orchymont, 1939b: 306 - Tanzania, Lake Victoria, Ukerewe I; Balfour-Browne 1950b: 55 [faunistic treatment]; Hebauer 1996: 22 [faunistic treatment]; Hansen 1999b: 171 [catalog]; Hebauer 2006: 27 [checklist].

DISTRIBUTION: Afrotropical: Cameroon, Democratic Republic of the Congo, Ghana, Guinea, Kenya, Rwanda, Senegal, Tanzania, Uganda.

Helochares strigellus Hebauer, 2002

Helochares (*Hydrobaticus*) *strigellus* Hebauer, 2002b: 14 - Liberia, Saclepea; Hebauer 2006: 27 [checklist]; Short and Hebauer 2006: 336 [catalog].

DISTRIBUTION: Afrotropical: Kenya, Liberia.

Helochares structus d'Orchymont, 1936

Helochares (*Hydrobaticus*) *structus* d'Orchymont, 1936b: 112 - Botswana, Kasane; Hebauer 1988: 156 [faunistic treatment]; Hebauer 1995a: 264 [faunistic treatment]; Hebauer 1996: 23 [faunistic treatment]; Hansen 1999b: 171 [catalog].

DISTRIBUTION: Afrotropical: Benin [in doubt], Botswana, Cameroon [in doubt], Congo, Gambia, Ghana [in doubt], Guinea, Ivory Coast, Liberia, Namibia, South Africa, Sudan, Tanzania, Zambia.

Helochares sublineatus Hebauer, 2002

Helochares (s. str.) *sublineatus* Hebauer 2002b: 15 - Ghana, Tamale; Hebauer 2006: 25 [checklist]; Short and Hebauer 2006: 337 [catalog].

DISTRIBUTION: Afrotropical: Ghana, Nigeria.

Remarks: The aedeagus in this species is quite unusual among *Helochares* (see fig. 8 in Hebauer 2002b).

Helochares subseriatus Hebauer, 2009

Helochares (*Hydrobaticus*) *subseriatus* Hebauer, 2009: 5 - Gabon, Bateke Plateau National Park, Camp, Mbie; Short and Fikáček 2011: 91 [catalog].

DISTRIBUTION: Afrotropical: Gabon.

Remarks: The species is described from a single female specimen.

Helochares subtilis d'Orchymont, 1936

Helochares (*Hydrobaticus*) *subtilis* d'Orchymont, 1936b: 112 - ?Botswana ["Kalahari"], "Tsotsoroga Pan"; Hebauer 1995a: 264 [faunistic treatment]; Hebauer 1996: 23 [faunistic treatment]; Hansen 1999b: 171 [catalog]; Hebauer 2006: 27 [checklist].

DISTRIBUTION: Afrotropical: Botswana, Cameroon, Democratic Republic of the Congo, Ethiopia, Namibia, Republic of the Congo, South Africa, Zimbabwe.

Helochares sufflavus Balfour-Browne, 1952

Helochares (*Hydrobaticus*) *sufflavus* Balfour-Browne, 1952a: 131 - Togo, Tohoun; Hebauer 1996: 23 [faunistic treatment]; Hansen 1999b: 171 [catalog]; Hebauer 2006: 27 [checklist].

DISTRIBUTION: Afrotropical: Togo.

Helochares sylvaticus Balfour-Browne, 1957

Helochares (*Hydrobaticus*) *sylvaticus* Balfour-Browne, 1957: 24 - Burundi ["Urundi"], Bururi; Hebauer 1996: 23 [faunistic treatment]; Hansen 1999b: 171 [catalog]; Hebauer 2006: 27 [checklist].

DISTRIBUTION: Afrotropical: Burundi, Democratic Republic of the Congo, Republic of the Congo.

Helochares tamsi Balfour-Browne, 1947

Helochares (*Hydrobaticus*) *tamsi* Balfour-Browne, 1947: 142 - São Tomé and Príncipe [West Africa], São Tomé; Hebauer 1996: 23 [faunistic treatment]; Hansen 1999b: 171 [catalog]; Hebauer 2006: 27 [checklist].

DISTRIBUTION: Afrotropical: Gabon, Kenya [in doubt], Republic of the Congo, São Tomé and Príncipe.

Helochares tatei (Blackburn, 1896)

Hydrobaticus tatei Blackburn, 1896: 258 - Australia, Palm Creek; Watts 1995: 126 [Lectotype designated].

Helochares (*Hydrobaticus*) *tatei* (Blackburn); Knisch 1924: 194 [catalog]; d'Orchymont 1943a: 5 [faunistic treatment]; Hansen 1999b: 171 [catalog].

DISTRIBUTION: Australasian: Australia (New South Wales, Northern Territory, Queensland, South Australia, Western Australia).

Helochares tenuistriatus Régimbart, 1908

Helochares (*Hydrobaticus*) *tenuistriatus* Régimbart, 1908a: 315 - Australia, Western Australia, Perth, Lake Monger ["Mongers Lake, N. de Subiaco"]; Knisch 1924: 194 [catalog]; d'Orchymont 1943a: 5 [faunistic treatment]; Watts 1995: 127 [faunistic treatment]; Hansen 1999b: 172 [catalog].

DISTRIBUTION: Australasian: Australia (Western Australia).

Helochares tertius Hebauer, 1996

Helochares (Helocharimorphus) tertius Hebauer, 1996: 9 - Republic of the Congo, Mt. Fouari reservation, near Gabon; Hansen 1999b: 172 [catalog]; Hebauer 2006: 27 [checklist].

DISTRIBUTION: Afrotropical: Democratic Republic of the Congo, Republic of the Congo.

Remarks: The species is described from a unique female.

Helochares thurmerae Watts, 1995

Helochares (*Hydrobaticus*) *thurmerae* Watts, 1995: 127 - Papua New Guinea, Morobe District, Gusap Markham Valley c. 90 ml W. of Lae; Hansen 1999b: 172 [catalog].

DISTRIBUTION: Australasian: Papua New Guinea.

Helochares tristis (MacLeay, 1871)

Hydrobaticus tristis MacLeay, 1871: 131 - Australia, Queensland, Gayndah.

Helochares (*Hydrobaticus*) *tristis* (MacLeay); Knisch 1924: 194 [checklist]; d'Orchymont 1943a: 2 [faunistic treatment]; Hansen 1999b: 172 [catalog].

Hydrobaticus australis Blackburn, 1888: 823 - Australia, South Australia, Port Lincoln; Watts 1995: 128 [lectotype designated; synonymy].

Helochares (*Hydrobaticus*) *australis* (Blackburn); Knisch 1924: 193 [catalog]; d'Orchymont 1943a: 3 [faunistic treatment].

DISTRIBUTION: Australasian: Australia (Australian Capital Territory, New South Wales, Northern Territory, Queensland, South Australia, Tasmania, Victoria, Western Australia).

Helochares trujillo Short and Girón, 2018

Helochares (*Hydrobaticus*) *trujillo* Short and Girón, 2018: 45 - Venezuela, Mérida State, Mérida, Monte Zerpa Area.

DISTRIBUTION: Neotropical: Venezuela.

Helochares uenoi Matsui, 1995

Helochares (*Hydrobaticus*) *uenoi* Matsui, 1995: 317 - Japan, Okinawa Islands, Yonaguni Island, Tindabana; Hansen 1999b: 172 [catalog]; Hansen 2004: 52 [catalog]; Fikáček et al. 2015: 62 [catalog].

DISTRIBUTION: Palearctic: Japan.

Helochares uhligi Hebauer, 1999

Helochares (s. str.) *uhligi* Hebauer 1999: 11 - South Africa, Cape Province, Karoo National Park, Mountain View River; Hebauer 2006: 26 [checklist]; Short and Hebauer 2006: 337 [catalog].

DISTRIBUTION: Afrotropical: South Africa.

Helochares vitalisi d'Orchymont, 1919

Helochares (s. str.) *vitalisi* d'Orchymont, 1919b: 78 (and 1921c: 13) - Cambodia, Phnom Penh; d'Orchymont 1928: 108 [faunistic treatment]; Hansen 1999b: 163 [catalog].

DISTRIBUTION: Indo-Malayan: Cambodia.

Helochares wagneri Hebauer, 2002

Helochares (*Hydrobaticus*) *wagneri* Hebauer, 2002b: 14 - Kenya, Kakamega Forest, 0°22'N, 34°50'E; Hebauer 2006: 27 [checklist]; Short and Hebauer 2006: 337 [catalog].

DISTRIBUTION: Afrotropical: Kenya.

Helochares wattsi Hebauer and Hendrich, 1999

Helochares (*Hydrobaticus*) *wattsi* Hebauer and Hendrich, 1999: 50 - Australia: Northern Territory, Kakadu National Park, Jim Jim Hwy, Black Jungle Spring; Short and Hebauer 2006: 337 [catalog].

DISTRIBUTION: Australasian: Australia (Northern Territory).

Remarks: The aedeagus in this species is quite unusual among *Helochares* (see fig. 4 in Hebauer and Hendrich 1999).

Helochares yangae Hebauer, Hendrich, and Balke, 1999

Helochares (*Hydrobaticus*) *yangae* Hebauer, Hendrich, and Balke, 1999: 340 - Malaysia, Pahang, Lake Cini, lakeside near Rimba Resort; Short and Hebauer 2006: 337 [catalog].

DISTRIBUTION: Indo-Malayan: Malaysia.

Helochares zamora Short and Girón, 2018

Helochares (*Hydrobaticus*) *zamora* Short and Girón, 2018: 46 - Ecuador, Zamora-Chinchipe Province, Zamora.

DISTRIBUTION: Neotropical: Ecuador.

Helopeltarium d'Orchymont, 1943

Helopeltarium ferrugineum d'Orchymont, 1943

Helopeltarium ferrugineum d'Orchymont, 1943f: 10 - Burma, Dawna Range (eastside), "Sukli".

DISTRIBUTION: Indo-Malayan: Myanmar [Burma].

Katasophistes Girón and Short, 2018

Katasophistes charynae Girón and Short, 2018

Katasophistes charynae Girón and Short, 2018: 136 - Peru, Madre de Dios, Parque Manu, Pakitza, 12°07'S 70°58'W.

DISTRIBUTION: Neotropical: Peru.

Katasophistes cuzco Girón and Short, 2018

Katasophistes cuzco Girón and Short, 2018: 138 - Peru, Cuzco, Quita Calzón, at km 164, 13°09'S 71°22'W.

DISTRIBUTION: Neotropical: Peru.

Katasophistes merida Girón and Short, 2018: 138

Katasophistes merida Girón and Short, 2018: 138 - Venezuela, Mérida State, ca. 12 km SE of Santo Domingo, 8°51.933'N, 70°37.131'W.

DISTRIBUTION: Neotropical: Venezuela.

Katasophistes superficialis Girón and Short, 2018

Katasophistes superficialis Girón and Short, 2018 - Ecuador, Pastaza Province: “AGIP platform Villano B, along transect 1 and 2.

DISTRIBUTION: Neotropical: Ecuador.

Nanosaphes Girón and Short, 2018

Nanosaphes castaneus Girón and Short, 2018

Nanosaphes castaneus Girón and Short, 2018: 146 - Brazil, Pará, Rio Xingu Camp, Altamira ca 60km S., 52°22'W, 3°39'S.

DISTRIBUTION: Neotropical: Brazil (Pará).

Nanosaphes hesperus Girón and Short, 2018

Nanosaphes hesperus Girón and Short, 2018: 148 - Suriname, Sipaliwini District, Camp 1, on Kutari River, 2°10.521'N, 56°47.244'W.

DISTRIBUTION: Neotropical: Suriname.

Nanosaphes punctatus Girón and Short, 2018

Nanosaphes punctatus Girón and Short, 2018: 151 - Suriname, Sipaliwini District, Brownsberg Nature Park, 04°56.871'N, 55°10.911'W.

DISTRIBUTION: Neotropical: Suriname.

Nanosaphes tricolor Girón and Short, 2018

Nanosaphes tricolor Girón and Short, 2018: 151 - Suriname, Sipaliwini District, Camp 4 (low), Kasikasima, trail to Kasikasima, N 2.97731°, W 55.38500°.

DISTRIBUTION: Neotropical: Suriname.

Novochares gen. n.

Novochares abbreviatus (Fabricius, 1801) comb. nov.

Hydrophilus abbreviatus Fabricius, 1801: 251 - [America meridionali].

Helochares (s. str.) *abbreviatus* (Fabricius, 1801); d'Orchymont 1939e: 258 [taxonomic treatment]; Fernández, 1982a: 34 [taxonomic treatment]; Hansen 1999b: 159 [catalog]; Short 2005: 215 [new record]; Clarkson and Ferreira-Jr. 2014: 400 [faunistic treatment].

Philydrus pallidus Castelnau, 1840: 53 - Brazil (secondary homonym of *Hydrophilus pallidus* Rossi, 1792); d'Orchymont 1936a: 10 [synonymy].

Philhydrus pallidus Castelnau; Gemminger and Harold, 1868: 482 [checklist].

Helochares pallidus (Castelnau); Fleutiaux and Sallé, 1889: 376 [checklist].

Enochrus (*Lumetus*) *pallidus* (Castelnau); Zaitzev 1908: 388 [checklist].

Helochares (*Hydrobaticus*) *rufobrunneus* Balfour-Browne, 1939: 293. - Lesser Antilles, Grenada, Balthazar; Spangler 1981b: 158 [synonymy].

DISTRIBUTION: Neotropical: Argentina, Bolivia, Brazil (Espírito Santo), Colombia, Costa Rica, Cuba, French Guiana, Lesser Antilles, Panama, Paraguay, Suriname, Venezuela.

Novochares atlanticus (Clarkson and Ferreira-Jr., 2014) comb. nov.

Helochares (s. str.) *atlanticus* Clarkson and Ferreira-Jr. 2014a: 401 - Brazil, São Paulo, Ubatuba, Parque Estadual da Serra do Mar, Núcleo Picinguaba.

DISTRIBUTION: Neotropical: Brazil (São Paulo).

Novochares atratus (Bruch, 1915) **comb. nov.**

Helochares atratus Bruch, 1915: 451 - Argentina, Buenos Aires province; Fernández 1982a: 35 [taxonomic treatment]; Hansen 1999b: 159 [catalog].

Helochares (s. str.) *atratus* Bruch; Clarkson and Ferreira-Jr. 2014: 400 [faunistic treatment].

Helochares (s. str.) *parhedrus* d'Orchymont, 1939: 259 - Argentina, Chaco de Santiago del Estero; not syn. of *gibbus* Brullé (= *ventricosus* Bruch), as in d'Orchymont 1926: 236); Fernández 1982a: 35 [synonymy; redescription].

DISTRIBUTION: Neotropical: Argentina, Brazil (Minas Gerais, Paraíba), Ecuador [in doubt]; Paraguay.

Novochares bolivianus (Fernández, 1989) **comb. nov.**

Helochares (s. str.) *bolivianus* Fernández, 1989: 146 - Bolivia, Santa Cruz Department, Gutiérrez Province, Nueva Moka; Hansen 1999b: 158 [catalog].

DISTRIBUTION: Neotropical: Bolivia.

Novochares carmona (Short, 2005) **comb. nov.**

Helochares (s. str.) *carmona* Short 2005: 215 - Costa Rica, Guanacaste Province, Laguna de Crocodilo, near Carmona, 10°03'31.0''N, 85°14'25.6''W; Short and Hebauer 2006: 335 [catalog].

DISTRIBUTION: Neotropical: Costa Rica.

Novochares chaquensis (Fernández, 1982) **comb. nov.**

Helochares (s. str.) *chaquensis* Fernández, 1982b: 87 - Argentina, Chaco Province, San Bernardo; Hansen 1999b: 159 [catalog]; Clarkson and Ferreira-Jr. 2014: 400 [faunistic treatment].

DISTRIBUTION: Neotropical: Argentina, Brazil (Mato Grosso do Sul).

Novochares cochlearis (Fernández, 1982) **comb. nov.**

Helochares (s. str.) *cochlearis* Fernández, 1982b: 89 - Argentina, Corrientes, Santo Tomé; Hansen 1999b: 159 [catalog].

DISTRIBUTION: Neotropical: Argentina, Paraguay.

Novochares coya (Fernández, 1982) **comb. nov.**

Helochares (s. str.) *coya* Fernández, 1982: 87 - Bolivia, Santa Cruz Department, Sara Province, Monteros; Hansen 1999b: 160 [catalog].

DISTRIBUTION: Neotropical: Bolivia.

Novochares guadelupensis (d'Orchymont, 1926) **comb. nov.**

Helochares (s. str.) *guadelupensis* d'Orchymont, 1926b: 233 - Lesser Antilles, Guadeloupe; Hansen 1999b: 160 [catalog].

DISTRIBUTION: Neotropical: Lesser Antilles (Guadeloupe).

Novochares inornatus (d'Orchymont, 1926) **comb. nov.**

Helochares (s. str.) *inornatus* d'Orchymont, 1926b: 235 - French Guiana, "Passoura"; Hansen 1999: 160 [catalog]; Clarkson and Ferreira-Jr. 2014: 400 [faunistic treatment].

DISTRIBUTION: Neotropical: Brazil (Amazonas, São Paulo), French Guiana.

Novochares oculatus (Sharp, 1882) **comb. nov.**

Helochares oculatus Sharp, 1882: 74 - Guatemala, Paso Antonio; Fernández, 1982a: 31 [specific rank confirmed; not syn. of *pallidus* Castelnau, as in d'Orchymont 1926b: 232; not. syn. of *abbreviatus* Fabricius, as in d'Orchymont 1936a: 10; lectotype designated].

Helochares (s. str.) *oculatus* Sharp, 1882: 74; Hansen 1999b: 162 [catalog]; Short 2005: 216 [new record]; Clarkson and Ferreira-Jr. 2014: 400 [faunistic treatment].

DISTRIBUTION: Neotropical: Argentina, Brazil (Pernambuco), Costa Rica, Guatemala, Panama; According to Hansen (1999b: 162), records from Mexico and the Antilles (Grenada, St. Vincent) need confirmation.

Novochares pallipes (Brullé, 1841) **comb. nov.**

Hydrophilus (*Philydrus*) *pallipes* Brullé, 1841: 58. - Uruguay, Montevideo.

Philhydrus pallipes (Brullé); Lacordaire 1854: 457.

Helochares pallipes (Brullé); Bedel, 1881: XCIV.

Helochares (s. str.) *pallipes* (Brullé); Fernández 1983: 444 [redescription; immatures description]; Hansen 1999b: 163 [catalog]; Clarkson and Ferreira-Jr. 2014: 400 [faunistic treatment].

DISTRIBUTION: Neotropical: Argentina, Brazil (Mato Grosso, Mato Grosso do Sul), Paraguay, Uruguay.

Novochares pichilingue (Fernández, 1989) **comb. nov.**

Helochares (s. str.) *pichilingue* Fernández, 1989: 147 - Ecuador, Los Ríos, Quevedo, Río Pichilingue; Hansen 1999b: 163 [catalog].

DISTRIBUTION: Neotropical: Ecuador.

Novochares sallaei (Sharp, 1882) **comb. nov.**

Helochares sallæi Sharp, 1882: 75 - Mexico, Cordova.

Helochares (s. str.) *Sellae* Sharp; Knisch, 1924a: 199 [catalog; misspelled].

Helochares (s. str.) *sallaei* Sharp; Hansen 1999b: 163 [catalog]; Short 2005: 217 [faunistic treatment].

Philhydrus estriatus Blatchley, 1917: 139. - U.S.A., Florida (west coast); Winters, 1927a: 24 [synonymy].

Enochrus (*Lumetus*) *estriatus* (Blatchley); Knisch 1924a: 208 [catalog].

DISTRIBUTION: Nearctic: U.S.A. (Florida). Neotropical: Belize, Costa Rica, Mexico.

Novochares tectiformis (Fernández, 1982) **comb. nov.**

Helochares (s. str.) *tectiformis* Fernández, 1982b: 88. - Argentina, Corrientes, Santo Tomé; Hansen 1999b: 163 [catalog]; Clarkson and Ferreira-Jr. 2014: 400 [faunistic treatment].

DISTRIBUTION: Neotropical: Argentina, Brazil (Mato Grosso do Sul), Paraguay, Venezuela.

Peltochares Régimbart, 1907

Peltochares atropiceus (Régimbart, 1903) comb. nov.

Helochares atropiceus Régimbart, 1903b: 53 - Vietnam ["Cochinchine"] (Ho Chi Minh ["Saigon"]; My Tho); Cambodia (Phnom Penh); Indonesia (Sumatra, Borneo, New Guinea); not syn. of *taprobanicus* Sharp, as in d'Orchymont 1923b: 419 and Hansen 1999: 163.

Helochares (s. str.) *atropiceus* Régimbart; Hebauer 2001: 10 [specific rank confirmed; lectotype designated]; Hansen 2004: 52 [checklist]; Hebauer and Ryndevich 2005: 45 [new record]; Fikáček et al. 2015: 61 [checklist]; Jia and Tang 2018b: 9 [redescription; new record].

Helochares (s. str.) *atropiceus* Sharp; Hebauer 2002a: 24 [author attribution in error; new record].

Helochares (s. str.) *ohkurai* Satô, 1976: 21 - Japan, Nansei-shoto archipelago ["Ryukyus"], Iriomote-jima Is., Ôhara-Ôtomi; Hansen 1999b: 162 [catalog]; Hebauer 2001: 11 [synonymy].

DISTRIBUTION: Australasian: Papua New Guinea ["Nouvelle Guinée"]. Indo-Malayan: Bangladesh, Cambodia, China (Guangdong, Guangxi, Guizhou, Hong Kong, Jiangxi, Macao), Indonesia (Borneo, Sumatra), Nepal, Thailand, Vietnam. Palearctic: Japan (Iriomote-jima).

Peltochares ciniensis (Hebauer, Hendrich, and Balke, 1999) **comb. nov.**

Helochares (s. str.) *ciniensis* Hebauer, Hendrich, and Balke, 1999: 341 - Malaysia, Pahang, Lake Cini, lakeside nr. Rimba Resort; Short and Hebauer 2006: 335 [catalog].

DISTRIBUTION: Indo-Malayan: Malaysia.

Peltochares conspicuus Régimbart, 1907

Peltochares conspicuus Régimbart, 1907: 49 - Gabon, Cape Lopez, Rembo N'Comi; Balfour-Browne 1950b: 60 [faunistic treatment]; Hansen 1999b: 172 [catalog]; Hebauer 2006: 27 [checklist].

DISTRIBUTION: Afrotropical: Democratic Republic of the Congo, Gabon, Ghana, Ivory Coast.

Remarks: We have seen Régimbart's syntype series for *Peltochares conspicuus*. It includes two specimens labeled 'Cape Lopez', one of them labeled '*Peltochares conspicuus* Rég.'; five specimens labeled Rembo N'Comi Fernand Vaz, one of them missing prothorax and head, and another one is missing the left elytron; one specimen labeled Rembo N'Comi Fernand Vaz (Gabon), missing prothorax and head; and one specimen labeled 'Gabon'. All specimens, except the last one, are pinned; the specimen labeled 'Gabon' is glued by its abdomen in a small pinned card. Here we designate as the Lectotype the specimen that bears the '*Peltochares conspicuus* Rég.' label, which even though is not completely clean, has all its appendages complete. One of the specimens missing its thorax and head was dissected to reveal the male genitalia, which is illustrated in Figs. 13G and 45A.

Peltochares discus (Hebauer, Hendrich, and Balke, 1999) **comb. nov.**

Helochares (s. str.) *discus* Hebauer, Hendrich, and Balke 1999: 342; Hebauer 2001b: 11 [taxonomic treatment]; Short and Hebauer 2006: 336 [catalog].

DISTRIBUTION: Indo-Malayan: Indonesia (Sumatra), Malaysia.

Peltochares foveicollis (Montrouzier, 1860) **comb. nov.**

Stagnicola foveicollis Montrouzier, 1860: 247 - New Caledonia, Île Art ["Nouvelle-Calédonie, Art"].

Helochares foveicollis (Montrouzier); Bedel 1880: CXLVIII [synonymy].

Philhydrus burrundiensis Blackburn, 1890: 447 - Australia, Nortern Territory, Burrundie; d'Orchymont 1943b: 6 [synonymy in doubt].

Neohydrobius burrundiensis (Blackburn); Blackburn 1898: 221 [new genus; new combination].

Helochares (s. str.) *burrundiensis* (Blackburn); d'Orchymont 1919b: 228 [synonymy].

Helochares (s. str.) *foveicollis* (Montrouzier); d'Orchymont 1937e: 154 [checklist]; Watts, 1995: 118 [taxonomic treatment]; Hansen 1999: 160 [catalog]; Short 2010: 312 [catalog].

DISTRIBUTION: Australasian: Australia (Australian Capital Territory, New South Wales, Northern Territory, Queensland, Western Australia), New Caledonia, Papua New Guinea.

Peltochares longipalpis (Murray, 1859) **comb. nov.**

Philhydrus (s. str.) *longipalpis* Murray, 1859: 123 - Nigeria, Calabar ["Old Calabar"].

Helochares longipalpis Murray; Régimbart 1903a: 26 [faunistic treatment].

Helochares (s. str.) *longipalpis* Murray; Balfour-Browne 1950b: 58 [faunistic treatment]; Balfour-Browne 1952a: 129 [faunistic treatment]; Balfour-Browne 1957: 22 [faunistic treatment]; Hansen and Hebauer 1988: 29 [in key]; Hebauer 1994: 112 [faunistic treatment]; Hebauer 1995a: 265 [faunistic treatment]; Hebauer 1996: 7 [faunistic treatment]; Hansen 1999b: 161 [catalog]; Hebauer 2001: 12 [taxonomic treatment]; Hebauer 2005: 39 [checklist]; Hebauer 2006: 25 [checklist]; Hansen 2004: 52 [checklist]; Fikáček et al. 2015: 61 [checklist]; Salah and Régil Cueto 2017: 265 [checklist].

Helochares filipalpis Sharp, 1903: 6 - South Sudan [Sudan], Jebel Ahmed Agha ["Gebel Ahmed Agha"]; d'Orchymont 1943c: 7 [synonymy].

DISTRIBUTION: Afrotropical: Angola, Benin, Botswana, Burkina Faso, Burundi, Cameroon, Central African Republic, Chad, Democratic Republic of the Congo, Ethiopia, Gabon, Gambia, Ghana, Guinea, Ivory Coast, Kenya, Liberia, Madagascar, Malawi, Mozambique, Namibia, Niger, Nigeria, Republic of the Congo, Rwanda, Senegal, Sierra Leone, Somalia, South Africa, South Sudan, Tanzania, Togo, Uganda, Western Sahara, Zambia, Zimbabwe. Palearctic: Canary Islands, Egypt, Israel.

Peltochares papuensis (Hebauer, 1995) **comb. nov.**

Helochares (s. str.) *papuensis* Hebauer, 1995: 8 - Indonesia, Papua [W. Neuguinea; Irian Jaya], Paniai province, Wanggar-Kali Bumi; Hansen 1999b: 163 [catalog].

DISTRIBUTION: Australasian: Indonesia (Papua).

Peltochares taprobanicus (Sharp, 1890) **comb. nov.**

Helochares (s. str.) *taprobanicus* Sharp, 1890: 351 - Sri Lanka, Colombo ["(Ceylon): Colombo"]; d'Orchymont 1928: 108 [faunistic treatment]; Hebauer 1995b: 8 [faunistic treatment]; Hansen 1999b: 163 [catalog]; Hebauer 2001: 11 [taxonomic treatment; lectotype designated].

Helochares (s. str.) *lacustris* Hebauer, Hendrich, and Balke 1999: 342; Hebauer 2001: 11 [synonymy]; Hebauer and Ryndevich 2005: 45 [new record]; Short and Hebauer 2006: 336 [catalog].

DISTRIBUTION: Indo-Malayan: Indonesia (Sumatra), Laos, Malaysia, Nepal, Sri Lanka, Thailand, Vietnam.

Primocerus Girón and Short, 2019

Primocerus cuspidis Girón and Short, 2019

Primocerus cuspidis Girón and Short, 2019: 144 - Venezuela, Amazonas, Tobogán de la Selva, old "Tobogancito", 5°23.207'N, 67°36.922'W.

DISTRIBUTION: Neotropical: Venezuela.

Primocerus gigas Girón and Short, 2019

Primocerus gigas Girón and Short, 2019: 145 - Venezuela, Amazonas, Cerro de la Neblina, camp II, 0°50'N, 65°59'W.

DISTRIBUTION: Neotropical: Venezuela.

Primocerus maipure Girón and Short, 2019

Primocerus maipure Girón and Short, 2019: 146 - Venezuela, Amazonas, ca. 15 Km S. of Puerto Ayacucho, 5°30.623'N, 67°36.109'W.

DISTRIBUTION: Neotropical: Venezuela.

