

Vinarski MV The birth of malacology. When and how?	1
Azman BAR, Wongkamhaeng K, Dumrongrojwattana P Description of <i>Floresorchestia samroiyodensis</i> , a new species of landhopper (Crustacea, Amphipoda, Talitridae) from Thailand	7
Rödel M-O, Emmrich M, Penner J, Schmitz A, Barej MF The taxonomic status of two West African <i>Leptopelis</i> species: <i>L. macrotis</i> Schiøtz, 1967 and <i>L. spiritusnoctis</i> Rödel, 2007 (Amphibia: Anura: Arthroleptidae)	21
Ozerov AL The Primary Types of Scathophagidae (Diptera) in the Museum für Naturkunde Berlin, and Senckenberg Deutsches Entomologisches Institut, Germany	33
Ziegler A, Mirantsev GV, Jangoux M, Kroh A Historical aspects of meetings, publication series, and digital resources dedicated to echinoderms	45
Krailas D, Namchote S, Koonchornboon T, Dechruksa W, Boonmekam D Trematodes obtained from the thiarid freshwater snail <i>Melanoides tuberculata</i> (Müller, 1774) as vector of human infections in Thailand	57
Voss M On the invalidity of <i>Halitherium schinzii</i> Kaup, 1838 (Mammalia, Sirenia), with comments on systematic consequences	87



Zoosystematics and Evolution

90 (1) 2014

Zoosystematics and Evolution

90 (1) 2014

<http://zse.pensoft.net>



ISSN 1435-1935 Zoosyst. Evol. 90 (1) 2014, 1–94

museum für naturkunde

Zoosystematics and Evolution

A Bulletin of Zoology since 1898

Instructions for authors

Scope

Zoosystematics and Evolution (formerly Mitteilungen aus dem Museum für Naturkunde in Berlin, Zoologische Reihe) edited by the *Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University Berlin* is an international, peer-reviewed, life science journal, devoted to whole-organism biology. It mainly publishes original research and review articles in the field of Metazoan taxonomy, biosystematics, evolution, morphology, development and biogeography at all taxonomic levels. Its scope encompasses primary information from collection-related research, viz. taxonomic descriptions and discoveries, revisions, annotated type catalogues, aspects of the history of science, and contributions on new methods and principles of systematics. Entomological papers will also be accepted for review, but authors should first consider submission to the Deutsche Entomologische Zeitschrift. Articles whose main topic is ecology, functional anatomy, physiology, or ethology are only acceptable when of clear systematic or evolutionary relevance and perspective. Review articles and contributions to a discussion forum are welcome, but authors are asked to contact the editors beforehand.

Authors and submission

- Conflicts of interest: Authors must disclose relevant competing interests, both financial and personal.
- Ownership: Authors must declare that the submitted work is their own and that copyright has not been breached in seeking its publication.
- Originality: Authors must declare that the submitted work has not previously been published, and is not being considered for publication elsewhere.

Language and style

- The language of publication is English. There is no general limitation of the length of manuscripts, but please contact the editor before submitting papers exceeding 30 printed pages (approximately 60 manuscript pages including figures).
- Manuscripts should be written in a clear, straightforward style and must not have been published or submitted elsewhere.
- The text should be 12 pt, double-spaced, one-sided, left justified and with a margin of at least 3 cm.
- Use a standard typeface, e.g. Times New Roman as little formatted as possible (without tabulators, several blank spaces, etc.). Avoid footnotes.
- Divide the text into sections using headlines and sub-headlines. Do not number the headlines. Inline headers should be set in italics and followed by a full stop.
- The names of genera and species must be in italics.
- Taxonomic descriptions must comply with the rules of the 4th edition of the ICZN (see <http://www.iczn.org/>).
- Enter the page number on every page.
- Submit figures with a minimum resolution of 300 dpi.
- The preferred file formats are PSD (Photoshop) and TIFF for colour and grayscale illustrations, and EPS for vector graphics.
- JPG files are only accepted in high resolution.

General manuscript structure

If appropriate, the manuscript should be structured using headlines and sub-headlines, but without numbering, according to the following sections:

- Title page
- Abstract
- Introduction
- Materials and Methods
- Results
- Discussion
- Acknowledgements
- References
- Tables with captions
- Figure captions

The publication process

Peer reviewing

Manuscripts are subject to peer review. All manuscripts submitted will be reviewed by at least two experts. Authors are welcome to make suggestions for competent reviewers.

Proofs

Prior to publication of your manuscript you will receive proofs in PDF format. Please correct and return the proofs within two weeks to the editorial office. We recommend using the standard proofreading marks or – in the case of a few corrections – using page and line numbers. Do not change the contents of your article. Corrections extending beyond production errors will be carried out at the expense of the author. The editorial office reserves the right to publish your article with only the editor’s corrections, if your corrections do not reach us in time.

Publishing

The print and the online versions of your paper are published simultaneously. It is accessible in open access at Pensoft: <http://zse.pensoft.net>

COPE Membership

This journal endorses the COPE (Committee on Publication Ethics) guidelines and will pursue cases of suspected research and publication misconduct (e.g. falsification, unethical experimentation, plagiarism, inappropriate image manipulation, redundant publication). For further information about COPE, please see the website for COPE at <http://www.publicationethics.org.uk>

Zoosystematics

and Evolution

90 (1) 2014

Zoosystematics and Evolution

A Bulletin of Zoology since 1898

Editor-in-Chief

Matthias Glaubrecht

Museum für Naturkunde, Berlin, Germany

phone: +49 (0)30/20 93 8400

fax: +49 (0)30/20 93 8565

e-mail: matthias.glaubrecht@mfn-berlin.de

Managing Editor

Lyubomir Penev

Pensoft Publishers, Sofia, Bulgaria

phone: +359-2-8704281

fax: +359-2-8704282

e-mail: penev@pensoft.net

Editorial Secretary

Yordanka Banalieva

Pensoft Publishers, Sofia, Bulgaria

phone: +359-2-8704281

fax: +359-2-8704282

e-mail: journals@pensoft.net

Editorial Board

Vertebrata – Collection & Museum Research –

Morphology & Development

Peter Bartsch – Museum für Naturkunde Berlin

Articulata – History of Science – Taxonomy & Systematics

Michael Ohl – Museum für Naturkunde Berlin

Mollusca – History of Science – Evolution & Biogeography

Matthias Glaubrecht – Museum für Naturkunde Berlin

Other Invertebrates

Carsten Lüter – Museum für Naturkunde Berlin

Zoosystematics and Evolution

2014. Volume 90. 2 Issues

ISSN: 1435-1935 (print), 1860-0743 (online)

Abbreviated keys title: Zoosyst. Evol.

In Focus

The cover picture shows *Leptopelis macrotis* Schiøtz, 1967 from Gola Rainforest National Park, Sierra Leone.

See paper of **Rödel et al.** The taxonomic status of two West African *Leptopelis* species: *L. macrotis* Schiøtz, 1967 and *L. spiritusnoctis* Rödel, 2007 (Amphibia: Anura: Arthroleptidae)

Cover design

Pensoft

Publisher



Zoosystematics and Evolution

A Bulletin of Zoology since 1898

Content of volume **90 (1)** 2014

Vinarski MV The birth of malacology. When and how?	1
Azman BAR, Wongkamhaeng K, Dumrongrojwattana P Description of <i>Floresorchestia samroiyeodensis</i> , a new species of landhopper (Crustacea, Amphipoda, Talitridae) from Thailand	7
Rödel M-O, Emmrich M, Penner J, Schmitz A, Barej MF The taxonomic status of two West African <i>Leptopelis</i> species: <i>L. macrotis</i> Schiøtz, 1967 and <i>L. spiritusnoctis</i> Rödel, 2007 (Amphibia: Anura: Arthroleptidae)	21
Ozerov AL The Primary Types of Scathophagidae (Diptera) in the Museum für Naturkunde Berlin, and Senckenberg Deutsches Entomologisches Institut, Germany	33
Ziegler A, Mirantsev GV, Jangoux M, Kroh A Historical aspects of meetings, publication series, and digital resources dedicated to echinoderms	45
Krailas D, Namchote S, Koonchornboon T, Dechruksa W, Boonmekam D Trematodes obtained from the thiarid freshwater snail <i>Melanoides tuberculata</i> (Müller, 1774) as vector of human infections in Thailand	57
Voss M On the invalidity of <i>Halitherium schinzii</i> Kaup, 1838 (Mammalia, Sirenia), with comments on systematic consequences	87

Abstract & Indexing Information

Biological Abstracts® (Thompson ISI)
BIOSIS Previews® (Thompson ISI)
Cambridge Scientific Abstracts (CSA/CIG)
Web of Science® (Thompson ISI)
Zoological Record™ (Thompson ISI)

The birth of malacology. When and how?

Maxim V. Vinarski¹

¹ Museum of Siberian Aquatic Molluscs, Omsk State Pedagogical University. 14, Tukhachevskogo embankment, Omsk, Russia, 644099

Corresponding author: Maxim V. Vinarski (radix.vinarski@gmail.com)

Abstract

Received 29 Aug 2013
Accepted 23 Nov 2013
Published 28 March 2014

Academic editor:
Matthias Glaubrecht

Key Words

Mollusks
Mollusca
Cuvier
Ducrotay de Blainville
anatomy
taxonomy
history of science
Rafinesque

In 1795, Georges Cuvier proposed a new classification of invertebrate animals based on anatomical data. He created a new concept of mollusks as representatives of a unique type of morphological organization of animals. Before Cuvier, the name “mollusks” was used only for cephalopods without external shells and slugs, whereas all shelled mollusks were placed in another taxon, Testacea. The Cuvier’s works (1795, 1798) are considered here as the starting point of transformation of classical conchology (= study of shells) into modern malacology (= study of molluscan animals as whole organisms). This process ended in 1825 when the very term “malacology” was finally established by Ducrotay de Blainville.

About two hundred years ago no students of mollusks might identify himself or herself as a “malacologist”. The very term “malacology” did not exist at the time, and the study of snails, clams and other testaceous animals, including barnacles and even foraminiferans, had been known under the name “conchology” or, more rarely, “testaceology” (Maton and Rackett 1804, Wood 1815, Burrow 1815). Most often “conchology” was defined as a branch of natural history devoted to the “study of shells, or Testaceous animals” (Da Costa 1776: 1). Some authors, although, restricted the scope of conchology exclusively to “the structure, properties, and methodical arrangement of shells, the external testaceous coverings of molluscan animals” (Pinnock 1824: 5). The term “malacology” has later origin, and it became common in the titles of handbooks and manuals in the 1840s (e.g., Porro 1838, Swainson 1840). In 1837, Fleming proposed even to get rid of the word “conchology” altogether as being unnecessary (Fleming 1837).

When, why, and how did the classical branch of natural science named “conchology” transform into a new

scientific discipline known as “malacology”? Glaubrecht (2009) recently ascribed the “explicit conceptual reform (i.e., distinction between conchology and malacology)” to none other than Edgar Allan Poe, a great American writer, who was an editor and compiler of a popular book on mollusks entitled “The Conchologist’s first book: A system of testaceous malacology” (Poe 1839). Though it was not more than a simple plagiarism of another book (Gould 1995), Poe seemingly wrote the preface and introduction where the “conceptual reform” was presented.

This observation, however, is not completely true at least due to the fact that the explicit distinction between conchology and malacology was proposed as early as in 1825 by a French zoologist Ducrotay de Blainville (1825), whose priority was acknowledged by Poe (1839). Moreover, the very term “malacology” was invented nine years earlier (in 1814) by an eccentric French-American naturalist Constantine Samuel Rafinesque-Schmaltz (see below). I believe, however, the conceptual shift from conchology to malacology should be examined in the sphere of

taxonomic ideas rather than in definitions and terminological subtleties. “Testaceous animals” as well as “Mollusca” are above all the taxonomic concepts, and historical shifts in their interpretation would help us to fix the point where malacology was born.

“Testaceous Animals” from Aristotle to Linnaeus

Aristotle was surely the first man of science to study mollusks seriously. In his famous “*Historia animalium*”, Aristotle gave a collection of his own thorough observations on external morphology, anatomy, reproduction, ecology and behavior of many soft-bodied animals that are classified today within the phylum Mollusca. Aristotle created the first universal classification of animals through his distinction between blooded (vertebrates) and bloodless (invertebrates) animals (Meyer 1855, Pellegrin 1986). The group of bloodless creatures included at least four *gene megista* (great families): insects, crustaceans, testaceans, and mollusks (“*Historia animalium*”, I, 6). The first two families correspond approximately to the contemporary taxa, whereas testaceans (Ostracodermata) and mollusks (Malakia) are merely two divisions of that large group known today as the phylum Mollusca. Aristotle’s Malakia included mostly cephalopods, while Ostracodermata embraced shelled gastropods and bivalves, as well as some other shelled organisms. Hence, the modern concept of mollusks did not exist in Aristotle’s time, and no serious emendations were made until the end of the 18th century. Leaving aside the numerous works of conchologists of the 17th–18th centuries (which did not substantively change this anatomical classification of invertebrates), the next reference point is Linnaeus’s work on classification of all known animals (Linnaeus 1758). One can find different taxa of mollusks (in modern sense) scattered among three orders of the classis Vermes created by Linnaeus (1758):

1. Order Intestina – genus *Teredo* along with such dissimilar creatures as *Lumbricus* (earthworm), *Hirudo* (leech), *Ascaris* (helminthes), and *Myxine* (hagfish).

2. Order Mollusca – essentially a direct descendant of Aristotle’s Malakia. The genuine molluscan genera (*Limax*, *Doris*, *Sepia* and others) were placed here, accompanied by such genera of soft-bodied aquatic animals from other invertebrate phyla, such as *Medusa*, *Asterias* (starfish), *Nereis*, and *Holothuria*.

3. Order Testacea – a species rich taxon including clams, snails, chitons as well as crustaceans (*Lepas*), annelids (*Serpula*) and scaphopods (*Dentalium*).

This is nothing but a reiteration of the classic system of Aristotle albeit more precisely developed. The presence or absence of the shell was the most important trait for classification, which is why Linnaeus distributed cephalopods between two orders. The shelled genera *Argonauta* and *Nautilus* were placed within Testacea, whereas the rest fell into the order Mollusca. Linnae-

us’ system of testaceous “vermes” was not strictly conchological, since he included some external characters of the mollusks’ soft bodies in the diagnoses of some higher taxa and even genera. For example, Linnaeus (1758) used shape and number of tentacles as diagnostic traits for several genera of nudibranchs. Several years later, O.F. Müller (1774) used tentacles and siphons (in bivalves) in his arrangement of freshwater mollusks. This author also transferred the Linnaean genus *Limax* (slugs) to the order Testacea on the basis of the apparent resemblance between shelled and non-shelled continental snails.

But the internal anatomy as a tool for classification of invertebrates was commonly ignored by taxonomists of Linnaeus’ time. Many naturalists of the 18th and even 19th centuries consciously rejected anatomical data in their taxonomic work (Stevens 1994). According to Foucault (2002), the ignorance of the anatomical traits of plants and animals was a distinguishing feature of the “Natural History” in the 17th and 18th centuries. Most taxonomists regarded internal anatomy as redundant and unnecessary for determination of the “Natural system”. A modern zoologist is hardly able to comprehend this ignorance as well as, for example, the rejection of the microscopic data by many prominent systematists of the 18th and 19th centuries (Gooday 1991, Stevens 1994).

Some conchologists declared that the system of mollusks based on anatomy is more scientific than the shell-based one (Da Costa 1776) but they considered the latter as the only useful system due to difficulties concerned with obtaining anatomical material of mollusks for study. For example, Maton and Rackett (1804: 177) believed that “innumerable testaceous animals must ever remain unknown to us, except by the *exuviae* accidentally thrown upon the shores after their death: many of them appear to inhabit inaccessible recesses of the ocean, and others part with life on the point of being removed from their native element”. The first attempts to collect animals from the oceanic floor were undertaken several decades later (Anderson and Rice 2006). Lamarck (1792: 471–472) also stressed that the anatomical material of most testaceous animals are not available for study, therefore their morphological classification (“*méthode distributive et distinctive... d’après la considération de animaux*”) had to be based on the shells. Furthermore, those rich and enjoyable collections of shells would become almost useless for natural history if the system of Testacea were to be based solely on internal morphology (Lamarck 1792). Da Costa (1776: 4) regarded the anatomical studies of mollusks as “too abstruse and unentertaining” to be worth pursuing.

The end of this anatomical ignorance is often thought to be inspired by Cuvier’s extensive studies on the comparative anatomy of animals. Foucault (2002) considers this as an obvious “epistemological” shift from the classical *Historia Naturalis* to the modern biology. “One day, towards the end of the eighteenth century, Cuvier was to topple the glass jars of the Museum,

smash them open and dissect all the forms of animal visibility that the Classical age had preserved in them” (Foucault 2002: 150).

The Cuvierian “Revolution” in the malacological systematics

Contrary to Foucault’s (2002) opinion, Cuvier started his anatomical research before he was given a position in the Muséum National d’Histoire Naturelle in Paris in 1795. Being a private tutor in Normandy (since 1788), he seized the opportunity to study the internal structure of different marine animals, including mollusks. His rather brief article devoted to description of molluscan anatomy appeared in 1795 (Fig. 1), and it may be regarded as the starting point of the true “revolution” in the malacological systematics. Cuvier described mollusks as representatives of a special type of organization of invertebrate animals (Cuvier called them “white-blooded animals”

and united both shelled and non-shelled groups in a single taxon (“class des mollusques”). The modern “conception of mollusks” as a distinct group of animals was thus created. Cuvier believed that the internal parts of mollusks are more important for classification than their shells, and his short diagnosis of Mollusca was as follows: “mollusks – a classis of animals that is characterized internally by oviparous reproduction, white blood, existence of heart, blood vessels and gills, liver; and externally – by mantle and tentacles” (Cuvier 1795: 447). His classis of mollusks was divided into three orders still without formal Latin names: “les céphalopodes”, “les gastéropodes”, and “les acéphales” that more or less correspond to the universally known taxa Cephalopoda, Gastropoda and Bivalvia. Dumeril (1806) was the first author to latinize these vernacular names of Cuvier.

A more detailed version of the system was presented in the next important work of Cuvier, «Tableau élémentaire de l’histoire naturelle des animaux» (Cuvier 1798), which listed all known genera of mollusks with their brief diagnoses and descriptions. Inevitably, the first Cuvierian version of the system of Mollusca was not free from errors. Though his new interpretation of mollusks was far closer to the modern one than the interpretations of Aristotle and Linnaeus, Cuvier still classified within «class des mollusques» such diverse and phylogenetically distant aquatic creatures as brachiopods, some crustaceans and tunicates (genera *Ascidia*, *Balanus*, *Lingula*, *Salpa*, *Terebratula*). In total, 59 genera of Mollusca were recognized, and the structure of shells was the main source of information for genera delineation. Most of the genera accepted by Cuvier (1798) had strictly conchological diagnoses.

The next important step of development of the system of mollusks was in 1812, when Cuvier explicitly expressed his great idea that all animals can be distributed among four large branches (embranchements) corresponding to four basic morphological groundplans (Cuvier 1812, Winsor 1976, Eigen 1997). These plans, or principal forms, are utterly independent from each other, and there are no intermediate forms among animals able to fill the gaps between the branches. As Cuvier wrote, any modification of a particular groundplan is slight and “change nothing of the essence of the plan” (Winsor 1976: 7). Mollusks became one of these four branches alongside with vertebrates, articulates and radiates. Cuvier, however, did not consider the four branches as separate phyla in the taxonomic sense, and their names remained vernacular, not latinized.

Cuvier published the last version of the system of Mollusca based on the type concept in 1817, and, somewhat changed, it was proclaimed again in 1830 (Cuvier 1817, 1830). In this system, six classes of mollusks were presented, including, again, phylogenetically distant from true mollusks taxa of tunicates, brachiopods and cirripedes (Table 1).

In 1825, Ducrotay de Blainville proposed a new term, “malacozoaires” (Malacozoa), to designate all these in-

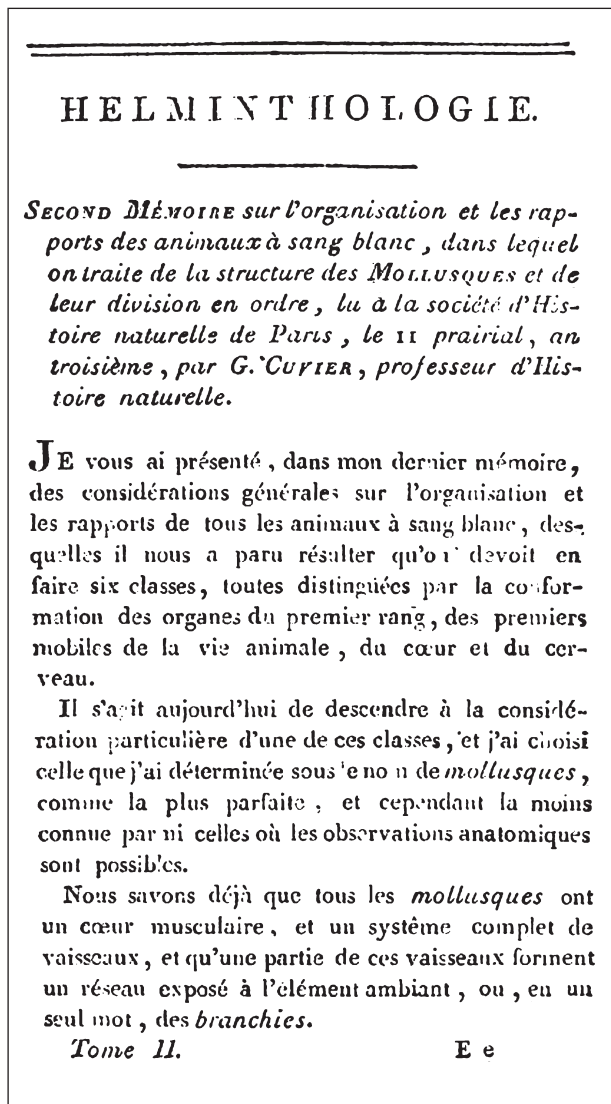


Figure 1. The title page of the Cuvier’s “mémoire” on classification of mollusks (Cuvier 1795).

Table 1. Cuvier's [1817] classification of molluscs

Group	Classes	Orders
Mollusques	Céphalopodes	none
	Ptéro-podes	none
	Gastéropodes	Nudibranches, Inferobranches, Tectibranches, Pulmonés, Pectinibranches, Scutibranches, Cyclobranches
	Acéphales	Acephales testacés (= Bivalvia), Acephalés sans coquilles (= Tunicata)
	Brachiopodes	none
	Cirrhopodes (= Cirripedia)	none

vertebrate animals with soft coverings that corresponded to the Cuvier's diagnosis of "les mollusques". Another term, malacology, was invented for designation of a branch of science devoted to study of malacozoaires. De Blainville wrote: "A branch of science devoted to this part of zoology [i.e. study of Malacozoa] still lacks a name; since *Molluscologie* cannot be used as being a hybrid [word], and since *Conchyliologie* is hardly better as it deals with only coverings of these animals, we propose here [a term] *Malacozoologie*, or, in abbreviated form, *Malacologie*..." (Blainville 1825: 2). In the Blainville's book, conchology, or *conchyliologie*, remains as a subordinated part of malacology.

Blainville clearly considered his term "Malacologie" as being entirely new. Most probably, he was not aware that nine years earlier, in 1814, the same word was introduced by Rafinesque in a rather obscure pamphlet published in Palermo (Italy) and entitled "Principes fondamentaux de somiologie ou les loix de la nomenclature et de la classification de l'empire organique" (see Robertson 1990, Dance 2011).

Rafinesque attempted to give a special name for each branch of zoology devoted to study of a particular taxon. Some of his terms sound highly exotic. For example, he introduced the term "plaxologie" for the studies of crustaceans, the term "anostologie" for a field of zoology devoted to all invertebrates and so on. "Malacologie" was proposed by Rafinesque to label the study of Malacosia, or mollusques (Rafinesque 1814: 48). Robertson (1990: 145) believes that "Rafinesque had more-or-less the same concept of "Mollusques" as Cuvier (1817)" but, strictly speaking, there was no a clear definition either for Malacosia or for Malacologie in the Rafinesque's brochure. If anything, this small booklet remained virtually unknown among the Rafinesque's colleagues, and Blainville (1825) nowhere demonstrated he knew it.

The birth of Malacology

Cuvier revolutionized invertebrate systematics through his pioneering studies in comparative anatomy, and should be considered the genuine "father of malacology." The conceptual shift from conchology to malacology took place between 1795 and 1825 when Cuvier developed his new and revolutionary ideas on systematization of invertebrates. This conceptual transition was concerned with

appearance of three new concepts not characteristic for conchology in its classical sense:

1. Mollusks represent a unique plan of organization of animals embracing both shelled and non-shelled species of animals with soft coverings and uniform internal structures. The shell as such is not essential for definition of Mollusca.

2. The shell is only a part of the whole body of a molluscan animal. Shell characters of mollusks are correlated with the structure of their internals that allows conchological traits to be useful for diagnostics and delineation of lower taxa, but shells have only secondary significance for arrangement of classes and order of Mollusca.

3. Shells are worth examining as objects of nature, but conchology as such constitutes merely a part of a broader branch of zoology that deserves a special name for its designation.

Zoologists in 1800-1810s did not express these three concepts explicitly, but all of them were implicitly contained in works of Cuvier and his associates. Rafinesque's and Blainville's formal establishment of malacology addressed this state of affairs and marked the birth of a new scientific discipline by a proper term. Thus, malacology was born nameless until Rafinesque and Blainville's time. This is not a rare case in the history of science. For example, Aristotle, the "father of zoology", contributed very much to biology without knowing the very word "biology", which did not appear until 1802. Similarly, Cuvier and Lamarck worked as true malacologists even before the word "malacology" was introduced to the dictionaries by Rafinesque and their compatriot Blainville.

Thus, the birth of malacology was not a sort of "saltation". Most probably, it was, in reality, a slow "tectonic" shift in zoological thinking that took at least three decades. This process ran parallel with a much larger one, the gradual transformation of "natural history" flourished in the Age of Reason to modern biology (Foucault 2002). Conchology, however, survived this transformation, and is still essential for countless paleontologists, museum curators and private shell collectors.

For those, who still seek for the "exact" date of birthday of malacology, I propose 10 May of 1795 (= 21 floréal an III), a day when Cuvier delivered his lecture on the arrangement of "vermes", including mollusks, before the Society of Natural History [see Cuvier 1830: 1]. Is there a better date to celebrate the beginnings of malacology?

Acknowledgements

I am grateful to Dr. Alan Kabat and an anonymous reviewer for their comments and polishing the English. I received a partial financial support for this study from the Russian Foundation for Basic Research (projects № 12-04-31564_mol_a; 12-04-98056-p_sibir_a) and the Russian Ministry of Education and Science (project № 4.2326.2011).

References

- Anderson TR, Rice T (2006) Deserts on the sea floor: Edward Forbes and his azoic hypothesis for a lifeless deep ocean. *Endeavour* 30(4): 131–137. doi: 10.1016/j.endeavour.2006.10.003
- Blainville HM (1825) *Manuel de malacologie et de conchologie*. E.G. Levrault, Paris-Strasbourg.
- Burrow EI (1815) *Elements of Conchology, according to the Linnaean system*. R. and A. Taylor, London. doi: 10.5962/bhl.title.11498
- Cuvier G (1795a) Mémoire sur la structure interne et externe, et sur les affinités des animaux auxquels on a donné le nom de Vers; lu à la société d'Histoire-Naturelle, le 21 floréal de l'an 3. *La Décade philosophique, littéraire et politique* 5(3): 385–396.
- Cuvier G (1795b) Second mémoire sur l'organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordre, lu à la société d'Histoire Naturelle de Paris, le 11 prairial an troisième. *Magazin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts* 2: 433–449.
- Cuvier G (1798) *Tableau élémentaire de l'histoire naturelle des animaux*. Baudoin, Paris. doi: 10.5962/bhl.title.11203
- Cuvier G (1812) Sur un nouveau rapprochement à établir entre les classes qui composent le Règne animal. *Annales du Muséum d'Histoire Naturelle* 19: 73–84.
- Cuvier G (1817) *Règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*. Déterville, Paris, 2: 1–532.
- Cuvier G (1830) *Règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*. Déterville, Crochard, Paris, 3: 1–504.
- Da Costa EM (1776) *Elements of Conchology: or, An introduction to the knowledge of shells*. B. White, London.
- Dance SP (2011) The curious case of Conchology versus Malacology. *American Conchologist* 35(1): 9–11.
- Duméril ACM (1806) *Zoologie analytique, ou Méthode naturelle de classification des animaux*. Allais, Paris.
- Eigen EA (1997) Overcoming first impressions: Georges Cuvier's types. *Journal of the History of Biology* 30: 179–209. doi: 10.1023/A:1004227517928
- Fleming J (1837) *Molluscous animals, including shell-fish; containing an exposition of their structure. systematical arrangement, physical distribution, and dietetical uses, with a reference to the extinct races. Forming the article "Mollusca" in the seventh edition of the Encyclopaedia Britannica*. Adam & Charles Black, Edinburgh.
- Foucault M (2002) *The order of things: An archaeology of the human sciences*. Routledge Classics, London, New York.
- Glaubrecht M (2009) On "Darwinian Mysteries" or molluscs as models in evolutionary biology: from local speciation to global radiation. *American Malacological Bulletin* 27 (1-2): 3–23. doi: 10.4003/006.027.0202
- Gooday G (1991) 'Nature' in the laboratory: domestication and discipline with the microscope in Victorian life science. *British Journal for the History of Science* 24: 307–341. doi: 10.1017/S0007087400027382
- Lamarck JBPA de M (1792) *Observations sur les coquilles, et sur quelques-uns des genres qu'on a établis dans l'ordre des vers testacés*. *Journal d'Histoire Naturelle* 2: 269–280.
- Lamarck JBPA de M (1801) *Système des animaux sans vertèbres, ou Tableau général des classes, des ordres et des genres de ces animaux*. Chez L'Auteur, Paris.
- Maton WG, Rackett T (1804) An historical account of testaceological writers. *Transactions of the Linnean Society* 7: 119–244. doi: 10.1111/j.1096-3642.1804.tb00287.x
- Meyer JB (1855) *Aristoteles Thierkunde*. G. Relmer, Berlin.
- Pellegrin P (1986) Aristotle's classification of animals: Biology and the conceptual unity in the Aristotelian corpus. University of California Press, Berkeley.
- Pinnock W (1824) *A catechism of conchology containing a pleasing description of the construction and classification of shells*. G. & W.B. Whittaker, London.
- Poe EA (1839) *The Conchologist's first book: A system of testaceous malacology etc*. Haswell, Barrington, and Haswell, Philadelphia.
- Porro C (1838) *Malacologia terrestre e fluviatile della Provincia Comasca*. Guglielmini e Redaelli, Milano. doi: 10.5962/bhl.title.12948
- Rafinesque-Schmaltz CS (1814) *Principes fondamentaux de somiologie ou les loix de la nomenclature et de la classification de l'empire organique etc*. F. Abate, Palermo.
- Robertson R (1990) Malacology or Conchology? *The Nautilus* 104(4): 145–146.
- Stevens PF (1994) *The development of biological systematics: Antoine-Laurent de Jussieu, Nature, and the Natural System*. Columbia University Press, New York.
- Swainson WA (1840) *Treatise on malacology: Or the natural classification of shells and shell-fish*. Longman etc., London.
- Winsor MP (1976) *Starfish, jellyfish and the order of life: Issues of nineteenth-century science*. Yale University Press, New Haven-London.
- Wood W (1815) *General Conchology, or A description of shells arranged according to the Linnaean system*. J. Booth, London.

Description of *Floresorchestia samroiyodensis*, a new species of landhopper (Crustacea, Amphipoda, Talitridae) from Thailand

Azman Abdul Rahim^{1,†}, Koraon Wongkamhaeng^{2,‡} and Pongrat Dumrongrojwattana^{3,§}

¹ Marine Ecosystem Research Centre (EKOMAR), Faculty of Science and Technology, Universiti Kebangsaan Malaysia
43600 Bangi, Selangor, Malaysia

² Marine and Coastal Resources Institute (MACORIN), Prince of Songkla University, 90112 Thailand

³ Department of Biology, Faculty of Science, Burapha University, Bangsaen, Chonburi 20131 Thailand

† <http://zoobank.org/9DF66EC5-44B0-4238-88EF-D7E1601234B7>

‡ <http://zoobank.org/801FBB8E-B12E-4C91-A592-ADEEB2417BEA>

§ <http://zoobank.org/7BB11A7C-C6DC-4681-8030-F9648DFC0A55>

<http://zoobank.org/64FD7F03-7892-4094-80C7-6930508E0CDE>

Corresponding author: Azman Abdul Rahim (abarahim@gmail.com)

Abstract

Received 26 Nov 2013
Accepted 4 Jan 2014
Published 28 March 2014

Academic editor:
Matthias Glaubrecht

A new species of landhopper from Thailand is described. Its main diagnostic features are its large eyes; antenna 1 short; antenna 2 slender; maxilliped palp article 4 reduced, button-shaped; mandible right lacinia mobilis 6-dentate; gnathopod 1 subchelate with palmate lobes on the carpus and propodus; gnathopod 2 subchelate; pereopods cuspidately, with dactylus of pereopod 4 thickened and pinched; epimera 2-3 with stridulating organ just above ventral margins; uropod 1 outer ramus with a row of 3-4 robust setae; telson apically incised.

Key Words

Amphipoda
Talitridae
Thailand
new species
Floresorchestia samroiyodensis
taxonomy

Introduction

Members of the talitrid amphipods are known to inhabit a wide range of habitats including forests, marshes and coastal environments (Bousfield 1982). Currently there are 59 recognised talitrid amphipod genera ranging from the palustral talitrids (marsh-hoppers), beach fleas (beach-hoppers), sand hoppers and the land hoppers (Lowry and Coleman 2012). Nevertheless, the landhoppers in Southeast Asian region particularly, is as yet poorly known. Only seven species have so far been recorded

in this region. The first known Southeast Asian region landhopper (*Parorchestia luzonensis*) was described by Baker (1915) from the summit of Mt. Maquilang, and in the same paper he described another species (*Parorchestia lagunae*) from the freshwater lake of central Luzon (Bay Lake), Philippines. Still in the early 20th century, another high altitude landhopper species *Parorchestia kinabaluensis*, was reported from Mt. Kinabalu, Sabah (Shoemaker 1935). Bussarawich et al. (1984) recorded two unnamed species of *Microrchestia* and *Floresorchestia* from the mangrove area of Southern Thailand. While

Miyamoto and Morino (2008) reported *Floresorchestia anomala* (Chevreux, 1901) from Malaysia. Recently, Lowry and Coleman (2012) described a new genus *Curiotalitrus* from rainforests in the Philippines. In this paper, we describe a 6-dentate cuspidactylate terrestrial amphipod discovered from a swamp forest in central Thailand.

Materials and methods

This study is based upon material collected from leaf litter of Khao Sam Roi Yod National Park (Fig. 1), Inner Gulf of Thailand in July 2011. Samples were collected using hand-nets and were then carefully transferred into plastic containers and fixed in 10% buffered formalin. In the laboratory, amphipod specimens were sorted out and stored in 70% alcohol. The animals were then examined under a compound microscope and later selected for dissection. The appendages of the dissected specimens were examined and figures were produced using a Leica DMLB light microscope with a camera lucida. All illustrations were digitally 'inked' following Coleman (2003). Setal and mouthpart classifications following Watling (1989). Figure legend: A, antenna; G, gnathopod; HD, head; LL, lower lip; MD, mandible; MX, maxilla; MP, maxilliped; P, pereopod; PL, pleopod; T, telson; U, uropod; UR, urosome; UL, upper lip; R, right; L, left; ♂, male; ♀, female. Type material is deposited at Prince of Songkla University Zoological Collection with the prefix PSUZC for museum numbers and the Universiti Kebangsaan Malaysia Muzium Zoologi with the prefix UKMMZ for museum numbers.

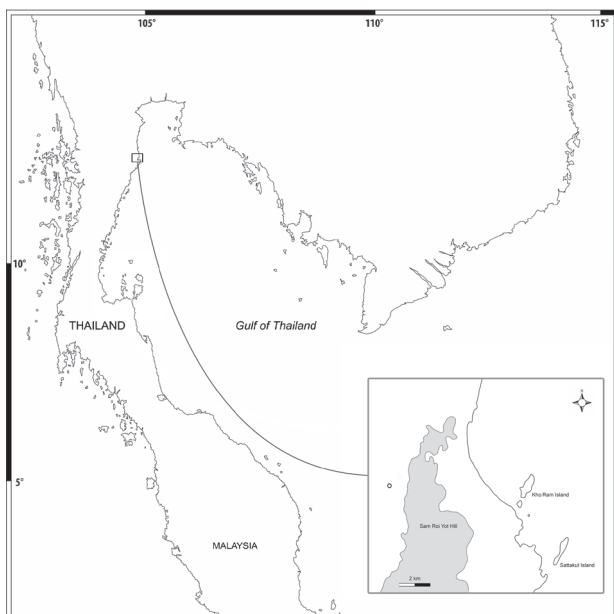


Figure 1. Map of the Inner Gulf of Thailand and the collection site (Sam Roi Yod National Park).

Systematic results

Suborder Senticauda Lowry & Myers, 2013

Infraorder Talitrida Rafinesque, 1815, emended Serejo 2004

Superfamily Talitroidea Bulycheva, 1957, emended Serejo 2004

Family Talitridae Rafinesque, 1815, emended Serejo 2004

Floresorchestia Bousfield, 1984

Floresorchestia samroiiodensis sp. n.

<http://zoobank.org/B4E6B5F4-A905-47D2-A2E7-9D048913A121>

http://species-id.net/wiki/Floresorchestia_samroiiodensis

(Figures 2-10)

Type material. Holotype, female, 10.6 mm, PSUZC-CR-0275, leaf litter of Khao Sam Roi Yod National Park, 12°14'36.93" N, 99°55'57.55" E, hand net, Pongrat Damrongrojwattana, 1 July 2011. Paratypes: 2 males, 13 females, 3 juveniles UKMMZ-1476, same station data.

Type locality: Khao Sam Roi Yod National Park, Sam Roi Yod district, Prachuap Khiri Khan Province, Thailand.

Diagnosis: Antenna 1 having 3 short articles of flagellum, reaching $\frac{1}{4}$ of peduncular article 5 of antenna 2; antenna 2 bearing more than 12 articles of flagellum; anterior coxal lobe of pereopod 6 not well developed; Mandible (female) right lacinia mobilis 6-dentate. Maxilliped palp



Figure 2. Live *Floresorchestia samroiiodensis* sp. n. in their natural habitat; photo taken by Mr. Komson Hongphattharakeeree.

article 2 distomedial lobe well developed, article 4 reduced, button-shaped. Gnathopod 1 parachelate; posterior margin of carpus and propodus each with lobe covered in palmate setae in male, posterior margin of merus, carpus and propodus each without lobe covered in palmate setae in female; palm slightly obtuse in male. Gnathopod 2 subchelate in male; mitten-shaped in female. Pereopods 2–4 coxae as wide as deep. Pereopods 3–7 cuspidate. Pereopods 6–7 longer than pereopods 3–5, with slender setae along posterior margin of dactyli. Pereopod 6 basis expanded in male. Epimera 2–3 with stridulating organ just above ventral margins (also presenting males where known). Pleopods well developed, similar in form and length; Uropod 1 peduncle distolateral robust seta present; inner ramus with marginal robust setae. Uropod 2 inner and outer rami with marginal robust setae. Uropod 3 ramus subequal in length to peduncle with 2 peduncular robust setae and 2 apical ones on ramus. Telson apically incised with marginal and apical robust setae, with 5 robust setae per lobe.

Description: (Based on holotype female, 10.6 mm, PSU-CR-0275)

Body compressed laterally, dorsal surface smooth. Head, height subequal to length. Eyes large, (greater than 1/3 head length). Antenna 1 short, ca. 1/3 of antenna 2; flagellum with 4 articles, shorter than peduncle; peduncular articles subequal in length. Antenna 2 peduncular articles narrow; article 5 longer than article 4; flagellum of 15 articles, longer than peduncle.

Upper lip broad, deep, apex rounded and densely pilose.

Lower lip broad, densely pilose on inner shoulder, distally in central trough and outer margin; lateral lobes long.

Left mandible incisor 5-toothed; molar process strong, with 15 striate (Sexually dimorphic in males; left lacinia mobilis with 4 teeth and right with 3 teeth). Right mandible incisor 6-toothed; molar process strong, with 16–17 striate.

Maxilla 1, inner plate slender with 2 terminal setae; outer plate with 9 articulating seta, medially with a row of 8 articulating seta.

Maxilla 2 plates narrow, inner plate slightly shorter than outer; inner plate with ca. 19 subapical robust setae, 1 plumose robust seta located at inner corner; outer plate with ca. 27 subapical robust setae more or less in 2 rows.

Maxilliped inner plate distally rounded, with apical and subapical plumose setae and 2 large conical robust setae; outer plate apically blunt, with a group of subapical setae.

Maxilliped palp broad; article 1 with 2 marginal and submarginal setae; article 2 with well-developed medial lobe, inner margin scalloped, with a row setae; outer margin of article 3 with several long setae, article 4 visible with robust setae apically.

Coxae 3–4 of medium depth, subquadrate, spinose lower margin slightly curvy or almost flat, posterior process

small and acute; coxa 5 deep, subequal to depth of coxa 4, anterior lobe large, posterior and ventral margins spinose, posterior lobe small; coxa 6 depth subequal to length, anterior lobe small, margin rounded distally; coxa 7 not deeper than coxa 6, gently curving below, weakly spinose.

Gnathopod 1, coxa anterior margin straight, ventral margin with 5 setae; basis straight almost parallel-sided; merus lacking tumescent lobe, posterior margin with 5 robust setae; carpus without tumescent protuberance; propodus without tumescent protuberance, anterior margin with a row of 7–8 robust setae, posterior margin with 6 robust setae; dactylus, 4 simple setae on anterodistal corner, inner lateral posterior margin with 1 robust seta, slightly acute.

Gnathopod 2 coxa as wide as deep with posterior process, convex ventral margin with 6 fine setae; basis expanded anteroproximally, posterior margin slightly straight; ischium subequal to merus in length; carpus elongate; propodus with posterodistal tumescent protuberance elongated distally, scabrous region from posteroproximal end to posterodistal end, outer lateral surface with several serrate setae, palm margin short, anterodistal corner with 3–4 simple setae; dactylus curved.

Sexual dimorphism present in gnathopods.

Gnathopod 1 of male short; basis strong, anterior margin with 4 setae and posterior margin with 2 setae; merus without posterior tumescent lobe; carpus deep, with posterior tumescence lobe; propodus slightly curved, shorter than carpus, posterodistal tumescent lobe large; subchelation strong, dactylus not exceeding palm and slightly obtuse.

Gnathopod 2 of male strongly subchelate, larger than 1; basis, anterior margin smooth, widened distally; ischium lobed anteriorly; merus subequal in length with ischium; propodus long ovate, bearing a row of small robust setae near dactylar hinge; palm oblique; dactylus curved, attenuated distally with smooth inner margin.

Pereopods 3–7 cuspidactylate. Pereopod 3 coxa subquadrate with posterior process, ventral margin slightly convex; basis longest; ischium shortest, anteroproximal margin notched; merus longer than carpus, anterior margin slightly convex, posterior margin straight; carpus anterior and posterior margins parallel; propodus slender, longer than carpus; dactylus subequal to ischium in length.

Pereopod 4 similar to pereopod 3, shorter, coxa wider than long, with posterior process, ventral margin straight; basis longest, convex; ischium shortest, anteroproximal margin notched; merus longer than carpus, anterior margin convex, posterior margin straight; carpus short; propodus slender, subequal to merus; dactylus posterior nail base with 1 simple seta.

Pereopod 5 coxa bilobed, anterior lobe larger than posterior lobe; basis oval; ischium shortest, posteroproximal margin notched; merus shorter to carpus in length, anterior margin straight, posterior margin slightly convex; carpus both margins parallel; propodus slender; dactylus short.

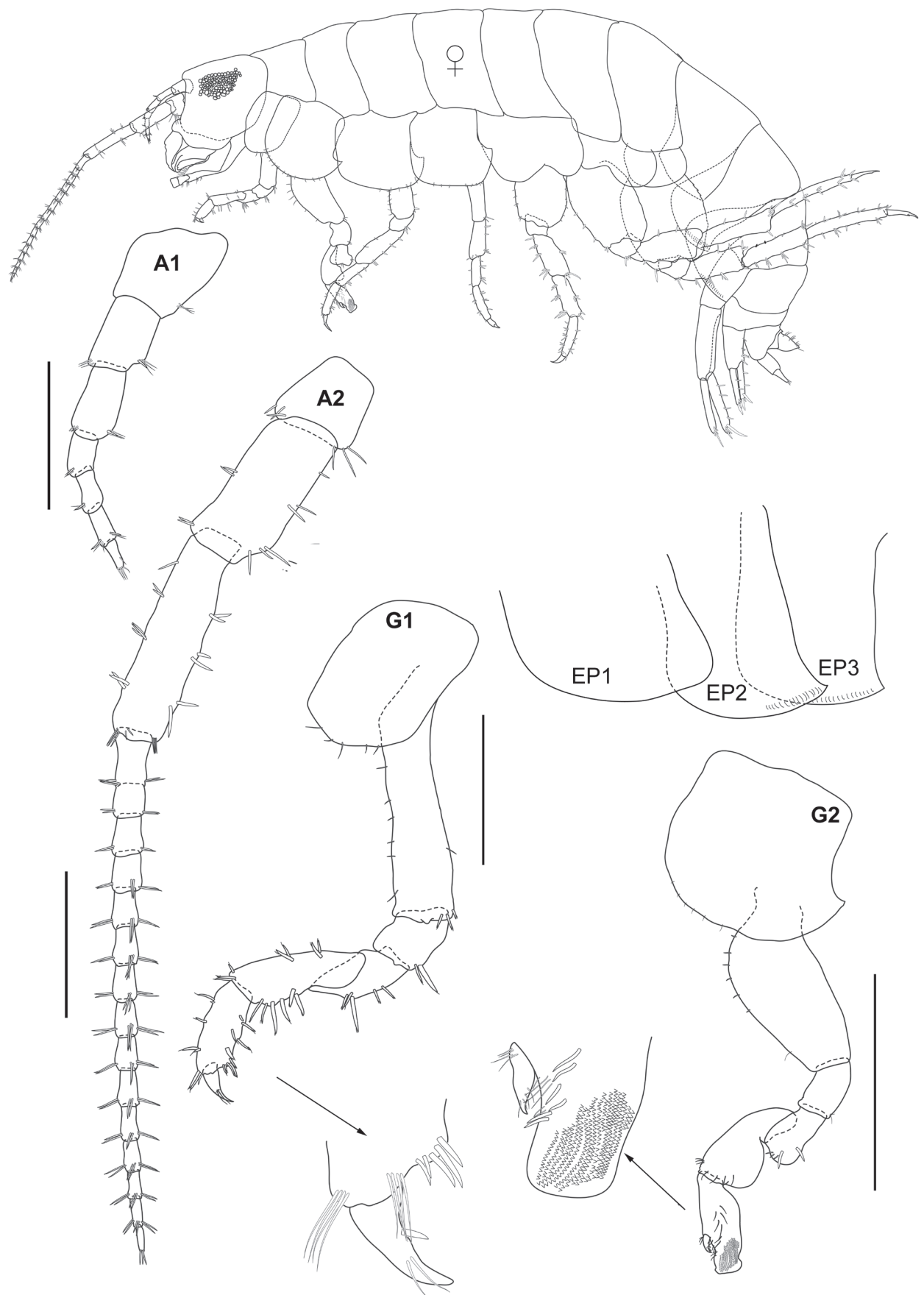


Figure 3. *Floresorchestia samroi yodensis* sp. n., holotype, female, (PSUZC-CR-0275) 10.6 mm. Khao Sam Roi Yod National Park. Scales for A1 and A2 represent 0.5 mm, G1 and G2 represent 0.2 mm.