Primocerus neutrum Girón and Short, 2019

Primocerus neutrum Girón and Short, 2019: 147 - Venezuela, Bolívar, along La Escalera, 6°2'10.5"N, 61°23'57.8"W.

DISTRIBUTION: Neotropical: Guyana, Suriname, Venezuela.

Primocerus ocellatus Girón and Short, 2019

Primocerus ocellatus Girón and Short, 2019: 148 - Venezuela, Amazonas, Cerro de la Neblina, Camp XII, near Pico Phelps.

DISTRIBUTION: Neotropical: Venezuela.

Primocerus petilus Girón and Short, 2019

Primocerus petilus Girón and Short, 2019: 148 - Brazil, Pará: Alenquer, Vale do Paraíso, ca. 55 km N. of Alenquer, 1.49292S, 54.51566W.

DISTRIBUTION: Neotropical: Brazil (Pará).

Primocerus pijiguaense Girón and Short, 2019

Primocerus pijiguaense Girón and Short, 2019: 149 - Venezuela, Bolívar, Los Pijiguaos, 6°35.617'N, 66°49.238'W

DISTRIBUTION: Neotropical: Venezuela.

Primocerus semipubescens Girón and Short, 2019

Primocerus semipubescens Girón and Short, 2019: 150 - Guyana, Region VIII, Ayanganna Airstrip, trail from Blackwater Creek Camp to Potaro River, 5°17.823'N, 59°50.000'W.

DISTRIBUTION: Neotropical: Guyana.

Primocerus striatolatus Girón and Short, 2019

Primocerus striatolatus Girón and Short, 2019: 151 - Suriname, Sipaliwini District, Camp 4 (high) Kasikasima, 2°58'36.7782"N, 55°24'40.986"W.

DISTRIBUTION: Neotropical: Suriname.

Quadriops Hansen, 1999

Quadriops acroreius Girón and Short, 2017

Quadriops acroreius Girón and Short, 2017: 123 - Suriname, Sipaliwini District, Camp 1: Upper Palemeu, 2°28'37.1994"N, 55°37'45.876"W.

DISTRIBUTION: Neotropical: Suriname, French Guiana.

Quadriops clusia Girón and Short, 2017

Quadriops clusia Girón and Short, 2017: 125 - Suriname, Brokopondo District, Brownsberg Nature Park, Leo Val trail, nr. pump station, 4.95069'N, -55.18599.

DISTRIBUTION: Neotropical: Guyana, Suriname, Brazil (Amazonas).

Quadriops dentatus Hansen, 1999

Quadriops dentatus Hansen, 1999a: 134 - Venezuela, Bolivar, 105 km S El Dorado; Hansen 1999b: 155 [catalog]; Girón and Short 2017: 127 [new records].

DISTRIBUTION: Neotropical: Venezuela, French Guiana, Suriname.

Quadriops depressus Hansen, 1999

Quadriops depressus Hansen, 1999: 136 - Peru, Departamento Loreto, 1.5km N Teniente Lopez 2°35.66'S,76°06.92'W; Hansen 1999b: 155 [catalog]; Girón and Short 2017: 128 [new records].

Quadriops amazonensis García, 2000: 59 - Venezuela, Amazonas, Municipio Guinia, Yavita, Caño Chivichi; Girón and Short 2017: 128 [synonymy]; Short and Hebauer 2006: 338 [catalog].

Quadriops politus Hansen, 1999: 135 - Peru, Departamento Loreto, Campamento San Jacinto, 2°18.75'S, 75°51.77'W; Hansen 1999b: 155; Girón and Short 2017: 128 [synonymy]

DISTRIBUTION: Neotropical: Ecuador, Peru, Venezuela.

Quadriops reticulatus Hansen, 1999

Quadriops reticulatus Hansen, 1999: 135 - Costa Rica, Puntarenas, Las Alturas (Stanford Biological Station), ca. 29km NE San Vito; Hansen 1999b: 155 [catalog]; Girón and Short 2017: 130 [new records].

DISTRIBUTION: Neotropical: Costa Rica, Panama.

Quadriops similaris Hansen, 1999

Quadriops similaris Hansen, 1999: 136 - Venezuela, Bolivar, 105 km S El Dorado; Hansen 1999b: 155 [catalog]; Girón and Short 2017: 134 [new records].

DISTRIBUTION: Neotropical: Venezuela, Guyana, Suriname, French Guiana.

Radicitus Short and García, 2014

Radicitus ayacucho Short and García, 2014

Radicitus ayacucho Short and García, 2014: 252 - Venezuela, Amazonas State, Tobogan de la Selva, 5°23.207'N, 67°36.922'W.

DISTRIBUTION: Venezuela.

Radicitus granitum Short and García, 2014

Radicitus granitum Short and García, 2014: 254 - Venezuela, Bolívar State, Los Pijiguaos, 6°35.617'N, 66°49.238'W.

DISTRIBUTION: Venezuela.

Radicitus surinamensis Short and García, 2014

Radicitus surinamensis Short and García, 2014: 257 - Suriname, Sipaliwini Department, Mt. Kasikasima, N 2°58.613', W 55°24.683'.

DISTRIBUTION: Suriname.

Sindolus Sharp, 1882

Sindolus femoratus (Brullé, 1841)

Hydrophilus (*Philydrus*) *femoratus* Brullé, 1841: 59 - Argentina ["province de Corrientes"].

Hydrobius femoratus (Brullé); Gemminger and Harold 1868a: 479 [checklist].

Helochares femoratus (Brullé); Bedel 1881: XCV.

Helochares (*Sindolus*) *femoratus* (Brullé); d'Orchymont 1926b: 236; Fernández and Kehr 1994 [annual life cycle]; Fernández and Kehr 1995 [spatial and temporal distribution]; Hansen 1999: 157 [catalog]; Clarkson and Ferreira-Jr 2014a: 403 [faunistic treatment].

? *Hydrobius spadiceus* Dejean, 1833: 134; nom. nud.; Mulsant 1844b: 380 [syn. of *Philhydrus spadiceus* Mulsant]

? *Philhydrus spadiceus* Mulsant, 1844b: 380 - French Guiana (Cayenne) and Colombia ["Nouvelle-Grenade"]; d'Orchymont 1929: 95 [synonym doubtful].

? *Enochrus* (*Lumetus*) *spadiceus* (Mulsant); Zaitzev 1908: 389 [catalog].

Helochares gravidus Bruch, 1915: 452 - Argentina, La Plata ("Tiro Federal"; Formosa (Puerto Bouvier); d'Orchymont 1926b: 236 [synomymy].

Helochares (*Sindolus*) *gravidus* Bruch; Knisch 1924: 199 [catalog].

DISTRIBUTION: Neotropical: Argentina, Brazil (Rio de Janeiro, Rio Grande do Sul), Colombia [in doubt; see d'Orchymont, 1943d: 56], French Guiana [in doubt; see d'Orchymont, 1943d: 56], Lesser Antilles (Antigua).

Sindolus mesostitialis (Fernández, 1981) comb. nov.

Helochares (*Sindolus*) *mesostitialis* Fernández, 1981: 189 - Argentina, Santa Fe, Dept. Garay, Colonia Mascias; Hansen 1999b: 158 [catalog]; Clarkson and Ferreira-Jr. 2014: 400 [faunistic treatment].

DISTRIBUTION: Neotropical: Argentina, Brazil (Mato Grosso do Sul).

Sindolus mini (Fernández, 1982) comb. nov.

Helochares (*Sindolus*) *mini* Fernández, 1982: 89 - Argentina, Santa Fe, Chaco prov., lag. La Cava, Barranqueras; Hansen 1999b: 158 [catalog].

DISTRIBUTION: Neotropical: Argentina, Paraguay.

Sindolus mundus Sharp, 1882

Sindolus mundus Sharp, 1882: 73 - Mexico, Oaxaca.

Helochares (*Sindolus*) *mundus* (Sharp); Knisch, 1924: 199 [checklist]; Hansen 1999b: 158 [catalog]; Short 2005: 219 [new records].

DISTRIBUTION: Neotropical: Costa Rica, Mexico, Nicaragua.

Sindolus optatus Sharp, 1882

Sindolus optatus Sharp, 1882: 72 - Guatemala, Paso Antonio.

Helochares (*Sindolus*) *optatus* (Sharp); Knisch 1924: 199 [checklist]; Hansen 1999b: 158 [catalog]; Short 2005: 220 [new records].

Helochares (s. str.) *guatemalensis* Knisch, 1921a: 68 - Guatemala; d'Orchymont 1937b: 253 [synonymy].

Helochares (*Sindolus*) *guatemalensis* Knisch; Knisch 1924: 199 [catalog].

DISTRIBUTION: Neotropical: Costa Rica, Guatemala, Mexico.

Sindolus spatulatus (Fernández, 1981) **comb. nov.**

Helochares (*Sindolus*) *spatulatus* Fernández, 1981: 191 - Argentina, Corrientes.

DISTRIBUTION: Neotropical: Argentina, Paraguay.

Sindolus talarum (Fernández, 1983)

Helochares (*Sindolus*) *talarum* Fernández, 1983: 440 - Argentina, Buenos Aires, lag. Los Talas; [original description includes description of immature stages].

DISTRIBUTION: Neotropical: Argentina.

Sindolus ventricosus Bruch, 1915

Hydrophilus (*Philydrus*) *gibbus* Brullé, 1841: 58 (primary homonym of *Hydrophilus gibbus* Illiger, 1801 and *Hydrophilus gibbus* Thunberg, 1820); d'Orchymont, 1926b: 236 (sub nom. *gibbus*; not syn. of *atratus* Bruch, as in Balfour-Browne 1939: 293).

Philhydrus gibbus (Brullé); Lacordaire 1854: 457.

Helochares gibbus (Brullé); Bedel 1881: XCV.

Helochares (*Sindolus*) *gibbus* (Brullé); d'Orchymont 1926b: 236.

Helochares ventricosus Bruch, 1915: 452; Fernández, 1982a: 36 [specific rank confirmed; lectotype designated; not syn. of *atratus* Bruch, as in Balfour-Browne, 1939: 293].

Helochares (*Sindolus*) *ventricosus* Bruch; Clarkson and Ferreira-Jr. 2014: 400 [faunistic treatment].

DISTRIBUTION: Neotropical: Argentina, Bolivia, Brazil (Amazonas, Mato Grosso do Sul), Paraguay, Uruguay.

Tobochares Short and García, 2007

Tobochares canaliculatus Kohlenberg and Short, 2017

Tobochares canaliculatus Kohlenberg and Short, 2017: 119 - Venezuela, Amazonas State, Tobogan de la Selva, old "tobogancito", 5°23.207'N, 67°36.922'W.

DISTRIBUTION: Neotropical: Venezuela.

Tobochares canthus Kohlenberg and Short, 2017

Tobochares canthus Kohlenberg and Short, 2017: 122 - Venezuela, Amazonas State, Tobogan de la Selva, old "tobogancito", 5°23.207'N, 67°36.922'W.

DISTRIBUTION: Neotropical: Venezuela.

Tobochares emarginatus Kohlenberg and Short, 2017

Tobochares emarginatus Kohlenberg and Short, 2017: 123 - Suriname: Sipaliwini District, Camp 4 (high) Kasikasima, N2°58.613', W55°24.683'.

DISTRIBUTION: Neotropical: Suriname.

Tobochares kasikasima Short, 2013

Tobochares kasikasima Short, 2013: 83 - Suriname, Sipaliwini District, Camp 4 (high) Kasikasima, N2°58.613', W55°24.683'; Kohlenberg and Short 2017: 124 [redescription].

DISTRIBUTION: Neotropical: Suriname.

Tobochares kusad Kohlenberg and Short, 2017

Tobochares kusad Kohlenberg and Short, 2017: 126 - Guyana: Region IX, Kusad Mts., Mokoro Creek, 2 48.531'N, 59 51.900'W.

DISTRIBUTION: Neotropical: Guyana.

Tobochares pallidus Kohlenberg and Short, 2017

Tobochares pallidus Kohlenberg and Short, 2017: 130 - Venezuela: Amazonas State, Tobogan de la Selva, old "tobogancito", 5°23.207'N, 67°36.922'W.

DISTRIBUTION: Neotropical: Venezuela.

Tobochares sipaliwini Short and Kadosoe, 2011

Tobochares sipaliwini Short and Kadosoe, 2011: 85 - Suriname, Sipaliwini District, Camp 2, on Sipaliwini River, Inselberg, 2 10.973'N, 56 47.235'W; Kohlenberg and Short 2017: 132 [redescription].

DISTRIBUTION: Neotropical: Suriname.

Tobochares sulcatus Short and García, 2007

Tobochares sulcatus Short and García, 2007: 4 - Venezuela: Amazonas State, Tobogan de la Selva, ca. 40 km S. Puerto Ayacucho, margin of Rio Coromoto; Short and Fikáček 2011: 91 [catalog].

DISTRIBUTION: Neotropical: Venezuela.

Troglochares Spangler, 1981

Troglochares ashmolei Spangler, 1981

Troglochares ashmolei Spangler, 1981: 318 - Ecuador, Morona-Santiago prov., Los Tayos Cave; Hansen 1999b: 156.

DISTRIBUTION. Neotropical: Ecuador.

ACKNOWLEDGEMENTS

We are grateful for the loan of valuable specimens by curators of collections including Mauricio García (MALUZ), Jesus Camacho (MALUZ), Luis Joly (MIZA), Vanessa Kadosoe and Paul Ouboter (NZCS), Robert Anderson (CMN). We are particularly thankful to the continued assistance of Charyn Micheli (USNM) for access to the Spangler collection and backlog and to Franz Hebauer for exchanging specimens years ago. Martin Fikáček has provided invaluable access to numerous references that would not be accessible otherwise. Rachel Smith dissected and imaged some of the *Chasmogenus* specimens that are presented here. Alex Kohlenberg produced some of the SEM images used here. This study was supported by US National Science Foundation grant DEB-1453452 to AEZS.

REFERENCES CITED

Anderson JME (1976) Aquatic Hydrophilidae (Coleoptera). The biology of some Australian species with descriptions of immature stages reared in the laboratory. Australian Journal of Entomology 15(2): 219–228. https://doi.org/10.1111/j.1440-6055.1976.tb01696.x

Archangelsky M (1997) Studies on the biology, ecology, and systematics of the immature stages of New World Hydrophiloidea (Coleoptera: Staphyliniformia). Bulletin of the Ohio Biological Survey 12(1): 1–207.

Balfour-Browne J (1939). Contribution to the Study of the Palpicornia. Part III. Annals and Magazine of natural History 11(4): 289–310. https://doi.org/10.1080/00222933908526990

Balfour-Browne J (1945) Aquatic Coleoptera of Oceania (Dytiscidae, Gyrinidae, and Palpicornia). Occasional Papers of the Bernice P. Bishop Museum 18(7): 103–132.

Balfour-Browne J (1947) New and interesting aquatic Coleoptera from the Sudan. Proceedings of the Royal Entomological Society of London (B) 16: 133–142. https://doi.org/10.1111/j.1365-3113.1947.tb00844.x

Balfour-Browne J (1948) New East African Palpicornia. Annals and Magazine of natural History 11(14): 817–833.

Balfour-Browne J (1950a) On the aquatic Coleoptera of Northern Rhodesia (Dytiscidae, Gyrinidae and Palpicornia). Occasional Papers of the national Museums of Southern Rhodesia 2(16): 359–399.

Balfour-Browne J (1950b) Palpicornia. Exploration du Parc National Albert. Mission G. F. de Witte (1933-35) 63: 1–84. http://www.apncb.be/archives/publications/exploration-national-park-albert/exploration-national-park-albert-first-series/mission-g.-f.-de-witte-1933-1935/1950-fascicule-63-palpicornia/balfour-complet.pdf

Balfour-Browne J (1951) Coleoptera: Haliplidae, Dytiscidae, Gyrinidae, Hydraenidae, Hydrophilidae (pp. 179–220, pl. 10–11). In British Museum (Natural History): Expedition to South-west Arabia 1937-1938. xiv + 504 pp. London.

Balfour-Browne J (1952a) Mission A. Villiers au Togo et au Dahomey (1950). VII. Coléoptères Hydrophilides. Bulletin de l'Institut français d'Afrique noire 14: 126–139.

Balfour-Browne J (1952b) Contribution à l'étude du peuplement de la Mauritanie. Coléoptères Hydrophilides. Bulletin de l'Institut français d'Afrique noire 14(2): 513–517.

Balfour-Browne J (1957) Contributions à l'étude de la faune entomologique du Ruanda-Urundi (Mission P. Basilewsky 1953). CXVIII. Coleoptera Hydrophilidae. Annales du Musée Royal du Congo Belge, Zool. 58: 14–25.

Balfour-Browne J (1958a) La Reserve naturelle integrale du Mont Nimba, Guinea. VI. Coléoptères Hydrophiloides. Mémoires de l'Institut français d'Afrique noire 53: 169–190.

Balfour-Browne J (1958b) New species of Malgassic Hydrophilidae (Col.). Mauritius Institute Bulletin 5: 134–147.

Balfour-Browne J (1959) Dr. Jan Bechyné expedition to French Guinea, 1951. Hydrophilidae. Entomologische Arbeiten aus dem Museum G. Frey 10: 302–320. https://biodiversitylibrary.org/page/45982912

Bedel L (1880) (Quelques modifications nouvelles à introduire dans la nomenclature des Hydrophilides). Annales de la Société Entomologique de France 5(10): CXLVII–CXLVIII. https://biodiversitylibrary.org/page/8232411

Bedel L (1881a) (1879-1881) Faune des Coléoptères du bassin de la Seine. Vol. 1. App. to Annales de la Société entomologique de France 24 + 360 pp. https://biodiversitylibrary.org/page/9314722

Bedel L (1881b) (Synonymie de quelques Hydrophilidæ et Sphæridiidæ exotiques décrits par Brullé). Annales de la Société Entomologique de France 6(1): XCIV–XCV. https://biodiversitylibrary.org/page/8996339

Bergroth E (1888) *Fåhraea* nov. gen. Hydrophilidarum. Deutsche entomologische Zeitschrift 32: 221. https://biodiversitylibrary.org/page/33177095

Bertrand H (1962) Contribution à l'étude des premiers états des Coléoptères aquatiques de la région éthiopienne (4e note). Bulletin de l'Institut Française d'Afrique Noire 24(4): 1065–1114.

Blackburn T (1888) Notes on Australian Coleoptera with descriptions of new species. Proceedings of the Linnean Society of New South Wales (2)3 (1889): 805–875. https://biodiversitylibrary.org/page/36009579

Blackburn T (1890) Notes on Australian Coleoptera, with descriptions of new species. Part III. Proceedings of the Linnean Society of New South Wales 2(4): 445–482. https://biodiversitylibrary.org/page/6240695

Blackburn T (1893) Notes on Australian Coleoptera, with descriptions of new species. Part XI. Proceedings of the Linnean Society of New South Wales 2(7) (1892): 65–150. https://biodiversitylibrary.org/page/6237149

Blackburn T (1896) Coleoptera (exclusive of the Carabidæ) (pp. 254–308). In Spencer, B. (ed.): Report on the work of the Horn Scientific Expedition to Central Australia. Part. II. - Zoology. iv + 431 pp., 29 pl. Dulau and Co., London; Melville, Mullen and Slade, Melbourne. https://biodiversitylibrary.org/page/57973709

Blatchley WS (1917) On some new or noteworthy Coleoptera from the west coast of Florida. Canadian Entomologist 49: 137–143. https://doi.org/10.4039/Ent49137-4

Boheman CH (1851) (1848-51) Insecta Caffrariæ annis 1838-1845 a J. A. Wahlberg collecta. Vol. 1. Coleoptera. 8 + 625 pp. Fritze & Norstedt, Holmiæ. (only pp. 299-625 issued in 1851) https://biodiversitylibrary.org/page/9907494

Brancsik K (1893) Beiträge zur Kenntniss Nossibés und dessen Fauna nach Sendungen und Mittheilungen des Herrn P. Frey. Jahresheft des naturwissenschaftlichen Vereins des Trencsiner Komitäts 15-16 (1892-93): 202-258, pl. 6 + 10-12.

Bruch C (1915) Nuevas especies de coleópteros hidrofílidos. Revista del Museo de la Plata 19(2): 447–470. https://publicaciones.fcnym.unlp.edu.ar/rmlp/article/view/1317/1520

Brullé A (1835) Histoire naturelle des Insectes. Vol. 5. Coléoptères II. 436 pp. - F. D. Pillot, Paris. https://biodiversitylibrary.org/page/24569590

Brullé A (1841) Famille des Hydrophiliens. In: d'Orbigny A. Voyage dans l'Amérique méridionale 6(2) Insectes. P Bertrand, Paris, France, pp. 52–59. https://biodiversitylibrary.org/page/2531016

Castelnau FL (1840) Histoire naturelle des Animaux articulés, Histoire naturelle des Insectes Coléoptères, Vol. 2. (Nécrophages-Trimères). 565 pp., 38 pl. P. Duménil, Paris. https://biodiversitylibrary.org/page/32717751

Chiesa A (1967) Compimento di una revisione di Hydrophilidae del Afghanistan (Coleoptera: Hydrophilidae). Annales historico-naturales Musei nationalis hungarici 59: 275–277.

Clarkson B, Ferreira-Jr N (2014a) A new species and records of *Helochares* (Insecta: Coleoptera: Hydrophilidae) from Southeastern Brazil. Zoologia 31(4): 400–404. http://www.scielo.br/pdf/zool/v31n4/12.pdf

Clarkson B, Ferreira-Jr N (2014b) Four new species and first nominal record of *Chasmogenus* Sharp, 1882 (Coleoptera: Hydrophilidae) from Brazil. Zootaxa 3765(5): 481–494. https://biotaxa.org/Zootaxa/article/view/zootaxa.3765.5.6

Clarkson B, Dias Dos Santos A, Ferreira-Jr N (2016) On Brazilian *Helobata* Bergroth, 1888 (Coleoptera: Hydrophilidae): description of two new species, new records, and key to species. Zootaxa 4126(4): 548–562. http://www.mapress.com/j/zt/article/view/zootaxa.4126.4.6

Cockerell TDA (1906a) Preoccupied Generic names of Coleoptera. Entomological News 17: 240–244. https://biodiversitylibrary.org/page/2562995

Cockerell TDA (1906b) Notes and News: Names of Coleoptera. Entomological News 17: 349. https://biodiversitylibrary.org/page/2563040

d'Orchymont A (1913a) H. Sauter's Formosa-Ausbeute. Hydrophilidae (Col.). Supplementa entomologica 2: 1–18, pl. 1.

d'Orchymont A (1913b) Contribution a l'etude des larves Hydrophilides. Annales de Biologie Lacustre 6: 173–214.

d'Orchymont A (1919a) Matériaux pour servir a l'étude de la faune entomologique de l'Indo-Chine. Palpicornia (Col.). Annales de la Société entomologique de Belgique 59: 70–83.

d'Orchymont A (1919b) Les genres Enochroides Kuw., Neohydrobius Blackb. et Hygrotrophus W. McLeay (Col. Palpicornia). Bulletin de la Société entomologique de France (1919): 226–230.

d'Orchymont A (1919c) Contribution a l'étude des sous-familles des Sphaeridiinae et des Hydrophilinae (Col. Hydrophilidae). Annales de la Societe Entomologique de France 88(1–2): 105–168. https://biodiversitylibrary.org/page/9486175

d'Orchymont A (1921) Matériaux pour servir a l'étude de la faune entomologique de l'Indo-Chine. Palpicornia (Col.). Faune entomologique de l'Indo-Chine française 5: 3-22. (= d'Orchymont 1919, Annales de la Société entomologique de Belgique 59: 70-83).

d'Orchymont A (1922) Zoological Results of the Abor Expedition. L. Coleoptera, X: Hydrophilidae. Records of the Indian Museum 8: 623–629.

d'Orchymont A (1923a) Hydrophilidae of India (Col.). A List of the Species in the Collection of the Agricultural Research Institute at Pusa (Bihar). Memoirs of the Department of Agriculture in India 7: 1–12.

d’Orchymont A (1923b) Neue oder interessante Sphaeridiinen und Hydrophilinen der Malayischen Region. Treubia 3: 416–421.

d’Orchymont A (1925a) Contribution à l'étude des Hydrophilides I. Bulletin et Annales de la Société Entomologique de Belgique 65: 63–77.

d’Orchymont A (1925b) Hydrophilides des Iles Philippines. Bulletin et Annales de la Société entomologique de Belgique 65: 200–202.

d’Orchymont A (1925c) Contribution à l'étude des Hydrophilides III. Bulletin et Annales de la Société entomologique de Belgique 65: 261–295.

d’Orchymont A (1926a) Notes on Philippine Hydrophilidae. Philippine Journal of Science 30(3): 361–385. http://philjournalsci.dost.gov.ph/images/pdf_upload/pjs1926/PJS_Vol_30_No3_Jul_1926.pdf

d’Orchymont A (1926b) Contribution à l'étude des Hydrophilides VI. Bulletin et Annales de la Société entomologique de Belgique 66: 201–248.

d’Orchymont A (1927a) Papers on Malayan aquatic biology. V. Notes on the Hydrophilidae in the Federated Malay States Museums. Journal of the Federated Malay States Museums, 13 (4), 246–252.

d’Orchymont A (1927b) Coléoptères Hydrophilides recueillis en Egypte. Bulletin de la Société royale entomologique d'Égypte 11: 3–7.

d'Orchymont A (1928) Catalogue of Indian Insects. Part 14 - Palpicornia. 2 + 146 pp. Government of India Central Publication Branch, Calcutta.

d'Orchymont A (1929). Contribution à l'étude des Palpicornia. VII. Bulletin et Annales de la Société Entomologique de Belgique 69: 79–96.

d'Orchymont A (1932) Zur Kenntnis der Kolbenwasserkäfer (Palpicornia) von Sumatra, Java und Bali. Archiv für Hydrobiologie, Supplement Band IX: 623–714, pl. XIV–XVII.

d'Orchymont A (1933) Contribution à l'étude des Palpicornia VIII. Bulletin et Annales de la Société entomologique de Belgique 73: 271–314, pl. 5.

d'Orchymont A (1936a) Quelques synonymies nouvelles d'Hydrophilidae (Col.). Bulletin du Musée royal d'Histoire naturelle de Belgique 12(23): 1–29. http://biblio.naturalsciences.be/rbins-publications/bulletin-of-the-royal-belgian-natural-history-museum/bulletin-of-the-royal-belgian-natural-history-museum-1930-1948/12-36/irscnb_p4087_0126ffp_12_bulletin-23.pdf

d'Orchymont A (1936b) Scientific results of the Vernay-Lang Kalahari Expedition, March to September, 1930. Hydrophilidae. Annals of the Transvaal Museum 17(2): 109–116, pl. I.

d’Orchymont A (1937a) Descriptions of three new Hydrophilidae from India. Records of the Indian Museum 39: 29–31.

d’Orchymont A (1937b) Contribution à l'étude des Palpicornia IX. Bulletin et Annales de la Société entomologique de Belgique 77: 213–255.

d'Orchymont A (1937c) Coleoptera Palpicornia from the Khewra Gorge, Salt Range, Punjab. Records of the Indian Museum 39: 33–41.

d'Orchymont A (1937d) Contributions à l'étude de la Faune du Mozambique. Voyage de M. P. Lesne (1928–1929). 26. note. Palpicornia. Memorias e Estudos do Museo zoologico da Universidade de Coimbra 96(1): 15 pp.

d'Orchymont A (1937e). Check List of the Palpicornia of Oceania (Coleoptera, Polyphaga). Occasional Papers of the Bernice P. Bishop Museum 13: 147–160.

d'Orchymont A (1939a) Revision des espèces du sous-genre *Crephelochares* d'*Helochares*. Bulletin et Annales de la Société entomologique de Belgique 79: 154–166.

d'Orchymont A (1939b) Notes sur des *Helochares* africains. Bulletin et Annales de la Société entomologique de Belgique 79: 293–323.

d'Orchymont A (1939c) L'*Helochares minutissimus* Kuwert, vrai. Bulletin et Annales de la Société entomologique de Belgique 79: 196–198.

d'Orchymont A (1939d) Revision des espèces du sous-genre *Crephelochares* d'*Helochares*. Bulletin et Annales de la Société entomologique de Belgique 79: 154-166.

d'Orchymont A (1939e) Notes sur quelques Palpicornia de la Republique Argentine. Revista de la Sociedad entomológica argentina 10: 253–264.

d'Orchymont A (1939f) *Helochares* (*Hydrobaticus*) *Andreinii* n. sp. *H. melanophthalmus* Régimbart, 1905 (nec Mulsant, non Reiche). Redia 25: 319–323.

d'Orchymont A (1940) Contribution à l'étude des Palpicornia XIV. Bulletin et Annales de la Société entomologique de Belgique 80: 157–197.

d'Orchymont A (1941) Revision des espèces du genre *Régimbartia* Zaitzev (Coleoptera Hydrophilidae). Bulletin du Musée royal d'Histoire naturelle de Belgique 17(4): 1–15.

d'Orchymont A (1943a) Nouvelles notes sur les *Helochares* (*Hydrobaticus*). (Coleoptera Palpicornia Hydrophilidae). Bulletin du Musée royal d'Histoire naturelle de Belgique 19(20): 1–12.

d'Orchymont A (1943b) Palpicornia (Coleoptera) V. Bulletin du Musée royal d'Histoire naturelle de Belgique 19(22): 1–8.

d'Orchymont A (1943c) Notes sur quelques *Helochares* (s. str.) (Coleoptera Palpicornia Hydrophilidae). Bulletin du Musée royal d'Histoire naturelle de Belgique 19(26): 1–8.

d'Orchymont A (1943d) Faune du Nord-Est Brésilien (récoltes du Dr. O Schubart). Palpicornia. Mémoires du Musée royal d'Histoire naturelle de Belgique (2)28: 1–85.

d'Orchymont A (1943e) Notes complémentaires sur les *Helochares* (*Hydrobaticus*) orientaux (Palpicornia Hydrophilidae). Bulletin du Musée royal d'Histoire naturelle de Belgique 19 (21): 1–12.

d'Orchymont A (1943f) Palpicornia (Coleoptera) VI. Bulletin du Musée royal d'histoire naturelle de Belgique 19(60): 1–12.

d'Orchymont A (1948) Report on the Palpicornia (Coleoptera), Mr. Omer-Cooper's Investigation of the Abyssinian Fresh Waters (Hugh Scott Expedition). Proceedings of the Zoological Society of London 117 (1947-48): 716-741. https://doi.org/10.1111/j.1096-3642.1948.tb00552.x

Darilmaz MC, Kiyak S (2006) *Helochares lividus*: new distributional records from Turkey (Coleoptera: Hydrophilidae). Entomological Problems, 36(1), 79.