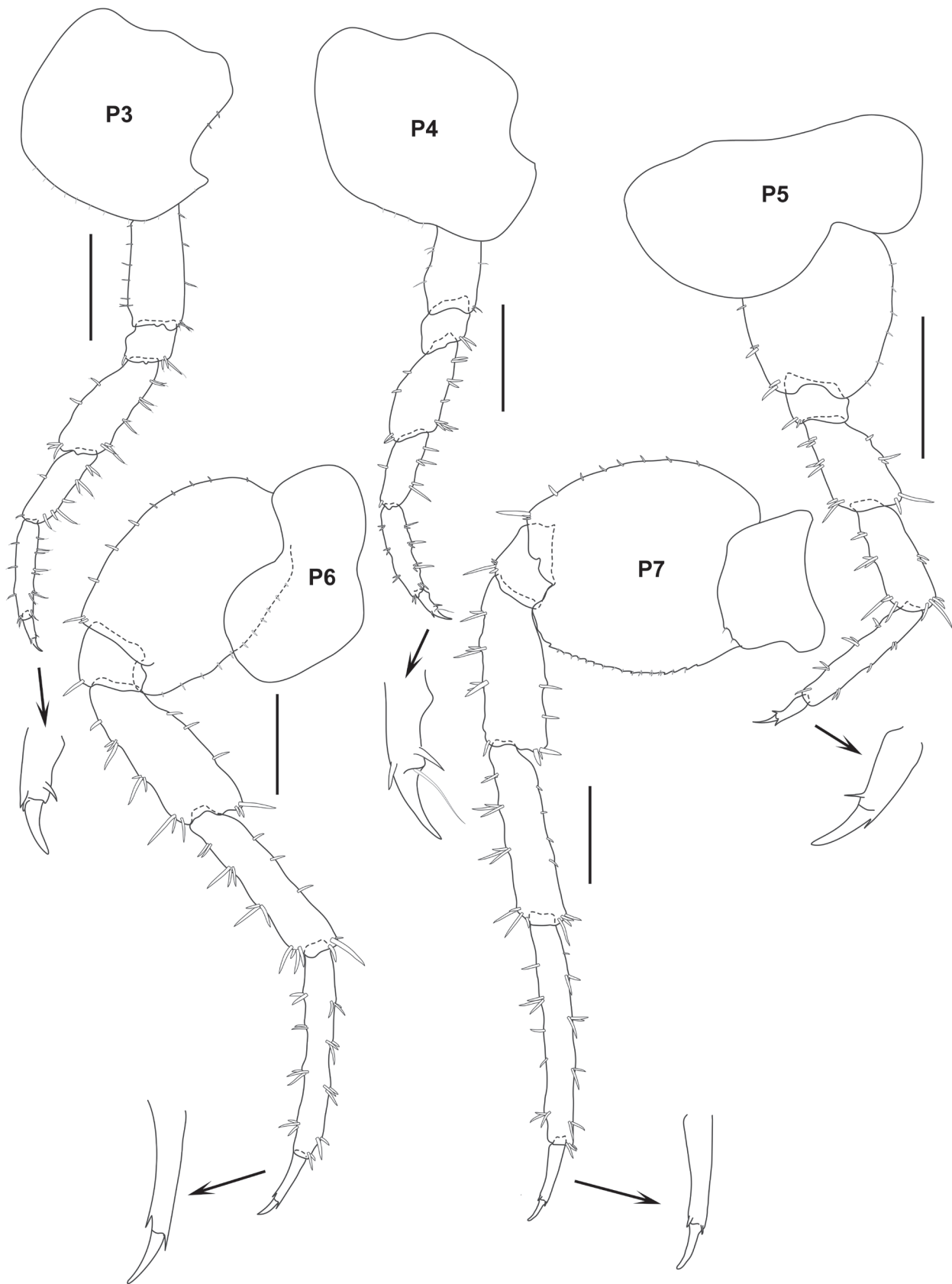


Figure 4. *Floresorchestia samroiiodensis* sp. n., holotype, female, (PSUZZ-CR-0275) 10.6 mm. Khao Sam Roi Yod National Park. All scales represent 0.5 mm.

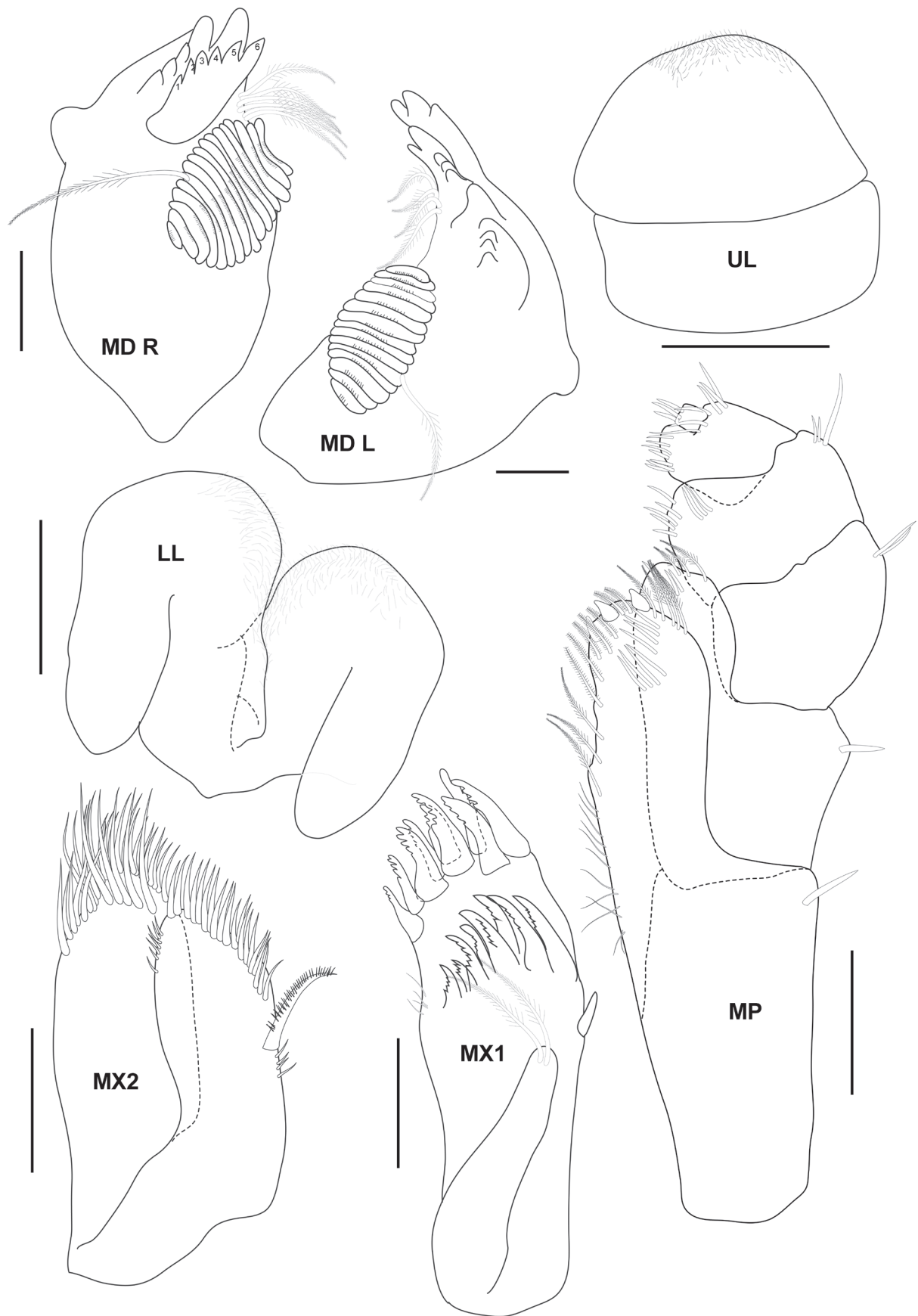


Figure 5. *Floresorchestia samroi yodensis* sp. n., holotype, female, (PSUZZ-CR-0275) 10.6 mm. Khao Sam Roi Yod National Park. Scales for IMD, MX1, MP and MX2 represent 0.1 mm; rMD, UL and LL represent 0.2 mm.

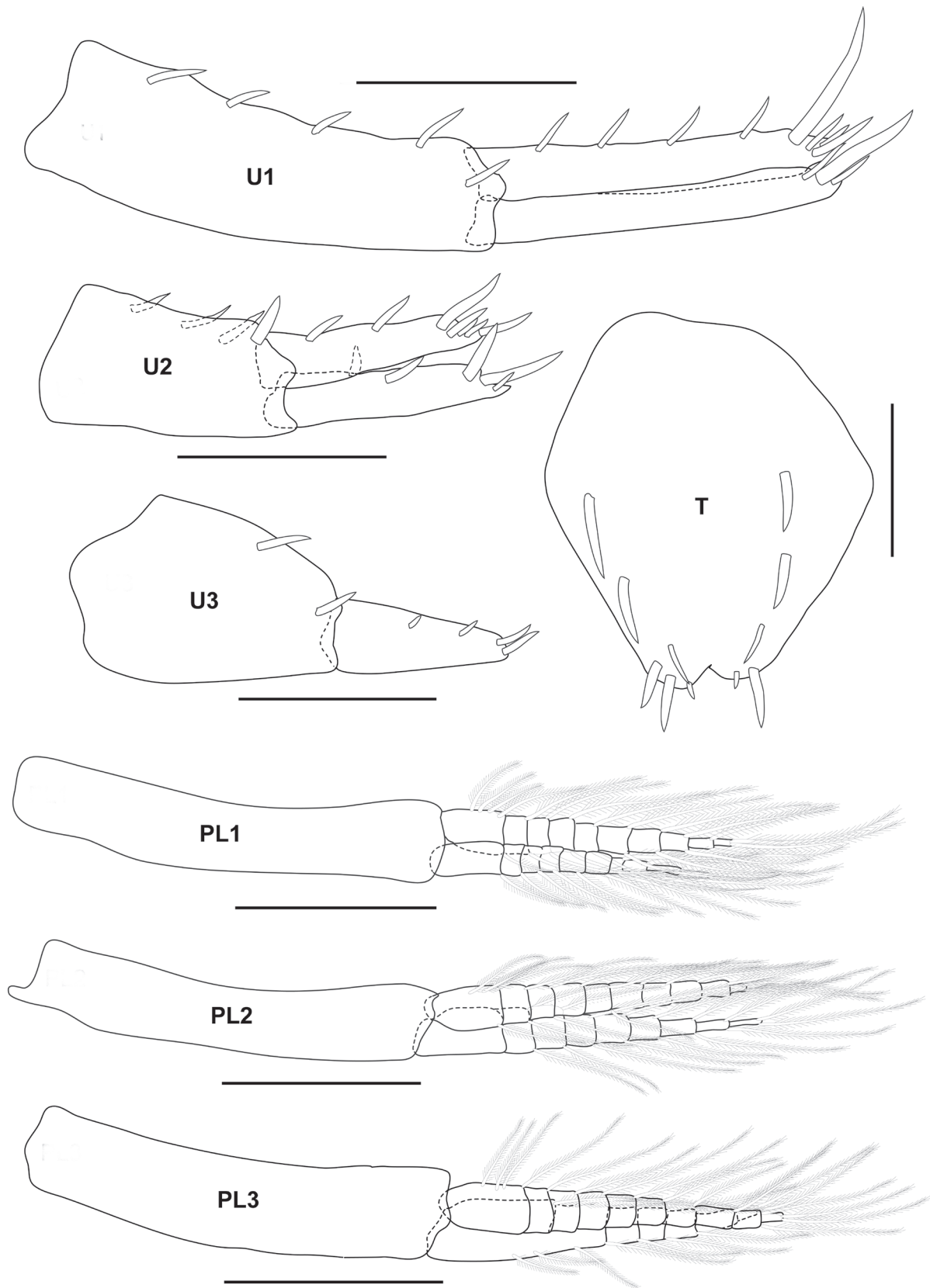


Figure 6. *Floresorchestia samroiiodensis* sp. n., holotype, female, (PSUZYCR-0275) 10.6 mm. Khao Sam Roi Yod National Park. Scales for U1, U2, PL1, PL2 and PL3 represent; 0.5 mm, U3 and T represent 0.2 mm.

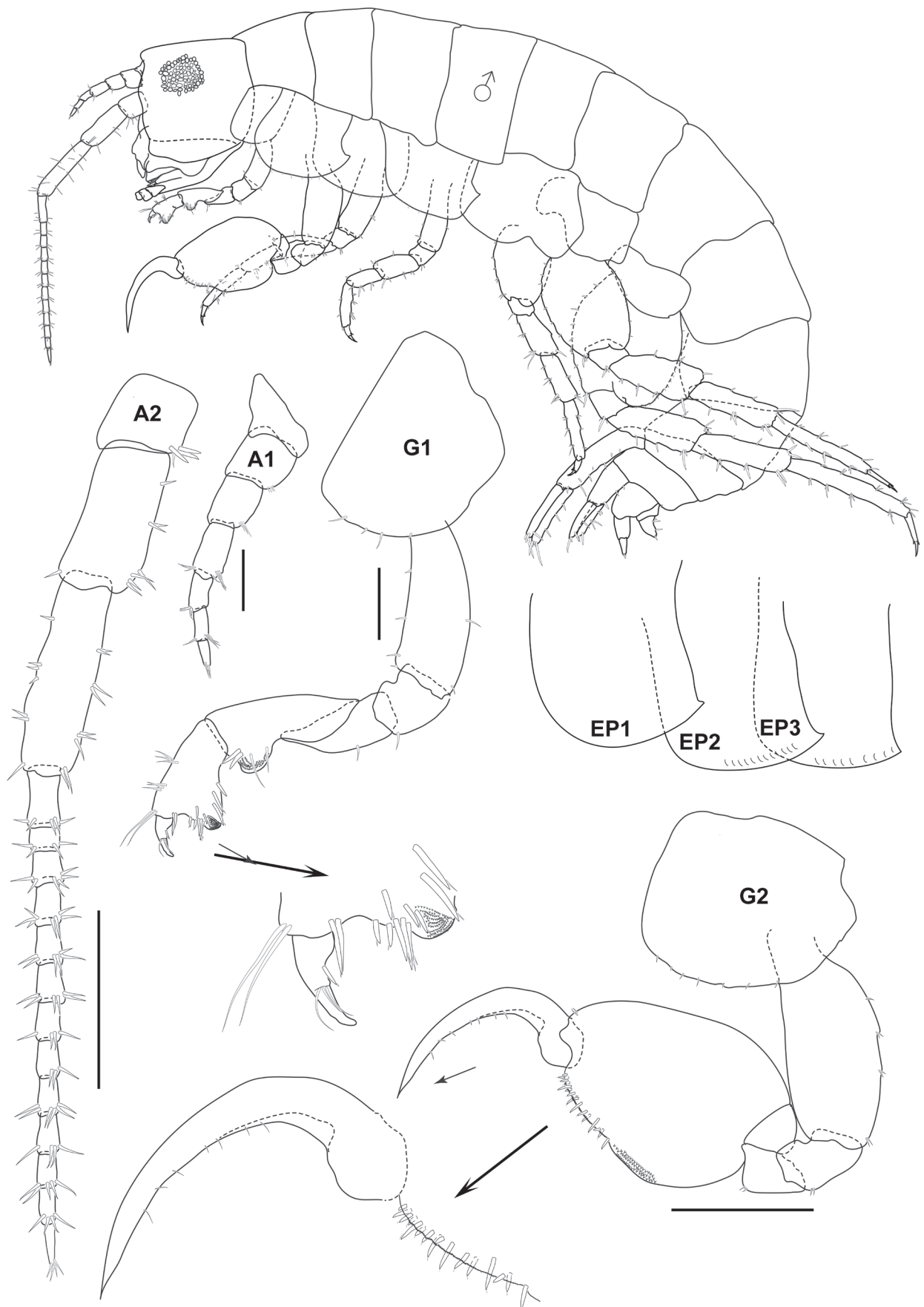


Figure 7. *Floresorchestia samroi yodensis* sp. n., allotype, male, (PSUZZC-CR-0274) 10.5 mm. Khao Sam Roi Yod National Park. Scales for A2 and G2 represent 0.5 mm; A1, G1 represent 0.2 mm.

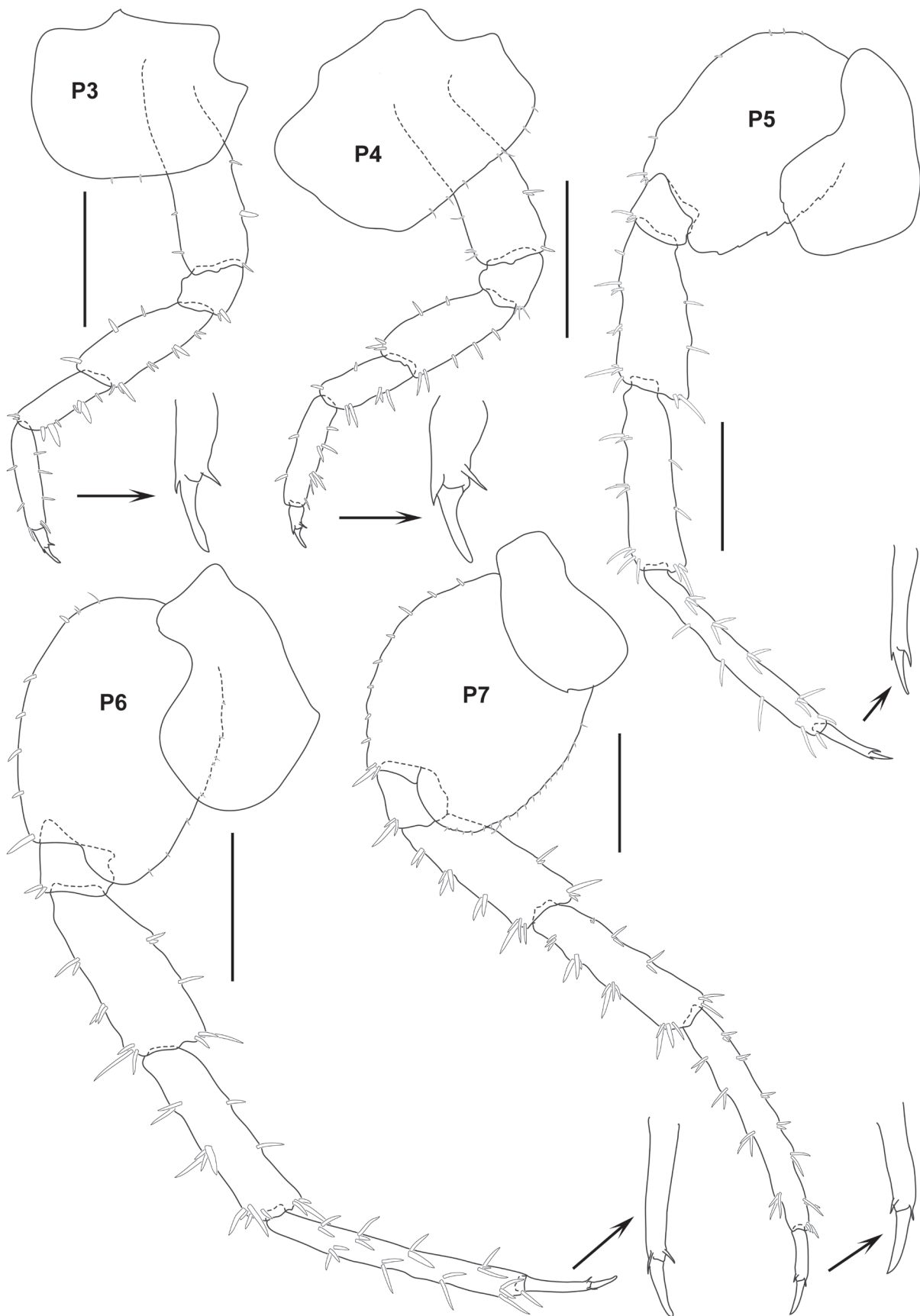


Figure 8. *Floresorchestia samroiiodensis* sp. n., allotype, male, (PSUZC-CR-0274) 10.5 mm. Khao Sam Roi Yod National Park. All scales represent 0.5 mm.

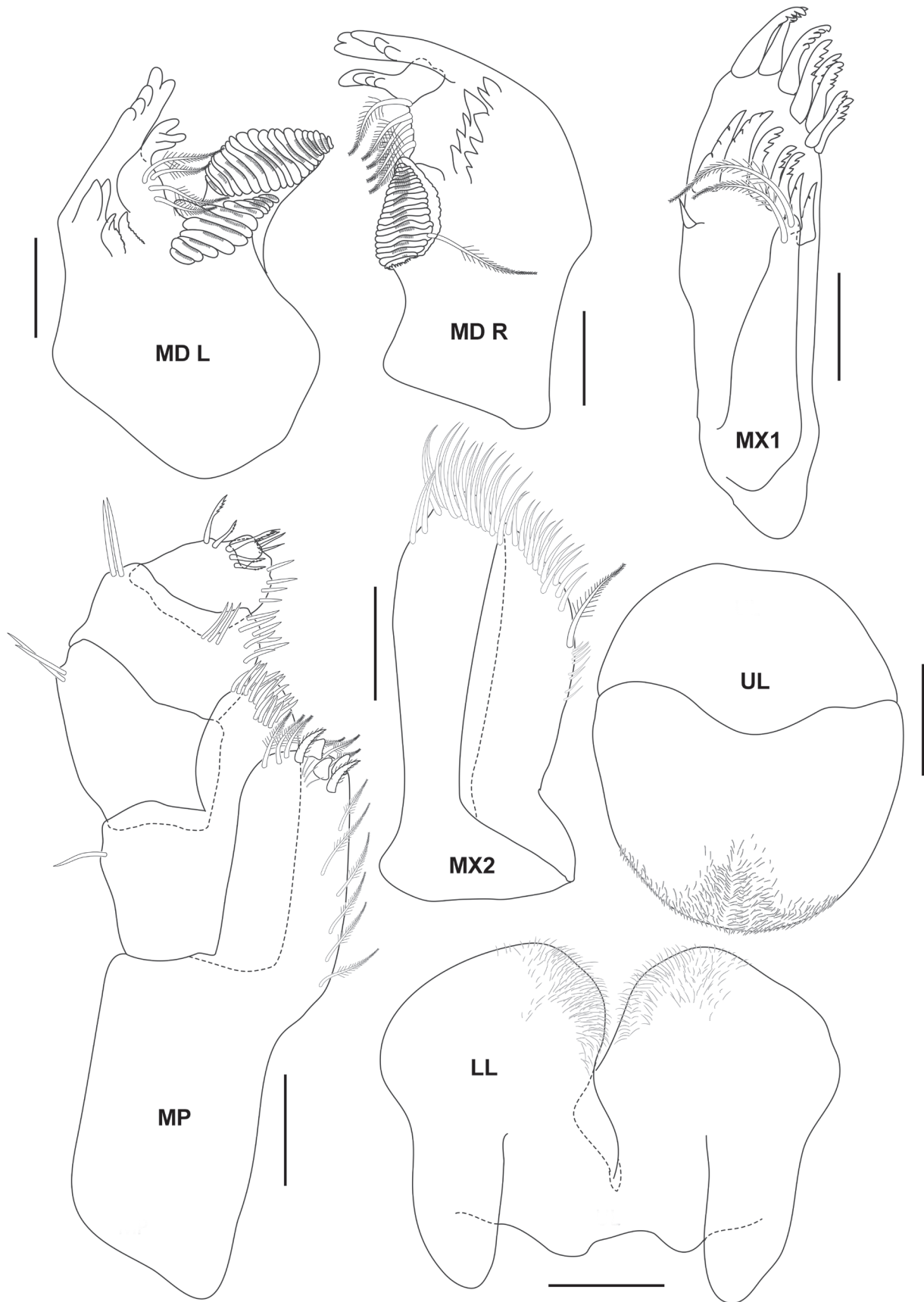


Figure 9. *Floresorchestia samroiensis* sp. n., allotype, male, (PSUZC-CR-0274) 10.5 mm. Khao Sam Roi Yod National Park. Scales for lMD, rMD and UL represent 0.1 mm; MP and MX1 represent 0.2 mm.