Darilmaz MC, İncekara Ü (2011) Checklist of Hydrophiloidea of Turkey (Coleoptera: Polyphaga). Journal of Natural History 45(11–12): 685–735. https://doi.org/10.1080/00222933.2010.535916

Devi MB, Devi OS, Fikáček M, Minoshima Y, Wanghengbam L (2016) Redescription and lectotype designation of *Chasmogenus abnormalis* (Sharp), with notes on its distribution. Zootaxa 4144(2): 296–300. http://dx.doi.org/10.11646/zootaxa.4144.2.12

de Villers CJ (1789) Caroli Linnaei Entomologia, faunae Suecicae descriptionibus aucta. Vol. 4. 556 + ccxiii pp., pl. xi. - Piestre et Delamolliere, Lugduni. https://biodiversitylibrary.org/page/12750672

Dejean PFMA (1833) (1833–37) Catalogue des Coléoptères de la collection de M. le Comte Dejean (2. ed.). 443 pp. (only pp. 1-176 issued in 1833; other parts issued in 1834 (pp. 177-256), 1835 (pp. 257-360) and 1837 (pp. 361-443)). Méquignon-Marvis Père et Fils, Paris. https://biodiversitylibrary.org/page/9322478

Erichson WF (1837–1839) Die Käfer der Mark Brandenburg. Vol. 1. viii + 740 pp. (only pp. 1–384 issued in 1837). F. H. Morin, Berlin. https://biodiversitylibrary.org/page/42139591

Erichson WF (1843) Beitrag zur Insecten-Fauna von Angola, in besondere Beziehung zur geographischen Verbreitung der Insecten in Afrika. Archiv für Naturgeschichte 9(1): 199–267. https://biodiversitylibrary.org/page/13703230

Fabricius JC (1787) Mantissa insectorum sistens eorum species nuper detectas adiectis characteribus genericis, differentiis specificis, emendationibus, observationibus, Vol. 1. 20 + 348 pp. C. G. Proft, Hafniae. https://biodiversitylibrary.org/page/12058315

Fabricius JC (1792) Entomologia systematica emandata et aucta. Secundum classes, ordines, genera, species adjectis synonimis, locis, observationibus descriptionibus, Vol. 1, pars 1. 20 + 330 pp. - C. G. Proft, Hafniae. https://biodiversitylibrary.org/page/52755135

Fabricius JC (1801) Systema Eleutheratorum: secundum ordines, genera, species, adiectis synonymis, locis, observationibus, descriptionibus (Vol. 2). Impensis bibliopolii academici novi. Vol. 1. 24 + 506 pp. Bibliopolii Academici Novi, Kiliae.

Fairmaire L, Laboulbène A (1854) (1854–56) Faune Entomologique Française ou Description des Insectes qui se trouvent en France. Vol. 1. Coléoptères. 35 + 665 pp. Deyrolle, Paris. https://books.google.com/books?id=lBqTM338UHsC&dq=Faune%20Entomologique%20Fran%C3%A7aise%20ou%20Description%20des%20Insectes%20qui%20se%20trouvent%20en%20France&pg=PR3#v=thumbnail&

Fauvel A (1895) Notes synonymiques. Revue d'Entomologie 14: 92–127. https://biodiversitylibrary.org/page/10977316

Fernández LA (1981) Dos especies nuevas del género *Helochares* (Coleoptera: Hydrophilidae). Limnobios 2(3): 189–192.

Fernández LA (1982a) Notas sobre el género *Helochares* (Insecta, Coleoptera: Hydrophilidae). Neotrópica 8(79): 31–40.

Fernández LA (1982b) Cinco especies nuevas del género *Helochares* (Coleoptera: Hydrophilidae). Physis (Buenos Aires), secc. b 40(99): 85–90.

Fernández LA (1983) *Helochares* (*Sindolus*) *talarum* sp. nov., y redescripción de *Helochares (Helochares) pallipes* (Brullé), con descripción de los estados preimaginales (Coleoptera: Hydrophilidae). Limnobios 2(6): 439–449.

Fernández LA (1986) Consideraciones sobre el género *Chasmogenus* Sharp y descripción de *Chasmogenus sapucay* sp. nov. (Coleoptera: Hydrophilidae). Neotrópica 32 189–193.

Fernández LA (1989) Notas sobre el género *Helochares*. II (Coleoptera: Hydrophilidae). Descripción de dos especies nuevas neotropicales. Clave para determinar las especies argentinas y de áreas vecinas. Revista de la Sociedad Entomológica Argentina 45(1–4): 145–151.

Fernández LA (2004) Larvae of Neotropical *Helochares* Mulsant (Coleoptera, Hydrophilidae): Description of *H. femoratus* (Brullé). Transactions of the American Entomological Society 130(1): 77–83. https://www.jstor.org/stable/25078837

Fernández LA, Bachmann AO (1987) Revisión del género *Helobata* Bergroth (Coleoptera: Hydrophilidae). Revista de la Sociedad Entomológica Argentina 44(2): 149–159.

Fernández LA, and Kehr AI (1994) The annual life cycle of an Argentinean population of *Helochares femoratus* (Brullé) (Coleoptera: Hydrophilidae). The Coleopterists Bulletin 48(1): 95–98. https://www.jstor.org/stable/4009006

Fernández LA, and Kehr AI (1995) Disposición espacial y su variabilidad con respecto al tiempo, de una población de *Helochares femoratus* (Brullé) (Coleoptera: Hydrophilidae). Revista de la Sociedad Entomológica Argentina 54(1-4): 67–73. https://biotaxa.org/RSEA/article/view/33511/29714

Fikáček M (2003) Commented review of immature stages of World Hydrophiloidea (Coleoptera: Staphyliniformia). Bachelor Seminar Work, Prague, Check Republic: Charles University.

Fikáček M, Gentili E, Short AE (2010) Order Coleoptera, family Hydrophilidae. Arthropod fauna of the UAE 3: 135–165.

Fikáček M, Minoshima, YN and Newton, AF (2014) A Review of *Andotypus* and *Austrotypus* gen. nov., Rygmodine genera with an Austral disjunction (Hydrophilidae: Rygmodinae). Annales Zoologici 64(4): 557–596. https://doi.org/10.3161/000345414X685893

Fikáček M, Angus RB, Gentili E (2015) Family Hydrophilidae Latreille, 1802. In: Löbl I, Löbl D (Eds) Catalogue of Palaearctic Coleoptera Volume 2, Revised and Updated Edition, Hydrophiloidea – Staphylinoidea. Brill, Leiden, Netherlands, 37–76.

Fleutiaux E, Sallé A (1889) (1889-90) Liste des Coléoptères de la Guadeloupe et descriptions d'espèces nouvelles. Annales de la Société entomologique de France (6)9: 351–484. (only pp. 351-424 issued in 1889). https://biodiversitylibrary.org/page/32438903

Forster JR (1771) Novæ species Insectorum. Centuria I. 8 + 100 pp. T. Davies; B. White, London.

Fourcroy AF (1785) Entomologia Parisiensis ... I. viii + 231 pp. Parisiis. https://biodiversitylibrary.org/page/25563905

Ganglbauer L (1904) Die Käfer von Mitteleuropa. Vol. 4 (part 1). 286 pp. Karl Gerold's Sohn, Wien. https://biodiversitylibrary.org/page/9334581

García M (2000a) Four new species of *Chasmogenus* Sharp, 1882 (Coleoptera: Hydrophilidae: Hydrophilinae) from Venezuela. Boletín del Centro de Investigaciones Biológicas Universidad del Zulia 34(1): 45–58. http://www.produccioncientificaluz.org/index.php/boletin/article/view/218

García M (2000b) Una nueva especie de *Quadriops* Hansen, 1999 (Coleoptera: Hydrophilidae: Hydrophilinae) de Venezuela. Boletín del Centro de Investigaciones Biológicas 34(1): 59–65. http://produccioncientificaluz.org/index.php/boletin/article/view/219

García M (2000c) Tres nuevas especies de *Helobata* Bergroth 1888 (Hydrophilidae: Hydrophilinae), de Venezuela. Boletín del Centro de Investigaciones Biológicas 34(2): 237–246. http://www.produccioncientificaluz.org/index.php/boletin/article/view/201

García M (2001) Nueva subtribu, género y especie de Hydrophilini (Coleoptera: Hydrophilidae) del extremo suroriental de Venezuela. Boletín del Centro de Investigaciones Biológicas 35(2): 151–160. http://produccioncientificaluz.org/index.php/boletin/article/view/3978

Gemminger M, Harold B de (1868) Catalogus Coleopterorum hucusque descriptorum synonymicus et systematicus. Vol. 2, pp. 425–752 + 6 unn. E. H. Gummi, Monachii. https://biodiversitylibrary.org/page/10174177

Gentili E, Hebauer F, Jäch MA, Ji L, Schödl S (1995) Hydrophilidae: 1. Checklist of the Hydrophilinae recorded from China (Coleoptera). In: Jäch MA, Ji L. (Eds) Water Beetles of China Vol. 1. Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, Vienna, 207–219.

Gentili E, Ostovan H, Ghahari H, Komarek A (2018) Annotated checklist of Iranian Hydrophilidae (Coleoptera: Polyphaga: Hydrophiloidea), Aquatic Insects 39(1): 55–88. https://doi.org/10.1080/01650424.2017.1415360

Girón JC, Short AEZ (2017) Revision of the Neotropical water scavenger beetle genus *Quadriops* Hansen, 1999 (Coleoptera: Hydrophilidae: Acidocerinae). ZooKeys 705: 115–141. https://zookeys.pensoft.net/articles.php?id=19815

Girón JC, Short AEZ (2018) Three new genera of acidocerine water scavenger beetles from tropical South America (Coleoptera, Hydrophilidae, Acidocerinae). ZooKeys 768: 113–158. https://doi.org/10.3897/zookeys.768.24423

Girón JC, Short AEZ (2019) Three additional new genera of acidocerine water scavenger beetles from the Guiana and Brazilian Shield regions of South America (Coleoptera: Hydrophilidae: Acidocerinae). ZooKeys 855: 109–154. https://doi.org/10.3897/zookeys.855.33013

Girón JC, Short AEZ (in prep.) New subgenera, new species and new records of the Neotropical water scavenger beetle genus *Tobochares* Short and García, 2007 (Coleoptera: Hydrophilidae: Acidocerinae).

Guillebeau F (1896) Descriptions de quelques espèces de Coléoptères inédites. Bulletin de la Société entomologique de France (1896): 226–232, 239–245. https://www.persee.fr/docAsPDF/bsef_0037-928x_1896_num_1_9_21849.pdf

Gyllenhal L (1808) Insecta svecica descripta a Leonardo Gyllenhal - Classis I. Coleoptera sive Eleuterata. Vol. 1, pars 1. 572 pp. F. J. Leverentz, Scaris. https://biodiversitylibrary.org/page/9330983

Hansen M (1982) Revisional notes on some European *Helochares* Muls. (Coleoptera: Hydrophilidae). Entomologica Scandinavica 13: 201–211. https://doi.org/10.1163/187631282X00129

Hansen M (1991) The hydrophiloid beetles. Phylogeny, classification and a revision of the genera (Coleoptera: Hydrophilidae). Biologiske Skrifter 40, 1–367.

Hansen M (1997) A new subfamily for a remarkable new genus and species of Hydrophilidae from New Guinea (Coleoptera: Hydrophilidae). Annales Zoologici 47: 107–110.

Hansen M (1999a) Fifteen new genera of Hydrophilidae (Coleoptera), with remarks on the generic classification of the family. Insect Systematics and Evolution 30(2): 121–172. https://doi.org/10.1163/187631200X00228

Hansen M (1999b) World catalogue of insects. Volume 2: Hydrophiloidea (s. str.) (Coleoptera). Apollo Books, Stenstrup, Denmark. 414 pp.

Hansen M (2004) Family Hydrophilidae. In: Löbl, I. and Smetana, A. (Eds) Catalogue of Palearctic Coleoptera. Vol. 2. Hydrophiloidea – Histeroidea – Staphylinoidea. Apollo Books, Stenstrup, Denmark, 44–68.

Hansen M, Hebauer F (1988) A new species of *Helochares* from Israel, with a key to the European and some Near East species (Coleoptera: Hydrophilidae). Insect Systematics and Evolution 19(1): 27–30. https://doi.org/10.1163/187631289X00023

Hebauer F (1988) Hydrophiloidea aus Namibia (Coleoptera; Hydrophilidae, Spercheidae). Bonner zoologische Beiträge 39: 153–161.

Hebauer F (1992) The species of the genus *Chasmogenus* Sharp, 1882 (Coleoptera, Hydrophilidae). Acta Coleopterologica 8(2): 61–92.

Hebauer F (1994) The Hydrophiloidea of Israel and the Sinai (Coleoptera, Hydrophiloidea). Zoology in the Middle East 10: 73–138. https://doi.org/10.1080/09397140.1994.10637663

Hebauer F (1995a) Die Hydrophilidae und Spercheidae Namibias Unter Berücksichtung des Materials der Namibia-Expedition des Museums für Naturkunde Berlin 1992, ergänzt durch Nachweise aus früheren Namibia- und Kalahari-Expeditionen (Coleoptera, Hydrophiloidea: Hydrophilidae et Spercheidae). Mitteilungen aus dem Zoologischen Museum in Berlin 71(2): 251–275. https://doi.org/10.1002/mmnz.19950710206

Hebauer F (1995b) Neues zu den Acidocerina Hansen (Helocharae d'Orchymont) der indomalaiischen Region (Coleoptera, Hydrophilidae). Acta Coleopterologica 11(3): 3–14.

Hebauer F (1996) Synopsis der afrikanischen Arten der Gattung *Helochares* Mulsant (Coleoptera, Hydrophilidae). Acta Coleopterologica 12(2): 3–38.

Hebauer F (1997) Annotated checklist of the Hydrophilidae and Helophoridae (Insecta: Coleoptera) of the Arabian Peninsula with a description of a new genus and species. Fauna of Saudi Arabia 16: 255–276.

Hebauer F (1998) Six new species of the genus *Helochares* Mulsant, 1844, subgenus *Hydrobaticus* Mac Leay, 1871 from Africa and Asia (Coleoptera: Hydrophilidae). Acta coleopterologica 14(2): 41–46.

Hebauer F (1999) Neue und wenig bekannte Hydrophiloidea aus dem südlichen Afrika (Coleoptera: Hydrophiloidea). Acta Coleopterologica 15(2): 7–16.

Hebauer F (2000) The genus *Megagraphydrus* Hansen, 1999, with description of new species (Coleoptera: Hydrophilidae). Acta Coleopterologica 16(2): 14–22.

Hebauer F (2001a) Beitrag zur Kenntnis der Hydrophilidae von Neuguinea. Ergebnisse der zoologischen Forschungsreisen von M. Balke und L. Hendrich nach West Neuguinea (Irian Jaya) in den Jahren 1990–1998 (Coleoptera: Hydrophilidae). Acta Coleopterologica 17(1): 3–72.

Hebauer F (2001b) The real *Helochares taprobanicus* Sharp 1890 and its allies (Coleoptera: Hydrophilidae). Latissimus 14: 10–16.

Hebauer F (2002a) Hydrophilidae of Northern India and Southern Himalaya (Coleoptera: Hydrophilidae). Acta Coleopterologica 18(1): 3–72.

Hebauer F (2002b) New Hydrophilidae of the Old World (Coleoptera, Hydrophilidae). Acta Coleopterologica 18(3): 3–24.

Hebauer F (2003a) A new species of the genus *Helochares* (Coleoptera, Hydrophilidae) from Africa. Special Bulletin of the Japanese Society of Coleopterology 6: 129–132.

Hebauer F (2003b) Checklist of the Malagasy *Helochares* with description of a new species (Coleoptera: Hydrophilidae). Acta Coleopterologica 19(1): 67–69.

Hebauer F (2005) Contribution to the knowledge of the Hydrophilidae of Malawi (Coleoptera: Hydrophilidae). Acta Coleopterologica 21(1): 37–40.

Hebauer F (2006a) Checklist of the Hydrophiloidea of Africa and adjacent archipelagos (Coleoptera: Epimetopidae, Georissidae, Helophoridae, Hydrochidae, Hydrophilidae, Spercheidae). Entomologische Zeitschrift 116(1): 19–36.

Hebauer F (2006b) Results of the Benin Mission 2001 and the Zambia Mission 2002 of F. and L. Kantner (Coleoptera: Hydrophilidae). Acta Coleopterologica 22(2): 11–24.

Hebauer F (2009) Five new species of the genus *Helochares* MacLeay, 1871 from Gabon and the Congo (Coleoptera: Hydrophilidae). Acta Coleopterologica 25(2): 3–8.

Hebauer F, Hendrich L (1999) Two new species of *Helochares* from Northern Australia (Coleoptera: Hydrophilidae). Entomological Problems 30 (1): 47–51.

Hebauer F, Ryndevich SK (2005) New data on the distribution of Old World Hydrophilidae (Coleoptera). Acta Coleopterologica 21(1): 43–51.

Hebauer F, Hendrich L, Balke M (1999) A contribution to the knowledge of the water beetle fauna (Col. Hydradephaga, Hydrophiloidea and Staphylinoidea) of a tropical freshwater lake: Tasek Cini, Pahang, West Malaysia. Raffles Bulletin of Zoology 47(2): 333–348.

Heer O (1841) (1838-1841). Fauna Coleopterorum Helvetica I. 12 + 652 pp. Orelii, Fuesslini et Sociorum, Turici (only pp. 361-652 issued in 1841). https://books.google.com/books?id=Qow-AAAAcAAJ&pg=PR3#v=onepage&q&f=false

Herbst JFW (1797) Natursystem aller bekannten in und ausländischen Insekten: als eine Fortsetzung der von Büffonschen Naturgeschichte: nach dem System des Ritters Carl von Linne bearbeitet - Der Käfer, 7. 346 + xi pp., 26 pl. Pauli, Berlin. https://doi.org/10.3931/e-rara-40522

Heyden L 1891. Hydrophilidae (pp. 66-75); Georyssidae (p. 75). In Reitter, E. (ed.): Catalogus Coleopterorum Europae, Caucasi et Armeniae rossicae. 8 + 420 pp. R. Friesländer & Sohn, Berlin; E. Reitter, Mödling; Revue d'Entomologie, Caen. https://archive.org/details/cataloguscoleop00weisgoog

Hope, F. W. 1845. On the Entomology of China, with Descriptions of the new Species sent to England by Dr. Cantor from Chusan and Canton. Transactions of the Entomological Society of London 4 (1845–47): 4–17, pl. 1. https://biodiversitylibrary.org/page/14690398

Horn GH (1873) Revision of the genera and species of the tribe Hydrobiini. Proceedings of the American Philosophical Society 13(90): 118–137. https://www.jstor.org/stable/981607

Horn GH (1890) Notes on some Hydrobiini of Boreal America. Transactions of the American entomological Society 17: 237–278, pl. 3–4. https://www.jstor.org/stable/25076544

International Commission on Zoological Nomenclature [ICZN] (1999) International Code of Zoological Nomenclature. International Trust for Zoological Nomenclature, 306 pp.

Illiger JCW (1798) Verzeichniss der Käfer Preussens. 41 + 510 pp. J. J. Gebauer, Halle. https://biodiversitylibrary.org/page/52579285

Inoue D, Nakajima J, Kudo Y, Utsunomiya Y, Kawahara J (2009) [Illustrated Guide of Aquatic Insects of Fukuoka Prefecture]. Gyobu, a Club of Fukuoka Prefectural Kitakyushu HighSchool, Kitakyushu. (In Japanese.)

Jäch MA (1984) Die Koleopterenfauna der Bergbäche von Südwest-Ceylon (Col.). Archiv für Hydrobiologie / Supplementum 69(2): 228–332.

Jasper SK, Vogtsberger RC (1996) First Texas records of five genera of aquatic beetles (Coleoptera: Noteridae, Dytiscidae, Hydrophilidae) with habitat notes. Entomological News 107: 49–60. https://biodiversitylibrary.org/page/2700315

Jia F (1998) A new genus *Pseudopelthydrus* gen. n. from Hainan Island, China (Coleoptera: Hydrophilidae: Hydrophilinae). Chinese Journal of Entomology 18: 225-230.

Jia F (2010) *Megagraphydrus puzhelongi*, sp n., a new water scavenger beetle from China (Coleoptera: Hydrophilidae: Hydrophilinae). Zootaxa 2498(1): 65–68. http://dx.doi.org/10.11646/zootaxa.2498.1.6

Jia F, Tang Y (2018a) A faunistic study of genus *Chasmogenus* Sharp, 1882 of China (Coleoptera, Hydrophilidae). ZooKeys 738: 59–66. https://doi.org/10.3897/zookeys.738.21711

Jia F, Tang Y (2018b) A revision of the Chinese *Helochares* (s. str.) Mulsant, 1844 (Coleoptera, Hydrophilidae). European Journal of Taxonomy 438: 1–27. https://doi.org/10.5852/ejt.2018.438

Klug JFC (1855) (Diagnosen neuer Coleoptera aus Mossambique). Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Konigl Preuss Akademie der Wissenschaften zu Berlin 1855: 643–660. https://biodiversitylibrary.org/page/11070837

Knisch A (1921) Die exotischen Hydrophiliden des Deutschen Entomologischen Museums (Col.). Archiv für Naturgeschichte. Abteilung A. 85(8): 55–88. https://biodiversitylibrary.org/page/13321515

Knisch A (1922) Hydrophiliden-Studien. (Op. 10.). Archiv für Naturgeschichte A 88(5): 87–126. https://biodiversitylibrary.org/page/45506050

Knisch A (1924a) Hydrophilidae. In: Junk W, Schenkling S (Eds) Coleopterorum Catalogus vol. 14, part 79. W. Junk, Berlin, Germany, 306 pp.

Knisch A (1924b) Neue Palpicornier aus dem südlichen Himalaya. (Col. Hydrophilidae. - Op. 15.). Wiener entomologische Zeitung 41: 29-41.

Knisch A (1924c) Neue neotropische Palpicornier. (Col. Hydrophilidae. - Op. 16.). Wiener entomologische Zeitung 41: 114–140.

Kohlenberg AT, Short AEZ (2017) Revision of the Neotropical water scavenger beetle genus *Tobochares* Short and García, 2007 (Coleoptera, Hydrophilidae, Acidocerinae). ZooKeys 669: 113–146. https://doi.org/10.3897/zookeys.669.11773

Komarek A (2003) Hydrophilidae: I. Checklist and key to Palearctic and Oriental genera of aquatic Hydrophilidae (Coleoptera). In: Jäch MA, Ji L (Eds) Water beetles of China, Vol. 3. Wien:

Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein, Wien. 383–395.

Komarek A (2018) Taxonomic revision of *Agraphydrus* Régimbart, 1903 II. The Indian Subcontinent. Koleopterologische Rundschau 88: 103–204. http://www.coleoptera.at/uploads/www.coleoptera.at/KOR_88_2018_0103-0204.pdf

Komarek A (2019) Taxonomic revision of *Agraphydrus* Régimbart, 1903 III. Southeast Asia (except Philippines) and Australian Region (Coleoptera: Hydrophilidae: Acidocerinae). Koleopterologische Rundschau 89: 151–316.

Komarek A, Hebauer F (2018) Taxonomic revision of *Agraphydrus* Régimbart, 1903 I. China and Taiwan (Coleoptera: Hydrophilidae: Acidocerinae). Zootaxa 4452(1): 1–101. http://dx.doi.org/10.11646/zootaxa.4452.1.1

Kuwert A (1888) Generalübersicht der Philydrus-Arten Europas und der Mittelmeerfauna. Deutsche entomologische Zeitschrift 32: 273–293. https://www.zobodat.at/pdf/Deutsche-Ent-Zeitschrift_32_1888_0273-0293.pdf

Kuwert A (1890a) Bestimmungs-Tabellen der europäischen Coleopteren. XIX. Heft. Hydrophilidae. I. Abteilung: Hydrophilini. Verhandlungen des naturforschenden Vereins in Brünn 28 (1889): 1–121. (Also issued as reprint: 121 pp. - Brünn.) https://biodiversitylibrary.org/page/43763386

Kuwert A (1890b) Bestimmungs-Tabellen der europäischen Coleopteren. XX. Heft. Hydrophilidae. II. Abteilung: Sphaeridiini und Helophorini. Verhandlungen des naturforschenden Vereins in Brünn 28 (1889): 159-328. (Also issued as reprint: 172 pp. - Brünn.) https://biodiversitylibrary.org/page/43763542

Lacordaire T (1854) Histoire naturelle des insectes: Genera des Coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes. Tome Premiere. Contenant les familles des Cicindélètes, Carabiques, Dytiscides, Gyrinides et Palpicornes. Librairie encyclopédique de Roret, Paris, 486 pp. https://biodiversitylibrary.org/page/9623497

Lawrence J, Ślipiński A (2013) Australian Beetles: morphology, classification and keys. CSIRO Publishing, Melbourne, Australia, 576 pp.

LeConte JL (1855) Synopsis of the Hydrophilidæ of the United States. Proceedings of the Academy of natural Sciences of Philadelphia 7: 356–375. https://biodiversitylibrary.org/page/1694470

LeConte JL (1861) New species of Coleoptera inhabiting the Pacific district of the United States. Proceedings of the Academy of Natural Sciences of Philadelphia 13: 338–359. https://biodiversitylibrary.org/page/1683467

Lee D-H, Ahn K-J (2009) *Agraphydrus narusei* (Satô) and *Crenitis apicalis* (Reitter) (Coleoptera: Hydrophilidae) new to Korea. Entomological Research 39(5): 317–320. https://doi.org/10.1111/j.1748-5967.2009.00233.x

Lee D-H, Ahn K-J (2017) Three water scavenger beetle species (Coleoptera: Hydrophilidae) new to Korea. Journal of Asia-Pacific Biodiversity 10(1): 39–43. https://doi.org/10.1016/j.japb.2016.12.004

MacLeay WS (1825) Annulosa Javanica or an attempt to illustrate the natural affinities and analogies of the Insects collected in Java by Thomas Horsfield, M.D. F.L. & G.S. and deposited by him in the Museum of the Honourable East-India Company. 50 pp., 1 pl. Kingsbury, Parbury, and Allen, London. https://biodiversitylibrary.org/page/41989352

MacLeay WS (1871) Notes on a collection of insects from Gayndah. Transactions of the Entomological Society of New South Wales 2: 79–205. https://biodiversitylibrary.org/page/16220374

Makhan D (2007) *Helobata soesilae* sp. nov. and *Helobata aschnakiranae* sp. nov. from Suriname (Coleoptera: Hydrophilidae). Calodema Supplementary Paper 14: 1–3. https://www.researchgate.net/publication/321107032_Helobata_soesilae_sp_nov_and_Helobata_aschnakiranae_sp_nov_from_Suriname_Coleoptera_Hydrophilidae

Mart A, İncekara U, Karaca H (2010) A new species and new records of Hydrophilidae (Coleoptera) from Turkey. Turkish Journal of Zoology 34: 297–303. https://dergipark.org.tr/tr/download/article-file/134666

Matsui E (1994) Three new species of the genus *Enochrus* from Japan and Taiwan (Coleoptera: Hydrophilidae). Transactions of the Shikoku entomological Society 20: 215–220.

Matsui E (1995) A New Species of the Genus *Helochares* (Coleoptera, Hydrophilidae) from Japan, with a Key to the Japanese Species of the Subgenus *Hydrovaticus*. Special Bulletin of the Japanese Society of Coleopterology 4: 317–322.

Minoshima YN (2016). Taxonomic review of *Agraphydrus* from Japan (Coleoptera: Hydrophilidae: Acidocerinae). Entomological Science 19(4): 351–366. https://doi.org/10.1111/ens.12213

Minoshima Y, Fujiwara J (2009) Discovery of water scavenger beetle genus *Megagraphydrus* Hansen (Coleoptera, Hydrophilidae) from Japan, with description of a new species. Elytra 37(1): 53–64. http://coleoptera.sakura.ne.jp/Elytra/37(1)053MinoshimaY_and_FujiwaraJ.pdf

Minoshima Y, Hayashi M (2011) Larval morphology of the Japanese species of the tribes Acidocerini, Hydrobiusini and Hydrophilini (Coleoptera: Hydrophilidae). Acta Entomologica Musei Nationalis Pragae 51 (Supplementum): 1–118. http://www.aemnp.eu/PDF/51_s/51_s_1.pdf

Minoshima Y, Hayashi M, Kobayashi N, Yoshitomi H (2013) Larval morphology and phylogenetic position of *Horelophopsis hanseni* Satô et Yoshitomi (Coleoptera, Hydrophilidae, Horelophopsinae). Systematic Entomology 38(4): 708–722. http://dx.doi.org/10.1111/syen.12025

Minoshima YN, Komarek A, Ôhara M (2015) A revision of *Megagraphydrus* Hansen (Coleoptera, Hydrophilidae): synonymization with *Agraphydrus* Régimbart and description of seven new species. Zootaxa 3930: 1–63. http://dx.doi.org/10.11646/zootaxa.3930.1.1

Montrouzier P (1860) Essai sur la faune entomologique de la Nouvelle-Calédonie et des îles de Pins, Art, Lifu, etc. Annales de la Société entomologique de France 3(8): 229–308. https://biodiversitylibrary.org/page/33971456

Motschulsky V (1845) Remarques sur la collection de Coléoptères Russes. 1. Article. - Bulletin de la Société impériale des Naturalistes de Moscou 18, 1 (1): 3-127, pl. I-III (errata: p. 549). https://biodiversitylibrary.org/page/44164948

Motschulsky V (1853) Hydrocanthares de la Russie. 15 pp. Société de Litérature Finnoise, Helsingfors.

Müller OF (1776) Zoologiae Danicae prodromus, seu Animalium Daniae et Norvegiae indigenarum; characteres, nomina, et synonyma imprimis popularium. xxxii + 274 pp. - Hallager, Havniæ. https://biodiversitylibrary.org/page/13227118

Mulsant E (1844a) Histoire Naturelle des Coléoptères de France. Palpicornies. 5 + 196 pp., 1 pl. (errata et addenda: 197). L. Maison, Paris; Ch. Savy Jeune, Lyon. https://biodiversitylibrary.org/page/9628710

Mulsant E (1844b) Description de quelques Palpicornes inédits. Annales de la Société d' Agriculture de Lyon 7: 372–382.

Olivier AG (1792) Encyclopédie méthodique. Dictionnaire des Insectes. Vol. 7 (Han-Mou). 827 pp. Pankouke, Paris. (Pl. 183, with illustrations of Hydrophilus, issued in 1797)

Panzer GWF (1795) Entomologica Germanica exhibens Insecta per Germaniam indigena I. Elevterata. 32 (unn.) + 368 + 2 (unn.) pp., 12 pl. - Felsegker, Norimbergae. (Including: Deutschlands Insectenfaune oder Entomologisches Taschenbuch für das Iahr 1795. 32 (unn.) pp., 12 pl.). https://biodiversitylibrary.org/page/12123973

Panzera O (1932) Descrizione delle larve di *Helochares griseus* Fabr. e *H. lividus* Forst. (Coleoptera-Hydrophilidae). Memorie della Società entomologica italiana 11(2): 52–63.

Paykull G (1798) Fauna Svecica, Insecta. Vol. 1. 8 + 358 + 2 pp. - Joh. F. Edman, Upsaliæ. https://biodiversitylibrary.org/page/51560628

Régimbart M (1900) Coléoptères aquatiques capturés dans l'île d'Aldabra, près des Comores, par le Dr Voeltzkow, de Strasbourg, et communiqués par le Dr Bergroth. Bulletin de la Société entomologique de France (1900): 49–52. https://books.google.com/books?id=0S9GAQAAMAAJ&pg=PA49#v=onepage&q&f=false

Régimbart M (1903a) Coléoptères aquatiques (Haliplidae, Dytiscidae, Gyrinidae et Hydrophilidae) recueillis dans le Sud de Madagascar par M. Ch. Alluaud (Juillet 1900 – Mai 1901). Annales de la Société Entomologique de France 72: 1–51. https://biodiversitylibrary.org/page/8247889

Régimbart M (1903b) Contribution a la faune Indo-Chinoise. 19e mémoire. Annales de la Société Entomologique de France 72: 52-64. https://biodiversitylibrary.org/page/8247940

Régimbart M (1906) Voyage de M. Ch. Alluaud dans l'Afrique Orientale. Dytiscidae, Gyrinidae, Hydrophilidae. Annales de la Société entomologique de France 75: 235–278. https://biodiversitylibrary.org/page/9207127

Régimbart M (1907) Hydrophilides provenant du Voyage de M. L. Fea dans l'Afrique Occidentale. Annali del Museo civico di Storia naturale di Genova 3(3)[43]: 46–62. https://biodiversitylibrary.org/page/7931482

Régimbart M (1908) Dytiscidae, Hydrophilidae et Gyrinidae (pp. 311–316). In Michaelsen W and Hartmeyer R: Die Fauna südwest-Australiens. Ergebnisse der Hamburger südwest-australischen Forschungsreise 1905. Band I, Lieferung 8. 488 pp., 3 pl. Gustav Fischer, Jena. https://biodiversitylibrary.org/page/1097855

Reiche L (1854) Catalogue des espèces d'Insectes Coléoptères recueillies par M. F. de Saulcy pendant son voyage en Orient. 19 pp. Gide et J. Baudry, Paris. https://books.google.com/books?id=6fxGAQAAMAAJ&pg=PA1&

Reiche L, Saulcy F de (1856) Espèces nouvelles ou peu connues de Coléoptères, recueillies par M. F. de Saulcy, membre de l'Institut, dans son voyage en Orient. Annales de la Société entomologique de France 3(4): 353–422, pl. 12. https://biodiversitylibrary.org/page/8248901

Reitter E (1909) Fauna Germanica. Die Käfer des Deutschen Reiches. Vol. 2. 392 pp., pl. 41–80. K. G. Lutz, Stuttgart.

Rey C (1885a) Descriptions de Coléoptères nouveaux ou peu connus de la tribu des Palpicornes. Annales de la Société linnéenne de Lyon 31 (1884): 13–32. https://books.google.com/books?id=ZyMYAAAAYAAJ&pg=PA13#v=onepage&q&f=false

Rey C (1885b) Histoire naturelle des Coléoptères de France (suite). Annales de la Société linnéenne de Lyon 31(1884): 213–396. https://books.google.com/books?id=6dNBAQAAMAAJ&pg=RA1-PA213#v=onepage&q&f=false

Ribera I, Hernando C, Cieslak A (2019) Aquatic Coleoptera of North Oman, with description of new species of Hydraenidae and Hydrophilidae. Acta Entomologica Musei Nationalis Pragae 59(1): 253–272. http://aemnp.eu/PDF/59_1/59_1_253.pdf

Ribera I, Fresneda J, Aguilera P, Hernando C (1996) Insecta: Coleoptera 8 (Familias 11–26): Coleópteros acuáticos. FAMILIAS: Gyrinidae, Haliplidae, Noteridae, Hygrobiidae, Dytiscidae, Hydraenidae, Helophoridae, Georissidae, Hydrochidae, Hydrophilidae, Elmidae, Dryopidae, Heteroceridae, Psephenidae, Scirtidae, Chrysomelidae Donaciinae. Catalogus de la Entomofauna Aragonesa 10: 3–22. http://molevol.cmima.csic.es/ribera/pdfs/ribera_etal1996_catalogus.pdf

Richmond EA (1920) Studies on the biology of the aquatic Hydrophilidae. Bulletin of the American Museum of Natural History 42(1): 1–93 + 16 pl. http://hdl.handle.net/2246/947

Rossi P (1792) Mantissa Insectorum, exhibens species nuper in Etruria collectas. Vol. 1. 148 pp. - Polloni, Pisis. https://biodiversitylibrary.org/page/33474928

Sahlberg J (1903) Messis hiemalis Coleopterorum Corcyraeorum. Enumeratio Coleopterorum mensibus Novembri-Februario 1895-1896 et 1898-1899 nec non primo vere 1896 in insula Corcyra collectorum. Öfversigt av finska Vetenskabssocietetens Förhandlingar 45(11): 1–85. https://biodiversitylibrary.org/page/15315790

Salah M, Régil Cueto JA (2017) An Annotated Checklist of the Aquatic Polyphaga (Coleoptera) of Egypt II. Family Hydrophilidae. The Coleopterists Bulletin, 71(2): 259–278. https://doi.org/10.1649/0010-065X-71.2.259

Satô M (1960) One new genus and two new species of the subtribe Helocharae from Japan (Coleoptera: Hydrophilidae). Transactions of the Shikoku Entomological Society 6(5): 76–80.

Satô M (1965) Some aquatic Coleoptera from Formosa, I. Special Bulletin of the Lepidopterological Society of Japan 1: 126–129.

Satô M (1976) Two *Helochares*-species from the Ryukyus (Hydrophilidae). Entomological Review of Japan 29: 21–24.

Satô M and Yoshitomi H (2004) Discovery of a second representative of the genus *Horelophopsis* (Coleoptera, Hydrophilidae) from the Ryukyu archipelago, Japan. Elytra 32(1): 41–49.

Schaufuss LW (1869) Beitrag zur Kenntniss der Coleopteren-Fauna der Balearen. 31 pp. Selbstverlag, Prag. https://books.google.com/books?id=NX-cN95KGtUC&lpg=PA3&ots=4j9hzxNFw5&dq=Beitrag%20zur%20Kenntniss%20der%20Coleopteren-Fauna%20der%20Balearen&pg=PA1#v=onepage&q&f=false

Schönherr CJ (1808) Synonymia Insectorum, oder: Versuch einer Synonymie Aller bisher bekannten Insecten, nach Fabricii Systema Eleutheratorum &c. geordnet, Vol. 1. Eleutherata oder Käfer. Part 2 (Spercheus-Cryptocephalus). x + 424 pp., 1 pl. C. F. Marquard, Stockholm. https://biodiversitylibrary.org/page/42206652

Scott, H 1913. The Percy Sladen Trust Expedition to the Indian Ocean in 1905, under the Leadership of Mr. J. Stanley Gardiner, M. A. Vol. 5. No. X. - Coleoptera, Hydrophilidae, Histeridae. Transactions of the Linnean Society of London 16(2): 193–235, pl. 14.

Seidel M, Arriaga-Varela E, Fikáček M (2016) Establishment of Cylominae Zaitzev, 1908 as a valid name for the subfamily Rygmodinae Orchymont, 1916 with an updated list of genera (Coleoptera: Hydrophilidae). Acta Entomologica Musei Nationalis Pragae 56: 159–165.

Sharp D (1873) The Water Beetles of Japan. Transactions of the Entomological Society of London (1873): 45–67. https://doi.org/10.1111/j.1365-2311.1873.tb00636.x

Sharp D (1882) Fam. Hydrophilidae. Biologia Centrali-Americana Insecta. Coleoptera 1(2): 53–80. https://biodiversitylibrary.org/page/577106

Sharp D (1890) On some aquatic Coleoptera from Ceylon. Transactions of the Entomological Society of London (1890): 339–359. https://doi.org/10.1111/j.1365-2311.1890.tb03026.x

Sharp D (1903) Water-beetles (Dytiscidae & Hydrophilidae) of the Swedish Zoological expedition to Egypt and the White Nile (No. 10: 10 pp.). In Jägerskiöld, L. A.: Results of the Swedish Zoological expedition to Egypt and the White Nile 1901 under the Direction of L. A. Jägerskiöld. Part I. Library of the Royal University of Uppsala, Uppsala. https://biodiversitylibrary.org/page/18760768

Short AEZ (2005) A review of the subtribe Acidocerina of Central America with special reference to Costa Rica (Coleoptera: Hydrophilidae). Koleopterologische Rundschau 75: 191–226. http://www.zobodat.at/pdf/KOR_75_2005_0191-0226.pdf

Short AEZ (2010). Hydrophilidae: Review of the subtribe Acidocerina of the Southwest Pacific islands (Coleoptera). In: Jäch MA, Balke M (eds.) Water Beetles of New Caledonia, part 1, Wien, 297–318.

Short AEZ (2013) Chapter 4 – Aquatic Beetles of the Grensgebergte and Kasikasima Regions, Suriname (Insecta: Coleoptera). In: Alonso LE, Larsen TH (Eds) A rapid biological assessment of the Upper Palumeu River watershed (Grensgebergte and Kasikasima) of Southeastern Suriname. RAP Bulletin of Biological Assessment 67, Conservation International, Arlington, VA, 79–89. http://www.bioone.org/doi/full/10.1896/054.067.0112

Short AEZ (2013) Chapter 4. Aquatic Beetles of the Grensgebergte and Kasikasima Regions, Suriname (Insecta: Coleoptera). In: Alonso LE, Larsen TH (Eds) A Rapid Biological Assessment of the Upper Palumeu River Watershed (Grensgebergte and Kasikasima) of Southeastern Suriname. RAP Bulletin of Biological Assessment. Vol. 67. Conservation International, Arlington, VA, pp. 79–89. https://bioone.org/ebooks/RAP-Bulletin-of-Biological-Assessment/A-Rapid-Biological-Assessment-of-the-Upper-Palumeu-River-Watershed/Chapter/Aquatic-Beetles-of-the-Grensgebergte-and-Kasikasima-Regions-Suriname-Insecta/10.1896/054.067.0112

Short AEZ (2018). Systematics of aquatic beetles (Coleoptera): current state and future directions. Systematic Entomology 43(1): 1–18. https://doi.org/10.1111/syen.12270

Short AEZ, Fikáček M (2011) World catalogue of the Hydrophiloidea (Coleoptera): additions and corrections II (2006–2010). Acta Entomologica Musei Nationalis Pragae 51(1): 83–122. http://www.aemnp.eu/PDF/51_1/51_1_83.pdf

Short AEZ, Fikáček M (2013) Molecular phylogeny, evolution and classification of the Hydrophilidae (Coleoptera). Systematic Entomology 38(4): 723–752. https://onlinelibrary.wiley.com/doi/abs/10.1111/syen.12024

Short AEZ, García M (2007) *Tobochares sulcatus*, a new genus and species of water scavenger beetle from Amazonas State, Venezuela (Coleoptera: Hydrophilidae). Aquatic Insects 29(1): 1–7. https://doi.org/10.1080/01650420701247869

Short AEZ, García M (2014) A new genus of egg case-carrying water scavenger beetle from the Guiana Shield (Coleoptera: Hydrophilidae: Acidocerinae). Zootaxa 3835(2): 251–262. https://biotaxa.org/Zootaxa/article/view/zootaxa.3835.2.5

Short AEZ, Girón JC (2018) Review of the *Helochares* (*Hydrobaticus*) MacLeay of the New World (Coleoptera: Hydrophilidae: Acidocerinae). Zootaxa 4407(1): 29–50. http://dx.doi.org/10.11646/zootaxa.4407.1.2

Short AEZ, Hebauer F (2006) World Catalogue of Hydrophiloidea – additions and corrections, 1 (1999–2005) (Coleoptera). Koleopterologische Rundschau 76: 315–359. http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.614.3424andrep=rep1andtype=pdf

Short AEZ, Kadosoe V (2011) Chapter 4. Aquatic Beetles of the Kwamalasamutu Region, Suriname (Insecta: Coleoptera). In: O'Shea, BJ, Alonso, LE, Larsen, TH (Eds) A Rapid Biological Assessment of the Kwamalasamutu region, Southwestern Suriname. RAP Bulletin of Biological Assessment 63, Conservation International, Arlington, VA, 79–90. http://www.bioone.org/doi/abs/10.1896/054.063.0107

Short AEZ, García M, Girón JC (2017) Revision of the Neotropical water scavenger beetle genus *Globulosis* García, 2001 (Coleoptera: Hydrophilidae: Acidocerinae). Zootaxa 4232(2): 271–281. https://biotaxa.org/Zootaxa/article/view/zootaxa.4232.2.10

Short AEZ, Toussaint EFA, Girón JC (in prep.) Phylogeny of the water scavenger beetle subfamily Acidocerinae (Coleoptera: Hydrophilidae).

Smith RR, Short AEZ, (in prep.) Taxonomic review of the water beetle genus *Chasmogenus* Sharp of Venezuela and the Guianas (Coleoptera: Hydrophilidae: Acidocerinae).

Solier AJJ (1834) Observations sur la tribu des Hydrophiliens, et principalement sur le genre *Hydrophilus* de Fabricius. Annales de la Société entomologique de France 3: 299–318. https://biodiversitylibrary.org/page/32515446

Spangler PJ (1979) A new genus of madicolous beetles from Ecuador (Coleoptera: Hydrophilidae: Hydrobiinae). Proceedings of the Biological Society of Washington 92(4): 753–761. https://www.biodiversitylibrary.org/item/110033#page/787/mode/1up

Spangler PJ (1981a) A new water beetle, *Troglochares ashmolei*, n. gen., n. sp., from Ecuador; the first known eyeless cavernicolous hydrophilid beetle (Coleoptera: Hydrophilidae). Proceedings of the Entomological Society of Washington, 83(2): 316–323. https://biodiversitylibrary.org/page/16364657

Spangler PJ (1981b) Supplement to the Aquatic and Semiaquatic Coleoptera of Cuba Collected by the Biospeleological Expeditions to Cuba by the Academies of Science of Cuba and Romania (pp. 145–171). In: Orghidan T et al.: Résultats des Expéditions Biospéologiques

Cubano-Roumaines à Cuba, 3. 191 pp. Academiell Republieli Socialiste România, Bucuresti.

Spangler PJ, Cross JL (1972) A description of the egg case and larva of the water scavenger beetle *Helobata striata* (Coleoptera: Hydrophilidae). Proceedings of the Biological Society of Washington 85: 413–418. https://biodiversitylibrary.org/page/34559933

Stephens JF (1829) (1828–29) Illustrations of British entomology; or, A synopsis of indigenous insects: containing their generic and specific distinctions. Mandibulata. Vol. 2. 200 pp., pl. 10–15. Baldwin and Cradock, London. (only pp. 113-200 and pl. 13-15 issued in 1829) https://biodiversitylibrary.org/page/35933523

Stephens JF (1839) A manual of British Coleoptera, or beetles: containing a brief description of all the species of beetles hitherto ascertained to inhabit Great Britain and Ireland together with a notice of their chief localities, times and places of appearances, etc. 12 + 443 pp. - Longman, Orme, Brown, Green, and Longmans. London. https://biodiversitylibrary.org/page/39160555

Stierlin G (1900) Coleoptera Helvetiae. Fauna Coleopterorum helvetica. Die Käfer-Fauna der Schweiz ... I. Theil. 12 + 667 pp. - Bolli & Böcherer, Schaffhausen. https://biodiversitylibrary.org/page/58080600

Thomson CG (1859) Skandinaviens Coleoptera. Vol. 1. 290 pp. Berlingska Boktryckeriet, Lund. https://biodiversitylibrary.org/page/54335801

Watts CHS (1995) Revision of the Australasian genera *Agraphydrus* Régimbart, *Chasmogenus* Sharp and *Helochares* Mulsant (Coleoptera: Hydrophilidae). Records of the South Australian Museum 28: 113–130. https://biodiversitylibrary.org/page/46866161

Watts CHS (2002) The larvae of some Australian aquatic Hydrophilidae (Coleoptera: Insects). Records of the South Australian Museum 35(2): 105–138. https://biodiversitylibrary.org/page/40639775

Winters FC (1927) Key to the subtribe Helocharæ Orchym. (Coleoptera-Hydrophilidæ) of Boreal America. Pan-Pacific Entomologist 4: 19–29. https://biodiversitylibrary.org/page/53384245

Wollaston TV (1867) Coleoptera Hesperidum, being an enumeration of the Coleopterous insects of the Cape Verde Archipelago. 39 + 285 pp. J. v. Voorst, London. https://biodiversitylibrary.org/page/33075137

Yoshitomi H, Nakajima J (2005) A new record of *Horelophopsis hanseni* (Coleoptera, Hydrophilidae) from Kyushu. Elytra 33(1): 376.

Zaitzev P (1908) Catalogue des Coléoptères aquatiques des familles des Dryopidae, Georyssidae, Cyathoceridae, Heteroceridae et Hydrophilidae. Horae Societatis Entomologicae Rossicae 38: 283–420. https://biodiversitylibrary.org/page/12380729

Chapter 4. The ecology and morphology of habitat transitions in acidocerine water scavenger beetles (Coleoptera: Hydrophilidae: Acidocerinae)

ABSTRACT

The ecological and morphological variation found within the water scavenger beetle subfamily Acidocerinae spans a range of extremes, from pond-adapted aquatic lineages to terrestrial rotting fruit specialists. This variation provides an ideal study system to test hypotheses about the role of habitat transitions in the evolution of aquatic beetles. Here we use phylogenetic comparative methods to estimate the number and direction of habitat shifts, determine the effect of habitat transitions on the diversification rate of the group, and analyze the effect of habitat transitions on a suite of morphological traits. We found that the ancestor of the Acidocerinae was likely a hygropetric inhabitant. There have been at least 13 shifts from hygropetric to aquatic habitats, with two reversals to hygropetric habitats, and two shifts from hygropetric habitats to terrestrial environments. Habitat shifting is not linked to any shifts in diversification rate within the Acidocerinae. Establishment in new habitats was coupled with morphological variation, with trends towards increases in length of the maxillary palpi and the extent of the metafemoral pubescence in aquatic taxa. Our study affirms that lineages moving between aquatic and terrestrial habitats face significant challenges and cannot go between the two directly, but must pass through an intermediate ecology and suite of morphological characters.

RESUMEN

La variación ecológica y morfológica en escarabajos acuáticos detritívoros de la subfamilia Acidocerinae abarca un rango de extremos, desde especies acuáticas adaptadas a estanques, hasta especies terrestres especializadas en frutos en descomposición. Esta variación provee un sistema de estudio ideal para probar hipótesis sobre el papel de las transiciones de hábitat en la evolución de los escarabajos acuáticos. En este trabajo usamos métodos filogenéticos comparativos para estimar el número y la dirección de las transiciones de hábitat, determinar el efecto de las transiciones de hábitat en la tasa de diversificación del grupo, y analizar el efecto de las transiciones de hábitat en un conjunto de caracteres morfológicos. Encontramos que el ancestro de los Acidocerinae era probablemente un habitante higropétrico. Ha habido al menos 13 transiciones desde hábitats higropétricos a hábitats acuáticos, con dos reversiones a hábitats higropétricos, y dos transiciones de hábitats higropétricos a hábitats terrestres. Las transiciones de hábitat no están relacionadas con cambios en la tasa de diversificación de los Acidocerinae. El establecimiento en nuevos hábitats estuvo acoplado con variación morfológica, con tendencias al incremento en la longitud de los palpos maxilares y la extensión de la cobertura de pubescencia en los metafémures en taxa acuáticos. Nuestro estudio afirma que linajes que se mueven entre hábitats acuáticos y terrestres enfrentan retos significativos y no pueden pasar del uno al otro directamente, sino que tienen que pasar por una ecología y morfología intermedias.

Keywords: aquatic beetles; morphology; phylogenetic comparative methods; habitat shifts

INTRODUCTION

Beetles have invaded aquatic habitats numerous times throughout their evolutionary history, leading to more than half a dozen major radiations that cumulatively contain more than 13,000 species (Bilton et al. 2019). Water scavenger beetles in the family Hydrophilidae constitute the second largest of these aquatic radiations with over 3,000 species (Short 2018). Since their origin 214 million years ago (Bloom et al. 2014), hydrophilids have successfully diversified in a wide range of freshwater aquatic habitats such as ponds and streams, in which the beetles swim freely or cling to submerged vegetation. In addition, they have also diversified in unusual "intermediate" habitats such as seepages and waterfalls, where they can crawl over the surface of rocks, submerged in a thin layer of running water. Furthermore, unlike many aquatic beetle radiations, some hydrophilid taxa still thrive a range of terrestrial environments including decaying vegetation and dung, always associated with humid substrates (Bloom et al. 2014, Hansen 1991, Short and Fikáček 2013, Fikáček 2019).

The broad diversity of habitats where hydrophilids live coincides with the broad variation observed in certain suites of morphological features. This morphological diversity is further matched with the ecological diversity, especially in relation to respiratory and locomotory requirements (Short and Liebherr 2007, Fikáček et al. 2013). For breathing, water scavenger beetles acquire atmospheric oxygen prior to becoming submerged, which it is held as an air bubble (compressible plastron) on the ventral surface of their bodies by means of a dense coat

of hydrofuge pubescence that covers their thorax, abdomen and part of their legs. The oxygen in the plastron needs to be replenished periodically, so the beetles swim to the surface and break the surface tension using their antenna to allow fresh air into the bubble (d'Orchymont 1933, Yee and Kehl 2015). Swimming behavior is facilitated by the presence of swimming hairs on the meso- and metatibiae (Hansen 1991, Fikáček 2019), and occasionally on the tarsi.

Given the tremendous breadth of ecologies and morphologies within the family, habitat transitions are one of the most intriguing evolutionary patterns in water scavenger beetles. When did those shifts occur? Is there a directionality to those shifts? How common or widespread is habitat shifting across the family? Which groups have shifted or are most likely to shift? Have those shifts had effects on the diversification and morphology of the beetles? To tackle these questions, we focus here on the subfamily Acidocerinae, which is sister to the primarily terrestrial Cylominae + Spaheridiinae; this larger clade (Acidocerinae+Cylominae + Spaheridiinae) is sister to the primarily aquatic Enochrinae (Short and Fikáček 2013). With representatives in nearly the entire range of habitats that have been recorded for hydrophilids, Acidocerinae constitutes an ideal study system to address habitat shifting in water scavenger beetles. Based on recent phylogenetic and taxonomic studies (Short et al. in prep.; see also Chapter 3), there have been multiple habitat shifts in the group, but the number and sequence of these shifts remains unknown. To better understand the evolutionary trajectory of the subfamily Acidocerinae, we used the most comprehensive time-calibrated phylogeny to date (Short et al. in prep.), along with phylogenetic comparative methods to address questions along the following three axes:

(1) What is the frequency, polarity, and phylogenetic placement of habitat transitions?

Although the majority of species of Acidocerinae are aquatic, recent studies have brought to light numerous taxa exclusively found on seepages (e.g., *Tobochares*, see Kohlenberg and Short 2017), *Ephydrolithus*, most *Primocerus* (see Girón and Short 2019), some *Agraphydrus* (see Komarek 2018), and there are at least two terrestrial lineages (*Quadriops* (see Girón and Short 2017) and one species of *Agraphydrus*) in the subfamily. However, neither the number of habitat shifts in the subfamily or the directionality of these shifts is known. Hygropetric habitats have been proposed as intermediate in the transition from aquatic to terrestrial environments (Short and Liebherr 2007). Because the Acidocerinae includes taxa in all three kinds of habitats, the lineage offers an ideal case to test the hypothesis that taxa cannot move from aquatic to terrestrial habitats directly but must pass through an intermediate stage.

(2) Do habitat transitions have an effect on diversification rates?

Prior studies have shown that there is no direct association between habitat shifting and changes in diversification rates in the Hydrophilidae (Bloom et al 2014). However, the phylogeny used by Bloom et al. (2014) was analyzed at the subfamily and tribe level, and therefore not able to recover shifts that occurred within subfamilies such as has happened within the Acidocerinae. Additionally, the phylogeny used in Bloom et al. (2014) includes only aquatic acidocerines, and therefore it is not comprehensive enough to use it for assessing ecological diversification within the subfamily. By densely sampling the ecological as well as taxonomic diversity of Acidocerinae, we will use a much more fine-scale approach to detecting potential shifts.

(3) Are habitat transitions correlated with variation in morphological traits?