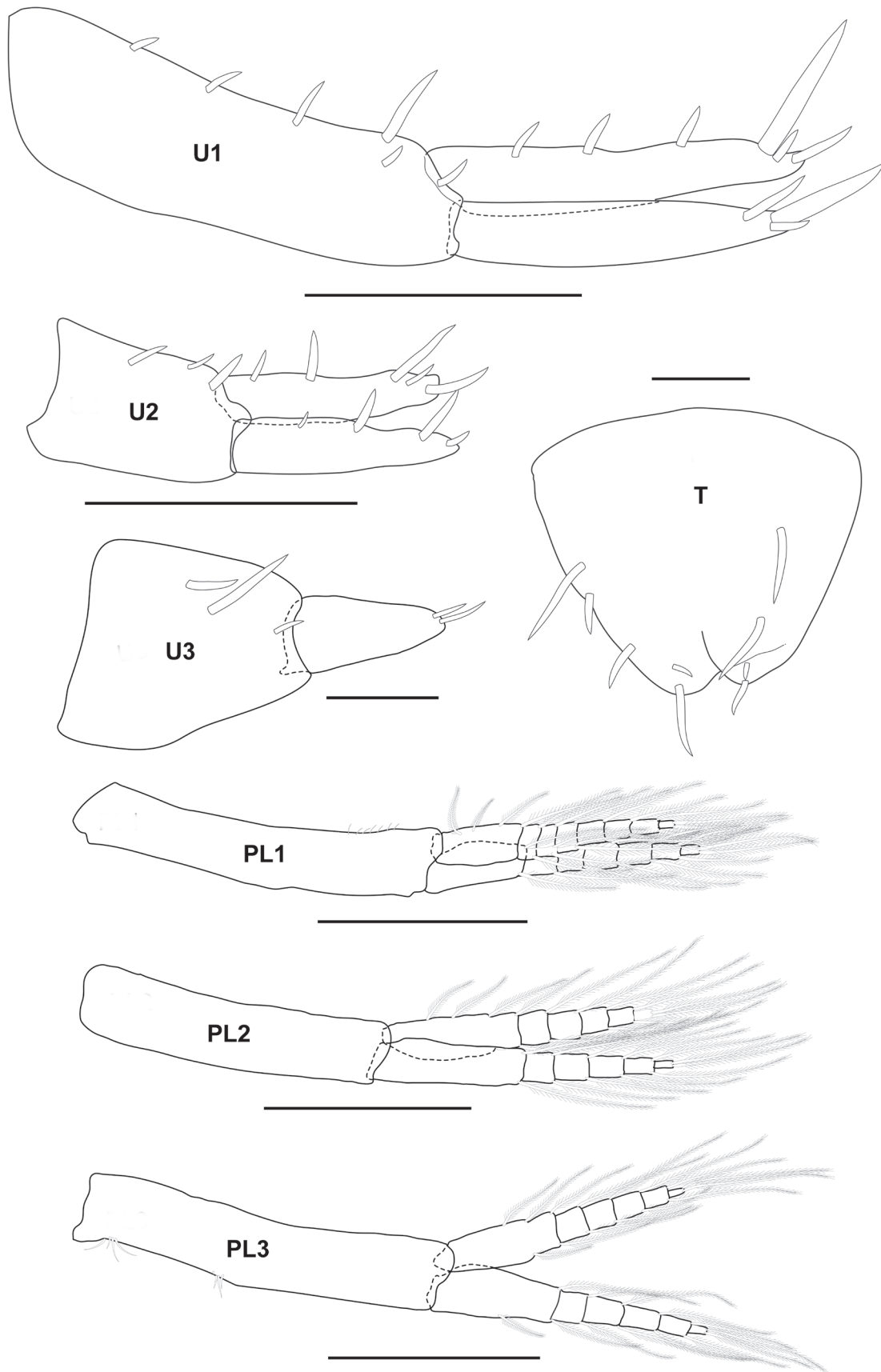


Figure 10. *Floresorchestia samroi yodensis* sp. n., allotype, male, (PSUZC-CR-0274) 10.5 mm. Khao Sam Roi Yod National Park. Scales for U1, U2, PL1, PL2 and PL3 represent 0.5 mm; U3 represent 0.1 mm; T represents 0.2 mm.

Pereopod 6 coxa bilobed, anterior lobe much smaller than posterior lobe; basis oval, anterior margin with short robust setae; ischium shortest, posteroproximal margin notched; merus slightly shorter than carpus in length, anterior margin straight, posterior margin slightly convex; carpus both margins parallel; propodus slender, longest; dactylus short.

Pereopod 7 coxa small, subquadrate; basis oval, posterodistal lobe broader than pereopod 5–6; ischium shortest; merus slightly shorter in length to carpus, anterior margin straight, posterior margin slightly convex; carpus anterior and posterior margins parallel; propodus slender, longest; dactylus narrow.

Epimeral plates, plate 1 smoothly rounded anterodistally and distally, posterodistal corner slightly protruded, hind margin slightly sigmoid; plate 2 slightly longer than plate 3, anterodistally rounded with a row of slits (16–21 slits) along ventral margin, posterodistal corner produced; plate 3 also with a row of slits (13–15 slits) along ventral margin and posterodistal corner produced.

Pleopods well developed, subsimilar in form and length. Peduncles sublinear; all pleopods biramous. Rami shorter than peduncles, with distinct segmentation.

Uropod 1, peduncle longer than rami, peduncle bearing 1 outer marginal robust setae and 4 inner marginal robust setae; rami slender, subequal in length, outer ramus lacking marginal robust setae, inner ramus with 4 robust marginal setae, both with large apical and subapical robust setae.

Uropod 2, peduncle subequal to rami in length; peduncle bearing 1 outer marginal and 3 inner marginal robust setae; rami slender, subequal in length, outer ramus and inner ramus with 2 marginal robust setae, apical robust setae with tapering acute tips.

Uropod 3, peduncle expanded proximally, narrowing distally, longer than deep, 2 robust setae set submarginally; ramus slightly shorter than peduncle, tapering distally, bearing 2 robust setae apically and another 2 along the margin.

Telson as broad as long, and apically shallow incised; each side with several robust setae (normally with 5–6).

Remarks. The new species is characterized by having the mandibular left lacinia mobilis 6-dentate; dactylus of pereopod 4 thickened and pinched, and also shows the following features: large eyes; antenna 1 short; antenna 2 slender; maxilliped palp article 4 reduced, button-shaped; gnathopod 1 subchelate with palmate lobes on the carpus and propodus; gnathopod 2 subchelate; pereopods cuspidactylate; epimera 2–3 with stridulating organ just above ventral margins; uropod 1 outer ramus with a row of 3–4 robust setae; telson apically incised. Individuals belonging to this new species are found underneath the moist environment of the forest leaf litter.

The species of *Floresorchestia* are known to be tropical and widespread which is, distributed in terrestrial habitats of rain forests of the tropical Indo-Pacific (Bousfield 1984) and also in the Caribbean Sea (Lowry and

Springthorpe 2009). Bousfield (1984) documented *Floresorchestia* for a group of described species with unique stridulating organs on the epimera. These epimeral slits are considered to be a powerful autapomorphy for *Floresorchestia* (Lowry & Bopiah, 2012) and they are found in various combinations: epimera 1–3; epimera 2–3 (most common); epimeron 2; epimeron 3. Recently Miyamoto and Morino (2008) and Lowry and Springthorpe (2009) have both discussed the morphology of the genus, refining characters and describing additional new species that brings a total of 16 valid species.

Floresorchestia samroiiodensis sp. n. shares several unique characters with *F. ancheidos* (K.H. Barnard, 1916) and *F. guadalupensis* (Ciavatti, 1989) in having the stridulating organs on epimera 2–3 and palmate lobes on the carpus and propodus of gnathopod 1. However the new species differs from any other members of *Floresorchestia* in its more developed dentitions (6-dentate) of lacinia mobilis on the female right mandible, as well as in having two rows of spine-like teeth in outer plate of maxilla 1, and the telson with 4–5 setae per lobe.

Acknowledgements

Thanks are due to Drs. Jaruwat Nabhitabhata, Pornsilp Pholphunthinn and Mr. Kwan Nualcharoen for their vital support, insight and expertise that greatly assisted the research. Appreciations are also extended to Dr. Charles Oliver Coleman from the Museum für Naturkunde Berlin, Germany and Dr. Jim Lowry from the Australian Museum, Sydney for reading the manuscript and for their invaluable comments and also for their assistance with literature. Universiti Kebangsaan Malaysia research grant (DIP-2012-020) has also provided travel grant to first author which helped in conducting field visit. Thanks to our colleague Mr. Komson Hongphattharakeeree in providing the amphipod photo for this study.

Reference

- Baker CF (1915) Two Amphipoda of Luzon. Philippine Journ. Sci. 10: 251–255.
- Bousfield EL (1982) The amphipod superfamily Talitroidea in the north-eastern Pacific region. I. Family Talitridae: systematics and distributional ecology. Publications in Biological Oceanography 11: 1–75.
- Bousfield EL (1984) Recent advances in the systematics and biogeography of landhoppers (Amphipoda: Talitridae) of the Indo-Pacific region. In: Radovsky FJ, Reven PH, Sohmer SH (Eds) Biogeography of the tropical Pacific, proceedings of a symposium. Bernice P. Bishop Museum, (Special Publication) 72: 171–210.
- Bulycheva AI (1957) Sea-fleas of the seas of the USSR and adjacent waters (Amphipoda - Talitroidea). Akademiya Nauk SSSR, Opre-deliteli po Faune SSSR 65: 1–185.
- Bussarawich S, Nateewathana A, Hylleberg J (1984) Distribution of Marine Benthic Amphipods Off Phuket Island, with Emphasis on Tin Mining and a Model of Species Individual Relationships. Phuket Marine Biological Center Research Bulletin 32:1–21.

- Chevreaux E (1901) Crustacés Amphipodes. In: Mission scientifique de M. Ch. Alluaud aux Iles Séchelles (Mars, Avril, Mai 1892). Mém. Soc. zool. France 14: 388–438.
- Ciavatti G (1989) Les Talitres (Crustacea, Amphipoda) des plages de la Guadeloupe. Description de deux espèces nouvelles. Ann. Inst. océanogr., Paris 65(2): 127–146.
- Coleman CO (2003) “Digital inking”: How to make perfect line drawings on computers. Organism Diversity & Evolution 3: 1–14. doi: 10.1078/1439-6092-00081
- Lowry JK, Bopiah A (2012) *Britorchestia*, a new talitrid genus from western Europe and the Mediterranean Sea and a revision of *Pseudorchestoidea* and *Sardorchestia* (Crustacea, Amphipoda, Talitridae). Zootaxa 3451: 60–67.
- Lowry JK, Coleman CO (2012) A new terrestrial talitrid genus from the Philippine Islands (Crustacea, Amphipoda, Talitrida, Talitridae) and the designation of two informal groups. Zootaxa 3400: 64–68.
- Lowry JK, Springthorpe RT (2009) The genus *Floresorchestia* (Amphipoda: Talitridae) on Cocos (Keeling) and Christmas Islands. Memoirs of Museum Victoria 66: 117–127.
- Lowry JK, Myers AA (2013) A Phylogeny and Classification of the Senticaudata subord. nov. (Crustacea: Amphipoda). Zootaxa 3610(1): 1–80. doi: 10.11646/zootaxa.3610.1.1
- Miyamoto H, Morino H (2008) Taxonomic studies on the Talitridae (Amphipoda) from Taiwan, III. The genus *Floresorchestia* Bousfield, 1984. Crustaceana 81(7): 837–860. doi: 10.1163/156854008784771667
- Serejo CS (2004) Cladistic revision of talitroidean amphipods (Crustacea, Gammaridea), with a proposal for a new classification. Zoologica Scripta 33: 551–586. doi: 10.1111/j.0300-3256.2004.00163.x
- Rafinesque CS (1815) Analyse de la Nature ou Tableau de l'Univers. Palerme, 224.
- Shoemaker CR (1935) A new species of amphipod - from Mt. Kinabalu, North Borneo. Bull. Raffles Mus., Singapore 10: 63–67.
- Watling L (1989) A classification system for crustacean setae based on the homology concept. In: Felgenhauer BE, Watling L, Thistle AB (Eds) Functional Morphology of Feeding and Grooming in Crustacea. Crustacean Issues 6: 15–27.

The taxonomic status of two West African *Leptopelis* species: *L. macrotis* Schiøtz, 1967 and *L. spiritusnoctis* Rödel, 2007 (Amphibia: Anura: Arthroleptidae)

Mark-Oliver Rödel¹, Mike Emmrich¹, Johannes Penner¹, Andreas Schmitz² and Michael F. Barej¹

¹ Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity, Invalidenstraße 43, 10115 Berlin, Germany

² Natural History Museum of Geneva, Department of Herpetology and Ichthyology, C.P. 6434, 1211 Geneva 6, Switzerland

Corresponding author: Mark-Oliver Rödel (mo.roedel@mf-n-berlin.de)

Abstract

Received 15 Nov 2013
Accepted 3 Dec 2013
Published 28 March 2014

Academic editor:
Matthias Glaubrecht

Key Words

Advertisement calls
DNA-barcoding
biogeography
Central Africa
rainforest
taxonomy
treefrogs
West Africa

We herein examine the taxonomic status of two West African forest-dwelling *Leptopelis* species. The small *L. spiritusnoctis*, described from the Upper Guinean forests of West Africa, was recently synonymized with *L. aubryi*, described from Gabon. The large *L. macrotis*, known from Ghana to Sierra Leone, was downgraded to a subspecies of *L. millsoni*, ranging from the Niger Delta to eastern Democratic Republic of Congo. These taxonomic decisions are in contrast to the general biogeographic pattern of African forest anurans and we consequently tested if the morphologically similar taxon pairs are indeed conspecifics by applying acoustic and molecular techniques. Both techniques confirmed that populations from West Africa differ significantly from their Central African morphological equivalents. Consequently, we herein resurrect *L. spiritusnoctis* as a valid species. The acoustic data indicate that *L. aubryi* may comprise a complex of cryptic species. We further advocate using the name *L. macrotis* for West African and *L. millsoni* for Central African populations of these larger arboreal frogs. However, we had neither genetic nor acoustic data from the type locality of *L. millsoni* available and could not clarify if these frogs belong to the more western or eastern taxon or even represent a Nigerian endemic. Thus, it is possible that West African populations need to be termed *L. millsoni* in the future. For populations east of the Cross River, Nigeria, the name *L. guineensis* would be available.

Introduction

In many older and recent herpetological papers the term West Africa is used to describe a region, ranging approximately from Senegal in the northwest, along the western coast of the continent to Gabon, or even further south to northern Angola. However, recent investigations showed that the Upper and parts of the Lower Guinean forests, as defined based on plant distributions (see Udvardy 1975, White 1983), comprise very unique amphibian faunas (Penner et al. 2011). The two zoogeographic regions, West and Central Africa, are roughly separated by the Cross River in easternmost Nigeria (Schiøtz 1967, Penner et al. 2011). However, it is presumably not this river, but a tongue of the Atlantic Ocean that reached far inland from ca. 50 to 100 MA (Scotese 2001) and has acted as a zoo-

geographic barrier. The amphibian faunas east and west of this salt water barrier could thus independently evolve for at least that time span. Nowadays, this is visible in ecologically and most often also morphologically very similar but distinct forest species in almost all groups of anuran amphibians: e.g. Bufonidae (e.g. Perret and Amiet 1971, Rödel and Ernst 2000, Barej et al. 2011), Arthroleptidae (e.g. Blackburn et al. 2008, 2009, 2010, Ernst et al. 2008), Phrynobatrachidae (e.g. Lamotte and Xavier 1966, Zimkus et al. 2010), Hyperoliidae (e.g. Schiøtz 1967, 2007, Seymour et al. 2001, Rödel et al. 2003) and Ranidae (e.g., Perret 1977, Rödel and Bangoura 2004).

Biogeographic subdivisions are even found within West Africa (Schiøtz 1967, Penner et al. 2011). Only very few forest anuran species are still believed to be distributed in the Upper and Lower Guinea forest bioregion

(Rödel and Ernst 2001, Rödel et al. 2002, Schiøtz 2007). However, in most cases there is already unpublished evidence that they actually comprise complexes of cryptic species, supporting the above sketched biogeographic borders (Rödel et al. unpubl. data). This biogeographic separation of ranges also applies for all forest-dwelling species of the predominantly arboreal arthroleptid genus *Leptopelis* (compare e.g. Schiøtz 1999, 2007 although there might be an overlap in southern Nigeria, see discussion). Thus, it was very surprising that in his seminal book on the treefrogs of Cameroon, Amiet (2012) synonymized a West African forest *Leptopelis*, *L. spiritusnoctis* Rödel, 2007, type locality Taï National Park, Ivory Coast (Rödel 2007), with a species known from central African forests, *L. aubryi* (Duméril, 1856), type locality Gabon (Duméril 1856, Guibé 1950). Amiet (2012) further downgraded another West African forest-dwelling species, *L. macrotis* Schiøtz, 1967, only known from the western part of the Upper Guinean forests (Schiøtz 1999, type locality: Gola Rainforest National Park, Sierra Leone), to a subspecies of the mostly central African *L. millsoni* (Boulenger, 1895), type locality being the Niger Delta, Nigeria (Boulenger 1895). These taxonomic conclusions were based on morphological similarities and the (visual) comparisons of published call descriptions (Amiet 2012). If the mentioned taxa are indeed conspecific, they would constitute very remarkable exceptions from the above outlined general biogeographic pattern in African forest anurans.

As detailed morphological descriptions of these species show, they are morphologically very similar to each other (Perret 1962, Schiøtz 1967, 1999, Rödel 2007; Amiet 2012, Figs 1 & 2). However, frogs of this genus are often only offering few and delicate morphological differences (Schiøtz 1967, 1999, Amiet 2012, Frétey et al. 2012). We thus tested Amiet's (2012) conclusions, using molecular

techniques and detailed comparisons of call characteristics. Both methods are well established to clarify the taxonomic status of anurans when morphology alone is not very informative (Schiøtz 1973, Vieites et al. 2009).

Material and methods

Origin of specimens. Specimens of all four species have been collected by ourselves in various West African countries and Cameroon, respectively, or were obtained from the collections of the Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK) and the Museum für Naturkunde, Berlin (ZMB; see Table 1). Vouchers were euthanized in a chlorobutanol solution and thereafter preserved in 70% ethanol and deposited in the collections mentioned above. Tissue samples (toe tips, muscle or liver samples) were separately stored in pure ethanol.

Molecular data. We analyzed 454 and 522 base pairs (bp) of the mitochondrial 16S ribosomal RNA gene (Table 1). DNA was extracted using either QIAamp or DNeasy tissue extraction kits (Qiagen) or High Pure PCR Template Preparation kits (Roche). We used the primers 16SA-L and 16SB-H of Palumbi et al. (1991) to amplify the 16S rRNA gene. Standard PCR protocols were used and PCR products were purified using QIAquick purification kits (Qiagen) or High Pure PCR Product Purification kits (Roche). Purified templates were directly sequenced using an automated sequencer (ABI 377 or ABI 3100). Sequences were aligned using ClustalX (Thompson et al. 1997; default parameters) and manually checked using the original chromatograph data in the program BioEdit (Hall 1999). Uncorrected pairwise sequence divergence was calculated using PAUP* 4beta10 (Swofford 2001).

Table 1. Origin, museum collection and GenBank accession numbers of the four West and Central African *Leptopelis* species compared herein.

Species	Catalogue	GenBank #	Locality	Country
<i>L. aubryi</i>	ZFMK 73157	KF888326	Barrage de Tchimbélé	Gabon
<i>L. aubryi</i>	ZFMK 73236	KF888327	Fougamou	Gabon
<i>L. aubryi</i>	ZFMK 75456	KF888328	N'guengué	Cameroon
<i>L. aubryi</i>	ZFMK 87728	KF888329	Nkoelon	Cameroon
<i>L. aubryi</i>	ZFMK 89560	KF888330	Big Massaka	Cameroon
<i>L. aubryi</i>	ZFMK 89562	KF888331	Big Massaka	Cameroon
<i>L. spiritusnoctis</i>	ZMB 79578	KF888332	near Banambala	Guinea
<i>L. spiritusnoctis</i>	ZMB 79579	KF888333	near Gbanshue	Liberia
<i>L. spiritusnoctis</i>	ZMB 79580	KF888334	Mt. Jideh	Liberia
<i>L. spiritusnoctis</i>	ZMB 79581	KF888335	Sapo National Park	Liberia
<i>L. spiritusnoctis</i>	ZMB 79582	KF888336	Sapo National Park	Liberia
<i>L. spiritusnoctis</i>	ZMB 79583	KF888337	Sapo National Park	Liberia
<i>L. macrotis</i>	ZMB 79584	KF888338	near Gpaole	Guinea
<i>L. macrotis</i>	ZMB 79585	KF888339	near Yomou	Guinea
<i>L. macrotis</i>	ZMB 79586	KF888340	Sapo National Park	Liberia
<i>L. macrotis</i>	ZMB 79587	KF888341	Mt. Jideh	Liberia
<i>L. millsoni</i>	ZFMK 87708	KF888342	Nkoelon	Cameroon

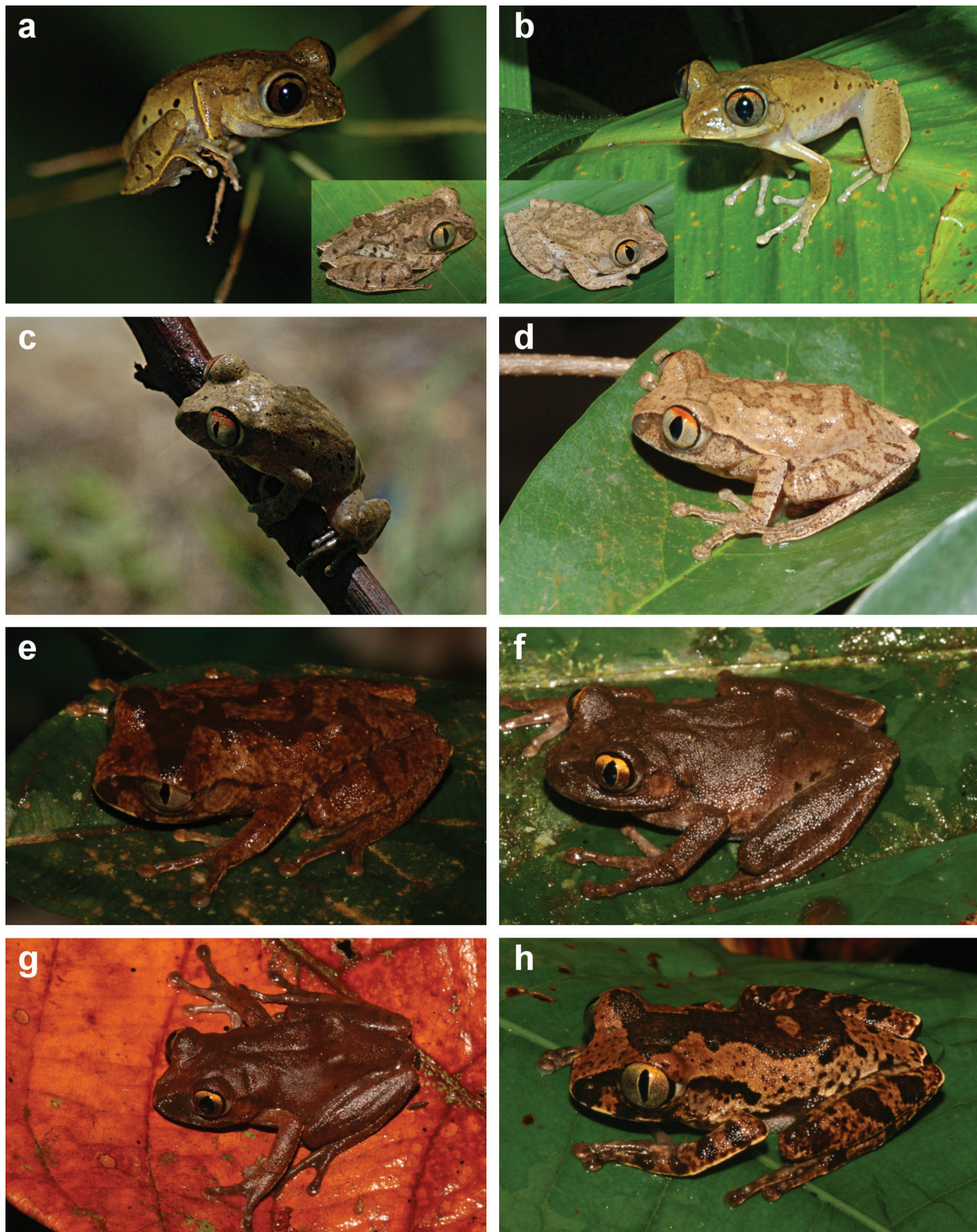


Figure 1. Life coloration and morphology in *Leptopelis aubryi* (a-c) and *L. spiritusnoctis* (d-h); a) *L. aubryi*, ZFMK 89562, call analyzed herein, and b) ZFMK 89560, call analyzed herein, both frogs from Big Massaka, Cameroon, large pictures color during night, inlet pictures color during daytime; c) *L. aubryi* (ZFMK 87728) from Nkoelon, Cameroon; d) *L. spiritusnoctis* (ZMB 79578) from Banambala, Guinea; e) *L. spiritusnoctis* (ZMB 79580) from Mt. Jideh, Liberia; f-h) *L. spiritusnoctis* (ZMB 79581-583) from Sapo National Park, Liberia.

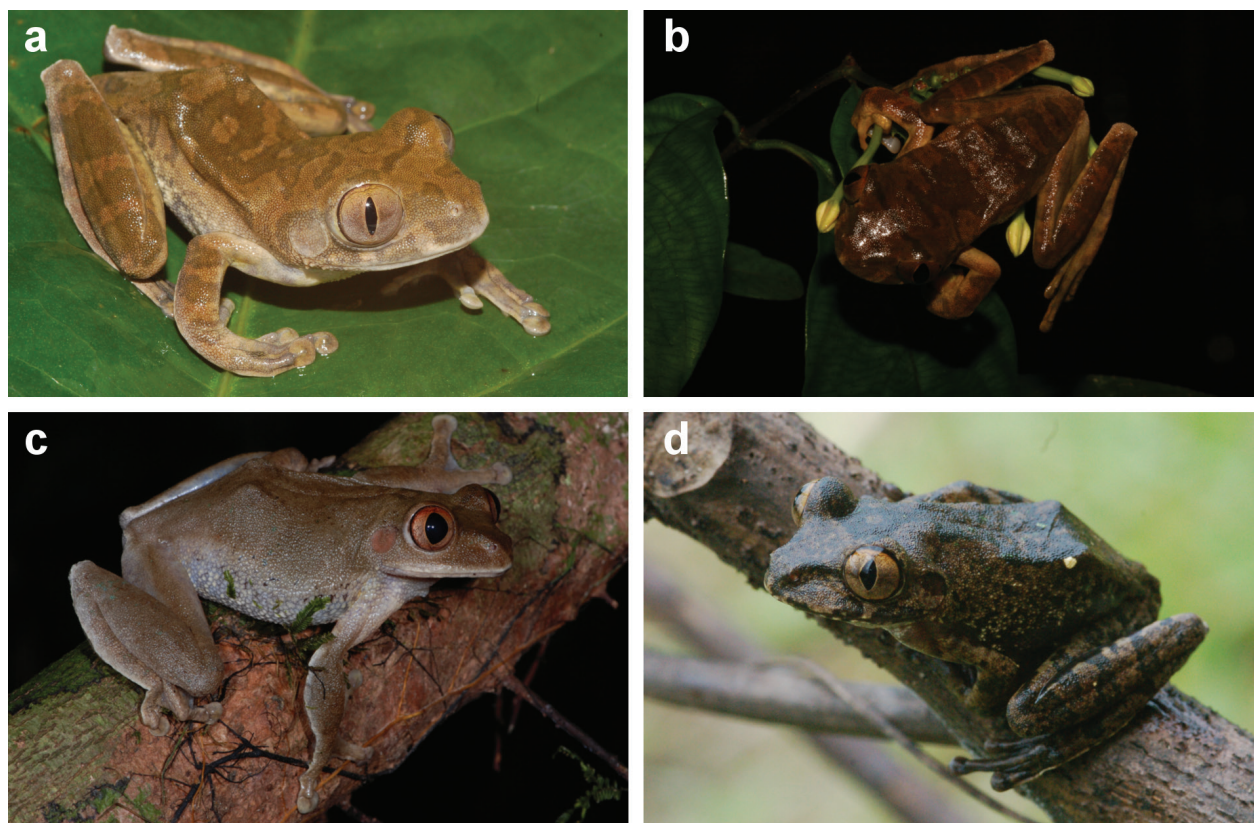


Figure 2. Life coloration and morphology in *Leptopelis macrotis* (a-c) and *L. millsoni* (d); *L. macrotis* from a) Yomou, Guinea (ZMB 79585); b) Mt. Jideh, Liberia (ZMB 79587); c) Gola Rainforest National Park, Sierra Leone (type locality, not collected); d) *L. millsoni* from Nkoelon, Cameroon (ZFMK 87708).

Acoustic data. Calls were either recorded by ourselves (various different recorders) and analyzed (44.1 kHz sample ratio, 16 bits resolution, FFT length = 256) with the software Soundruler 0.9.6 (Gridi-Papp 2007), extracted from the original call collection of A. Schiøtz (analyzed like our own recordings) or data have been gathered from literature (Schiøtz 1967, 1999, Amiet and Schiøtz 1974, Bosch et al. 2000). Values are presented as mean \pm standard deviation; figures were prepared using the Soundruler 0.9.6 (Gridi-Papp 2007). The majority of collected call characteristics are mainly used by females to discriminate between conspecific and heterospecific calls (Duellman and Trueb 1986, Gerhardt 1991, Littlejohn 2001, Ryan and Rand 2001). Thirteen call characteristics were measured: call duration, minimum frequency, maximum frequency, overall frequency range, dominant frequency, fundamental frequency, start value of dominant frequency, end value of dominant frequency, change in dominant frequency, number of pulses per call, pulse duration, interval of pulses and pulses per second.

Results

Molecular data. We analyzed 454 bp of the mitochondrial 16S ribosomal RNA gene for the *L. macrotis* / *L. millsoni* comparison and 522 bp for the *L. spiritusnoctis* / *L. aubryi* comparison. The uncorrected pairwise sequence

divergence between *L. aubryi* (N = 6) and *L. spiritusnoctis* (N = 6) ranged from 5.74–6.56% ($6.23 \pm 0.22\%$; N = 36). The intraspecific variation in *L. aubryi* ranged from 0–2.12% ($0.86 \pm 0.94\%$; N = 15). The intraspecific variation in *L. spiritusnoctis* ranged from 0–0.62% ($0.27 \pm 0.23\%$; N = 15). The uncorrected pairwise sequence divergence between *L. macrotis* (N = 4) and *L. millsoni* (N = 1) ranged from 11.07–11.30% (mean \pm sd: $11.24 \pm 0.12\%$; N = 4). The intraspecific variation in *L. macrotis* ranged from 0–0.22% ($0.11 \pm 0.12\%$; N = 6).

Acoustic data. For *L. aubryi* and *L. spiritusnoctis* we could analyze the “chuck” (Fig. 3) and “buzz” (Fig. 4) calls (compare Amiet and Schiøtz 1974 and Grafe et al. 2000 for intraspecific call variability in *Leptopelis*). Both call types showed distinct differences in a variety of different call characteristics between populations of different origin (Table 2). At first sight the “chuck” call of *L. aubryi* (N = 22) and *L. spiritusnoctis* (N = 13) looked similar (Schiøtz 1967). Both calls are short single notes. However, the call of *L. spiritusnoctis* (Ivory Coast) was almost twice as long (18.8 ± 4.2 ms) compared to the chuck of *L. aubryi* (10.0 ± 2.0 ms) from Cameroon (Fig. 3). Likewise the dominant frequency differed between these populations (Table 2). The “buzz” call of these two species also showed differences. The “buzz” of *L. spiritusnoctis* (N = 22) was longer (334.5 ± 122.5 ms) than in *L. aubryi* (duration 51–105 ms; N = 3) and comprised more pulses (Fig.

Table 2. Comparison of call characteristics of *Leptopelis spiritusnoctis* and calls assigned to *L. aubryi* (compare text). “Chucks” are interpreted as advertisement calls whereas “buzz” are regarded as territorial calls (compare Grafe et al. 2000). We summarize the mean \pm standard deviation values (range if only two values available) of call duration (CD); minimum frequency (minF); maximum frequency (maxF); frequency range (FR); dominant frequency (DF); fundamental frequency (FF); start value of the dominant frequency (sDF); end of the dominant frequency (eDF); change in frequency (CF); number of pulses per call (PC); pulse duration (PD); pulse interval (PI) and pulses per second (Pps). All call duration values are provided in [ms], and frequency values in [Hz], N= sample size (number of calls analyzed). We further provide the country where the calls have been recorded, as well as the data source. A. Schiøtz’s call data were analyzed based on his original recordings. Not all values were available for all recordings.

Species and call type	CD	minF	maxF	FR	DF	FF	sDF	eDF	CF	PC	PD	PI	Pps	Country	source
<i>spiritusnoctis</i> (chuck; N= 13)	18.8 \pm 4.2	2307.7 \pm 46.3	3143.4 \pm 80.5	835.5 \pm 62.5	2726.4 \pm 156.7	2726.4 \pm 156.7	2786.1 \pm 126.0	2660.2 \pm 215.4	(-)125.9 \pm 119.8					Ivory Coast	this paper
<i>aubryi</i> (chuck; N= 4)	43.0 \pm 8.0	1353.0	2019.0	1540.0 \pm 321.0	2049.0 \pm 461.0					162.0 \pm 225.0	13.0 \pm 2.0		281.0 \pm 31.0	Equatorial Guinea	Bosch et al. (2000)
<i>aubryi</i> (chuck; N= 22)	10.0 \pm 2.0	1512.3 \pm 238.4	3771.2 \pm 292.3	2259.1 \pm 440.8	2984.6 \pm 238.0	2984.6 \pm 238.0	3004.2 \pm 249.3	3009.8 \pm 217.2	5.6 \pm 159.8					Cameroon	this paper
<i>aubryi</i> (chuck; N= 1)	35.0	2547.0	3394.0	847.0	2842.0		2842.0	3015.0	173.0					eastern Nigeria	A. Schiøtz
<i>spiritusnoctis</i> (buzz; N= 22)	334.5 \pm 122.5	2525.0 \pm 114.0	3297.9 \pm 86.5	773.0 \pm 122.0	2996.9 \pm 26.2	2996.9 \pm 26.2	2799.5 \pm 43.5	2998.9 \pm 27.5	199.4 \pm 50.6	15.2 \pm 5.5	11.40 \pm 3.43	12.69 \pm 3.49	45.4 \pm 1.1	Ivory Coast	this paper
<i>aubryi</i> (buzz; N= 3)	51.0 – 105.0	2191.0	3562.0	1370.7	2906.3	2906.3	2719.0	2906.0	187.0	2.33 \pm 0.58	3.97 \pm 1.38	46.24 \pm 2.22	0.03 \pm 0.01	Cameroon	this paper

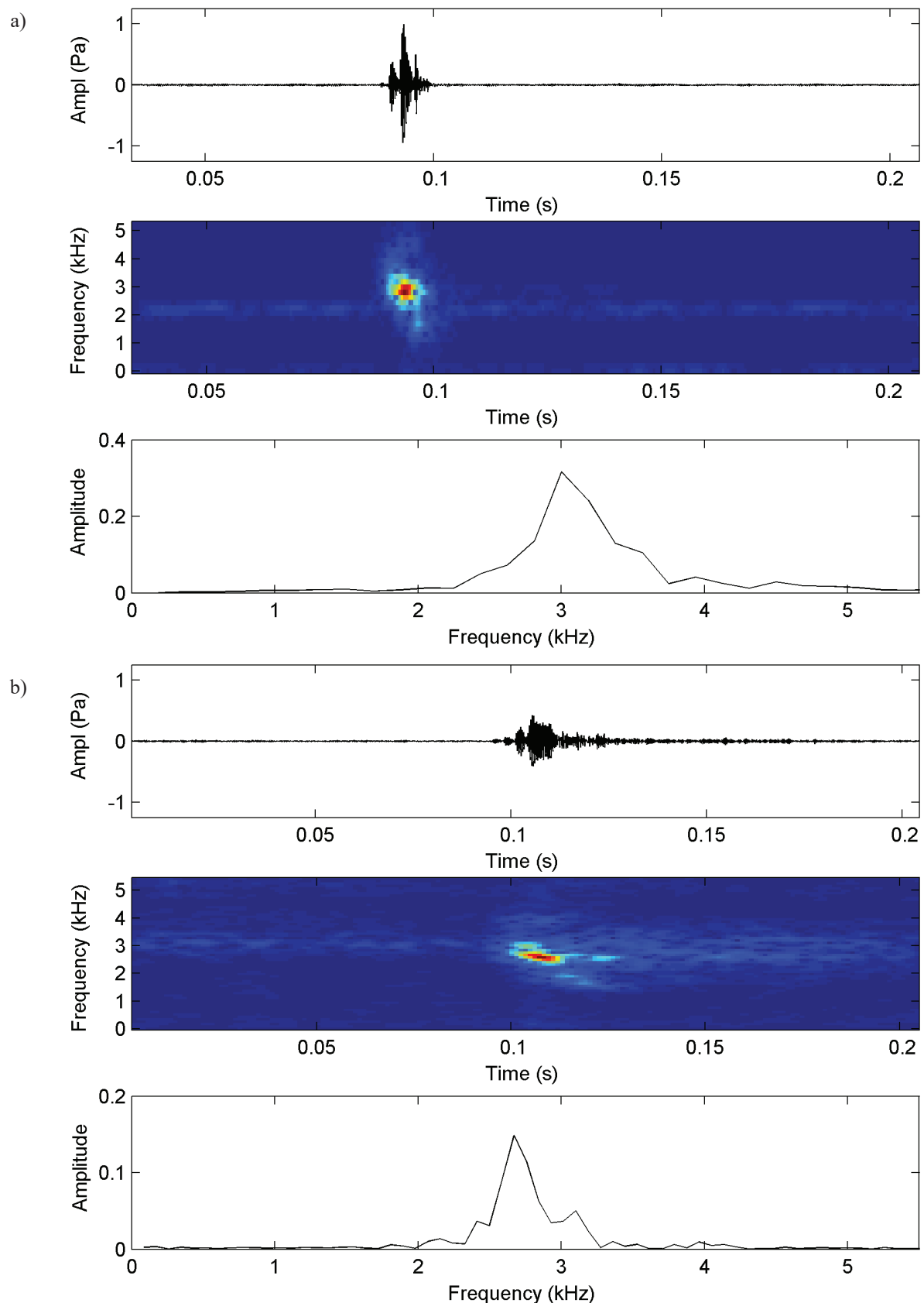


Figure 3. Oscillograms, audio spectrograms and power spectrograms of the “chuck” call of *Leptopelis aubryi* (ZFMK 89560) from Big Massaka, Cameroon (a) and *Leptopelis spiritusnoctis* from Taï National Park, Ivory Coast (b). This audio files are also available from the Tierstimmenarchiv at the Museum für Naturkunde, Berlin, through the following links: a) http://www.tierstimmenarchiv.de/recordings/Leptopelis_aubryi_DIG0174_01_short.mp3 (Suppl. material 2), b) http://www.tierstimmenarchiv.de/recordings/Leptopelis_spiritusnoctis_DIG0174_02_short.mp3 (Suppl. material 5).

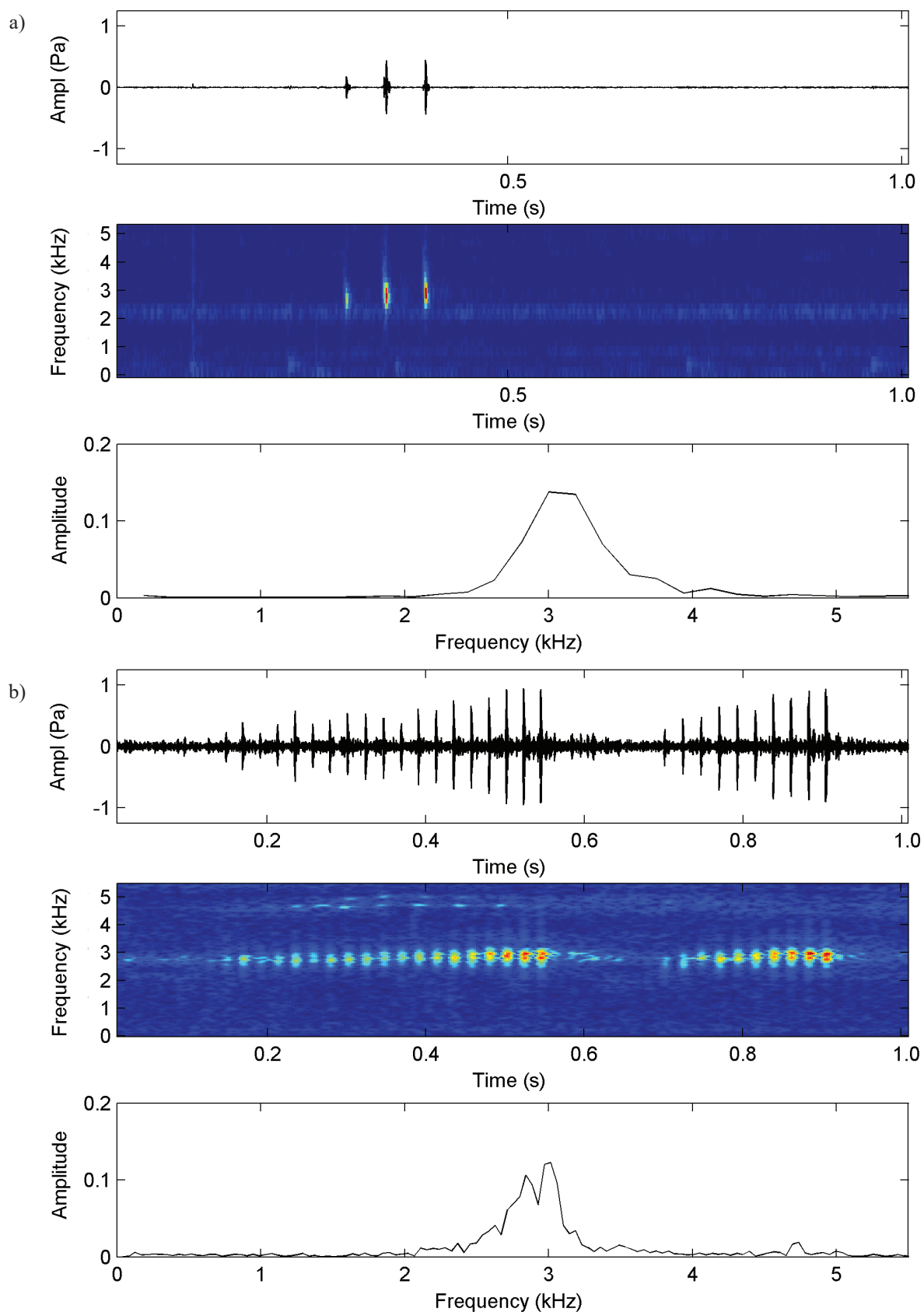


Figure 4. Oscillograms, audio spectrograms and power spectrograms of the buzz calls of *Leptopelis aubryi* (ZFMK 89560) from Big Massaka, Cameroon (a) and of *Leptopelis spiritusnoctis* (two calls) from Taï National Park, Ivory Coast (b). This audio files are also available from the Tierstimmenarchiv at the Museum für Naturkunde, Berlin, through the following links: a) http://www.tierstimmenarchiv.de/recordings/Leptopelis_aubryi_DIG0174_03_short.mp3 (Suppl. material 1), b) http://www.tierstimmenarchiv.de/recordings/Leptopelis_spiritusnoctis_DIG0174_04_short.mp3 (Suppl. material 4).

4; Table 2). However, the “chuck” calls of “*L. aubryi*” from different localities were extremely variable (Table 2). In contrast to our *L. aubryi* records from Cameroon “chucks” from eastern Nigeria and Equatorial Guinea (recordings A. Schiøtz and Bosch et al. 2000, respectively) were three to four times longer than in Cameroon (Table 2) and also differed in the dominant frequencies (Table 2). Some parameters of a particular *L. aubryi* population had similar values compared to *L. spiritusnoctis* calls. However, each “*aubryi*” population showed distinct differences to the *L. spiritusnoctis* calls, which exhibit only very little variation (Table 2; MOR, JP, MFB own experiences of calls heard throughout West Africa).

From *L. macrotis* we only know of one call type (Fig. 5). Our *L. macrotis* calls ($N = 3$; recorded in Cavally Forest Reserve, Ivory Coast) had the following call characteristics (always: mean \pm sd): call duration 388.0 ± 19.0 ms; note duration 92.0 ± 10.0 ms; duration of interval between notes 204.0 ± 15.0 ms; minimum frequency 1300.3 ± 18.5 Hz; maximum frequency 2432.0 ± 19.1 Hz; frequency range 1132.0 ± 19.1 Hz; dominant frequency and fundamental frequency 1729.8 ± 22.2 Hz; the dominant frequency starts at 1715.5 ± 22.2 Hz and ends with 1744.2 ± 27.2 Hz.

From *L. millsoni* we had no own recording available. The call of *L. millsoni* is described as a nasal “himp”,

consisting of a single tonal long note (approximately 170 ms) with a high frequency range (Amiet and Schiøtz 1974). *L. macrotis* calls, sounding like the meowing of a suffering cat to the human ear (“mmau”), consists of two (instead of one in *L. millsoni*) short, tonal notes with a smaller frequency range. In comparison to the spectra of *L. millsoni* the dominant frequency in *L. macrotis* (approximately 1500 Hz) seems to be similar, but *L. millsoni* may have a much lower fundamental frequency (approximately 250 Hz).