In general, the external morphology of the adults is extremely homogeneous within acidocerine genera, so that obvious variable external characters have been traditionally used for classification (e.g., length of maxillary palpomeres, number of antennomeres, presence of elytral striae, emargination of fifth abdominal ventrite). These characters have never been studied in a phylogenetic context within the subfamily, and there is no evidence that those characters actually define monophyletic groups. On the other hand, some morphological features seem to change consistently in acidocerines according to their ecological habits: species from hygropetric and terrestrial environments tend to have shorter maxillary palpi and reduced metafemoral pubescence in comparison with aquatic taxa. Based on these observations we set out to test the hypotheses presented in Table 4.1.

Table 4.1. Summary of morphological characters selected for this study and hypotheses for their evolutionary change.

Morphological character	Predictions	Rational
Antennomere number	Phylogenetically conserved	The ancestral condition in Hydrophilidae is nine antennomeres. There are several instances of reduction to eight antennomeres in the family.
Maxillary palpomere 3	There is an effect of habitat transition on trait values	Observed trend: relatively long and slender in aquatic species to short and stout in species from hygropetric and terrestrial habitats
Metafemoral pubescence	There is an effect of habitat transition on trait values	Observed trend: reduction of coverage in species from hygropetric and terrestrial habitats
Elytral striae	Phylogenetically conserved	Has been used for taxonomic purposes, therefore should group monophyletic taxa.
Apex of fifth abdominal ventrite	Phylogenetically conserved	Has been used for taxonomic purposes, therefore should group monophyletic taxa.

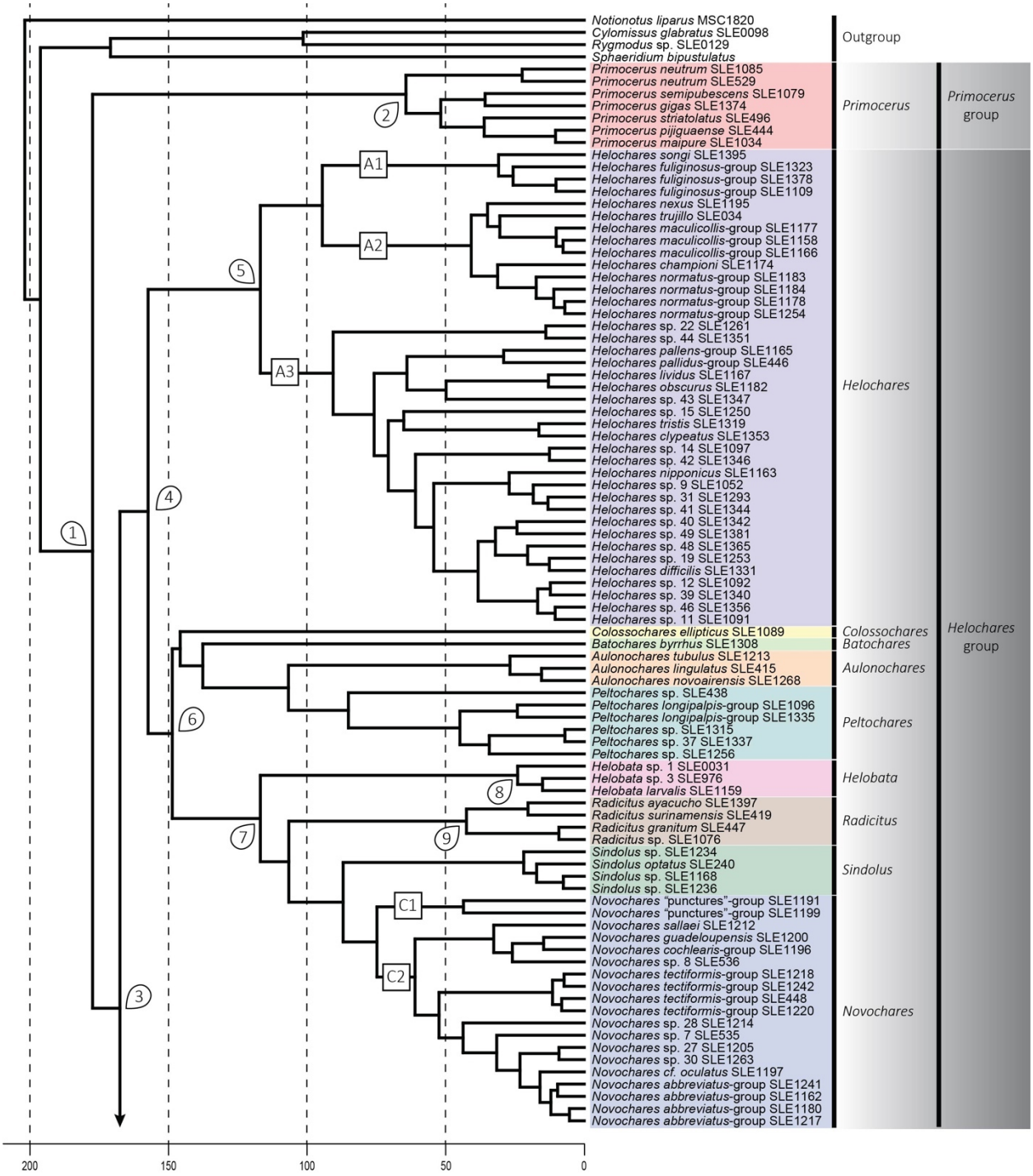


Figure 4.1. Part one of pruned version of thetime-calibrated Bayesian phylogeny by Short et al. (in prep.) used in this study. Includes only genera in the *Primocerus*- and *Helochares*-group of genera. Major nodes are labeled with numbers.

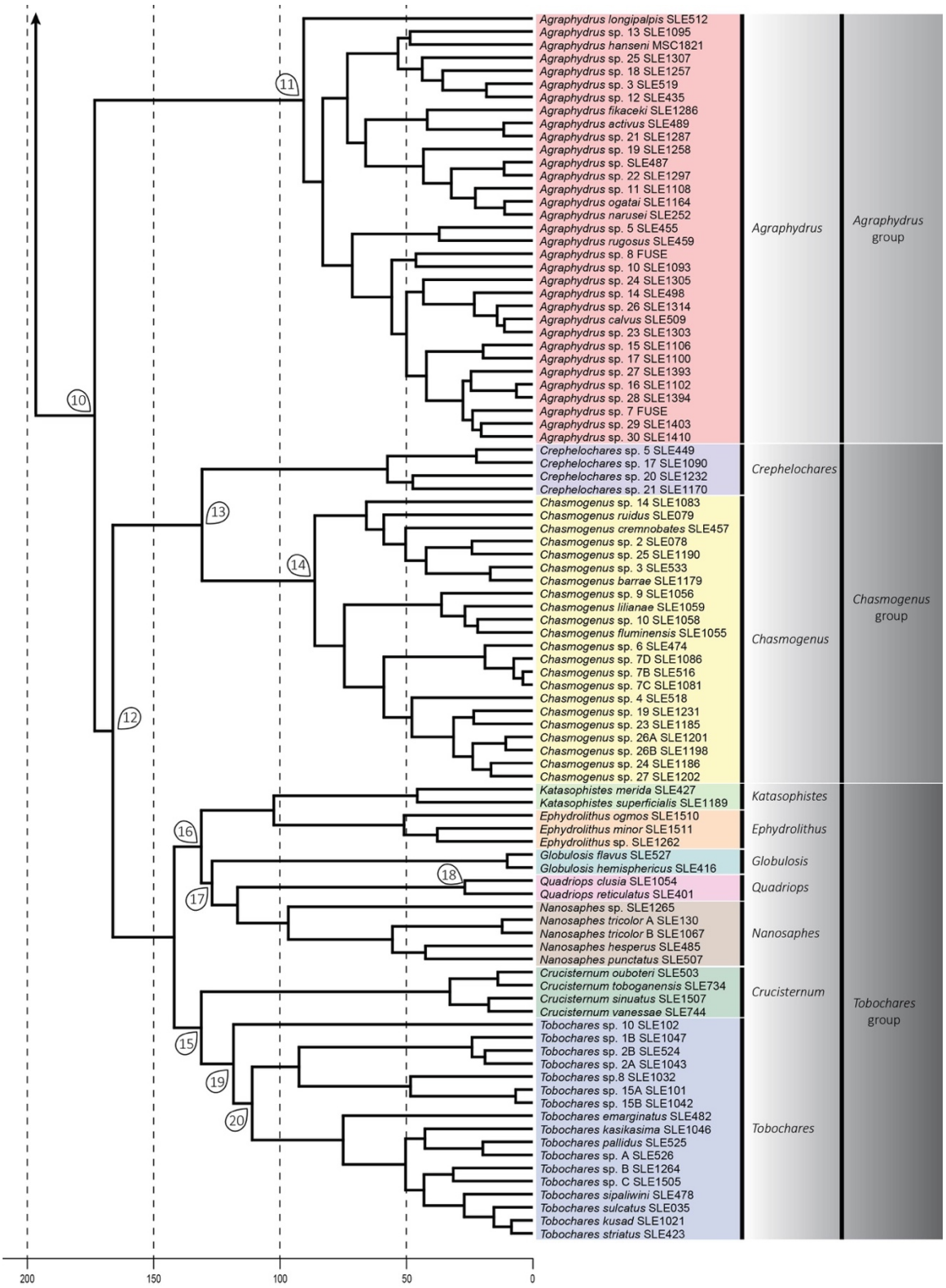


Figure 4.2. Part two of pruned version of the time-calibrated Bayesian phylogeny by Short et al. (in prep.) used in this study. Includes genera in the *Agraphydrus*-, *Chasmogenus*-, and *Tobochares*-group of genera. Major nodes are labeled with numbers continuing from Fig. 1.

MATERIALS AND METHODS

Analyses were performed in R version 3.5.2 (R Core Team 2018), interfaced through RStudio version 1.1.463 (RStudio Team 2016). For all analyses in this study, we used the Bayesian time-calibrated phylogeny of the Acidocerinae (Short et al. in prep.). The phylogeny is based on DNA sequence data for the mitochondrial gene COI, and the nuclear genes 18S, 28S, H3, and CAD, for 216 terminals of which are outgroups. Twenty out of the 23 recognized genera of Acidocerinae are represented in the tree. The phylogeny was pruned using the function `drop.tip` in the R package ape version 5.0 (Paradis 2004, Paradis and Schliep 2019) to include only terminals for which voucher specimens with the structures of interest were available. The pruned tree contains 181 acidocerine terminals and four outgroup taxa (Fig. 4.1, 4.2) (list of terminals in Appendix 1).

Habitat transitions

We coded the habitat of each terminal in the pruned tree as a categorical trait with three states: aquatic (including ponds, marshes, forest pools, streams, stream margins etc.), hygropetric (seepages, thin layer of water flowing over the surface of rocks), or terrestrial (decaying plant material not submerged in water) (Short and Liebherr 2007). We based each habitat coding on a combination of (1) original label data on the voucher specimens, (2) species accounts from primary literature, and (3) personal field observations. To estimate the number and direction of ecological shifts as well as where in the phylogenetic history of the Acidocerinae these shifts occurred, we reconstructed ancestral states for habitat.

Models of variation in transition rates among states for discrete characters were fitted using the likelihood `fitDiscrete` function in the R package GEIGER version 2.0.6.1 (Harmon et al. 2008). For a visual depiction and rate matrices for the models tested see Fig. 4.3; Table 4.2 presents descriptions of the different models. Akaike weights (AICw) were obtained for each of the models tested using the `aic.w` function in GEIGER to determine the model with the best fit: higher AICw indicate better support. The best model was then used to generate 10,000 ancestral state histories (stochastic character mapping; Huelsenbeck et al. 2003) with the `simmap` function in the R package phytools version 0.6-99 (Revell 2012) and summarized with the function `summary` in the same package.

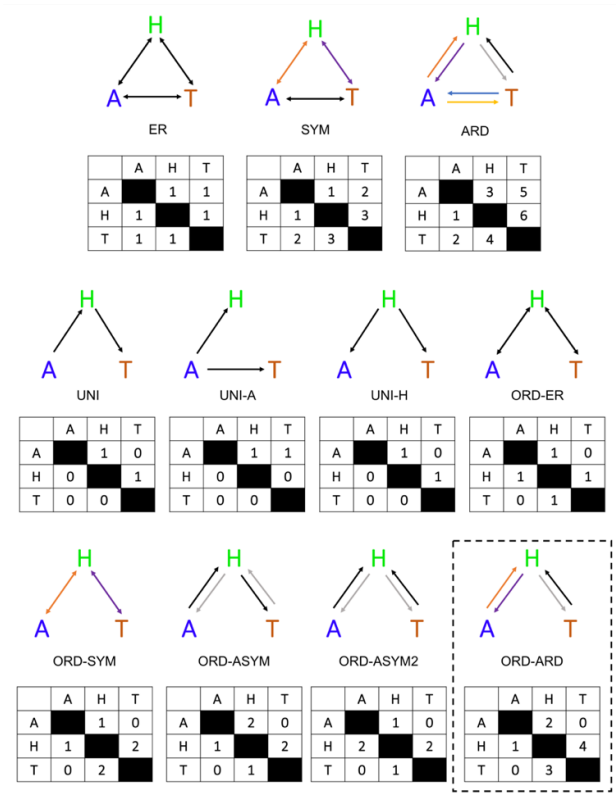


Figure 4.3. Summary of tested models of transition rates including rate matrices for each model. The preferred model (ORD-ARD) in the bottom right corner is highlighted with a dashed outline. For a description of each model see Table 2. A (aquatic), H (hygropetric), T (terrestrial).

Table 4.2. Summary of transition rates models tested for habitat.

Model	Number of rate parameters	Description
ER	1	All transition rates between states are equal
SYM	3	Transitions forward and backward are equal between states, but different among state pairs
ARD	6	All transition rates between states are different
UNI	1	Only forward transitions aquatic-hygropetric and hygropetric-terrestrial are allowed at the same rate
UNI-A	1	Only forward transitions aquatic-hygropetric and aquatic-terrestrial are allowed at the same rate
UNI-H	1	Only forward transitions hygropetric-aquatic and hygropetric-terrestrial are allowed at the same rate
ORD-ER	1	Transitions forward and backward between hygropetric-aquatic and hygropetric-terrestrial are allowed at the same rate; transitions aquatic - terrestrial are not allowed
ORD-SYM	2	Transitions forward and backward are equal between states, but different among state pairs; transitions aquatic - terrestrial are not allowed
ORD-ASYM	2	Transitions forward (aquatic->hygropetric->terrestrial) and backward (terrestrial->hygropetric->aquatic) occur at different rates; transitions aquatic - terrestrial are not allowed
ORD-ASYM2	2	Transitions towards hygropetric and from hygropetric occur at different rates; transitions aquatic - terrestrial are not allowed
ORD-ARD	4	Transitions forward and backward and transitions hygropetric-aquatic and hygropetric-terrestrial occur at different rates; transitions aquatic - terrestrial are not allowed

Diversification rate analysis

The birth (b), death (d), and net diversification rates (b-d) were calculated using the command `birthdeath` in the R package ape version 5.0 (Paradis 2004, Paradis and Schliep 2019). To visualize the pattern of lineage diversification in Acidocerinae, we generated a lineage-through-time (LTT) plot using the function `ltt` in phytools version 0.6-99 (Revell 2012). The function also returns the value of gamma (a measure of the relative position of internal nodes within a phylogeny; Pybus and Harvey 2000) and a p-value for the Constant Rate test hypothesis. In addition, we obtained a confidence interval for LTT based on a set of 1,000 simulated trees assuming a pure-birth process of the same duration and resulting in the same number of species.

Trees were simulated with the phytools function `pbtree`, and the confidence interval was obtained with the function `ltt95`.

To detect diversification rate shifts in the phylogeny, we used the function `medusa` in GEIGER, which fits increasingly complex diversification models (using stepwise addition) to a phylogeny with richness information, using the Akaike Information Criterion to retain the best model. We ran an analysis including all the terminals (with outgroups), and another excluding the outgroups, assuming complete sampling for the phylogeny (without providing species numbers). We also generated a reduced phylogeny, by pruning the tree to retain only the earliest diverging representative of each major acidocerine clade and ran one analysis with the number of described species per each clade, and another with estimated numbers of species based on our knowledge about the group (Table 4.3). We visually inspected the identified shifts against ecological information to determine if habitat is involved in changes in diversification rates.

Table 4.3. Number of currently described species and estimated number of species for major clades of Acidocerinae.

Clade	Number of described species	Estimated number of species
Primocerus	9	12
Helochares (Clade A1)	4	6
Helochares (Clade A2)	9	11
Helochares (Clade A3)	140	190
Colossochares	2	3
Batochares	3	5
Aulonochares	3	5
Peltochares	8	20
Helobata	13	16

Radicitus	3	6
Sindolus	8	10
Novochares (Clade C1)	5	10
Novochares (Clade C2)	15	40
Agraphydrus	168	210
Crephelochares	29	40
Chasmogenus	16	55
Katasophistes	4	10
Ephydrolithus	5	10
Globulosis	3	5
Quadriops	6	8
Nanosaphes	4	8
Crucisternum	7	12
Tobochares	10	40

Evolution of morphological features

Five external morphological features were chosen based on their variation across the Acidocerinae (Fig. 4.4). The full character matrix is presented in Appendix 1.

Antennomere number: The plesiomorphic number of antennomeres in hydrophilids is nine, with some taxa exhibiting a reduction to eight or, rarely, seven (Hansen 1991, Short and Fikáček 2013). Acidocerine taxa possess either nine (Fig. 4.4A) or eight (Fig. 4.4B) antennomeres and this character has been traditionally used for taxonomic purposes (e.g., Hebauer 1992). The character is coded as categorical and binary.

Maxillary palpomere: The maxillary palpi in all water scavenger beetles are composed of four palpomeres, with the first palpomere being extremely small and palpomeres 2–4 clearly visible and elongated. In acidocerines, palpomeres 2–4 are approximately of the same length and overall proportions. The length of the palpi vary substantially from short and stout (nearly half

width of the head; Fig. 4.4C) to long and slender (nearly 2 × width of the head; Fig. 4.4D). The total length of the maxillary palpi relative to the width of the head has been traditionally used as a taxonomic character, including diagnosing genera (e.g., d'Orchymont 1919). We calculated the length/width ratio of the maxillary palpomere 3 (penultimate) of each specimen, in order to remove the effect of body size variation across the subfamily (1.5–14.0 mm). The maximum length and maximum width of palpomere 3 were measured using the ocular graticule of an Olympus SZX 16 stereo microscope. The magnification at which the measurements were taken depended on the size of the specimen, but both measurements (length and width) were taken at the same magnification for each specimen. The character is coded as continuous.

Metafemoral pubescence: The extent of the coverage of hydrofuge pubescence over the surface of the metafemora tends to be reduced in some hydrophilid groups, especially those associated with terrestrial habitats (e.g., Protosternini, Sphaeridiinae, Megasternini; Short and Fikáček 2013). There is broad variation in this character in acidocerines (e.g., *Primocerus*, *Agraphydrus*). We calculated the area of the anterior surface of the metafemora covered by hydrofuge pubescence by taking a photo of one of the metafemora of each specimen. This was done using an Olympus DP72 digital camera attached to an Olympus SZX 16 stereo microscope. For each image the total area and the area covered by hydrofuge pubescence were traced and measured using the online tool SketchAndCalc (Dobbs 2011); the percentage of area covered by pubescence (Fig. 4.4E–H) was calculated based on those measurements; it is a continuous character.

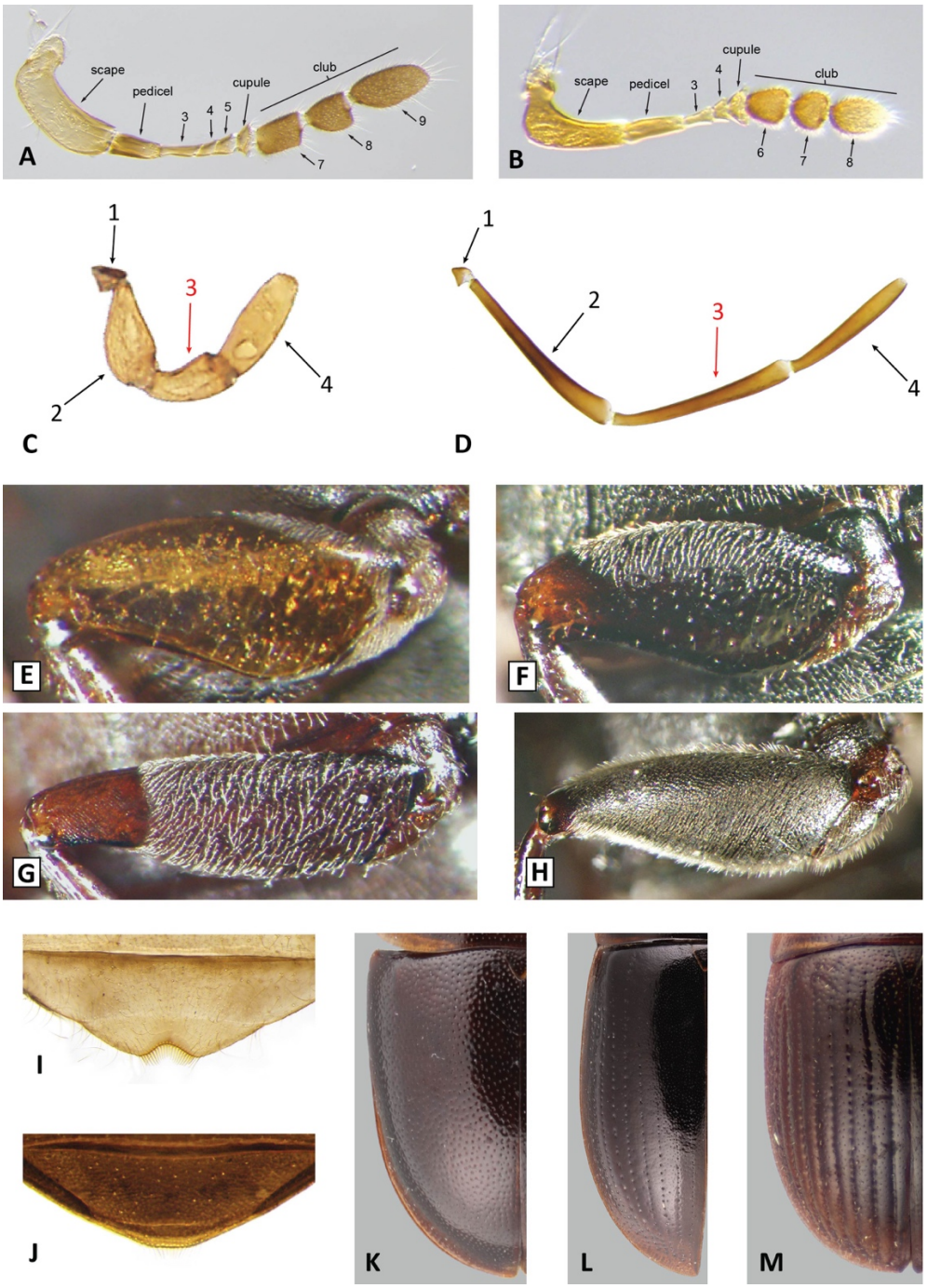


Figure 4.4. Morphological features analyzed in this study. **A–B** antennae: **A** nine antennomeres (*Aulonochares tubulus*), **B** eight antennomeres (*Chasmogenus crenmobates*); **C–D** maxillary palpi: **C** short and stout (length/width ratio of maxillary palpomere 3 = 1.9; *Quadriops reticulatus*), **D** long and slender (length/width ratio of maxillary palpomere 3 = 8.9; *Aulonochares tubulus*); **E–H** metafemoral pubescence: **E** mostly glabrous (11% coverage; *Tobochares* sp.), **F** partly covered (30% coverage; *Radicitus* sp.), **G** partly covered (78% coverage; *Katasophistes superficialis*), **H** mostly covered (96% coverage; *Helochares maculicollis*); **I–J** apex of fifth abdominal ventrite: **I** emargination present (*Aulonochares tubulus*), **J** emargination absent (*Ephydrolithus hamadae*). **K–M** left elytron in dorsal view: **K** elytral striae present (*Tobochares kusad*), **L** elytral striae present (*Novochares* sp.), **M** elytral striae absent (*Quadiops acroreius*).

Apex of fifth abdominal ventrite: The presence of an emargination at the apex of the fifth (apical) abdominal ventrite has been considered an important taxonomic character in the family (e.g., Hansen 1991). There is variation in this character across Acidocerinae, but it is not clear whether the emargination is homologous or even circumscribes monophyletic groups. We coded this character as categorical and binary: emargination present (Fig. 4.4I), emargination absent (Fig. 4.4J).

Elytral striae: Several features of the elytral punctation in Acidocerinae have been traditionally important for taxonomic diagnoses (e.g., Hebauer 1996). We coded the presence or absence of well-defined striae (longitudinally aligned serial punctures forming rows, sometimes impressed) along at least part of the elytra, as categorical and binary (elytral striae absent (Fig. 4.4K), elytral striae present (Fig. 4.4L, M)).

Ancestral states were reconstructed for each morphological trait. For binary characters, model testing and stochastic maps were implemented as described above for habitat. Only ER and ARD transition models were tested, given that for binary characters ER and SYM are equivalent. For continuous characters univariate models for continuous character evolution were fitted using the `fitContinuous` function in GEIGER version 2.0.6.1 (Harmon et al. 2008). We evaluated Brownian motion (BM), 'early-burst' (EB), and Ornstein-Uhlenbeck (OU) models, calculating Akaike weights as described above to determine the best fit model, which was then used for estimating ancestral states using the function `fastAnc` in phytools version 0.6-99 (Revell 2012). Ancestral character estimated values, including the estimated 95% confidence interval, were obtained for each major node of the acidocerine phylogeny. The traits

were mapped onto the phylogeny with the `contMap` function in phtyools and plotted using a color palette generated with the package viridis 0.5.1 (Garnier 2018).

Phylogenetic signal

To test whether morphological traits are phylogenetically conserved, we estimated phylogenetic signal. For discrete characters (e.g., antennomere number, elytral striae, and apex of fifth abdominal ventrite), we calculated the D statistic (Fritz and Purvis 2010) using the `phylo.d` function of the R package caper version 1.0.1. (Orme 2018); a dataset for each character was previously assembled using the command `comparative.data` in the same package. D values and values for the probability of D resulting from Brownian phylogenetic structure were obtained. For continuous characters (e.g., maxillary palpomere 3 and metafemoral pubescence), analyses were carried out using the function `phylosig` in phytools version 0.6-99 (Revell 2012). Values for Blomberg's K (Blomberg et al. 2003) and Pagel's lambda (Pagel 1999), with their corresponding p-values, were obtained.

Tests for correlation between habitat and morphological traits

We tested whether changes in morphological features are influenced by habitat type. Current methods to estimate character correlations between two categorical variables are limited to binary traits, so we binarized our coding for habitat by merging together two of the states at a time, for a new set of three binary characters for habitat (Fig. 4.5):

- Eco1 (aquatic+terrestrial vs. hygropetric): where aquatic and terrestrial species are considered together as the extremes of the habitat continuum, different from a putatively intermediate condition (Fig. 4.5A).

- Eco2 (aquatic+hygropetric vs. terrestrial): both water-related habitats are considered as the same unit, separate from the terrestrial state (Fig. 4.5B).

- Eco3 (hygropetric+terrestrial vs. aquatic): aquatic as the ancestral condition for hydrophilids is considered different from the derived hygropetric and terrestrial habitats (Fig. 4.5C).

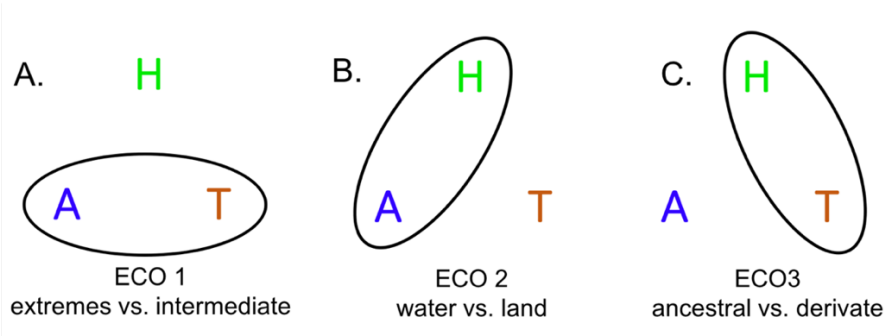


Figure 4.5. Schematic for binarized habitats: **A** Eco1: aquatic+terrestrial vs. hygropetric, **B** Eco2 aquatic+hygropetric vs. terrestrial, **C** Eco3 (hygropetric+terrestrial vs. aquatic. A (aquatic), H (hygropetric), T (terrestrial).

Each of these new habitat categories were tested for phylogenetic signal by calculating the D statistic as described above, obtaining values for the D statistic and for the probability of D resulting from Brownian phylogenetic structure. Correlation was then tested for each binary habitat with each morphological binary trait by fitting and testing Pagel's model for independent evolution of two binary characters (Pagel 1994; Fig. 6). The function fitPagel of the R package phytools version 0.6-99 (Revell 2012) was used, setting the method to fitDiscrete from GEIGER

version 2.0.6.1 (Harmon et al. 2008) and the model to those resulting from the initial model testing. Values of log likelihood and AICw were obtained for each model along with the likelihood ratio and p-value for the test.