Discussion

The overall morphological and presumed acoustic similarity between *Leptopelis aubryi* with *L. spiritusnoctis* and that of *L. millsoni* with *L. macrotis* (Figs 1 & 2) led Amiet (2012) to consider the West African taxa to be a synonym or subspecies, respectively, of the similar Central African taxon. In fact, this judgment is not new and in particular *L. spiritusnoctis* (termed *L. hyloides* prior to Rödel 2007, see Rödel 2007 for discussion of the taxonomic history of this taxon) was treated as a synonym of *L. aubryi* (e.g. Lamotte and Perret 1961, Schiøtz 1963, Perret 1966). Likewise, West African populations (e.g. from south-eastern Guinea) of the large forest *Leptopelis*

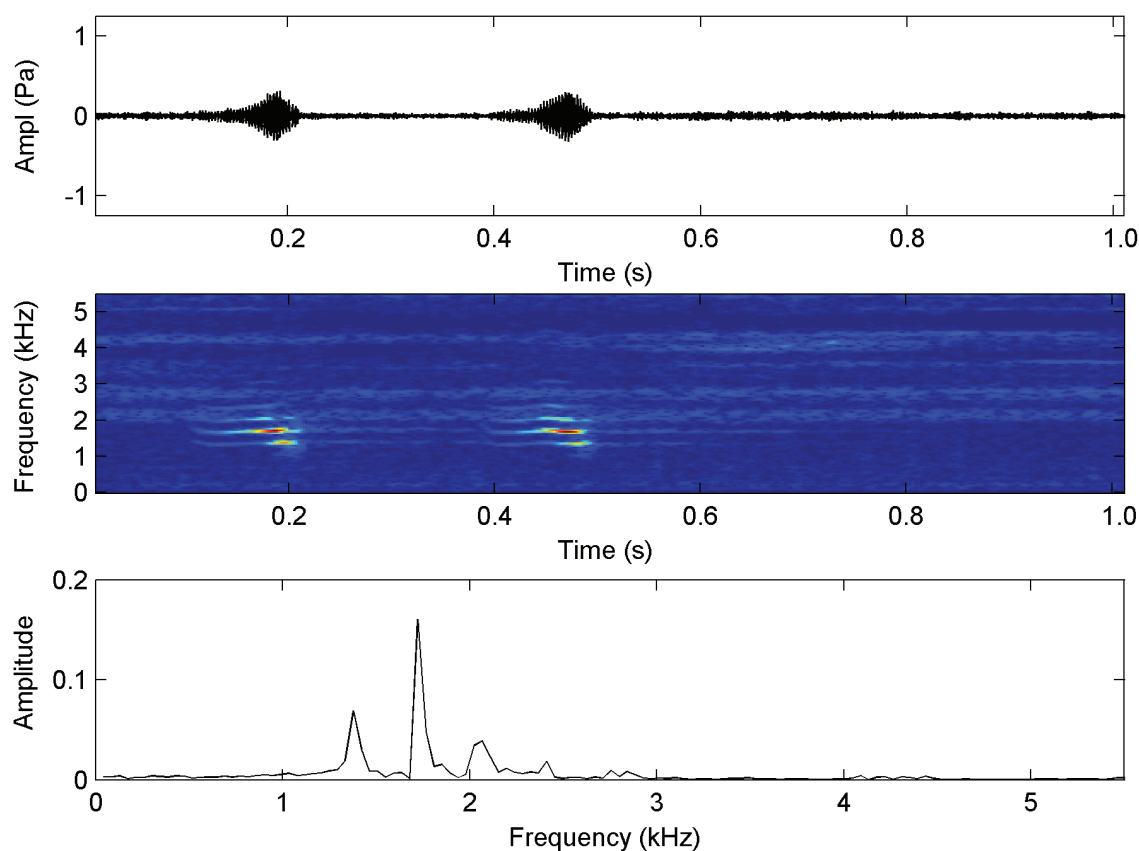


Figure 5. Oscillograms, audiospectrograms and power spectrograms of the advertisement call (“mmau”) of *Leptopelis macrotis* from Cavally Forest Reserve, Ivory Coast. This audio file is also available from the Tierstimmenarchiv at the Museum für Naturkunde, Berlin, through the following link http://www.tierstimmenarchiv.de/recordings/Leptopelis_macrotis_DIG0174_05_short.mp3 (Suppl. material 3).

have been assigned to *L. millsoni*, until Schiøtz (1967) described them as a distinct species. Thus, we can see the reasoning for the doubts on the validity of these two species. In contrast, as already outlined in the introduction, the distribution of the forest anurans, *L. millsoni* and *L. aubryi*, far into West Africa would be a remarkable exception from the almost general biogeographic pattern of western African anuran species (compare Schiøtz 1967, 2007, Penner et al. 2011).

Nevertheless, the Cross River in eastern Nigeria is not an all-or-nothing barrier, and a few Central African forest anurans indeed managed to occur further West reaching the Niger Delta or even beyond (e.g. *Hymenochirus boettgeri*, *Amietophrynus camerunensis*, *Nectophryne afra*, *Conraua crassipes*, *Acanthixalus spinosus*, *Afixalus paradosalis*; Akani et al. 2004, Onadeko and Rödel 2009). Also a few species of the Upper Guinean forests managed to cross the Dahomey Gap (a natural forest gap at the Gulf of Guinea coast roughly aligned with the countries Togo and Bénin; see Schiøtz 1967, Penner et al. 2011) to the east and reach the Niger River (e.g. *Leptopelis* cf. *occidentalis*, *Phrynobatrachus* cf. *plicatus*; Onadeko and Rödel 2009) or even Cameroon (e.g. *Hyperolius concolor*, *H. gutturalis*, *H. fusciventris*, *Phlyctimantis boulengeri*; Schiøtz 1967, 1999). The latter are farmbrush species (species tolerating forest degradation and commonly are most abundant in the forest-savanna ecotone; Schiøtz 1967, 1999, Rödel 2000, Rödel and Ernst 2001) and thus not strictly bound to forest vegetation and respective barriers (compare Schiøtz 2007), although different subspecies of the *Hyperolius* species are accepted to occur in West and Central Africa (e.g. Schiøtz 1967, 2007). The four *Leptopelis* species treated in this paper are strictly forest-dwelling.

Our molecular and acoustic data presented herein, clearly support the view that West and Central Africa comprise distinct anuran faunas, including the *Leptopelis* populations in question. The genetic distances between *L. aubryi* and *L. spiritusnoctis* in the studied 16S gene fragment (5.74–6.56%) and *L. millsoni* and *L. macrotis* (11.07–11.30%), respectively, by far exceed the values which are commonly assumed to indicate distinct species (3–5% in 16S; see Vieites et al. 2009 for general statement and e.g. Blackburn et al. 2008, Zimkus 2009, Rödel et al. 2012a, Zimkus and Gvodzik 2013 for values between distinct western African anuran species). Furthermore, our detailed call analyses revealed distinct differences between these taxa in almost all examined call parameters, in particular in parameters with low intraspecific variability (i.e. fundamental frequency, dominant frequency, call duration; Gerhardt 1991, Ryan and Rand 2001). That *L. spiritusnoctis* and *L. aubryi* have very different calls was already mentioned by Schiøtz (1967, 1999) and Amiet and Schiøtz (1974). In contrast Amiet and Schiøtz (1974) regarded the calls of *L. millsoni* and *L. macrotis* as almost identical. This could not be confirmed herein.

Taxonomic conclusions. Based on the molecular and acoustic data presented we conclude that synonymizing *L. spiri-*

tusnoctis with *L. aubryi* was not justified and thus resurrect *L. spiritusnoctis* for the small forest-dwelling *Leptopelis* species in the Upper Guinean forest zone (see Rödel 2007 for the distribution). Although our genetic samples of *L. aubryi* from Gabon and Cameroon were relatively similar (maximum difference in the 16S sequence being 2.12%), the large variation of call characteristics in *L. aubryi* might be an indication that this name currently covers a complex of cryptic species, indicating the needs for further taxonomic studies. Various names currently regarded as synonyms of *L. aubryi*, are available (see Frost 2013).

The downgrading of *L. macrotis* as a subspecies of *L. millsoni*, as currently understood, was likewise erroneous. However, the situation is more complex. West and Central African populations clearly represent distinct species. Currently, we cannot decide to which species the name *L. millsoni* (type locality is the Niger delta, geographically a part of the western species assemblage) should be applied. Unfortunately, so far we do not have genetic samples from Nigeria. Thus, we do not know which species occurs in Nigeria and we cannot even exclude that southern Nigeria harbors taxa which are morphologically similar, but distinct on the basis of genetics and acoustics from those adjacent to the east and west (compare e.g. Rödel et al. 2012b). To resolve this problem new material, tissue samples and call recordings, from the *L. millsoni* type locality are needed. If *L. millsoni* would be the valid name for the West African species, the name *L. guineensis* Ahl, 1929 (type: ZMB 20047; type locality: Makomo, Equatorial Guinea) would be available for the Central African species (Ahl 1929, Perret 1962). With respect to taxonomic stability we suggest to continue using the name *L. macrotis* and *L. millsoni* as defined by Schiøtz (1967, 1999) until new material becomes available.

Acknowledgements

We thank the various authorities from Cameroon, Ivory Coast, Guinea and Liberia for collection permits, and A. Schiøtz for making his call recordings available, through the sound library of the Cornell University. W. Böhme and D. Rödder (ZFMK) permitted tissue sampling from ZFMK vouchers. We thank Julia Barej for the permission to use her photos of life frogs. Jörn Köhler and Frank Glaw provided helpful critique.

References

- Ahl E (1929) Zur Kenntnis der afrikanischen Baumfrosch-Gattung *Leptopelis*. Sitzungsberichte der Gesellschaft naturforschender Freunde Berlin 1929: 185–222.
- Akani GC, Politano E, Luiselli L (2004) Amphibians recorded in forest swamp areas of the River Niger Delta (southeastern Nigeria), and the effects of habitat alteration from oil industry development on species richness and diversity. Applied Herpetology 2: 1–22.
- Amiet J-L (2012) Les rainettes du Cameroun. Édition J.-L. Amiet & La Nef des Livres, Nyons, Saint Nazaire.

- Amiet J-L, Schiøtz A (1974) Voix d'Amphibiens camerounais III. Hyperoliidae: genre *Leptopelis*. Annales de la Faculté des Sciences du Cameroun 17: 131–163.
- Barej MF, Schmitz A, Menegon M, Hillers A, Hinkel H, Böhme W, Rödel M-O (2011) Dusted off – the African *Amietophrynus superciliosus*-species complex of giant toads. Zootaxa 2772: 1–32.
- Blackburn DC, Kosuch J, Schmitz A, Burger M, Wagner P, Gonwouo LN, Hillers A, Rödel M-O (2008) A new species of *Cardioglossa* (Anura: Arthroleptidae) from the Upper Guinean forests of West Africa. Copeia 2008: 603–612.
- Blackburn DC, Gonwouo LN, Ernst R, Rödel M-O (2009) A new squeaker frog (Arthroleptidae: *Arthroleptis*) from the Cameroon volcanic line with redescrptions of *Arthroleptis adolfifriederici* Nieden, 1911 “1910” and *A. variabilis* Matschie, 1893. Breviora 515: 1–22.
- Blackburn DC, Gvoždík V, Leaché AD (2010) A new squeaker frog (Arthroleptidae: *Arthroleptis*) from the mountains of Cameroon and Nigeria. Herpetologica 66: 335–348.
- Bosch J, de la Riva I, Márquez R (2000) Advertisement calls of seven species of hyperoliid frogs, from Equatorial Guinea. Amphibia-Reptilia 21: 246–255.
- Boulenger GA (1895) Third report on additions to the batrachian collection in the Natural History Museum. Proceedings of the Zoological Society London 1894: 640–646 + 2 plates.
- Duellman WJ, Trueb L (1986) Biology of amphibians. Johns Hopkins University Press, New York.
- Duméril AHA (1856) Note sur les reptiles du Gabon. Revue et Magasin de Zoologie Pure et Appliquée, sér. 2, 8: 553–562.
- Ernst R, Agyei AC, Rödel M-O (2008) A new giant species of *Arthroleptis* (Amphibia: Anura: Arthroleptidae) from the Krokosua Hills Forest Reserve, south-western Ghana. Zootaxa 1697: 58–68.
- Frétey T, Dewynter M, Blanc C (2012) Amphibiens d'Afrique centrale et d'Angola – Clé de détermination illustrée des amphibiens du Gabon et du Mbini. Biotope, Mèze (Collection Parthénopé), Paris.
- Frost DR (2013) Amphibian species of the World: an online reference. Version 5.6 (9 January 2013). <http://research.amnh.org/herpetology/amphibia/index.html> [accessed on 8 November 2013]
- Gerhardt HC (1991) Female mate choice in treefrogs: static and dynamic acoustic criteria. Animal Behaviour 42: 615–635.
- Grafe TU, Steffen JO, Stoll C (2000) Vocal repertoire and effect of advertisement call intensity on calling behaviour in the West African tree frog, *Leptopelis viridis*. Amphibia-Reptilia 21: 13–23.
- Gridi-Papp M (2007) SoundRuler: Acoustic analysis for research and teaching. <http://soundruler.sourceforge.net> [accessed on 22 October 2013]
- Guibé J (1950) Catalogue des types d'amphibiens du Muséum national d'Histoire naturelle. Paris, nationally printed: 1–71.
- Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41: 95–98.
- Lamotte M, Perret J-L (1961) Contribution à l'étude des batraciens de l'Ouest Africain XIII. Les formes larvaires de quelques espèces de *Leptopelis*: *L. aubryi*, *L. viridis*, *L. anchietae*, *L. ocellatus* et *L. calcaratus*. Bulletin de l'Institut fondamental d'Afrique noire, Sér. A 23: 855–885.
- Lamotte M, Xavier F (1966) Étude comparée de deux espèces de *Phrynobatrachus* souvent confondues: *Phr. plicatus* Günther et *Phr. auritus* Boulenger. Bulletin de l'Institut fondamental d'Afrique noire, Sér. A 28: 1605–1619.
- Littlejohn MJ (2001) Patterns of differentiation in temporal properties of acoustic signals of anurans. In: Ryan MJ (Ed) Anuran communication. Smithsonian Institution Press, Washington D.C.: 102–120.
- Onadeko AB, Rödel M-O (2009) Anuran surveys in south-western Nigeria. Salamandra 45: 1–14.
- Palumbi SR, Martin A, Romano S, McMillan WO, Stice L, Grabowski G (1991) The simple fool's guide to PCR, Version 2.0. Privately published document compiled by S. Palumbi, department of Zoology, University of Hawaii, Honolulu, HI, 96822.
- Penner J, Wegmann M, Hillers A, Schmidt M, Rödel M-O (2011) A hotspot revisited – a biogeographical analysis of West African amphibians. Diversity and Distributions 17: 1077–1088.
- Perret J-L (1962) Révision des types de *Leptopelis* et note sur quelques *Hyperolius* (Amphibia Salientia) de la région camerounaise, conservés au Museum de Berlin. Revue Zoologique Botanique africaine 64: 235–246.
- Perret J-L (1966) Les amphibiens du Cameroun. Zoologische Jahrbücher (Systematik) 8: 289–464.
- Perret J-L (1977) Les *Hylarana* (Amphibiens, Ranidés) du Cameroun. Revue suisse de Zoologie 84: 841–868.
- Perret J-L, Amiet J-L (1971) Remarques sur les *Bufo* (Amphibiens Anoures) du Cameroun. – Annales de la Faculté des Sciences du Cameroun 5: 47–55.
- Rödel M-O (2000) Herpetofauna of West Africa, Vol. I: Amphibians of the West African savanna. Edition Chimaira, Frankfurt am Main.
- Rödel M-O (2007) The identity of *Hylambates hyloides* Boulenger, 1906 and description of a new small species of *Leptopelis* from West Africa. Mitteilungen aus dem Museum für Naturkunde Berlin, Zoologische Reihe 83: 90–100.
- Rödel M-O, Bangoura MA (2004) A conservation assessment of amphibians in the Forêt Classée du Pic de Fon, Simandou Range, south-eastern Republic of Guinea, with the description of a new *Ammirana* species (Amphibia Anura Ranidae). Tropical Zoology 17: 201–232.
- Rödel M-O, Doherty-Bone T, Talla Kouete M, Janzen P, Garrett K, Browne R, Gonwouo NL, Barej MF, Sandberger L (2012a) A new small *Phrynobatrachus* (Amphibia: Anura: Phrynobatrachidae) from southern Cameroon. Zootaxa 3431: 54–68.
- Rödel M-O, Ernst R (2000) *Bufo taiensis* n. sp., eine neue Kröte aus dem Taï-Nationalpark, Elfenbeinküste. herpetofauna 22 (125): 9–16.
- Rödel M-O, Ernst R (2001) Redescription of the tadpole of *Phlyctimantis boulengeri* Perret, 1986, with preliminary comments on the biology of the species. Alytes 18: 178–186.
- Rödel M-O, Kosuch J, Veith M, Ernst R (2003) First record of the genus *Acanthixalus* Laurent, 1944 from the Upper Guinean rain forest, West Africa, with the description of a new species. Journal of Herpetology 37: 43–52.
- Rödel M-O, Krätz D, Ernst R (2002) The tadpole of *Ptychadena aequiplicata* (Werner, 1898) with the description of a new reproductive mode for the genus (Amphibia, Anura, Ranidae). Alytes 20: 1–12.
- Rödel M-O, Onadeko AB, Barej MF, Sandberger L (2012b) A new polymorphic *Phrynobatrachus* (Amphibia: Anura: Phrynobatrachidae) from western Nigeria. Zootaxa 3328: 55–65.
- Ryan MJ, Rand AS (2001) Feature weighting in signal recognition and discrimination by Túngara frogs. In: Ryan MJ (Ed) Anuran communication. Smithsonian Institution Press, Washington D.C., 86–101.
- Schiøtz A (1963) The amphibians of Nigeria. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening 125: 1–92 + 4 plates.
- Schiøtz A (1967) The treefrogs (Rhacophoridae) of West Africa. Spolia zoologica Musei Haunienses 25: 1–346.

- Schiotz A (1973) Evolution of anuran mating calls, ecological aspects. In: Vial JL (Ed) *Evolutionary biology of the anurans, Contemporary research on major problems*. University of Missouri Press, Columbia: 311–319.
- Schiotz A (1999) *Treefrogs of Africa*. Edition Chimaira, Frankfurt am Main.
- Schiotz A (2007) Zoogeography of the treefrogs in Africa's tropical forests. *Alytes* 25: 1–37.
- Scotese CR (2001) PALEOMAP Project. Version 1 (2010). <http://www.scotese.com> [accessed on 11 November 2013]
- Seymour CL, De Klerk HM, Channing A, Crowe TM (2001) The biogeography of the Anura of sub-equatorial Africa and the prioritisation of areas for their conservation. *Biodiversity and Conservation* 10: 2045–2076.
- Swofford DL (2001) *Paup*: Phylogenetic analysis using parsimony (and other methods)*, version 4. Sinauer Associates, Sunderland / Massachusetts.
- Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG (1997) The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* 24: 4876–4882.
- Udvardy MDF (1975) A classification of the biogeographical provinces of the World. *IUCN Occasional Paper* 18: 1–50.
- Vieites DR, Wollenberg KC, Andreone F, Köhler J, Glaw F, Vences M (2009) Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. *Proceedings of the National Academy of Sciences USA* 106: 8267–8272.
- White F (1983) *The vegetation map of Africa*. UNESCO, Paris.
- Zimkus B (2009) Biogeographical analysis of Cameroonian puddle frogs and description of a new species of *Phrynobatrachus* (Anura: Phrynobatrachidae) endemic to Mount Oku, Cameroon. *Zoological Journal of the Linnean Society* 157: 795–813.
- Zimkus BM, Gvodzik V (2013) Sky Islands of the Cameroon Volcanic Line: a diversification hot spot for puddle frogs (Phrynobatrachidae: *Phrynobatrachus*). *Zoologica Scripta*, 42: 591–611.
- Zimkus BM, Rödel M-O, Hillers A (2010) Complex patterns of continental speciation: molecular phylogenetics and biogeography of sub-Saharan puddle frogs (*Phrynobatrachus*). *Molecular Phylogenetics and Evolution* 55: 883–900.

Supplementary material 1

Buzz call of *Leptopelis aubryi* (ZFMK 89560) from Big Massaka Cameroon

Authors: Mark-Oliver Rödel, Mike Emmrich, Johannes Penner, Andreas Schmitz, Michael F. Barej

Data type: multimedia

Explanation note: This audio file is also available from the Tierstimmenarchiv at the Museum für Naturkunde, Berlin, through the following link: http://www.tierstimmenarchiv.de/recordings/Leptopelis_aubryi_DIG0174_03_short.mp3.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <http://id.pensoft.net/suppl/efaa4ed0-b67d-11e3-b3d7-677993a45e50>

Supplementary material 2

Chuck call of *Leptopelis aubryi* (ZFMK 89560) from Big Massaka, Cameroon

Authors: Mark-Oliver Rödel, Mike Emmrich, Johannes Penner, Andreas Schmitz, Michael F. Barej

Data type: multimedia

Explanation note: This audio file is also available from the Tierstimmenarchiv at the Museum für Naturkunde, Berlin, through the following link: http://www.tierstimmenarchiv.de/recordings/Leptopelis_aubryi_DIG0174_01_short.mp3.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <http://id.pensoft.net/suppl/f70dc990-b67d-11e3-be98-bfa608e0b81c>

Supplementary material 3

Advertisement call of *Leptopelis macrotis* from Cavally Forest Reserve, Ivory Coast

Authors: Mark-Oliver Rödel, Mike Emmrich, Johannes Penner, Andreas Schmitz, Michael F. Barej

Data type: multimedia

Explanation note: This audio file is also available from the Tierstimmenarchiv at the Museum für Naturkunde, Berlin, through the following link: http://www.tierstimmenarchiv.de/recordings/Leptopelis_macrotis_DIG0174_05_short.mp3.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <http://id.pensoft.net/suppl/f8233130-b67d-11e3-83b8-f99820085417>

Supplementary material 4

Two buzz calls of *Leptopelis spiritusnoctis* from Tai National Park, Ivory Coast

Authors: Mark-Oliver Rödel, Mike Emmrich, Johannes Penner, Andreas Schmitz, Michael F. Barej

Data type: multimedia

Explanation note: This audio file is also available from the Tierstimmenarchiv at the Museum für Naturkunde, Berlin, through the following link: http://www.tierstimmenarchiv.de/recordings/Leptopelis_spiritusnoctis_DIG0174_04_short.mp3.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while

maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <http://id.pensoft.net/suppl/f8f6fbf0-b67d-11e3-bf64-7bda05088d06>

Supplementary material 5

Chuck call of *Leptopelis spiritusnoctis* from Tai National Park, Ivory Coast

Authors: Mark-Oliver Rödel, Mike Emmrich, Johannes Penner, Andreas Schmitz, Michael F. Barej

Data type: multimedia

Explanation note: This audio file is also available from the Tierstimmenarchiv at the Museum für Naturkunde, Berlin, through the following link: http://www.tierstimmenarchiv.de/recordings/Leptopelis_spiritusnoctis_DIG0174_02_short.mp3.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <http://id.pensoft.net/suppl/f9b6f090-b67d-11e3-9cb7-1b2703913844>

The Primary Types of Scathophagidae (Diptera) in the Museum für Naturkunde Berlin, and Senckenberg Deutsches Entomologisches Institut, Germany

Andrey L. Ozerov¹

¹ Zoological Museum, Moscow State University, Bol'shaya Nikitskaya 6, Moscow 125009, Russia

Corresponding author: Andrey L. Ozerov (ozarov2455@rambler.ru)

Abstract

Received 12 Nov 2013
Accepted 8 Jan 2014
Published 28 March 2014

Academic editor:
Michael Ohl

Key Words

Diptera
Scathophagidae
Museum für Naturkunde Berlin
Senckenberg Deutsches
Entomologisches Institut
collection
type specimens

The primary types (holotypes, lectotypes, and syntypes) of the Diptera family *Scathophagidae* housed in the Museum für Naturkunde der Humboldt-Universität zu Berlin and Senckenberg Deutsches Entomologisches Institut, Müncheberg, both in Germany, are revised. 50 species of Scathophagidae are enumerated. The species are listed alphabetically, and the account concludes with a systematic nomenclatural summary. Detailed information is given on the specimens, their labelling and their condition. 28 lectotypes are designated [*Acanthocnema latipennis* Becker, 1894 (Poland); *Amaurosoma articulata* Becker, 1894 (Poland); *Amaurosoma inermis* Becker, 1894 (Latvia or Estonia); *Amaurosoma minuta* Becker, 1894 (Latvia or Estonia); *Amaurosoma nigrifrontata* Becker, 1894 (Italy); *Amaurosoma nutans* Becker, 1894 (Poland); *Cochliarium castanipes* Becker, 1894 (Switzerland); *Cochliarium lasiostoma* Becker, 1894 (Switzerland); *Cordylura aberrans* Becker, 1894 (Sweden); *Cordylura bezzii* Sack, 1937 (Italy); *Cordylura biseta* Loew, 1864 (Denmark or Germany); *Cordylura dasyprocta* Loew, 1864 (Sweden); *Cordylura femoralis* Loew, 1864 (Austria); *Cordylura glaucescens* Loew, 1864 (Germany); *Cordylura melaleuca* Loew, 1873 (Greece); *Cordylura melanacra* Loew, 1873 (Poland); *Cordylura nigriventris* Loew, 1864 (Poland); *Cordylura opaca* Loew, 1864 (Austria); *Cordylura pecticornis* Loew, 1864 (Russia); *Cordylura umbrosa* Loew, 1873 (Slovakia); *Cordylura unicolor* Loew, 1864 (Spain); *Parallelomma longicornis* Hendel, 1913 (Taiwan); *Parallelomma media* Becker, 1894 (Poland); *Pselaphephila loewi* Becker, 1894 (Poland); *Scatophaga dasythrix* Becker, 1894 (Russia); *Scatophaga islandica* Becker, 1894 (Iceland); *Scatophaga mollis* Becker, 1894 (Russia); *Scatophaga ordinata* Becker, 1894 (Switzerland)]. Three new synonyms are established: *Amaurosoma nigrifrontata* Becker, 1894 is a new junior synonym of *Nanna tibiella* (Zetterstedt, 1838); *Cordylura rubifrontata* Becker, 1894 is a new junior synonym of *Cordylura aberrans* (Becker, 1894); *Cordylura unicolor* Loew, 1864 is a new junior synonym of *Cordylura albipes* (Fallén, 1819).

Introduction

The Museum für Naturkunde an der Humboldt-Universität zu Berlin (ZMHB) and Senckenberg Deutsches Entomologisches Institut (SDEI) contain the most important Diptera collections in Europe. These include the collections of Friedrich Hermann Loew (1807–1878) and Theodor Becker (1840–1928), two of the leading European dipterists of their day, who described numbers of Scathophagidae and whose collections are of significant value.

Also, there are type specimens of scathophagid species described by P. Sack (1865–1946), L. Oldenberg (1863–1931), F. G. Hendel (1874–1936), E. M. Hering (1893–1967), and types of several species described by myself in 1997, 1999, and 2013 in both the ZMHB and SDEI.

Each specimen in Loew's and Becker's collections, which were handed over to ZMHB, has its own number, but each number may refer to a single specimen or to a series of conspecific specimens. There are notebooks that give the key to these code numbers: the "Catalog Gen-

eral Musei Zoologici Berolinensis" (Diptera I, II) for Loew's collection and four notebooks for Becker's collection (Becker Catalog Diptera: Tome I (1882–1887; Nos 1–14179), Tome II (1887–1893; Nos 14180–33839), Tome III (1894–1906; Nos 13840–53642), and Tome IV (1906–1914; Nos 53641–62427)). These notebooks contain information about the number of specimens, localities, dates of capture and year.

Loew's collection also contains many syntypes of scathophagid species described by Zetterstedt in 1838 and 1846. This material requires special examination together with Zetterstedt's own collection in the Museum of Zoology of Lund University (Sweden) and is not discussed in this paper except for those specimens which were described by Loew or Becker as new species (for example *Cordylura aberrans* Becker, 1894 or *Cordylura dasyprocta* Loew, 1864, see below).

The Scathophagidae types in the ZMHB and SDEI were examined by the late J.R. Vockeroth in 1954–1964 who designated numerous lectotypes, but these designations were not published.

All the species discussed here are listed alphabetically. Detailed information is given on the specimens, their labelling and their condition. Finally, the current taxonomic identity is provided.

The following abbreviations are used for the depositories of specimens used or discussed in this paper: MNHP – Muséum National d'Histoire Naturelle, Paris, France; NMW – Naturhistorisches Museum Wien, Vienna, Austria; SDEI – Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany; ZISP – Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russia; ZMHB – Museum für Naturkunde, Berlin, Germany; ZMUH – Zoological Museum, Helsinki University, Helsinki, Finland. ZMUM – Zoological Museum, Moscow State University, Moscow, Russia.

List of the taxa

***aberrans* Becker, 1894: 91 (*Cordylura*).**

Described from an unspecified number of both sexes: "Zett., Dipt. Sc. V. 2001, 6, *Cord. rufimana*".

ZMHB material: 1 male syntype was found in Loew's collection among *C. rufimana*. It is labelled "Lappon. Bohem.", "2633", "*Cordylura rufimana*", "*Cordilura rufimana* Meig det. F. Šifner ♂". There is every reason to believe that this specimen is a syntype of *Cordylura aberrans*. Therefore this male (thorax damaged in posterior part, scutellum missing; right wing missing, left hind leg glued to the pin, abdomen dissected and stored in a microvial with glycerol on the same pin) has been labelled and is designated herewith as lectotype. Type-locality: "Lapponia" (Sweden). Genitalia was examined and found to be conspecific with that shown in Hackman's figures for *C. aberrans* (Hackman 1956: 21, fig. 77).

Current name: A good species of *Cordilura* Fallén, 1810, correctly recognised by recent authors.

***alata* Becker, 1914: 127 (*Scopeuma*).**

Described from 6 specimens of both sexes from Kenya. 4 of them are in MNHP and a lectotype was designated from these type-specimens (Ozerov 2010b: 301).

ZMHB material: male and female syntypes, both in very good condition, are conspecific with lectotype and have been labelled as paralectotypes. Both specimens have the same labels: "Afrique or. anglaise, Mt Kenya, verst Ouest, zone des forêts, Alluaud & Jeanne", "Forêts Moyennes, Bambous supér, 2800–3200 m, Janv. 1912, St 41", "Scatophaga alata Beck. det. Becker".

Current name: *Scathophaga alata* (Becker, 1914).

***albidohirta* Becker, 1907a: 254 (*Scatophaga*).**

Described from "8 Exemplare aus Ost-Zaidam in O.Tibet: Kurlyk am Fl.Baingol (24 und 28.V.95), Fl. Bomyn oder Itschegyn (Ende VI.95), zwischen dem See Itsche und dem Fl. Orogyn (1–8.VII.95), am Fl. Orogyn südlich von W.-Nan-schan (3–20.VII.95); Gobi in Chines. Turkestan: Kara-Tübe, westlich von Hami (15. IX.95) [Roborowski]". 7 of them are in ZISP and a lectotype was designated from these syntypes (Ozerov and Krivosheina 2011: 105).

ZMHB material: a male syntype (half of left wing, mid and hind left legs missing, abdomen dissected and glued on card on the same pin), labelled "оз. Иче — р Орогын с Цайдам, ц Гоби РобКозлов 1–3 VII 95", "Gobi. Asien 51896. VII", "albidohirta Beck.", "ZMU Berl.", "Scatophaga albidohirta Beck. SYN-TYPE labelled 1954 by J.R. Vockeroth", is conspecific with the lectotype and has been labelled as paralectotype.

Current name: *Scatophaga albidohirta* (Becker, 1907).

***amica* Ozerov, 1999: 511 (*Langechristia*).**

Described from a single female from Russian Far East.

SDEI material: holotype female, labelled "RUSSIA: Primorskiy Kray Sichote-Alin, Biol. Stat. 30 km SE Chuguyevka, 44.05 N, 134.12 E), 650 m, Malaisefalle 31.V.–03.VI.1993 leg. C. Lange & J. Ziegler", "Holotypus ♀ *Langechristia amica* sp.nov. det. A.L. Ozerov, 1997". Type-locality: 30 km SE Chuguyevka (44.05N, 134.2E), 650 m (Primorskiy Kray, Russia).

Current name: *Langechristia amica* Ozerov, 1999.

***arctica* Becker, 1897: 398 (*Scatophaga*).**

Described from an unspecified number specimens of both sexes taken on Novaya Zemlya. 2 syntypes are housed in ZISP and a lectotype was designated from these type-specimens (Ozerov and Krivosheina 2013: 143), which is conspecific with *Scathophaga miltisetosa* (Holmgren, 1883).

ZMHB material: a male syntype (left mid leg missing), labelled "Novaja Semlja, mons Tschernyschew, G. Ja-

cobson, 5.VIII.96”, “41956”, “arctica Becker”, “Scathophaga arctica Beck. SYNTYPE labelled 1954 by J.R. Vockeroth”, “Scathophaga apicalis Curt. Det. 1962 J.R. Vockeroth”, has been labelled as paralectotype. It is *Scathophaga multisetosa*.

Current name: A junior synonym of *Scathophaga multisetosa* (Holmgren, 1883) as currently understood.

arctica Becker, 1907b: 412 (*Pselaphephila*).

Described from an unspecified number of male specimens from “Ost-Grönland”.

ZMHB material: male syntype in good condition, labelled “♂ Hekla Havn [in English =Hekla Harbor 70.47N 26.18W] 29–7.[18]92. Deichmann”, “36008”, “Pselaph. arctica Beck. det. Becker”, “Gonarticus arcticus Beck. det. J.R. Vockeroth 1954”, “Pselaphephila arctica PARALECTOTYPE labelled 1954 by J.R. Vockeroth”. I have labelled it as syntype.

Current name: *Gonarticus arcticus* (Becker, 1907).

articulata Becker, 1894: 117 (*Amaurosoma*).

Described from an unspecified number of male specimens from “Schlesien”.

ZMHB material: 2 male syntypes. One male syntype in very good condition, labelled “Rothkirch 6/V 29986”, “Amaurosoma LECTOTYPE articulata Beck. Designated by J.R. Vockeroth 19”, “Amaurosoma articulatum (Ztt.) ♂ Det. F. Šifner”, has been labelled and is designated herewith as lectotype of *Amaurosoma articulata*. Type-locality: “Rothkirch” (Czerwony Kościół [near Legnica: ca. 51.186N, 16.061E], Poland). The second male (good condition), labelled “Rothkirch 6/V 29986”, “PARALECTOTYPE Amaurosoma articulata Beck. labelled by J.R. V.”, “Nanna articulata Beck. Det. J.R. Vockeroth 1962”, has been labelled as paralectotype.

Current name: *Nanna articulata* (Becker, 1894), correctly recognised by recent authors.

bezzii Sack, 1937: 18 (*Cordylura*).

Described an unspecified number of both sexes from “Livrio (Adamellagruppe)”.

ZMHB material: 2 males, 1 female syntypes. One male is in very good condition, labelled “Livrio 16.VI.00”, “Italien VI. 46052”, “Cordylura Bezzii. Beck det. Becker”, “Homotype Cordylura bezzii Sack Compared by J.R. Vockeroth 1956”, “Bucephalina bezzii Sack det. 1957 J.R. Vockeroth”, “Syntypus”. The other male has labels “Livrio 16.VI.00”, “Italien VI. 46052”, “Typus”, “Homotype Cordylura bezzii Sack Compared by J.R. Vockeroth 1956”, “Bucephalina (Neogimnomera) bezzii Sack det. 1957 J.R. Vockeroth”. The female has labels “Livrio 11.VII.00”, “48264”, “Cordylura Bezzii Beck. det. Becker”, “Cordylura Bezzii in lit Bek.”, “Bucephalina bezzii Sack det. 1957 J.R. Vockeroth”,

“Syntypus”. All three syntypes have been labelled as paralectotypes.

SDEI material: 2 males and 2 females syntypes, all in very good condition. One of males is labelled “Livrio 16.VI.00”, “Cordylura Bezzii in litt. Beck”, “Cordylura Bezzii sp.n. det. Sack”, “coll. Oldenberg”, “Typus ♂”, “Cordylura bezzii Sack LECTOTYPE Designated by J.R. Vockeroth 19”, “Lectotypus”. I have designated it herewith and labelled it as lectotype of *Cordylura bezzii*. Type-locality: Livrio (Italy). Male and female syntypes both labelled “Livrio 16.VI.00”, “coll. Oldenberg”, “Cordylura Bezzii sp.n. det. Sack”, “Cordylura bezzii Sack PARALECTOTYPE labelled 1954 by J.R. Vockeroth”, “Paralectotypus”, and one female syntype with labels “Livrio 16.VI.00”, “coll. Oldenberg”, “Cordylura Bezzii Beck det. Bezzii”, “Cordylura Bezzii sp.n. det. Sack”, “Typus ♀”, “Cordylura bezzii Sack PARALECTOTYPE labelled 1954 by J.R. Vockeroth”, “Paralectotypus”, have all been labelled as paralectotypes.

Current name: a good species. Šifner (2008: 116) listed it in the genus *Bucephalina* Malloch, 1919, which I consider as a subgenus of *Cordilura*.

biseta Loew, 1864: 21 (*Cordylura*).

Described from male and female syntypes from “Dänemark, ganz Deutschland”.

ZMHB material: one well preserved male, labelled “P. Seitz 27.4.51” or “P. Sulz, 27.4.51” (a family name, difficult to read), “Coll. H. Loew”, “11399”, “Cordylura biseta m.”, “Type”, “Cordilura picipes Meigen det. Šifner ♂”. It has been labelled and is herewith designated as lectotype. It is *Cordilura picipes* (Meigen, 1826).

Current name: A junior synonym of *Cordilura picipes* (Meigen, 1826), correctly recognised by recent authors.

breviventris Loew, 1873: 250 (*Cordylura*).

Described from male sex, number not stated, taken from “Sarepta”. Studied by Ozerov (2010c: 5), who designated a lectotype.

ZMHB material: lectotype male (abdomen dissected and glued on card on the same pin, right fore and hind tibiae missing), labelled “Sarepta Christ”, “11434”, “Cordylura breviventrus Lw.”, “Coll. H. Loew”, “Type”, “Cordylura breviventrus Loew LECTOTYPE designated by J.R. Vockeroth 19”. Type-locality: “Gegend von Sarepta” [=Krasnoarmeisk in Volgogradskaya Oblast’, ca. 48.512N 44.554E] (Russia).

Current name: synonymized with *Spathephilus nigriventrus* (Loew, 1864) by Ozerov (2010c: 5).

castanipes Becker, 1894: 185 (*Cochliarium*).

Described an unspecified number of both sexes from “St. Moritz”.

ZMHB material: 2 male and 1 female syntypes, all in excellent condition. The male labelled “St. Moritz 5/7 10777” [= 5 July 1886], *Cochliarium castanipes* Becker LECTOTYPE Designated by J.R. Vockeroth 19”, “Zool. Mus. Berlin”, has been labelled and is herewith designated as lectotype. Type-locality: “St. Moritz” (Switzerland).

The male with labels “St. Moritz 1/7 10294”, *Cochliarium castanipes* Becker PARALECTOTYPE labelled 1954 by J.R. Vockeroth” and the female “St. Moritz 30/6 10132”, *Cochliarium castanipes* Becker PARALECTOTYPE labelled 1954 by J.R. Vockeroth” have been labelled as paralectotypes.

Current name: *Gimnomera castanipes* (Becker, 1894).

***dasyprocta* Loew, 1864: 25 (*Cordylura*).**

Described from an unspecified number of both sexes from “Sweden” taken from the syntypes of *Cordylura caudata* Zetterstedt, 1838.

ZMHB material: 3 males and 1 female syntypes. A male (right mid leg missing, right wing slightly torn) labelled “Cord. caudata Zett. Lappon. Bohem.*”, “Coll. H. Loew”, “11438”, “*Cordylura dasyprocta* m.”, “type”, “*Cordylura dasyprocta* Lw. Lectotype Designated by J.R. Vockeroth 19”, has been labelled and is herewith designated as lectotype of *Cordylura dasyprocta*. Type-locality: “Sweden”.

One male (good condition) labelled “Palmén”, “Lapponia”, “Coll. H. Loew”, “Type”, “*Cordylura dasyprocta* Lw. PARALECTOTYPE labelled 1954 by J.R. Vockeroth”, conspecific with lectotype, one male syntype (badly damaged: head, abdomen, wings, right mid leg and both hind legs missing) labelled “C. caudata Zett. Lapp. Boh.*”, “Coll. H. Loew”, “type”, “*Cordylura dasyprocta* Lw. PARALECTOTYPE labelled 1954 by J.R. Vockeroth”, which seems to be conspecific with the lectotype, and female syntype (good condition) labelled “Bhn”, “Dv”, “caudata Ztt. Boh. *”, “Coll. H. Loew”, “type”, “*Cordylura dasyprocta* Lw. PARALECTOTYPE labelled 1954 by J.R. Vockeroth”, conspecific with lectotype; all three have been labelled as paralectotypes.

Current name: *Okeniella dasyprocta* (Loew, 1864), correctly recognised by recent authors.

***dasythrix* Becker, 1894: 173 (*Scatophaga*).**

Described from an unspecified number of both sexes from “aus der Behringstrasse”.

ZMHB material: one well preserved male, labelled “xxx Miednaja blizko w Behrynga. July P. Dybowski 1882” (xxx = illegible), “30030”, “*Scatophaga dasythrix* Becker LECTOTYPE Designated by J.R. Vockeroth 19”, has been labelled and is herewith designated as lectotype of *Scatophaga dasythrix*. Type-locality: Island Medny (Comandor Is., Russia).

Current name: *Scathophaga dasythrix* (Becker, 1894), correctly recognised by recent authors.

***fascipes* Becker, 1894: 160 (*Spathiophora*).**

In the original paper described from an unspecified number of both sexes: “Zett., Cord. hydromyzina var. b, Dipt. Scand. V. 2037, 35” and only specimens mentioned by Zetterstedt for his var. B can be considered as syntypes. Four specimens are mentioned in “Becker Catalog Diptera” (No 30109) as *Spathiophora fascipes* from “Dorpat”; one of them was sent to F. Hendel.

ZMHB material: 2 females, both in very good condition. One of them labelled “15/7 86”, “Dorpat” 30109”, “hydromyzina Fall. Det. 1954 J.R. Vockeroth”. The other female is identical labelled but with the date “1/7 86”. Both are *Spaziphora hydromyzina* (Fallén, 1819).

There is a male labelled by J.R. Vockeroth as lectotype of *Spathiophora fascipes*. This specimen was taken from “Rügen”, was mentioned in “Becker Catalog Diptera” under No 30112 as *Spaziphora hydromyzina* Fallén.

All these 3 specimens are not from Zetterstedt’s collection and therefore they cannot be syntypes of *S. fascipes*.

Current name: *Spaziphora hydromyzina* (Fallén, 1819) as currently understood.

***femoralis* Loew, 1864: 18 (*Cordylura*).**

Described from an unspecified number of females from “Kärnthen”. A single specimen is mentioned in the “Catalog General Musei Zoologici Berolinensis” as *Cordylura femoralis* (No.11387). It has been studied, labelled and is herewith designated as lectotype.

ZMHB material: lectotype female (both hind legs missing, abdomen glued back on to the body, right wing damaged) labelled “Schneeb Jul. 55”, “11387”, “Coll. H. Loew”, “*Cordylura femoralis* Lw.”, “Holotypus Nr.”, “*Norellisoma femorale* (Loew) ♀ Det. F. Šifner 1970”. Type-locality: “Kärnthen” (Austria, Carinthia, Schneeberg).

Current name: *Norellisoma femorale* (Loew, 1864).

***fulvifrons* Ozerov, 1997: 1427 (*Cordilura*).**

Described from 2 males and 1 female from Khabarovskiy Kray (Russia).

SDEI material: holotype male (Ozerov 1997: 1427, original designation) in excellent condition, labelled “RUSSIA: Khabarovskiy Kray Boitsovo 20 km N Bikin Bolsoi Solntsepyok Hill 47.02N 134.21E 25.V.1993 leg. C. Lange & J. Ziegler”. Type-locality: Boitsovo 47.02N 134.21E (Russia, Khabarovskiy Kray). Paratype female with the same label but with the date 24–27.V.1993 is conspecific with the holotype. The second male paratype is kept in ZMUM (Ozerov 1997: 1427).

Current name: *Cordilura fulvifrons* Ozerov, 1997.

***glaucescens* Loew, 1864: 23 (*Cordylura*).**

Described from an unspecified number of the female sex from “Kreuth; Gerstaecker”. A single specimen is mentioned in the “Catalog General Musei Zoologici Berolinensis” as *Cordylura glaucescens* (No.11412). It has been studied, labelled and is herewith designated as lectotype.

ZMHB material: lectotype female (condition very good, but right postpedicel and left hind leg missing), labelled “Kreuth Gerst. 7/8”, “Coll. H. Loew”, “11412”, “*Cordylura glaucescens* Lw.” “Holotypus”. Type-locality: “Kreuth” (Germany, Bavaria, Kreuth village).

Note: The fore tibia of this species has only one (preapical) anteroventral seta. See also below under *latipennis* Becker.

Current name: *Acanthocnema glaucescens* (Loew, 1864).

***incola* Becker, 1900: 54 (*Scatophaga*).**

Described from 4 male syntypes from “Kantaika und der Insel Nikander” [river Khantayka: ca. 68.1019N 86.6293E; Nikandrovsk’s Is: ca. 70.6722N 83.2370E (Russia, West Siberia)]. Most of the males are in ZMUH (Hackman 1956: 20) and a lectotype will be selected from the syntypes in this Museum.

ZMHB material: 1 male syntype (half of right wing broken off and glued on the determination label, right mid leg missing), labelled “246”, “Ins. Nikandr.”, “J. Sahlb.”, “*Scatophaga incola* Beck. det. Becker”, “*Scatophaga incola* Becker PARALECTOTYPE labelled 1954 by J.R. Vockeroth”. It has been labelled by me as a syntype of *Scatophaga incola*.

Current name: *Scathophaga incola* (Becker, 1900).

***inermis* Becker, 1894: 119 (*Amaurosoma*).**

Described from an unspecified number of both sexes from “aus Livland und Schlesien”.

ZMHB material: 4 syntypes: 2 males and 2 females, all in very good condition and conspecific.

A male labelled “Livland 29991”, “2/5 87”, “84”, “*Amaurosoma* LECTOTYPE *inermis* Beck. Designated by Vockeroth 19” has been labelled and is herewith designated as lectotype of *Amaurosoma inermis*. Type-locality: “Livland” (Latvia or Estonia). A female labelled “Livland 29991”, “V/8 88”, “PARALECTOTYPE *Amaurosoma inermis* Beck. labelled J.R.V.”, “*Nanna inermis* Beck. Det. J.R. Vockeroth 1962”, a female with the same labels, but without “84” and with “V/12 89”, and a male (abdomen dissected and stored in glycerol in a microvial on the same pin) labelled “Livland 29991”, “8/5 88”, “PARALECTOTYPE *Amaurosoma inermis* Beck. labelled J.R.V.”, “*Nanna inermis* Beck. Det. J.R. Vockeroth 1962”, “Paralectotypus”, “Zool. Mus. Berlin”, have been labelled as paralectotypes; all three are conspecific with the lectotype.

Current name: *Nanna inermis* (Becker, 1894), correctly recognised by recent authors.

***islandica* Becker, 1894: 175 (*Scatophaga*).**

Described from “Ein Pärchen aus Island und Labrador”.

ZMHB material: male and female syntypes. Male (left mid leg missing, end of abdomen dissected and stored in a microvial of glycerol on the same pin) labelled “Island xxx” (xxx = illegible, possibly collector’s name), “*Scatophag[a] borealis* nov. sp.”, “Coll. H. Loew”, “11452”, “*Islandica* Becker”, “*Scatophaga intermedia* Walker ♂ Det. F. Šifner”, has been labelled and is herewith designated as lectotype. Type-locality: “Island” [= Iceland]. It is *Scathophaga litorea* (Fallén, 1819). Female (left hind leg, tibia and tarsus of right hind leg missing, end of abdomen dissected and glued on card), labelled “Labrador.”, “Coll. H. Loew”, “*Scatophaga islandica* Becker”, “*Scatophaga villipes* Zetterstedt ♀ Det. F. Šifner” and provided with a green label, has been labelled as paralectotype; it is conspecific with the lectotype.

Current name: A junior synonym of *Scathophaga litorea* (Fallén, 1819), as currently understood.

***lasiosoma* Becker, 1894: 184 (*Cochliarium*).**

Described from “Ein Pärchen aus St. Moritz”.

ZMHB material: both syntypes. Male (condition excellent), labelled “St. Moritz 28/6 9779” [= 28 June 1886], “*Cochliarium lasiosoma* Becker LECTOTYPE Designated by Vockeroth 19”, has been labelled and is herewith designated as lectotype. Type-locality: “St. Moritz” (Switzerland). Female (right mid leg missing), labelled “St. Moritz 28/6 9753”, “*Cochliarium lasiosoma* Becker PARALECTOTYPE labelled 1954 by J.R. Vockeroth”, is conspecific with the lectotype and has been labelled as paralectotype.

Current name: *Gimnomera lasiosoma* (Becker, 1894).

***latipennis* Becker, 1894: 138 (*Acanthocnema*).**

Described from an unspecified number of the female sex taken “Schlesien. Wölfelsfall bei Glatz”.

ZMHB material: a female in excellent condition, labelled “Wölfelsfall 7/7 23793” [= 7 July 1889], “*Acanthocnema latipennis* Becker LECTOTYPE Designated by Vockeroth 19” has been labelled and is herewith designated as lectotype. Type-locality: “Wölfelsfall bei Glatz” (Wodospad Wilczki west of Międzygórze southeast of Bystrzyca Kłodzka, Poland).