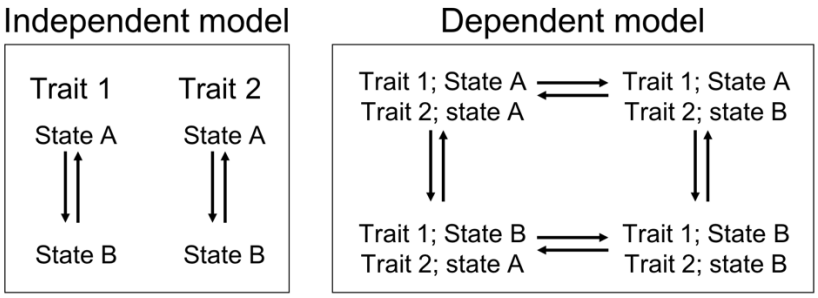


Figure 4.6. Schematic of transition rates tested by Pagel's model for independent evolution of two binary characters.

For continuous traits (e.g., maxillary palpomere 3 and metafemoral pubescence) we tested the original multistate habitat coding by performing Phylogenetic Analyses of Variance (Garland et al. 1993) on the log-transformed trait values using the command `aov.phylo` in GEIGER (Harmon et al. 2008), with 10,000 simulations. Visual inspection of the mapped continuous traits on the phylogeny, with overlaid habitat shifts was performed to assess the effect, if any, of habitat transition on trait values.

RESULTS

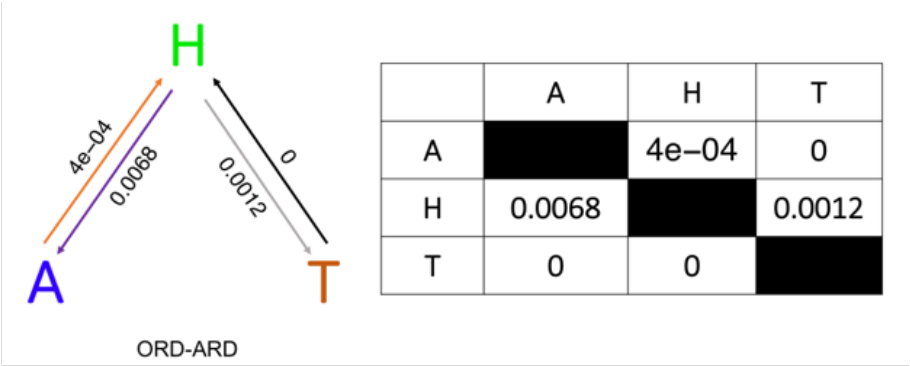
Habitat transitions

The tested models for habitat with their calculated values of Log-likelihood, AICc, and AICw are presented in Table 4.4. The model ORD-ARD of variation in transition rates among

states was the best fit for habitat. The model allows transitions hygropetric-aquatic, hygropetric-terrestrial, transitions forward (aquatic -> hygropetric -> terrestrial) and transitions backward (terrestrial -> hygropetric -> aquatic), all at different rates (Fig. 4.3); direct transitions aquatic-terrestrial are not permitted under model ORD-ARD. Transitions aquatic to hygropetric occurred at a rate of 4.4e-04; transitions hygropetric to aquatic at 0.0068; transitions hygropetric to terrestrial at 1.2e-03; transitions terrestrial to hygropetric at 3.6e-15 (essentially 0) (Fig. 4.7).

Table 4.4. Log-likelihood, AICc and AICw values for models of character evolution for multistate habitat. Values in bold indicate the model with the best fit. Values are rounded to the nearest hundredth.

Model	Log-likelihood	AICc	AICw score
ER	-74.31	150.65	0.00
SYM	-69.65	145.43	0.06
ARD	-61.59	135.65	0.00
UNI	-69.57	141.16	0.00
UNI-A	-74.30	150.62	0.00
UNI-H	-74.47	150.96	0.00
ORD-ER	-71.10	144.21	0.00
ORD-SYM	-70.91	145.88	0.00
ORD-ASYM	-63.87	131.81	0.40
ORD-ASYM2	-66.66	137.39	0.02
ORD-ARD	**-61.59**	**131.40**	**0.50**



	A	H	T
A		4e−04	0
H	0.0068		0.0012
T	0	0	

Figure 4.7. Transition rates obtained for habitat under the ORD-ARD model.

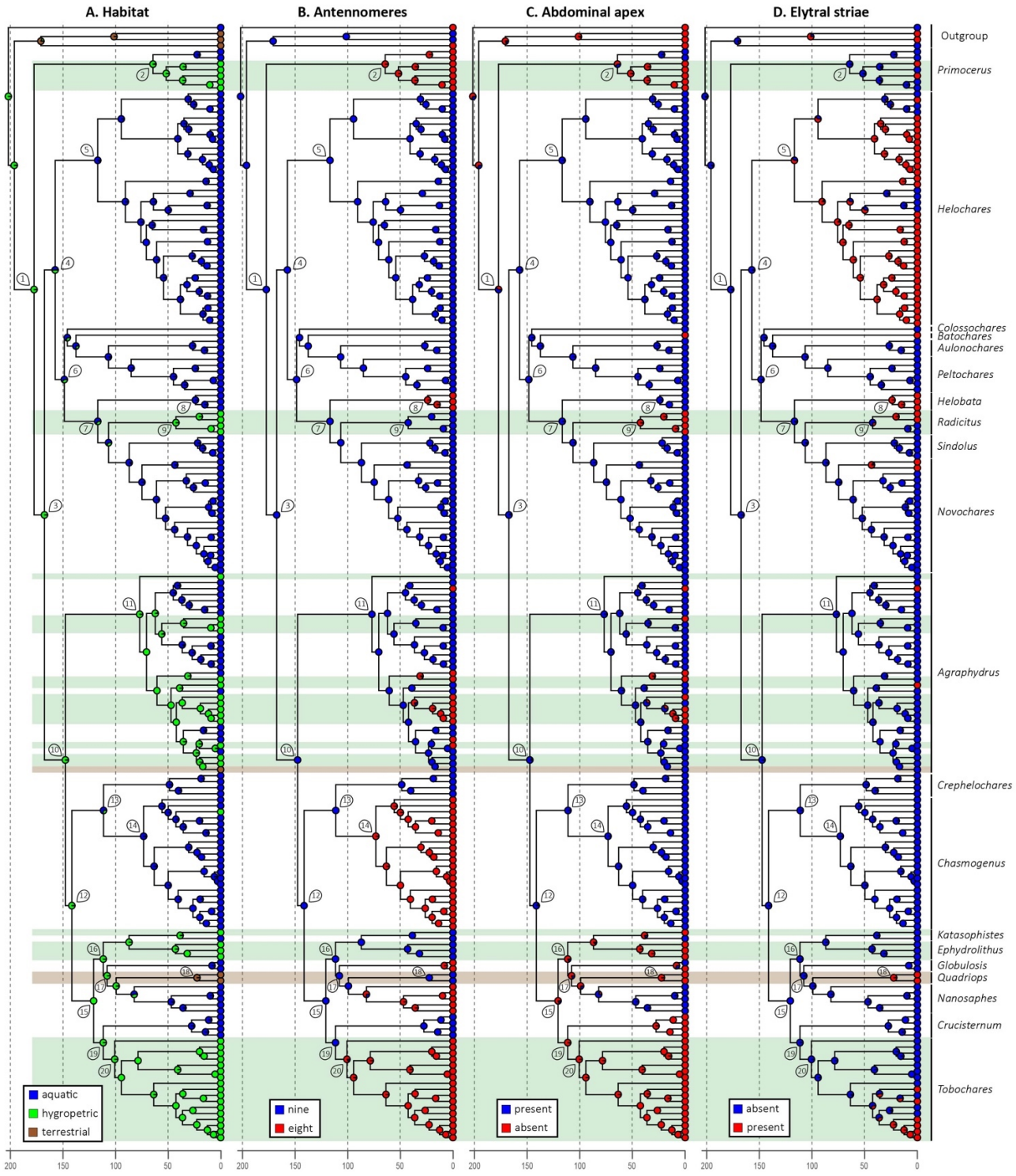


Figure 4.8. Stochastic character mapping throughout the acidocerine phylogeny: **A** habitat, **B** number of antennomeres, **C** emargination of the abdominal apex, **D** presence of elytral striae. Node numbers correspond to major clades for which values are presented in Tables 4.5 and 4.8. Green shading highlights clades where habitat remained hygropetric; brown shading indicates terrestrial terminals.

Stochastic character mapping (Fig. 4.8A) indicates that under the ORD-ARD model the most recent common ancestor of the Acidocerinae was most likely a hygropetric inhabitant. There are 13 transitions to aquatic habitats: one in *Primocerus*, one in the *Helochares*-group with a reversal to seepage in *Radicitus*, six in *Agraphydrus*, one in *Chasmogenus*-group with a reversal in *Chasmogenus cremnobates*, one in *Katasophistes superficialis*, one in *Globulosis*, one in *Nanosaphes*, and one in *Crucisternum*. In addition, there are two transitions to terrestrial habitats, one in one species of *Agraphydrus* and one in *Quadriops*, both directly from seepage. Posterior probabilities at each major node of the phylogeny are presented in Table 4.5.

Table 4.5. Posterior probabilities of transition between habitat states at each major node of the acidocerine phylogeny.

Node number	Clade	aquatic	hygropetric	terrestrial
1	Acidocerinae	0.0013	**0.9987**	0.0000
2	*Primocerus*	0.0284	**0.9716**	0.0000
3	*Helochares-Tobochares*	0.0079	**0.9921**	0.0000
4	*Helochares* group	**0.5218**	0.4782	0.0000
5	*Helochares*	**0.9406**	0.0594	0.0000
6	*Colossocares-Novochares*	**0.6281**	0.3719	0.0000
7	*Helobata-Novochares*	**0.6611**	0.3389	0.0000
8	*Helobata*	**0.9959**	0.0041	0.0000
9	*Radicitus*	0.0054	0.9946	0.0000
10	*Agraphydrus-Tobochares*	0.0025	**0.9975**	0.0000
11	*Agraphydrus*	0.0001	**0.9999**	0.0000
12	*Crephelochares-Tobochares*	0.0045	**0.9955**	0.0000
13	*Chasmogenus* group	**0.7255**	0.2745	0.0000
14	*Chasmogenus*	**0.9763**	0.0237	0.0000
15	*Tobochares* group	0.0000	**1.0000**	0.0000
16	*Katasophistes-Nanosaphes*	0.0002	**0.9998**	0.0000
17	*Globulosis-Nanosaphes*	0.0057	**0.9943**	0.0000
18	*Quadriops*	0.0000	0.0050	**0.9950**
19	*Crucisternum-Tobochares*	0.0013	**0.9987**	0.0000
20	*Tobochares*	0.0001	**0.9999**	0.0000

Diversification rates in Acidocerinae and the effect of habitat transitions

Calculated values of birth (b = 0.022), death (d = 0), and net diversification rate (b-d = 0.022) were obtained. A lineage-through-time (LTT) plot to visualize the pattern of lineage diversification in Acidocerinae is presented in Fig. 4.9. The resulting gamma statistic was -1.24; the p-value for the Constant Rate test (Pybus and Harvey 2000) was 0.21, which indicates that the diversification of Acidocerinae conforms to the null hypothesis of constant birth and death.

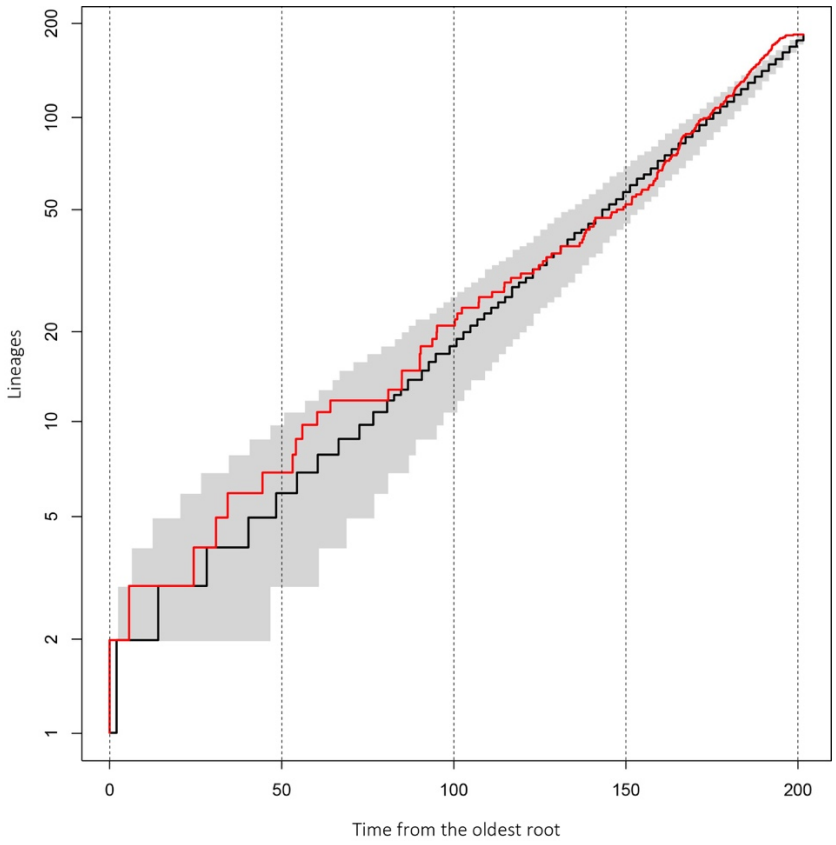


Figure 4.9. Lineage-through-time (LTT) plot for the acidocerine phylogeny. Y axis is on a log-scale. Solid black line indicates the expectation under pure birth. Solid red line indicates the observed diversification of acidocerines. Shaded area indicates the 95% confidence interval estimated from 1000 simulations.

When the diversification rate was estimated including the outgroups and assuming the phylogeny was fully sampled, the Medusa analysis detected one rate increase for the acidocerine clade with respect to the outgroups. When the outgroups were not included in the analysis, the Medusa algorithm did not detect any shifts in diversification rates within Acidocerinae (Fig. 4.10A). For the reduced dataset including one terminal per each major clade, when the described numbers of species were considered, the Medusa analysis found one rate decrease in the clade composed of *Colossochares*, *Batochares*, *Aulonochares*, and *Peltochares* and a rate increase in *Helochares* Clade A3 (Fig. 4.10B, Table 4.6). When the estimated numbers of species were considered for the reduced phylogeny, the Medusa analysis only found a rate decrease in the *Colossochares*–*Peltochares* clade (Fig. 4.10C, Table 4.6). Figure 4.10 also shows the habitats mapped onto the tree, where it is clear that diversification rate shifts do not overlap with diversification rate shifts.

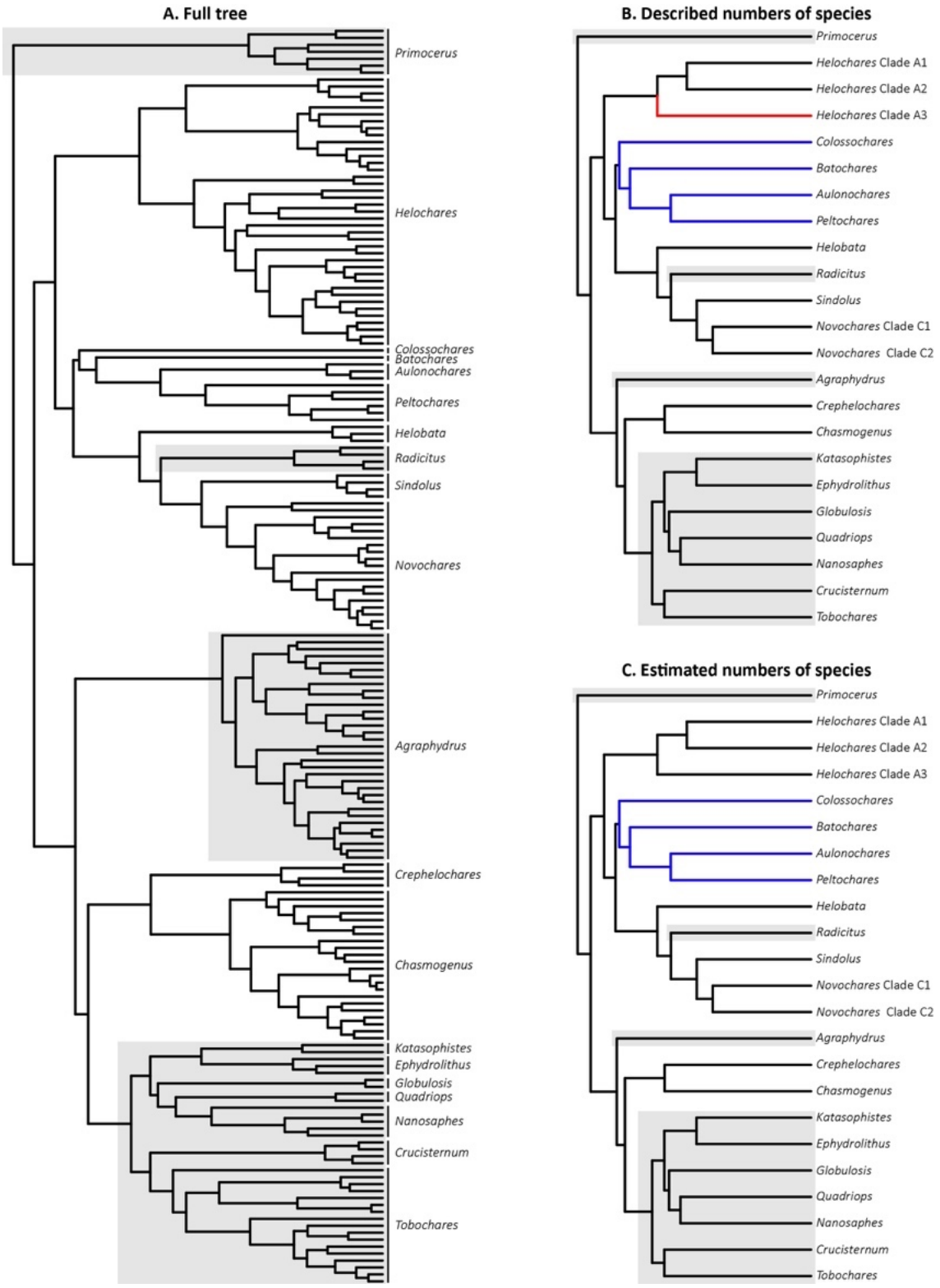


Figure 4.10. Phylogeny of Acidocerinae with mapped diversification rate shifts and ecological shifts. **A** full phylogeny without outgroups, **B** reduced dataset with numbers of described species, **C** reduced dataset with estimated numbers of species. Increases in diversification rates are highlighted in red, whereas decreases are highlighted in blue.

Table 4.6. Results from medusa analyses.

Dataset	Log-likelihood	r	r low	r high
Full tree with outgroups	-19.25	0.0044	0.00	0.01
Shift 1 [increase]	-856.74	0.0233	0.02	0.03
Full tree without outgroups	-852.55	0.0232	0.02	0.03
Reduced tree, number of described spp.	-140.31	0.0265	0.02	0.03
Shift 1 [decrease]	-18.76	0.0133	0.01	0.02
Shift 2 [increase]	-5.94	0.0423	0.03	0.07
Reduced tree, estimated number of spp.	-158.24	0.0333	0.03	0.04
Shift 1 [decrease]	-21.79	0.0191	0.01	0.03

Evolution of morphological features

Models of variation in transition rates among states were tested for all morphological characters included in this analysis. The equal rates (ER) model was the best fit for presence/absence of both abdominal emargination (transition rate = 0.002) and elytral striae (transition rate = 0.003). The all rates different model (ARD) was the best fit for the number of antennomeres with a transition rate from nine to eight of 2.4e-03, and from eight to nine antennomeres of 3.1e-81 (essentially 0). For maxillary palpomere 3 the best fit was the Ornstein–Uhlenbeck model (OU), whereas for metafemoral pubescence the best fit was the early burst model (EB). Results of model testing are presented in Table 4.7. The best fit models were used for reconstructing ancestral states. The resulting posterior probability values of the ancestral state reconstructions are presented in Table 4.8 for the major nodes of the acidocerine phylogeny as illustrated in Figure 4.8B–D.

Table 4.7. Log-likelihood, AICc and AICw values for models of character evolution for morphological traits. Values in bold indicate the model with the best fit. Values are rounded to the nearest hundredth.

Morphological feature	Model	Log-likelihood	AICc	AICw score
Antennomeres	ER	-48.73	99.49	0.05
	ARD	**-44.82**	**93.70**	**0.95**
Abdominal apex	**ER**	**-51.60**	**105.22**	**0.71**
	ARD	-51.45	106.96	0.29
Elytral striae	**ER**	**-58.32**	**118.67**	**0.73**
	ARD	-58.32	120.70	0.27
Maxillary palps	BM	-283.60	571.27	0.32
	EB	-283.60	573.33	0.12
	OU	**-282.02**	**570.16**	**0.56**
Metafemoral coverage	BM	-743.96	1491.99	0.00
	EB	**-733.54**	**1473.21**	**1.00**
	OU	-743.96	1494.06	0.00

Table 4.8. Posterior probabilities of transition between character states at each major node of the acidocerine phylogeny for binary traits. Values are rounded to the nearest hundredth.

Node number	Clade	Antennomere number		Elytral striae		Emargination of fifth abdominal ventrite	
		nine	eight	absent	present	absent	present
1	Acidocerinae	**1.00**	0.00	**0.98**	0.02	0.39	**0.61**
2	*Primocerus*	0.01	**0.99**	**0.97**	0.03	**0.62**	0.38
3	*Helochares-Tobochares*	**1.00**	0.00	**0.99**	0.01	0.08	**0.92**
4	*Helochares* group	**1.00**	0.00	**0.97**	0.03	0.01	**0.99**
5	*Helochares*	**1.00**	0.00	0.40	**0.60**	0.00	**1.00**
6	*Colossocares-Novochares*	**1.00**	0.00	**0.97**	0.03	0.00	**1.00**
7	*Helobata-Novochares*	**1.00**	0.00	**0.92**	0.08	0.00	**1.00**
8	*Helobata*	0.00	**0.99**	0.01	**0.99**	0.00	**1.00**
9	*Radicitus*	**1.00**	0.00	**0.75**	0.25	**0.98**	0.02
10	*Agraphydrus-Tobochares*	**1.00**	0.00	**1.00**	0.00	0.07	**0.93**
11	*Agraphydrus*	**1.00**	0.00	**1.00**	0.00	0.00	**1.00**
12	*Crephelochares-Tobochares*	**1.00**	0.00	**1.00**	0.00	0.09	**0.91**
13	*Chasmogenus* group	**1.00**	0.00	**1.00**	0.00	0.01	**0.99**
14	*Chasmogenus*	0.01	**0.99**	**1.00**	0.00	0.00	**1.00**
15	*Tobochares* group	**1.00**	0.00	**1.00**	0.00	**0.83**	0.17
16	*Katasophistes-Nanosaphes*	**1.00**	0.00	**1.00**	0.00	**0.83**	0.17
17	*Globulosis-Nanosaphes*	**1.00**	0.00	**1.00**	0.00	**0.80**	0.20
18	*Quadriops*	**1.00**	0.00	0.02	**0.98**	**1.00**	0.00
19	*Crucisternum-Tobochares*	**1.00**	0.00	**1.00**	0.00	**1.00**	0.03
20	*Tobochares*	0.13	**0.87**	**1.00**	0.00	**1.00**	0.00

Antennomere number: The best fit model for the number of antennomeres was ARD (Table 4.8). The summary of the ancestral histories generated under ARD indicates that the most recent common ancestor (MRCA) of the Acidocerinae had nine antennomeres. There are eleven transitions from nine to eight antennomeres in the tree: in *Primocerus*, *Helobata*, five clades of *Agraphydrus*, *Chasmogenus*, *Globulosis*, *Nanosaphes*, and *Tobochares* (Fig. 4.8B). No reversals were recovered.

Apex of fifth abdominal ventrite: The best fit model for the presence of a medial emargination in the apical margin of the fifth ventrite was ER (Table 4.8). Under this model the MRCA of the Acidocerinae most likely had an emarginated abdominal apex. Shifts towards more likely to have entire apical margins occur in the ancestors of *Primocerus*, *Batochares*, *Radicitus*, two clades plus three terminals of *Agraphydrus*, and the ancestor of the *Tobochares*-group (Fig. 4.8C). There is one shift from more likely to be absent to more likely to be present in the ancestor of *Nanosaphes*. The emargination is also retained in one species of *Katasophistes* and one species of *Globulosis*.

Elytral striae: The best fit model for the presence of elytral striae was ER (Table 4.8). According to the ancestral state reconstruction the most recent common ancestor of the Acidocerinae lacked elytral striae. Shifts towards more likely to have elytral striae occurred in *Helochares*, *Helobata*, a clade of *Radicitus*, a clade of *Novochares*, *Quadriops*, and a clade of *Tobochares* (Fig. 4.8D).

Maxillary palpomere 3: For this character the best fit model was OU (Table 4.8). The parameter estimates for the model were: optimal value $\theta = 4.45$; pull towards optimum $\alpha = 0.003$; rate $\sigma^2 = 0.031$. Under the OU model the most recent common ancestor of the Acidocerinae was recovered as most likely to have moderate palpi (length/width ratio = 4.66; 95% CI = (3.28–6.04)). Transitions to more elongate palpi occurred in *Peltochares*, *Helobata*, most *Novochares*, and some *Chasmogenus*, whereas transitions from moderate to short and stout occurred in some *Primocerus*, *Radicitus*, *Agraphydrus*, some *Chasmogenus*, and most of the *Tobochares*-group. Length-width values and confidence intervals are recorded in Table 4.9, and their variation is depicted in Fig. 4.11.

Metafemoral pubescence: For this character the best fit model was EB (Table 4.8). The parameter estimates for the model were: Brownian rate (σ^2) = 49.05, ancestral state value for the clade (z_0) = 54.23, and rate change through time or rate decay (r) = -0.015. Under the EB model the MRCA of the Acidocerinae was recovered as most likely to have moderately covered metafemora (63.60; 95% CI = (46.98–80.23)). There are trends to higher values in some *Primocerus*, *Helochares*-group, part of *Agraphydrus*, *Chasmogenus*-group, *Katasophistes*, *Globulosis*, *Nanosaphes*, and *Crucisternum*, and trends to lower values in *Radicitus*, some *Agraphydrus*, *Ephydrolithus*, *Quadriops*, and *Tobochares* (Table 4.9 and Fig. 4.11).

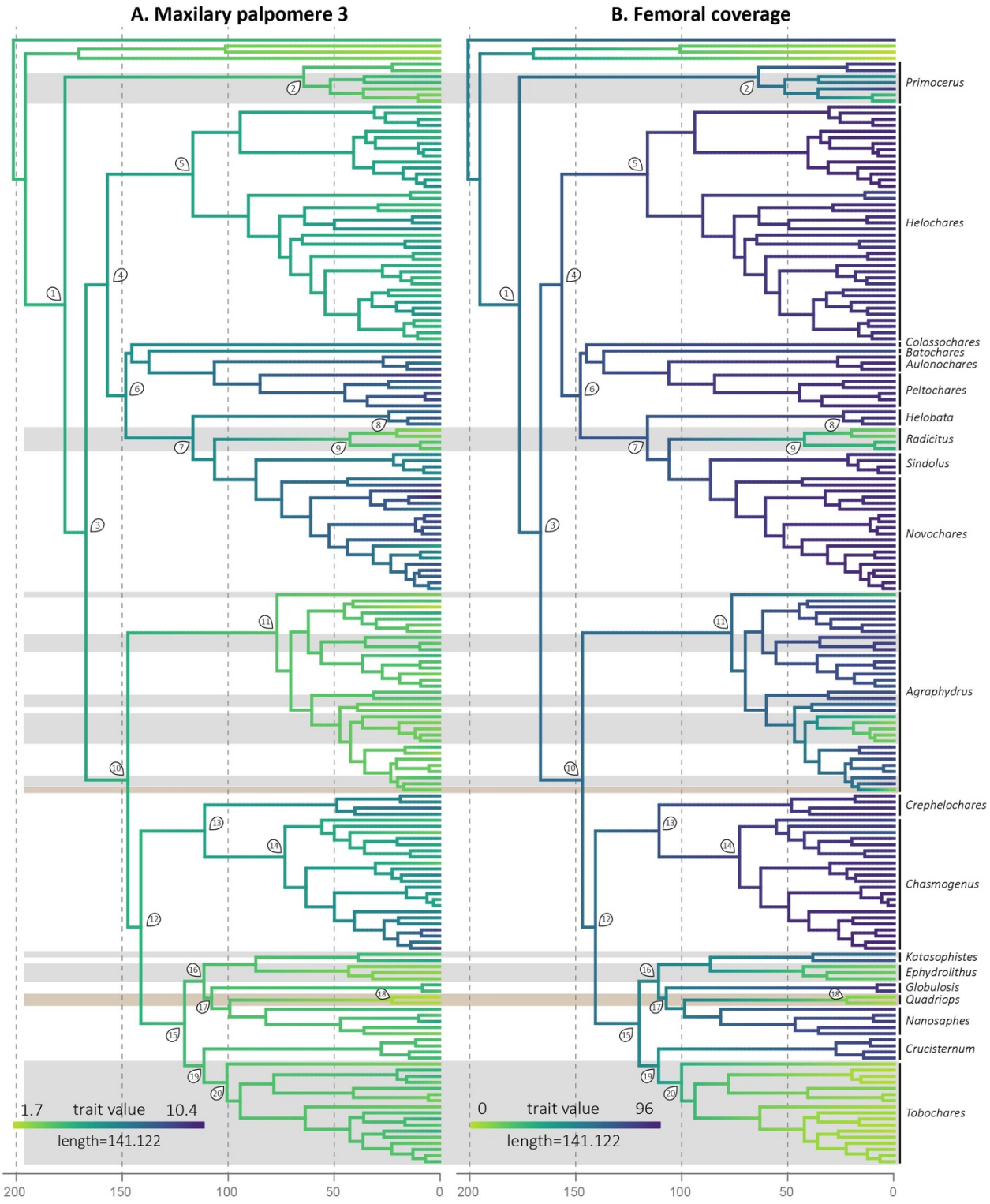


Figure 4.11. Continuous character mapping: **A** maxillary palpomere 3, **B** metafemoral pubescence. Node numbers correspond to major clades for which values are presented in Table 4.9. Gray shading highlights clades where habitat remained hygropetric; brown shading indicates terrestrial terminals; not shaded clades come from aquatic habitats.

Table 4.9. Ancestral character estimates (ACE) at each major node of the acidocerine phylogeny for continuous traits with 95% confidence interval. Values are rounded to the nearest hundredth.

Node number	Clade	Maxillary palpomere 3		Metafemoral pubescence	
		ACE	95% CI	ACE	95% CI
1	Acidocerinae	4.66	3.28–6.04	63.60	46.98–80.23
2	*Primocerus*	3.82	2.51–5.14	65.68	49.82–81.53
3	*Helochares-Tobochares*	4.92	3.71–6.14	67.62	53.01–82.23
4	*Helochares* group	5.39	4.20–6.59	73.15	58.79–87.50
5	*Helochares*	5.06	3.70–6.43	83.99	67.56–100.43
6	*Colossocares-Novochares*	5.87	4.67–7.07	75.57	61.09–90.05
7	*Helobata-Novochares*	6.29	4.93–7.66	74.71	58.28–91.14
8	*Helobata*	7.94	6.96–8.91	87.74	76.02–99.46
9	*Radicitus*	3.72	2.49–4.96	32.12	17.26–46.98
10	*Agraphydrus-Tobochares*	4.54	3.32–5.76	64.86	50.15–79.57
11	*Agraphydrus*	3.56	2.41–4.70	65.59	51.80–79.38
12	*Crephelochares-Tobochares*	4.50	3.30–5.70	63.94	49.49–78.39
13	*Chasmogenus* group	5.17	3.75–6.58	76.90	59.86–93.94
14	*Chasmogenus*	5.25	4.12–6.38	86.02	72.42–99.63
15	*Tobochares* group	3.94	2.83–5.04	51.96	38.66–65.27
16	*Katasophistes-Nanosaphes*	3.79	2.67–4.90	53.66	40.18–67.14
17	*Globulosis-Nanosaphes*	3.75	2.60–4.90	55.10	41.22–68.99
18	*Quadriops*	2.11	1.08–3.13	11.82	-0.55–24.20
19	*Crucisternum-Tobochares*	3.83	2.67–5.00	44.95	30.88–59.02
20	*Tobochares*	3.71	2.52–4.91	32.12	17.76–46.48

Phylogenetic signal

Values for the D statistic (Fritz and Purvis 2010) for discrete traits are provided in Table 4.10. The D value is 0 when a trait is phylogenetically conserved as expected under a Brownian motion model of evolution; it can be smaller than 0 for highly conserved traits. D is 1 when the trait is randomly distributed throughout the phylogeny; greater than 1 when a trait is overdispersed. According to the values obtained for the D statistic, all the evaluated traits are phylogenetically conserved ($D < 0$).

Table 4.10. Values of the D statistic for binary characters. Prob. indicates the probability that the calculated D value results from Brownian phylogenetic structure. Values are rounded to the nearest hundredth.

Character	Calculated D value	Prob.
Antennomere number	-0.57	1
Presence of elytral striae	-0.30	0.92
Emargination of fifth abdominal ventrite	-0.48	0.99

Values of Blomberg's K, and Pagel's lambda, both measurements of phylogenetic signal for continuous traits are presented in Table 4.11. Pagel's lambda is 0 when characters evolve independent of the phylogeny; a value of 1 indicates evolution under Brownian motion. When Blomberg's K is lower than 1 it means that related species resemble each other less than what it would be expected from evolution under Brownian motion; values greater than 1 indicate that related species are more similar to each other than the expectation under Brownian motion. The values obtained for both metrics indicate that both maxillary palpomere 3 and metafemoral pubescence show significant phylogenetic signal; both characters have evolved under a pattern of Brownian motion, meaning that closely related species tend to be more similar to each other in their trait values.

Table 4.11. Values of indices of phylogenetic signal for continuous morphological traits. Values of K and lambda are rounded to the nearest hundredth.

Character	K	P value	Lambda	P value
Maxillary palpomere 3	0.94	0.001	0.92	0.001
Metafemoral pubescence	1.91	0.001	1.01	0.001

Tests for correlation between habitat and morphological traits

In order to test for correlation between habitat and discrete binary morphological features, habitat was binarized into three new characters as shown in Figure 4.5. We tested

these binarized ecological characters for phylogenetic signal. Resulting values are presented in Table 4.12. According to the values obtained for the D statistic for binarized ecological characters, there is strong phylogenetic signal in all cases.

Table 4.12. Values of the D statistic for binarized ecological characters. Prob. indicates the probability that the calculated D value results from Brownian phylogenetic structure. Values are rounded to the nearest hundredth.

Character	Calculated D value	Prob.
Eco1	-0.41	0.97
Eco2	-0.77	0.90
Eco3	-0.41	0.97

Pagel's test for independent evolution of two binary characters (Pagel 1994) was implemented. The test involves the comparison of two models: the independent model (in which the rates of change in each trait do not depend on the state of the other trait), and the dependent model (in which the rates of change in one trait depend on the state of the other trait) (Fig. 4.6). The number of antennomeres and the presence of elytral striae are correlated with habitat when coded either as Eco1 (extremes vs. intermediate) or Eco3 (ancestral vs. derived) (Fig. 4.5). The presence of an apical emargination on the fifth abdominal ventrite is only correlated with Eco3. Eco2 shows no correlation with any of the tested morphological traits.

Table 4.13. Values of log likelihood and AICw for each model. Likelihood ratio and p-value for the correlation test between habitat and morphological traits. Significant values are highlighted in bold. Values are rounded to the nearest hundredth, except for the p-value rounded to the nearest thousandth.

Trait	Habitat	Model	Log-likelihood	AICw	Likelihood ratio	p-value
Antennomeres	Eco1	Independent	-96.06	0.07	13.11	**0.011**
		Dependent	-89.50	0.93		
	Eco2	Independent	-60.85	0.95	2.25	0.691
		Dependent	-59.73	0.05		
	Eco3	Independent	-96.85	0.28	9.89	**0.042**
		Dependent	-91.91	0.72		

Abdominal apex	Eco1	Independent	-108.30	0.62	3.00	0.223
		Dependent	-106.80	0.38		
	Eco2	Independent	-67.85	0.58	3.32	0.190
		Dependent	-66.19	0.42		
	Eco3	Independent	-109.94	0.28	5.89	**0.052**
		Dependent	-106.99	0.72		
Elytral striae	Eco1	Independent	-115.03	0.02	11.87	**0.002**
		Dependent	-109.09	0.98		
	Eco2	Independent	-74.58	0.65	2.72	0.257
		Dependent	-73.22	0.35		
	Eco3	Independent	-116.66	0.01	13.30	**0.001**
		Dependent	-110.01	0.99		

To test continuous traits for correlation with habitat, phylogenetic analyses of variance were performed. The results are presented in Table 4.14. According to the results of the analyses of variance, habitat has a significant effect in both the proportions of the maxillary palpomere 3 and the extent of the femoral coverage, when the phylogeny is taken into account.

Table 4.14. Results of phylogenetic ANOVA between continuous characters and multistate habitat. Pp-value is the p-value taking the phylogeny into account. Values are rounded to the nearest hundredth.

Morphological trait	Mean (SE)	p-value	Pp-value
Maxillary palpomere 3	0.99 (0.02)	7.63e-20	9.99e-05 ***
Femoral coverage	14.79 (0.08)	1.08e-43	9.99e-05 ***

DISCUSSION

Hygropetric habitats facilitate aquatic-terrestrial transitions

Our analyses confirm that multiple habitat shifts have occurred throughout the evolutionary history of the Acidocerinae, and that most of those shifts originated from

hygropetric habitats. The best fit model (ORD-ARD) allows transitions hygropetric-aquatic, hygropetric-terrestrial, transitions forward (aquatic -> hygropetric -> terrestrial) and transitions backward (terrestrial -> hygropetric -> aquatic), all at different rates (Fig. 3); the model does not permit direct transitions between aquatic and terrestrial habitats. Even though the resulting transition rates are relatively low (4.4e-04 to 0.0068; Fig. 7), there is a trend for transitions to be higher from hygropetric to aquatic and from hygropetric to terrestrial, which is congruent with the most recent ancestor for Acidocerinae being resolved as a hygropetric inhabitant. In this sense, hygropetric habitats seem to allow for certain ecological plasticity that can go either towards aquatic or towards terrestrial habitats, but more frequently results in transitions towards aquatic environments.

Given that the best fit model does not allow for direct aquatic-terrestrial transitions, the resulting rates are evidence for hygropetric habitats as necessary intermediate steps between aquatic and terrestrial habitats, which is congruent with previous observations in other hydrophilid subfamilies (Short and Liebherr 2007). The relatively high AICw value obtained for the second-best fit model ORD-ASYM suggests that the asymmetrical model where transitions forward (aquatic->hygropetric->terrestrial; transition rate = 0.00061) and backward (terrestrial->hygropetric->aquatic; transition rate = 0.0065) are different, is nearly as good fit to the data as the best-fit model ORD-ARD, but given that transitions to terrestrial habitats occur less frequently, the ORD-ASYM model is a poorer fit to the data.

Habitat transitions have occurred in all five genus-groups as defined by Short et al. (in prep.; see Fig. 4.8) but have been particularly recurrent in the *Agraphydrus*- and *Tobochares*-groups, which are also the only lineages with known terrestrial representatives. The recent explosion in the number of new species described over the last five years in both these groups (e.g., Komarek and Hebauer 2018, Komarek 2018, Komarek 2019, Kohlenberg and Short 2017, Girón and Short 2018, Girón and Short in prep.) highlights the importance of exploring the usually overlooked hygropetric habitats, for the knowledge of water scavenger beetles. It also highlights how these assemblages of tiny beetles can be so immensely diverse, not only in numbers of species, but in ecology and morphology.

Habitat transitions do not affect diversification rate

Our results indicate that the diversification of the subfamily Acidocerinae exhibits a pattern concordant with the pure-birth model in which speciation (birth; b = 0.022) is constant through time and extinction (death) does not occur (d = 0) (Pybus and Harvey 2000). The resulting gamma statistic (-1.24) indicates that the internal nodes of the phylogeny are closer to the root than the expectation under a pure birth process (Pybus and Harvey 2000), which occurs when the extinction rate (d) is 0 and the speciation rate (b) is constant (pure-birth model). The p-value obtained for the Constant Rate test (p = 0.21), show that the hypothesis of constant rates cannot be rejected for our dataset. Given the high rate of type II errors reported for the Constant

Rates test by Pybus and Harvey (2000), this p-value cannot be considered as evidence in favor of the constant rates model.

When the outgroups were left unpruned from the tree, we obtained one increase in diversification rate for the acidocerine clade with respect to the outgroup taxa. This is an artifact of the severely limited outgroup sampling relative to the diversity of the outgroup lineages and the assumption of total coverage of the phylogeny. When the outgroups were excluded from the analysis, no shifts in diversification rate were detected within the Acidocerinae. This is consistent with our LTT plot, as there are no evident decreases or increases throughout the graph, as well as with the constant speciation rate obtained for our data. For the reduced dataset, which included one terminal per each major clade, when the analysis was implemented for the described numbers of species, we recovered one rate decrease in the clade composed of *Colossochares*, *Batochares*, *Aulonochares*, and *Peltochares* (Fig. 4.10B), and one rate increase in *Helochares* Clade A3 (Fig. 4.10B; Short et al. in prep.). The *Colossochares*–*Peltochares* clade has a comparatively low number of species, whereas *Helochares* Clade A3 is the most speciose clade of *Helochares*, which is reflected in these rate shifts. When the estimated numbers of species were considered for the reduced phylogeny, we found the same rate decrease in the *Colossochares*–*Peltochares* clade, but no other rate shifts in the phylogeny. Most importantly, none of the shifts in diversification rates recovered by our analyses corresponded to habitat-shifting events, indicating that the observed habitat shifts have not impacted the diversification of the Acidocerinae.

Although it has been argued that the Medusa algorithm is flawed and that it has a high false-discovery rate (May and Moore 2016), we did not obtain unexpected results for our datasets, as each rate increase or decrease can be putatively explained by either our sampling or by the numbers of species of the clades involved. More detailed analyses, using additional methods to estimate associations between traits and diversification rates (e.g., FitzJohn 2012) may allow further exploration of the relationship between habitat transitions and diversification rates in this group.

Habitat-Morphology Correlations

Given that all the traits considered here, including habitat, showed high phylogenetic signal it is not surprising that morphological characters are correlated with habitat. Even though a cause and effect relationship cannot be concluded from these correlations alone, when trends in both morphology and habitat are considered together, it is evident that particular habitats are often associated with particular phenotypes.

For each binary morphological trait we examined, we found a trend towards reduction (number of antennomeres), loss (apical emargination of the abdomen), or gain (presence of elytral striae), with no reversals, which is evident in the ancestral state reconstructions (Fig. 4.7B–D). In all cases, we found a trend for the morphology to shift more frequently in clades with ancestors that remained in hygropetric habitats (e.g., *Agraphydrus*- and *Tobochares*-group; Fig.

4.7C), which probably had more time to acquire new adaptations. For these morphological systems, our initial hypotheses are supported (Table 4.1), as it is now clear that the number of antennomeres, the presence of an emargination in the apex of the abdomen, and the presence of elytral striae are, for the most part, limited to particular clades in the phylogeny. Therefore, these character systems are supported as being useful for diagnosing monophyletic groups. Nevertheless, this utility should be considered carefully, as there remains homoplasy whereby unrelated species (and genera) exhibit the same character states (e.g., elytral striae are present in *Radicitus* and *Tobochares*), or contrasting character states are present within the same genus (e.g., abdominal emargination present in some but not all *Nanosaphes* and *Globulosis*).

The same plasticity that we found for habitat was evidenced in both continuous characters (e.g., maxillary palpomere 3, metafemoral pubescence). Furthermore, there is a clear trend for trait values to increase (e.g., more pubescence and longer palps) in aquatic taxa and decrease in hygropetric and terrestrial terminals (Fig. 11), suggesting a strong and directional influence of habitat in both traits. We hypothesize that the reduction in the length of the maxillary palpi may be a product of the interaction of the beetle with the substrate when finding food; it is likely that in aquatic environments, as resources and beetles are floating, having longer palpi may be useful for reaching longer distances, whereas shorter and stouter palpi may be advantageous when the beetles are directly in contact with the substrate for most of the time. The extent of the metafemoral hydrofuge coverage is likely related to the size of the bubble needed by the beetles in different environments. A beetle in aquatic circumstances may need a larger air storage, achieved by pubescence covering most of the metafemur, to be able to

submerge, spend some time under water, and go back to the surface to refill the bubble; in contrast, in hygropetric situations it is likely the beetles spend less time being submerged, or are only partly submerged, and in terrestrial systems, there is no longer any need to carry an air store.

The correlations that we recovered in the Acidocerinae seem to be biologically meaningful, as not only did we recover high correlation values, but there is also replicated co-distribution between habitat and the morphological traits we analyzed throughout the phylogeny. Therefore, according to the scenario proposed by Maddison and FitzJohn (2015) it is reasonable to conclude that habitat is adaptively or functionally linked to morphology in acidocerines.

Yoder et al. (2010) summarize a series of steps linking ecological opportunity to adaptive radiation through a series of ecological, demographic and evolutionary processes, that represent evidence towards an adaptive relationship. The Acidocerinae follow a path in which new habitats (aquatic and terrestrial) became available to the hygropetric ancestor, which may have released morphological constraints to the length of the palpomeres and selected towards increasing the area covered by hydrofuge pubescence in order to be able to hold larger bubbles of air, leading to increases in trait variation and further morphological diversification. This process has taken nearly 170 million years for the subfamily, and has occurred throughout the world, which doesn't fit the "rapid diversification" condition to advocate for the Acidocerinae as an adaptive radiation.

CONCLUSIONS

Habitat shifts have occurred multiple times across the evolutionary history of the Acidocerinae, with hygropetric habitats recovered as the ancestral state for the subfamily, and as a necessary step in the transition from aquatic to terrestrial habitats. Habitat shifts do not have an effect in the diversification rates of the Acidocerinae. Establishment in new habitats was coupled with morphological variation, with trends to increases in length of the maxillary palpi and the extent of the metafemoral pubescence in aquatic taxa.

ACKNOWLEDGEMENTS

We are grateful to Mark Holder for advice at several points during the development of this project. Tutorials created by Liam Revell were fundamental for the implementation of most analyses carried out here.

REFERENCES CITED

Bilton DT, Ribera I, Short AEZ (2019) Water beetles as models in ecology and evolution. Annual Review of Entomology 64: 359–377. https://doi.org/10.1146/annurev-ento-011118-111829

Blomberg SP, Garland T, Ives AR (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57: 717–745. https://doi.org/10.1111/j.0014-3820.2003.tb00285.x

Bloom DD, Fikáček M, Short AEZ (2014) Clade age and diversification rate variation explain disparity in species richness among water scavenger beetle (Hydrophilidae) lineages. PLOS ONE 9: e98430. https://doi.org/10.1371/journal.pone.0098430

Dobbs EM (2011) www.SketchAndCalc.com. SketchAndCalc. Available from: https://www.sketchandcalc.com (October17, 2019).

Fikáček M (2019) Hydrophilidae Leach, 1815. In: Lawrence, J.,y Slipinski, A. (Eds.). Australian Beetles Volume 2: Archostemata, Myxophaga, Polyphaga: Staphyliniformia - Scarabaeiformia. CSIRO Publishing.

Fikáček M, Minoshima Y, Vondráček D, Gunter N, Leschen RA (2013) Morphology of adults and larvae and integrative taxonomy of southern hemisphere genera *Tormus* and *Afrotormus* (Coleoptera: Hydrophilidae). Acta Entomologica Musei Natioalis Pragae 53: 75–126.

FitzJohn RG (2012) Diversitree: comparative phylogenetic analyses of diversification in R. Methods in Ecology and Evolution 3: 1084–1092. https://doi.org/10.1111/j.2041-210X.2012.00234.x

Fritz SA, Purvis A (2010) Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. Conservation Biology 24: 1042–1051. https://doi.org/10.1111/j.1523-1739.2010.01455.x

Garland T, Dickerman AW, Janis CM, Jones JA (1993) Phylogenetic Analysis of Covariance by Computer Simulation. Systematic Biology 42: 265–292. https://doi.org/10.1093/sysbio/42.3.265

Garnier S (2018) viridis: Default Color Maps from “matplotlib”. R package version 0.5.1. Available from: https://cran.r-project.org/web/packages/viridis/viridis.pdf.

Girón JC, Short AEZ (2018) Three new genera of acidocerine water scavenger beetles from tropical South America (Coleoptera, Hydrophilidae, Acidocerinae). ZooKeys 768: 113–158. https://doi.org/10.3897/zookeys.768.24423

Girón JC, Short AEZ (2019) Three additional new genera of acidocerine water scavenger beetles from the Guiana and Brazilian Shield regions of South America (Coleoptera, Hydrophilidae, Acidocerinae). ZooKeys 855: 109–154. https://doi.org/10.3897/zookeys.855.33013

Gould SJ (1970) Dollo on Dollo’s law: Irreversibility and the status of evolutionary laws. Journal of the History of Biology 3: 189–212. https://doi.org/10.1007/BF00137351

Hansen M (1991) The hydrophiloid beetles. Phylogeny, classification and a revision of the genera (Coleoptera: Hydrophilidae). Biologiske Skrifter 40: 1–367.

Hansen TF (1997) Stabilizing selection and the comparative analysis of adaptation. Evolution 51: 1341–1351. https://doi.org/10.1111/j.1558-5646.1997.tb01457.x

Harmon LJ (2018) Phylogenetic comparative methods: learning from trees. 1.0 edition. CreateSpace Independent Publishing Platform, 286 pp. Available from: https://lukejharmon.github.io/pcm/.

Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W (2008) GEIGER: investigating evolutionary radiations. Bioinformatics 24: 129–131. https://doi.org/10.1093/bioinformatics/btm538

Harmon LJ, Losos JB, Davies TJ, Gillespie RG, Gittleman JL, Jennings WB, Kozak KH, McPeek MA, Moreno-Roark F, Near TJ, Purvis A, Ricklefs RE, Schluter D, Ii JAS, Seehausen O, Sidlauskas BL, Torres-Carvajal O, Weir JT, Mooers AØ (2010) Early bursts of body size and shape evolution are rare in comparative data. Evolution 64: 2385–2396. https://doi.org/10.1111/j.1558-5646.2010.01025.x

Hebauer F (1992) The species of the genus *Chasmogenus* Sharp, 1882 (Coleoptera: Hydrophilidae). Acta Coleopterologica 8: 61–92.

Hebauer F (1996) Synopsis der afrikanischen Arten der Gattung *Helochares* Mulsant (Coleoptera, Hydrophilidae). Acta Coleopterologica 12: 3–38.

Huelsenbeck JP, Nielsen R, Bollback JP (2003) Stochastic mapping of morphological characters. Systematic Biology 52: 131–158. https://doi.org/10.1080/10635150390192780

Kohlenberg AT, Short AEZ (2017) Revision of the Neotropical water scavenger beetle genus *Tobochares* Short & García, 2007 (Coleoptera, Hydrophilidae, Acidocerinae). ZooKeys 669: 113–146. https://doi.org/10.3897/zookeys.669.11773

Komarek A (2018) Taxonomic revision of *Agraphydrus* Régimbart, 1903 II. The Indian Subcontinent. Koleopterologische Rundschau 88: 103–204.

Komarek A (2019) Taxonomic revision of *Agraphydrus* Régimbart, 1903 III. Southeast Asia (except Philippines) and Australian Region (Coleoptera: Hydrophilidae: Acidocerinae). Koleopterologische Rundschau 89: 151–316.

Komarek A, Hebauer F (2018) Taxonomic revision of *Agraphydrus* Régimbart, 1903 I. China and Taiwan (Coleoptera: Hydrophilidae: Acidocerinae). Zootaxa 4452: 1–101. http://dx.doi.org/10.11646/zootaxa.4452.1.1

Maddison WP, FitzJohn RG (2015) The unsolved challenge to phylogenetic correlation tests for categorical characters. Systematic Biology 64: 127–136. https://doi.org/10.1093/sysbio/syu070

May MR, Moore BR (2016) How well can we detect lineage-specific diversification-rate shifts? a simulation study of sequential AIC methods. Systematic Biology 65: 1076–1084. https://doi.org/10.1093/sysbio/syw026

McKenna DD, Farrell BD, Caterino MS, Farnum CW, Hawks DC, Maddison DR, Seago AE, Short AEZ, Newton AF, Thayer MK (2015) Phylogeny and evolution of Staphyliniformia and Scarabaeiformia: forest litter as a stepping stone for diversification of nonphytophagous beetles. Systematic Entomology 40: 35–60. https://doi.org/10.1111/syen.12093

d'Orchymont A (1919) Contribution a l'étude des sous-familles des Sphaeridiinae et des Hydrophilinae (Col. Hydrophilidae). Annales de la Société Entomologique de France 88: 105–168.

d'Orchymont A (1933) La respiration des Palpicornes aquatiques. Bulletin et Annales de la Société entomologique de Belgique 73: 17–31.

Orme D (2018) The caper package: comparative analysis of phylogenetics and evolution in R. Available from: https://cran.r-project.org/web/packages/caper/vignettes/caper.pdf.

Pagel M (1994) Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. Proceedings of the Royal Society of London. Series B: Biological Sciences 255: 37–45. https://doi.org/10.1098/rspb.1994.0006

Pagel M (1999) Inferring the historical patterns of biological evolution. Nature 401: 877–884. https://doi.org/10.1038/44766

Paradis E (2004) APE: Analyses of Phylogenetics and Evolution in R language. Bioinformatics 20: 289–290. https://doi.org/10.1093/bioinformatics/btg412

Paradis E, Schliep K (2019) ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35: 526–528. https://doi.org/10.1093/bioinformatics/bty633

Pybus OG, Harvey PH (2000) Testing macroevolutionary models using incomplete molecular phylogenies. Proceedings of the Royal Society of London. Series B: Biological Sciences 267: 2267–2272. https://doi.org/10.1098/rspb.2000.1278

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: https://www.R-project.org/.

Revell LJ (2012) phytools: an R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3: 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

RStudio Team (2016) RStudio: Integrated Development for R. RStudio, Inc., Boston, MA. Available from: http://www.rstudio.com/.

Seidel M, Arriaga-Varela E, Fikáček M (2016) Establishment of Cylominae Zaitzev, 1908 as a valid name for the subfamily Rygmodinae Orchymont, 1916 with an updated list of genera (Coleoptera: Hydrophilidae). Acta Entomologica Musei Nationalis Pragae 56: 159–165.

Short AEZ (2018) Systematics of aquatic beetles (Coleoptera): current state and future directions. Systematic Entomology 43: 1–18. https://doi.org/10.1111/syen.12270

Short AEZ, Liebherr JK (2007) Systematics and biology of the endemic water scavenger beetles of Hawaii (Coleoptera: Hydrophilidae, Hydrophilini). Systematic Entomology 32: 601–624. https://doi.org/10.1111/j.1365-3113.2007.00403.x

Short AEZ, Fikáček M (2013) Molecular phylogeny, evolution and classification of the Hydrophilidae (Coleoptera). Systematic Entomology 38: 723–752. https://doi.org/10.1111/syen.12024

Yee DA, Kehl S (2015) Chapter 39 - Order Coleoptera. In: Thorp JH, Rogers DC Eds, Thorp and Covich's Freshwater Invertebrates (Fourth Edition). Academic Press, Boston, 1003–1042. https://doi.org/10.1016/B978-0-12-385026-3.00039-5

Yoder JB, Clancey E, Roches SD, Eastman JM, Gentry L, Godsoe W, Hagey TJ, Jochimsen D, Oswald BP, Robertson J, Sarver B a. J, Schenk JJ, Spear SF, Harmon LJ (2010) Ecological opportunity and the origin of adaptive radiations. Journal of Evolutionary Biology 23: 1581–1596. https://doi.org/10.1111/j.1420-9101.2010.02029.x

APPENDIX 1.

Data matrix with multistate habitat and five morphological characters for 181 acidocerine terminals and four outgroup taxa.

Data matrix with multistate habitat and five morphological characters for 181 acidocerine terminals and four outgroup taxa. SLE numbers correspond to DNA extraction code numbers. Data for maxillary palpomere 3 correspond to the length/ratio of measurements. Data for metafemoral coverage correspond to percentage of area of the anterior surface of the metafemur covered by hydrofuge pubescence.

Species	Habitat	Number of antennomeres	Elytral striae	Emargination of abdominal apex	Maxillary palpomere 3	Metafemoral coverage
Notionotus liparus MSC1820	aquatic	eight	absent	absent	4.07	84.08
Cylomissus glabratus SLE0098	terrestrial	nine	present	absent	2.64	6.01
Rygmodus sp. SLE0129	terrestrial	nine	present	absent	2.07	0.50
Sphaeridium bipustulatus	terrestrial	eight	absent	absent	2.75	0.50
Primocerus neutrum SLE1085	aquatic	eight	absent	present	3.94	90.34
Primocerus neutrum SLE529	aquatic	eight	absent	present	3.30	86.40
Primocerus semipubescens SLE1079	hygropetric	eight	present	absent	4.64	48.05
Primocerus gigas SLE1374	hygropetric	eight	absent	absent	4.15	60.54
Primocerus striatolatus SLE496	hygropetric	eight	present	absent	3.24	85.07
Primocerus pijiguaense SLE444	hygropetric	eight	absent	absent	2.89	24.33
Primocerus maipure SLE1034	hygropetric	eight	absent	absent	2.97	27.80
Helochares songi SLE1395	aquatic	nine	absent	present	4.75	92.88
Helochares fuliginosus-group SLE1323	aquatic	nine	present	present	4.23	91.37
Helochares fuliginosus-group SLE1378	aquatic	nine	absent	present	4.51	92.95
Helochares fuliginosus-group SLE1109	aquatic	nine	absent	present	5.97	94.89
Helochares nexus SLE1195	aquatic	nine	present	present	4.46	93.40
Helochares trujillo SLE034	aquatic	nine	present	present	4.41	93.11
Helochares maculicollis-group SLE1177	aquatic	nine	present	present	5.30	95.78
Helochares maculicollis-group SLE1158	aquatic	nine	present	present	5.55	93.99
Helochares maculicollis-group SLE1166	aquatic	nine	present	present	4.64	93.04

Helochares championi SLE1174	aquatic	nine	present	present	4.79	95.11
Helochares normatus-group SLE1183	aquatic	nine	present	present	5.69	95.16
Helochares normatus-group SLE1184	aquatic	nine	present	present	5.19	94.66
Helochares normatus-group SLE1178	aquatic	nine	present	present	5.11	95.40
Helochares normatus-group SLE1254	aquatic	nine	present	present	6.57	95.38
Helochares sp. 22 SLE1261	aquatic	nine	present	present	4.23	83.75
Helochares sp. 44 SLE1351	aquatic	nine	present	present	4.48	83.34
Helochares pallens-group SLE1165	aquatic	nine	absent	present	4.05	92.70
Helochares pallidus-group SLE446	aquatic	nine	absent	present	4.24	92.73
Helochares lividus SLE1167	aquatic	nine	absent	present	6.24	92.04
Helochares obscurus SLE1182	aquatic	nine	absent	present	5.81	92.92
Helochares sp. 43 SLE1347	aquatic	nine	present	present	6.64	87.51
Helochares sp. 15 SLE1250	aquatic	nine	present	present	4.13	89.35
Helochares tristis SLE1319	aquatic	nine	present	present	4.97	87.16
Helochares clypeatus SLE1353	aquatic	nine	present	present	5.83	87.82
Helochares sp. 14 SLE1097	aquatic	nine	present	present	4.74	92.07
Helochares sp. 42 SLE1346	aquatic	nine	present	present	4.26	91.28
Helochares nipponicus SLE1163	aquatic	nine	present	present	4.59	91.03
Helochares sp. 9 SLE1052	aquatic	nine	present	present	5.13	91.14
Helochares sp. 31 SLE1293	aquatic	nine	present	present	4.04	88.01
Helochares sp. 41 SLE1344	aquatic	nine	present	present	4.62	88.60
Helochares sp. 40 SLE1342	aquatic	nine	present	present	4.55	90.55
Helochares sp. 49 SLE1381	aquatic	nine	present	present	4.61	88.01
Helochares sp. 48 SLE1365	aquatic	nine	present	present	5.82	89.10
Helochares sp. 19 SLE1253	aquatic	nine	present	present	5.63	89.55
Helochares difficilis SLE1331	aquatic	nine	present	present	6.18	90.84
Helochares sp. 12 SLE1092	aquatic	nine	present	present	4.35	91.38
Helochares sp. 39 SLE1340	aquatic	nine	present	present	4.45	90.97
Helochares sp. 46 SLE1356	aquatic	nine	present	present	4.65	88.94
Helochares sp. 11 SLE1091	aquatic	nine	present	present	3.94	91.02
Colossochares ellipticus SLE1089	aquatic	nine	absent	present	6.73	88.41
Batochares byrrhus SLE1308	aquatic	nine	present	absent	6.18	79.50
Aulonochares tubulus SLE1213	aquatic	nine	absent	present	8.74	91.69
Aulonochares lingulatus SLE415	aquatic	nine	absent	present	6.89	93.30
Aulonochares novoairensis SLE1268	aquatic	nine	absent	present	8.95	91.84
Peltochares sp. SLE438	aquatic	nine	absent	present	9.93	92.09
Peltochares longipalpis-group SLE1096	aquatic	nine	absent	present	8.70	91.12
Peltochares longipalpis-group SLE1335	aquatic	nine	absent	present	7.24	91.45
Peltochares sp. SLE1315	aquatic	nine	absent	present	9.24	93.37

Peltochares sp. 37 SLE1337	aquatic	nine	absent	present	8.87	91.51
Peltochares sp. SLE1256	aquatic	nine	absent	present	8.18	92.78
Helobata sp. 1 SLE0031	aquatic	eight	present	present	8.10	87.78
Helobata sp. 3 SLE976	aquatic	eight	present	present	8.62	90.09
Helobata larvalis SLE1159	aquatic	eight	present	present	7.61	89.97
Radicitus ayacucho SLE1397	hygropetric	nine	present	absent	2.46	14.91
Radicitus surinamensis SLE419	hygropetric	nine	present	absent	2.93	15.64
Radicitus granitum SLE447	hygropetric	nine	absent	absent	3.59	25.17
Radicitus sp. SLE1076	hygropetric	nine	absent	absent	3.28	30.19
Sindolus sp. SLE1234	aquatic	nine	absent	present	6.39	90.01
Sindolus optatus SLE240	aquatic	nine	absent	present	6.74	90.96
Sindolus sp. SLE1168	aquatic	nine	absent	present	7.09	93.55
Sindolus sp. SLE1236	aquatic	nine	absent	present	5.94	92.06
Novochares "punctures"-group SLE1191	aquatic	nine	present	present	6.52	92.54
Novochares "punctures"-group SLE1199	aquatic	nine	present	present	9.32	93.17
Novochares sallaei SLE1212	aquatic	nine	absent	present	9.54	93.15
Novochares guadelupensis SLE1200	aquatic	nine	absent	present	10.39	91.65
Novochares cochlearis-group SLE1196	aquatic	nine	absent	present	7.82	92.05
Novochares sp. 8 SLE536	aquatic	nine	absent	present	7.05	92.40
Novochares tectiformis-group SLE1218	aquatic	nine	absent	present	8.82	94.44
Novochares tectiformis-group SLE1242	aquatic	nine	absent	present	9.39	94.25
Novochares tectiformis-group SLE448	aquatic	nine	absent	present	8.74	93.42
Novochares tectiformis-group SLE1220	aquatic	nine	absent	present	8.39	92.60
Novochares sp. 28 SLE1214	aquatic	nine	absent	present	9.42	91.88
Novochares sp. 7 SLE535	aquatic	nine	absent	present	5.08	93.16
Novochares sp. 27 SLE1205	aquatic	nine	absent	present	6.61	92.65
Novochares sp. 30 SLE1263	aquatic	nine	absent	present	6.50	92.39
Novochares cf. oculatus SLE1197	aquatic	nine	absent	present	8.76	94.60
Novochares abbreviatus-group SLE1241	aquatic	nine	absent	present	8.98	93.24
Novochares abbreviatus-group SLE1162	aquatic	nine	absent	present	8.07	93.96
Novochares abbreviatus-group SLE1180	aquatic	nine	absent	present	8.43	94.93
Novochares abbreviatus-group SLE1217	aquatic	nine	absent	present	6.42	94.45
Agraphydrus longipalpis SLE512	hygropetric	nine	absent	present	2.82	25.53
Agraphydrus sp. 13 SLE1095	aquatic	nine	absent	present	3.86	72.33
Agraphydrus hanseni MSC1821	aquatic	eight	present	absent	1.73	87.02
Agraphydrus sp. 25 SLE1307	aquatic	nine	absent	present	4.72	85.06
Agraphydrus sp. 18 SLE1257	aquatic	nine	absent	present	3.96	87.42
Agraphydrus sp. 3 SLE519	aquatic	nine	absent	present	3.20	83.58
Agraphydrus sp. 12 SLE435	aquatic	nine	absent	present	3.36	85.63

Agraphydrus fikaceki SLE1286	hygropetric	nine	absent	absent	3.60	84.95
Agraphydrus activus SLE489	hygropetric	nine	absent	present	3.34	82.64
Agraphydrus sp. 21 SLE1287	hygropetric	nine	absent	present	4.01	89.52
Agraphydrus sp. 19 SLE1258	aquatic	nine	absent	present	4.40	78.45
Agraphydrus sp. SLE487	aquatic	nine	absent	present	3.64	84.11
Agraphydrus sp. 22 SLE1297	aquatic	nine	absent	present	3.64	80.90
Agraphydrus sp. 11 SLE1108	aquatic	nine	absent	present	2.90	80.86
Agraphydrus ogatai SLE1164	aquatic	nine	absent	present	3.28	74.61
Agraphydrus narusei SLE252	aquatic	nine	absent	present	4.00	76.34
Agraphydrus sp. 5 SLE455	aquatic	eight	absent	absent	3.63	79.15
Agraphydrus rugosus SLE459	hygropetric	eight	absent	absent	3.74	84.59
Agraphydrus sp. 8 FUSE	hygropetric	nine	present	present	3.20	71.23
Agraphydrus sp. 10 SLE1093	aquatic	nine	absent	present	2.95	84.61
Agraphydrus sp. 24 SLE1305	hygropetric	eight	absent	absent	3.52	24.99
Agraphydrus sp. 14 SLE498	hygropetric	eight	absent	present	2.77	10.86
Agraphydrus sp. 26 SLE1314	hygropetric	eight	absent	absent	2.75	15.05
Agraphydrus calvus SLE509	hygropetric	eight	absent	absent	3.14	11.86
Agraphydrus sp. 23 SLE1303	hygropetric	eight	absent	absent	3.27	14.62
Agraphydrus sp. 15 SLE1106	aquatic	nine	absent	present	4.19	85.08
Agraphydrus sp. 17 SLE1100	aquatic	nine	absent	present	2.39	85.88
Agraphydrus sp. 27 SLE1393	aquatic	eight	absent	present	3.30	82.81
Agraphydrus sp. 16 SLE1102	hygropetric	eight	absent	present	2.97	74.57
Agraphydrus sp. 28 SLE1394	aquatic	nine	absent	present	3.43	72.23
Agraphydrus sp. 7 FUSE	hygropetric	nine	absent	present	3.75	76.65
Agraphydrus sp. 29 SLE1403	hygropetric	nine	absent	present	3.33	84.39
Agraphydrus sp. 30 SLE1410	terrestrial	nine	absent	present	2.94	12.41
Crephelochares sp. 5 SLE449	aquatic	nine	absent	present	6.75	91.00
Crephelochares sp. 17 SLE1090	aquatic	nine	absent	present	6.39	91.67
Crephelochares sp. 20 SLE1232	aquatic	nine	absent	present	7.67	91.97
Crephelochares sp. 21 SLE1170	aquatic	nine	absent	present	5.99	92.91
Chasmogenus sp. 14 SLE1083	aquatic	eight	absent	present	4.06	84.26
Chasmogenus ruidus SLE079	aquatic	eight	absent	present	5.06	86.54
Chasmogenus cremnobates SLE457	hygropetric	eight	absent	present	3.13	74.29
Chasmogenus sp. 2 SLE078	aquatic	eight	absent	present	5.90	90.52
Chasmogenus sp. 25 SLE1190	aquatic	eight	absent	present	4.87	92.77
Chasmogenus sp. 3 SLE533	aquatic	eight	absent	present	4.97	90.02
Chasmogenus barrae SLE1179	aquatic	eight	absent	present	4.87	89.50
Chasmogenus sp. 9 SLE1056	aquatic	eight	absent	present	3.51	91.41
Chasmogenus lilianae SLE1059	aquatic	eight	absent	present	5.61	93.75

Chasmogenus sp. 10 SLE1058	aquatic	eight	absent	present	6.35	90.61
Chasmogenus fluminensis SLE1055	aquatic	eight	absent	present	5.40	91.30
Chasmogenus sp. 6 SLE474	aquatic	eight	absent	present	5.97	91.26
Chasmogenus sp. 7D SLE1086	aquatic	eight	absent	present	5.91	95.23
Chasmogenus sp. 7B SLE516	aquatic	eight	absent	present	4.45	92.61
Chasmogenus sp. 7C SLE1081	aquatic	eight	absent	present	5.19	93.40
Chasmogenus sp. 4 SLE518	aquatic	eight	absent	present	6.66	94.05
Chasmogenus sp. 19 SLE1231	aquatic	eight	absent	present	6.13	94.15
Chasmogenus sp. 23 SLE1185	aquatic	eight	absent	present	6.62	95.80
Chasmogenus sp. 26A SLE1201	aquatic	eight	absent	present	9.06	94.17
Chasmogenus sp. 26B SLE1198	aquatic	eight	absent	present	7.99	96.03
Chasmogenus sp. 24 SLE1186	aquatic	eight	absent	present	6.45	94.90
Chasmogenus sp. 27 SLE1202	aquatic	eight	absent	present	9.35	94.40
Katasophistes merida SLE427	hygropetric	nine	absent	absent	3.56	65.86
Katasophistes superficialis SLE1189	aquatic	nine	absent	present	5.03	78.00
Ephydrolithus ogmos SLE1510	hygropetric	nine	present	absent	2.67	13.55
Ephydrolithus minor SLE1511	hygropetric	nine	absent	absent	2.42	14.44
Ephydrolithus sp. SLE1262	hygropetric	nine	absent	absent	2.81	16.44
Globulosis flavus SLE527	aquatic	eight	absent	present	4.61	90.21
Globulosis hemisphericus SLE416	aquatic	eight	absent	absent	3.64	89.44
Quadriops clusia SLE1054	terrestrial	nine	present	absent	1.82	6.67
Quadriops reticulatus SLE401	terrestrial	nine	present	absent	1.94	4.15
Nanosaphes sp. SLE1265	aquatic	eight	absent	present	4.25	89.98
Nanosaphes tricolor SLE130	aquatic	eight	absent	present	3.50	82.22
Nanosaphes tricolor SLE1067	aquatic	eight	absent	present	5.02	86.54
Nanosaphes hesperus SLE485	aquatic	eight	absent	present	3.93	87.30
Nanosaphes punctatus SLE507	aquatic	eight	absent	present	2.86	82.01
Crucisternum ouboteri SLE503	aquatic	nine	absent	absent	3.76	84.51
Crucisternum toboganensis SLE734	aquatic	nine	absent	absent	3.64	85.92
Crucisternum sinuatus SLE1507	aquatic	nine	absent	absent	3.96	85.34
Crucisternum vanessae SLE744	aquatic	nine	absent	absent	3.93	80.18
Tobochares sp. 10 SLE102	hygropetric	eight	absent	absent	2.83	3.30
Tobochares sp. 1B SLE1047	hygropetric	eight	absent	absent	4.41	2.23
Tobochares sp. 2B SLE524	hygropetric	eight	absent	absent	4.39	2.55
Tobochares sp. 2A SLE1043	hygropetric	eight	absent	absent	3.21	2.03
Tobochares sp. 8 SLE1032	hygropetric	eight	absent	absent	3.88	10.70
Tobochares sp. 15A SLE101	hygropetric	eight	absent	absent	3.34	6.02
Tobochares sp. 15B SLE1042	hygropetric	eight	absent	absent	2.85	6.64
Tobochares emarginatus SLE482	hygropetric	eight	absent	absent	3.07	2.81

Tobochares kasikasima SLE1046	hygropetric	eight	present	absent	3.70	5.34
Tobochares pallidus SLE525	hygropetric	eight	absent	absent	4.62	3.92
Tobochares sp. A SLE526	hygropetric	eight	present	absent	3.45	2.38
Tobochares sp. B SLE1264	hygropetric	eight	absent	absent	4.46	1.60
Tobochares sp. C SLE1505	hygropetric	eight	absent	absent	3.33	5.78
Tobochares sipaliwini SLE478	hygropetric	eight	present	absent	3.17	4.37
Tobochares sulcatus SLE035	hygropetric	eight	present	absent	3.83	5.18
Tobochares kusad SLE1021	hygropetric	eight	present	absent	3.22	6.78
Tobochares striatus SLE423	hygropetric	eight	present	absent	4.01	5.99

APPENDIX 2.

Data matrix with binarized habitat for 181 acidocerine terminals and four outgroup taxa.

Data matrix with binarized habitat for 181 acidocerine terminals and four outgroup taxa. SLE numbers correspond to DNA extraction code numbers.

Species	Eco1	Eco2	Eco3
Notionotus liparus MSC1820	extreme	water	ancestral
Cylomissus glabratus SLE0098	extreme	land	derivate
Rygmodus sp. SLE0129	extreme	land	derivate
Sphaeridium bipustulatus	extreme	land	derivate
Primocerus neutrum SLE1085	extreme	water	ancestral
Primocerus neutrum SLE529	extreme	water	ancestral
Primocerus semipubescens SLE1079	intermediate	water	derivate
Primocerus gigas SLE1374	intermediate	water	derivate
Primocerus striatolatus SLE496	intermediate	water	derivate
Primocerus pijiguaense SLE444	intermediate	water	derivate
Primocerus maipure SLE1034	intermediate	water	derivate
Helochares songi SLE1395	extreme	water	ancestral
Helochares fuliginosus-group SLE1323	extreme	water	ancestral
Helochares fuliginosus-group SLE1378	extreme	water	ancestral
Helochares fuliginosus-group SLE1109	extreme	water	ancestral
Helochares nexus SLE1195	extreme	water	ancestral
Helochares trujillo SLE034	extreme	water	ancestral
Helochares maculicollis-group SLE1177	extreme	water	ancestral
Helochares maculicollis-group SLE1158	extreme	water	ancestral
Helochares maculicollis-group SLE1166	extreme	water	ancestral
Helochares championi SLE1174	extreme	water	ancestral
Helochares normatus-group SLE1183	extreme	water	ancestral
Helochares normatus-group SLE1184	extreme	water	ancestral
Helochares normatus-group SLE1178	extreme	water	ancestral
Helochares normatus-group SLE1254	extreme	water	ancestral
Helochares sp. 22 SLE1261	extreme	water	ancestral
Helochares sp. 44 SLE1351	extreme	water	ancestral
Helochares pallens-group SLE1165	extreme	water	ancestral
Helochares pallidus-group SLE446	extreme	water	ancestral
Helochares lividus SLE1167	extreme	water	ancestral
Helochares obscurus SLE1182	extreme	water	ancestral

Helochares sp. 43 SLE1347	extreme	water	ancestral
Helochares sp. 15 SLE1250	extreme	water	ancestral
Helochares tristis SLE1319	extreme	water	ancestral
Helochares clypeatus SLE1353	extreme	water	ancestral
Helochares sp. 14 SLE1097	extreme	water	ancestral
Helochares sp. 42 SLE1346	extreme	water	ancestral
Helochares nipponicus SLE1163	extreme	water	ancestral
Helochares sp. 9 SLE1052	extreme	water	ancestral
Helochares sp. 31 SLE1293	extreme	water	ancestral
Helochares sp. 41 SLE1344	extreme	water	ancestral
Helochares sp. 40 SLE1342	extreme	water	ancestral
Helochares sp. 49 SLE1381	extreme	water	ancestral
Helochares sp. 48 SLE1365	extreme	water	ancestral
Helochares sp. 19 SLE1253	extreme	water	ancestral
Helochares difficilis SLE1331	extreme	water	ancestral
Helochares sp. 12 SLE1092	extreme	water	ancestral
Helochares sp. 39 SLE1340	extreme	water	ancestral
Helochares sp. 46 SLE1356	extreme	water	ancestral
Helochares sp. 11 SLE1091	extreme	water	ancestral
Colossochares ellipticus SLE1089	extreme	water	ancestral
Batochares byrrhus SLE1308	extreme	water	ancestral
Aulonochares tubulus SLE1213	extreme	water	ancestral
Aulonochares lingulatus SLE415	extreme	water	ancestral
Aulonochares novoairensis SLE1268	extreme	water	ancestral
Peltochares sp. SLE438	extreme	water	ancestral
Peltochares longipalpis-group SLE1096	extreme	water	ancestral
Peltochares longipalpis-group SLE1335	extreme	water	ancestral
Peltochares sp. SLE1315	extreme	water	ancestral
Peltochares sp. 37 SLE1337	extreme	water	ancestral
Peltochares sp. SLE1256	extreme	water	ancestral
Helobata sp. 1 SLE0031	extreme	water	ancestral
Helobata sp. 3 SLE976	extreme	water	ancestral
Helobata larvalis SLE1159	extreme	water	ancestral
Radicitus ayacucho SLE1397	intermediate	water	derivate
Radicitus surinamensis SLE419	intermediate	water	derivate
Radicitus granitum SLE447	intermediate	water	derivate
Radicitus sp. SLE1076	intermediate	water	derivate
Sindolus sp. SLE1234	extreme	water	ancestral
Sindolus optatus SLE240	extreme	water	ancestral

Sindolus sp. SLE1168	extreme	water	ancestral
Sindolus sp. SLE1236	extreme	water	ancestral
Novochares "punctures"-group SLE1191	extreme	water	ancestral
Novochares "punctures"-group SLE1199	extreme	water	ancestral
Novochares sallaei SLE1212	extreme	water	ancestral
Novochares guadelupensis SLE1200	extreme	water	ancestral
Novochares cochlearis-group SLE1196	extreme	water	ancestral
Novochares sp. 8 SLE536	extreme	water	ancestral
Novochares tectiformis-group SLE1218	extreme	water	ancestral
Novochares tectiformis-group SLE1242	extreme	water	ancestral
Novochares tectiformis-group SLE448	extreme	water	ancestral
Novochares tectiformis-group SLE1220	extreme	water	ancestral
Novochares sp. 28 SLE1214	extreme	water	ancestral
Novochares sp. 7 SLE535	extreme	water	ancestral
Novochares sp. 27 SLE1205	extreme	water	ancestral
Novochares sp. 30 SLE1263	extreme	water	ancestral
Novochares cf. oculatus SLE1197	extreme	water	ancestral
Novochares abbreviatus-group SLE1241	extreme	water	ancestral
Novochares abbreviatus-group SLE1162	extreme	water	ancestral
Novochares abbreviatus-group SLE1180	extreme	water	ancestral
Novochares abbreviatus-group SLE1217	extreme	water	ancestral
Agraphydrus longipalpis SLE512	intermediate	water	derivate
Agraphydrus sp. 13 SLE1095	extreme	water	ancestral
Agraphydrus hanseni MSC1821	extreme	water	ancestral
Agraphydrus sp. 25 SLE1307	extreme	water	ancestral
Agraphydrus sp. 18 SLE1257	extreme	water	ancestral
Agraphydrus sp. 3 SLE519	extreme	water	ancestral
Agraphydrus sp. 12 SLE435	extreme	water	ancestral
Agraphydrus fikaceki SLE1286	intermediate	water	derivate
Agraphydrus activus SLE489	intermediate	water	derivate
Agraphydrus sp. 21 SLE1287	intermediate	water	derivate
Agraphydrus sp. 19 SLE1258	extreme	water	ancestral
Agraphydrus sp. SLE487	extreme	water	ancestral
Agraphydrus sp. 22 SLE1297	extreme	water	ancestral
Agraphydrus sp. 11 SLE1108	extreme	water	ancestral
Agraphydrus ogatai SLE1164	extreme	water	ancestral
Agraphydrus narusei SLE252	extreme	water	ancestral
Agraphydrus sp. 5 SLE455	extreme	water	ancestral
Agraphydrus rugosus SLE459	intermediate	water	derivate

Agraphydrus sp. 8 FUSE	intermediate	water	derivate
Agraphydrus sp. 10 SLE1093	extreme	water	ancestral
Agraphydrus sp. 24 SLE1305	intermediate	water	derivate
Agraphydrus sp. 14 SLE498	intermediate	water	derivate
Agraphydrus sp. 26 SLE1314	intermediate	water	derivate
Agraphydrus calvus SLE509	intermediate	water	derivate
Agraphydrus sp. 23 SLE1303	intermediate	water	derivate
Agraphydrus sp. 15 SLE1106	extreme	water	ancestral
Agraphydrus sp. 17 SLE1100	extreme	water	ancestral
Agraphydrus sp. 27 SLE1393	extreme	water	ancestral
Agraphydrus sp. 16 SLE1102	intermediate	water	derivate
Agraphydrus sp. 28 SLE1394	extreme	water	ancestral
Agraphydrus sp. 7 FUSE	intermediate	water	derivate
Agraphydrus sp. 29 SLE1403	intermediate	water	derivate
Agraphydrus sp. 30 SLE1410	extreme	land	derivate
Crephelochares sp. 5 SLE449	extreme	water	ancestral
Crephelochares sp. 17 SLE1090	extreme	water	ancestral
Crephelochares sp. 20 SLE1232	extreme	water	ancestral
Crephelochares sp. 21 SLE1170	extreme	water	ancestral
Chasmogenus sp. 14 SLE1083	extreme	water	ancestral
Chasmogenus ruidus SLE079	extreme	water	ancestral
Chasmogenus cremnobates SLE457	intermediate	water	derivate
Chasmogenus sp. 2 SLE078	extreme	water	ancestral
Chasmogenus sp. 25 SLE1190	extreme	water	ancestral
Chasmogenus sp. 3 SLE533	extreme	water	ancestral
Chasmogenus barrae SLE1179	extreme	water	ancestral
Chasmogenus sp. 9 SLE1056	extreme	water	ancestral
Chasmogenus lilianae SLE1059	extreme	water	ancestral
Chasmogenus sp. 10 SLE1058	extreme	water	ancestral
Chasmogenus fluminensis SLE1055	extreme	water	ancestral
Chasmogenus sp. 6 SLE474	extreme	water	ancestral
Chasmogenus sp. 7D SLE1086	extreme	water	ancestral
Chasmogenus sp. 7B SLE516	extreme	water	ancestral
Chasmogenus sp. 7C SLE1081	extreme	water	ancestral
Chasmogenus sp. 4 SLE518	extreme	water	ancestral
Chasmogenus sp. 19 SLE1231	extreme	water	ancestral
Chasmogenus sp. 23 SLE1185	extreme	water	ancestral
Chasmogenus sp. 26A SLE1201	extreme	water	ancestral
Chasmogenus sp. 26B SLE1198	extreme	water	ancestral

Chasmogenus sp. 24 SLE1186	extreme	water	ancestral
Chasmogenus sp. 27 SLE1202	extreme	water	ancestral
Katasophistes merida SLE427	intermediate	water	derivate
Katasophistes superficialis SLE1189	extreme	water	ancestral
Ephydrolithus ogmos SLE1510	intermediate	water	derivate
Ephydrolithus minor SLE1511	intermediate	water	derivate
Ephydrolithus sp. SLE1262	intermediate	water	derivate
Globulosis flavus SLE527	extreme	water	ancestral
Globulosis hemisphericus SLE416	extreme	water	ancestral
Quadriops clusia SLE1054	extreme	land	derivate
Quadriops reticulatus SLE401	extreme	land	derivate
Nanosaphes sp. SLE1265	extreme	water	ancestral
Nanosaphes tricolor SLE130	extreme	water	ancestral
Nanosaphes tricolor SLE1067	extreme	water	ancestral
Nanosaphes hesperus SLE485	extreme	water	ancestral
Nanosaphes punctatus SLE507	extreme	water	ancestral
Crucisternum ouboteri SLE503	extreme	water	ancestral
Crucisternum toboganensis SLE734	extreme	water	ancestral
Crucisternum sinuatus SLE1507	extreme	water	ancestral
Crucisternum vanessae SLE744	extreme	water	ancestral
Tobochares sp. 10 SLE102	intermediate	water	derivate
Tobochares sp. 1B SLE1047	intermediate	water	derivate
Tobochares sp. 2B SLE524	intermediate	water	derivate
Tobochares sp. 2A SLE1043	intermediate	water	derivate
Tobochares sp. 8 SLE1032	intermediate	water	derivate
Tobochares sp. 15A SLE101	intermediate	water	derivate
Tobochares sp. 15B SLE1042	intermediate	water	derivate
Tobochares emarginatus SLE482	intermediate	water	derivate
Tobochares kasikasima SLE1046	intermediate	water	derivate
Tobochares pallidus SLE525	intermediate	water	derivate
Tobochares sp. A SLE526	intermediate	water	derivate
Tobochares sp. B SLE1264	intermediate	water	derivate
Tobochares sp. C SLE1505	intermediate	water	derivate
Tobochares sipaliwini SLE478	intermediate	water	derivate
Tobochares sulcatus SLE035	intermediate	water	derivate
Tobochares kusad SLE1021	intermediate	water	derivate
Tobochares striatus SLE423	intermediate	water	derivate