Current name: It is a good species of *Acanthocnema*, not a synonym of *Acanthocnema glaucescens* Loew as considered by Gorodkov (1986), Suwa (1986), and Šifner (2008). The fore tibia of *A. latipennis* has two anteroventral setae (one at middle, the other preapical). Figures of the male sternite 5 and genitalia of *A. latipennis* are given by Suwa (1986: figs 8, 10, 20, 22) as *Acanthocnema glaucescens* Loew.

***lesgiae* Becker, 1894: 129 (*Norellia*).**

Described from 2 males “vom Kaukasus aus Lesgia”.

ZMHB material: Lectotype male (designated by Ozerov 2010a: 231), labelled “Caucas Lesgia”, “Zool. Mus. Berlin”, “Norellia HOLOTYPE lesgiae Beck lab [= labelled by] Vockeroth”. Type-locality: “Lesgia” (= Dagestan, Russia). Fore right and left mid legs missing.

Current name: *Norellisoma lesgiae* (Becker, 1894).

loewi Becker, 1894: 123 (*Pselaphephila*).

Described from an unspecified number of both sexes without any statement giving a specific locality, but most probably from “Schlesien” or “Posen”, now part of Poland: “... diesen Exemplaren aber keinerlei Notiz beigegeben ist, so nehme ich an, dass diese Thiere entweder aus Schlesien oder aus Posen stammen.”.

ZMHB material: 3 syntypes. A male, double pinned (condition good), labelled “Coll. H. Loew”, “Zool. Mus. Berlin”, “Type”, “Pselaphephila loewi Becker LECTOTYPE Designated by J.R. Vockeroth 19”, has been labelled and is herewith designated as lectotype. Type-locality: Poland.

A female, double pinned (right eye broken), labelled “Coll. H. Loew”, “11436”, “Cordylura immunda Lw. Besch. II”, “an ♀ praecedentis”, “Zool. Mus. Berlin”, “Type”, “Pselaphephila loewi Becker PARALECTOTYPE labelled 1954 by J.R. Vockeroth”, and a male, (damaged: abdomen, right wing and left mid leg glued on card, right fore and right hind legs missing), labelled “Coll. H. Loew”, “Zool. Mus. Berlin”, “Type”, “Pselaphephila loewi Becker PARALECTOTYPE labelled 1954 by J.R. Vockeroth”, have been labelled as paralectotypes. Both are conspecific with the lectotype.

Current name: *Nanna loewi* (Becker, 1894).

longicornis Hendel, 1913: 77 (*Parallelomma*).

Described from 11 male syntypes taken “aus Hoozan. 7. Februar”. Šifner (2009: 290) incorrectly designated a holotype for this species and 6 paratypes (3 males and 3 females) taken at “Hoozan” and “Chip-Chip”, all deposited in NMW. Only the males from “Hoozan” in this material may be syntypes. Hendel loaned material for study from SDEI, and a lectotype is being designated from syntypes in this Institution.

SDEI material: 5 male syntypes.

A male syntype (right wing absent), labelled “Hoozan Formosa Sauter, 1911”, “7.II”, “coll. Oldenberg”, “PARALECTOTYPE *Parallelomma longicornis* Hendel”, “*Parallelomma longicornis* Hendel”, “*Megaphthalma longicornis* Hend. Det. 1956 J.R. Vockeroth”, has been labelled and is herewith designated as lectotype. Type-locality: “Hoozan” (Taiwan). The other four syntypes have been labelled as paralectotypes: male (all left legs missing), labelled “Hoozan Formosa Sauter, 1911”, “7.II”, “Hendel det.”, “Typus”, “PARALECTOTYPE *Parallelomma longicornis* Hendel”, “*Parallelomma longicornis*

Hendel”, “*Megaphthalma longicornis* Hendel Det. 1965 J.R. Vockeroth”; male (right mid leg and both hind legs missing), labelled “Hoozan Formosa Sauter, 1911”, “7.II”, “Hendel det.”, “Typus”, “Lectotypus”, “*Parallelomma longicornis* Hendel”, “*Parallelomma longicornis* H. det. Hendel”, “*Parallelomma longicornis* Hendel LECTOTYPE Designated Vockeroth 19”; male (right postpedicel and right mid leg missing), labelled “Hoozan Formosa Sauter, 1911”, “7.II”, “coll. Oldenberg”, “PARALECTOTYPE *Parallelomma longicornis* Hendel”, “*Parallelomma longicornis* Hendel”, “*Megaphthalma longicornis* Hend. Det. 1956 J.R. Vockeroth”; male (right mid leg missing, both postpedicels damaged), labelled “Hoozan Formosa Sauter, 1911”, “7.II”, “Hendel det.”, “Typus”, “Paralectotypus”, “*Parallelomma longicornis* Hendel”.

There are several additional specimens in SDEI identified as *Parallelomma longicornis*, but these are females or males taken on other dates and so none can be a syntype.

ZMHB material: 4 females from “Kosempo”, cannot be syntypes.

Current name: Vockeroth (1977: 437) listed this species in the genus *Megaphthalma* Becker, 1894. Šifner (2009: 290) placed it in a monotypic genus *Suwaia* Šifner, 2009. I follow Vockeroth’s assignment.

media Becker, 1894: 96 (*Parallelomma*).

Described from an unspecified number of the male sex from “Aus Schlesien, Umgegend von Liegnitz”.

ZMHB material: a male in excellent condition, labelled “Rothkirch 11/6 31511”, “media Beck.”, “Typus”, Zool. Mus. Berlin”, “*Chylizosoma media* Beck. Det. 1954 J.R. Vockeroth”, “*Chylizosoma medium* Beck. ♂ Det. F. Šifner”, “Holotypus ♂ *Parallelomma media* Becker, 1894: 96 det. A.L. Ozerov, 2010” has been labelled and is herewith designated as lectotype. Type-locality: “Rothkirch” (Czerwony Kościół (51.186215N, 16.06128E), Poland).

Current name: *Parallelomma medium* Becker, 1894.

melaleuca Loew, 1873: 245 (*Cordylura*).

Described from an unspecified number of females from “Griechenland”. A single specimen is mentioned in the “Catalog General Musei Zoologici Berolinensis” as *Cordylura melaleuca* (No 11381). It has been studied, labelled and is herewith designated as lectotype.

ZMHB material: The lectotype is male, not female, damaged (head and legs missing, thorax largely consumed by a beetle pest), labelled “Corfu Erber”, “11381”, “Coll. H.Loew”, “*Cordylura melaleuca* Lw.”, “Type”, “*Cordylura melaleuca* Loew LECTOTYPE Designated Vockeroth 19”. Type-locality: Corfu I. (Greece). It is conspecific with *Norellia tipularia* (Fabricius, 1794).

Current name: A junior synonym of *Norellia tipularia* (Fabricius, 1794), as currently understood.

melanacra Loew, 1873: 247 (*Cordylura*).

Described from an unspecified number of both sexes from “Schlesien”.

ZMHB material: A female syntype in very good condition, labelled “Rosenthal 14.4.51”, “Coll. H.Loew”, “Type”, “*Cordylura melanacra* Loew LECTOTYPE Designated by Vockeroth 19”, “*Scoliaphleps ustulata* (Ztt.). ♂ [sic] Det. F. Šifner” has been labelled and is herewith designated as lectotype. Type-locality: “Rosenthal” [now Rózanka, part of Międzyzylesie, near Kłodzko (Poland)]. It is conspecific with *Cordilura ustulata* (Zetterstedt, 1838).

Current name: A junior synonym of *Cordilura ustulata* (Zetterstedt, 1838), as currently understood.

mensurata Becker, 1894: 119 (*Amaurosoma*).

Described from an unspecified number of both sexes from “Schlesien”.

ZMHB material: 1 type specimen. It was sent on loan to F. Šifner in 2007; not examined by me.

Current name: According by Šifner (2008: 151) it is a junior synonym of *Nanna armillata* (Zetterstedt, 1846).

minuta Becker, 1894: 116 (*Amaurosoma*).

Described from an unspecified number of the male sex “Aus Livland”.

ZMHB material: a male (abdomen, tarsomeres 2–5 of right fore leg and of both hind legs missing), labelled “7/5”, “Livland 29984”, “110”, “*Amaurosoma* LECTOTYPE minuta Becker Designated by Vockeroth 19”, “*Nanna flavipes* Fall. Det. J.R. Vockeroth 1962” has been labelled and is herewith designated as lectotype. Type-locality: “Livland” (Latvia or Estonia).

Current name: Recently synonymized with *Nanna flavipes* (Fallén, 1819) by Ozerov (2010c: 7).

mollis Becker, 1894: 171 (*Scatophaga*).

Described from an unspecified number of both sexes from “Sibirien”.

ZMHB material: 8 syntypes: 6 males, 2 females. Male in very good condition, labelled “Sibiria Schnabl”, “Coll. H. Loew”, “*Scatophaga mollis* Becker LECTOTYPE Designated by J.R. Vockeroth 19”, has been labelled and is herewith designated as lectotype. Type-locality: “Sibiria” (Russia).

All other syntypes have been labelled as paralectotypes: 2 males, both in good condition and labelled “Sibiria Schnabl”, “Coll. H. Loew”, “*Scatophaga mollis* Becker PARALECTOTYPE labelled 1954 by J.R. Vockeroth”; female (right wing damaged), labelled “Sibiria Schnabl”, “11453”, “Coll. H. Loew”, “*Scatina mollis* Lw.”, “*Scatophaga mollis* Becker PARALECTOTYPE labelled 1954 by J.R. Vockeroth”; 3 males (one without right postpedicel), all in good condition, and female (left hind leg, left wing, and abdomen missing), each

labelled “Sibiria Schnabl”, “Coll. H. Loew”. All paralectotypes are conspecific with the lectotype.

Current name: A good species of *Scathophaga* Meigen, 1803.

nigrifrontata Becker, 1894: 120 (*Amaurosoma*).

Described from “Ein Pärchen aus Süd-Tirol vom Lusier Pass”.

ZMHB material: both syntypes. Male (head missing), labelled “Lusier Pass 19/6 90 25520” [= 19 June 1890], “*Amaurosoma nigrifrontata* Becker LECTOTYPE Designated by Vockeroth 19”, has been labelled and is herewith designated as lectotype. Type-locality: “Süd-Tirol vom Lusier Pass” [now Passo di Lusia (Italy, Trentino)]. The female is in very good condition, labelled “Lusier Pass 19/6 90 25522”, “PARALECTOTYPE *Amaurosoma nigrifrontata* Beck. labelled [by] Vockeroth”, “*Nanna nigrifrontata* Beck. Det. 1962 J.R.Vockeroth” has been labelled as paralectotype. Both specimens are conspecific with *Nanna tibiella* (Zetterstedt, 1838).

Current name: A new junior synonym of *Nanna tibiella* (Zetterstedt, 1838), **syn.n.**

nigriventris Loew, 1864: 19 (*Cordylura*).

Described from an unspecified number of females from “Posen”. A single specimen is mentioned in the “Catalog General Musei Zoologici Berolinensis” as *Cordylura nigriventris* (No 11392). It was studied by Ozerov (2010c: 5), has been labelled and is herewith designated as lectotype.

ZMHB material: lectotype female (left mid leg and right hind tarsal segments 2–5 are missing and the apex of the right wing is damaged), labelled “23/5 43.”, “11392”, “Coll. H. Loew”, “Type”, “*Cordylura nigriventris* m.”, “*Cordylura nigriventris* Lw. LECTOTYPE Designated by Vockeroth 19”, “Zool. Mus. Berlin”. Type-locality: “Posen” (Poland, Poznań).

Current name: *Spathephilus nigriventris* (Loew, 1864).

nutans Becker, 1894: 120 (*Amaurosoma*).

Described from “Ein Männchen aus Kärnthen in der Sammlung des Herrn Prof. Tief; ein Männchen aus Schlesien”.

ZMHB material: there is one male, near the box label “nutans Becker”, labelled “Liegnitz 10/5 30636” [10 May 1893]. It was mentioned by Vockeroth as lectotype of *Amaurosoma nutans* and is highly probably a syntype. In the Becker’s Catalogue there is an entry “Panten bei Liegnitz” (now Pątnów Legnicki near Legnica). It has been labelled and is herewith designated as lectotype. Type-locality: Legnica (formerly Liegnitz), Poland. It was correctly determined by Vockeroth as *Nanna tibiella* (Zetterstedt).

Current name: A junior synonym of *Nanna tibiella* (Zetterstedt, 1838). Synonymized by Šifner (2008: 155).

***obscurinervis* Becker, 1900: 55 (*Scatophaga*).**

Described from “2 Pärchen von der Insel Nikander und Dudinka” [Russia, West Siberia]. Most syntypes are deposited in ZMUH (Hackman 1956: 20) and a lectotype will be selected from the syntypes in this Museum.

ZMHB material: female syntype (damaged, left wing, left mid leg, both hind legs missing, abdomen glued to the mount), labelled “250”, “J. Sahlb.”, “Ins. Nikandr.”, “42482”, “*obscurinervis* Beck.”, “*Scatophaga obscurinervis* Becker PARALECTOTYPE labelled 1954 by J.R. Vockeroth”. It has been labelled as a syntype.

Current name: *Scathophaga obscurinervis* (Becker, 1900).

***opaca* Loew, 1864: 19 (*Cordylura*).**

Described from an unspecified number of females from “Kärnten”. A single specimen is mentioned in the “Catalog General Musei Zoologici Berolinensis” as *Cordylura opaca* (No 11385). It has been studied, labelled and is herewith designated as lectotype.

ZMHB material: the lectotype female has been mainly consumed by a beetle pest, and all that remain are the head, legs (except right hind leg), and some small fragments of thorax, labelled “Saualp aug. 55”, “Coll. H.Loew”, “11385”, “*Cordylura opaca* Lw”, “Type”, “*Cordylura opaca* Loew LECTOTYPE Designated by J.R. Vockeroth 19”. Type-locality: Saualpe (Kärnten [Carinthia], Austria).

Current name: because of its poor condition, the identity of the lectotype is difficult to determine. The name was synonymized by Becker (1905: 13) with *Norellisoma lituratum* (Meigen, 1826). I can see no reason for disputing this synonymy, and have accepted it.

***ordinata* Becker, 1894: 168 (*Scatophaga*).**

Described from an unspecified number of both sexes from “St. Moritz”.

ZMHB material: male and female syntypes. The male (slightly wrinkled, abdomen dissected and placed in a microvial of glycerine), labelled “St. Moritz 26/6 9629” [26 June 1886], “*Scatophaga ordinata* Becker LECTOTYPE Designated by J.R. Vockeroth 19”, “*Scopaeuma taeniopum* Rond. det. 1954 J.R. Vockeroth”, has been labelled and is herewith designated as lectotype. Type-locality: St. Moritz (Switzerland). I agree with the determination by Vockeroth that it conspecific with *S. taeniopa* (Rondani, 1867). The female is in good condition and is labelled “St. Moritz 28/6 9819”, “*Scatophaga ordinata* Becker PARALECTOTYPE labelled 1954 by J.R. Vockeroth”, “*Scatophaga taeniopa* Rond. det. 1962 J.R. Vockeroth”, and has been labelled as paralectotype; Vockeroth’s determination is correct.

Current name: A junior synonym of *Scathophaga taeniopa* (Rondani, 1867).

***paridis* Hering, 1923: 200 (*Parallelomma*).**

Described from a female holotype (Hering 1923: 200, original designation) and some female paratypes taken from “Berlin (Jungfernheide, 4. VII. 20), und Güntersberg a. Oder [now Osiecznica near Krosno (Poland)], 6. VII. 20”.

ZMHB material: holotype and 1 paratype, each labelled by Hering accordingly, but both are males, not females. Holotype male in good condition, but abdomen dissected and placed in a microvial of glycerine, labelled “Jungfernheide. 4.7.20 Nr. 1513 Mt. Hering. MZ”, “Paris quadrif”, “*Parallelomma paridis* m. type det. Mart Hering”, “coll. Hypon. M. Hering”, “Type ♀”, “Zool. Mus. Berlin”, “HOLOTYPUS ♂ *Parallelomma paridis* Hering 1923: 200 det. A.L. Ozerov, 2010”, “*Parallelomma vittatum* (Meigen) ♂ det. A.L. Ozerov, 2010”. Type-locality: Jungfernheide, Berlin (Germany). Photos of the original labels of the holotype were given by Ozerov (2010d: 311).

Male paratype in good condition, labelled “Jungfernheide. 4.7.20 Nr. 1513 Mt. Hering. MZ”, “Paris quadrif”, “*Parallelomma paridis* m. det. Mart Hering”, “coll. Hypon. M. Hering”, “Paratypus”, “Zool. Mus. Berlin”, “Chylizos. vittatum Meig. ♂ Det. F. Šifner”, “PARATYPUS ♂ *Parallelomma paridis* Hering 1923: 200 det. A.L. Ozerov, 2010”, “*Parallelomma vittatum* (Meigen) ♂ det. A.L. Ozerov, 2010”.

Current name: A junior synonym of *Parallelomma vittatum* (Meigen, 1826), as currently understood.

***picticornis* Loew, 1864: 22 (*Cordylura*).**

Described from an unspecified number of females from “Sibirien”. A single specimen is mentioned in the “Catalog General Musei Zoologici Berolinensis” as *Cordylura picticornis* (No 11369). It has been studied, labelled and is herewith designated as lectotype.

ZMHB material: lectotype female in very good condition, labelled “11369”, “Coll. H. Loew”, “*Cordylura picticornis* m.”, “Type”, “*Cordylura picticornis* Lw. LECTOTYPE Designated by J.R. Vockeroth 19” and provided with a small black label. Type-locality: “Sibiria” (Russia).

Current name: *Cordylura picticornis* (Loew, 1864), correctly recognised by recent authors.

***pictipennis* Oldenberg, 1923: 307 (*Scatophaga*).**

Described from a single male „oberhalb Gastein zwischen Böckstein und Nassfeld, nahe dem Bärenfall“.

SDEI material: holotype male in very good condition (abdomen in a microvial of glycerine), labelled “Gastein 10.7.07“, “*pictipenne* Old.”, “n.sp.”, “coll. Oldenberg”, “*Scatophaga*”, “Typus”, “Holotypus”, “*Scatophaga* HOMOTYPE maculipennis Ringd. Compared by J.R.Vockeroth 1954”. Type-locality: Gastein valley (Austria).

Current name: *Scathophaga pictipennis* (Oldenberg, 1923), correctly recognised by recent authors.

***rubifrontata* Becker, 1894: 91 (*Cordylura*).**

Described from “Ein Weibchen in der Loew’schen Sammlung aus Kultuk”.

ZMHB material: female holotype (abdomen dissected and glued on card, right hind tibia and tarsus missing), labelled “Kultuk v. Maak”, “*rubifrontata* Beck.”, “Type”, “Coll. H. Loew”, “13885”, “*Cordylura* sp. nov. an var. praec.”, “*Cordilura ciliata* Meigen det. Šifner, ♀”. Type-locality: Kultuk (Russia, Baikal Area, 51.7221N 103.6951E). Conspecific with *Cordilura aberrans* Becker, 1894, not with *Cordilura ciliata* (Meigen, 1826), as was determined and published by Šifner (2008: 118).

Current name: A new junior synonym of *Cordilura aberrans* (Becker, 1894), **syn.n.**

***sahlbergi* Becker, 1900: 51 (*Lasioscelus*).**

Described from “5 Exemplare aus Kantaika u. Dudinka” [Russia, West Siberia]. Most syntypes are in Helsinki University Museum (ZMHU) and a lectotype will be selected from the syntypes in this Museum.

ZMHB material: 1 male and 1 female syntypes. Male (head missing, both wings damaged), labelled “185”, “Dudinka”, “J.Sahlb.”, “*Sahlbergi* Beck.”, “42487”, “*Lasioscelus sahlbergi* Beck. PARALECTOTYPE labelled 1954 by J.R. Vockeroth”, “*Pogonota sahlbergi* Beck. Det. 1963 J.R. Vockeroth”; and female (both wings damaged), labelled “69”, “Kantaika”, “J.Sahlb.”, “*Lasioscelus Sahlbergi* Beck.”, “42487”, “*Lasioscelus sahlbergi* Beck. PARALECTOTYPE labelled 1954 by J.R. Vockeroth”, “*Pogonota sahlbergi* Beck. Det. 1963 J.R. Vockeroth”, “*Lasioscelus sahlbergi* Becker ♀ Det. F. Šifner 1973”. Both have been labelled as syntypes.

Current name: *Pogonota sahlbergi* (Becker, 1900), correctly recognised by recent authors.

***septentrionalis* Becker, 1897: 397 (*Scatophaga*).**

Described from 5 specimens of both sexes “vom Tschernyschew-Berge auf Nowaja-Semlja. 5. Aug. 1896”. 3 syntypes are in ZISP and a lectotype was designated from these syntypes (Ozerov and Krivosheina 2013: 146).

ZMHB material: 1 male and 1 female syntypes. Male (right wing, right mid and hind legs missing), labelled “N. Semlja mons Tshernyschewi J. Jacobs on 5.VIII.96”, “41955”, “*Scatophaga septentrionalis* Beck. SYNTYPE labelled 1954 by J.R. Vockeroth”, “*Scopeuma varipes* Holm. Det. 1954 J.R. Vockeroth”. Female (right wing damaged), labelled “N. Semlja mons Tshernyschewi J. Jacobs on 5.VIII.96”, “41955”, “*septentrionalis* Beck.”, “*Scatophaga septentrionalis* Beck. SYNTYPE labelled 1954 by J.R. Vockeroth”, “*Scopeuma varipes* Holm. Det. 1954 J.R. Vockeroth”. Both are conspecific with *Scathophaga varipes* (Holmgren, 1883) and have been labelled as paralectotypes.

Current name: A junior synonym of *Scathophaga varipes* (Holmgren, 1883).

***socialis* Becker, 1894: 90 (*Cordylura*).**

Described from an unspecified number of both sexes [“*C. pudica*. Zett. Dipt. Sc. V. 1998, 3 [“*Succia meridionalis*... in Scania... ad Hafniam” (Sweden, Denmark)]; Rond., Prodr. VII, 14, 4. [“unicum exemplar germanicum” (Germany)]]”. Šifner (2008: 123) wrote that these syntypes were kept in ZMHB.

ZMHB and SDEI material: no type-material found.

Current name: A good species of *Cordilura*, correctly recognised by recent authors.

***speciosa* Ozerov, 1999: 511 (*Langechristia*).**

Described from a single female from Primorskiy Kray (Russia).

SDEI material: holotype female (left fore leg, except coxa missing, right wing damaged), labelled “RUSSIA: Primorskiy Kray Sichote-Alin, Biol. Stat. 30 km SE Chuguyevka, 44.05 N, 134.12 E 650 m, Malaisefalle 31.V.–03.VI.1993 leg. C. Lange & J. Ziegler”. Type-locality: 30 km SE Chuguyevka (44.05N, 134.12E) (Russia, Primorskiy Kray).

Current name: *Langechristia speciosa* Ozerov, 1999.

***tinctinervis* Becker, 1894: 178 (*Coniosternum*).**

Described from “Ein Männchen und zwei Weibchen in der Sammlung des Prof. Strobl.”, locality not stated.

ZMHB material: 1 female syntype. This female (right mid leg missing), labelled “v. G Strobl aus Seitenstetten [Austria]”, “8/5 88”, “*tinctinervis* Beck”, “*Coniosternum tinctinervis* Beck. LECTOTYPE Designated by J.R. Vockeroth 19”, has been labelled as syntype.

Current name: *Scathophaga tinctinervis* (Becker, 1894).

***umbrosa* Loew, 1873: 246 (*Cordylura*).**

Described from an unspecified number of females from “Ungarn... bei Losoncz”. A single specimen is mentioned in the “Catalog General Musei Zoologici Berolinensis” as *Cordylura umbrosa* (No 11398). It has been studied, labelled and is herewith designated as lectotype.

ZMHB material: male lectotype (both wing damaged at middle), with a small green label and labelled “11398”, “Coll. H. Loew”, “Losoncz Kowarz”, “*Cordylura umbraculata* Lw.”, “Type”, “*Cordylura umbrosa* Loew LECTOTYPE Designated by J.R. Vockeroth 19”, “*Cordylura umbrosa* Loew det. Šifner ♂”. Type-locality: “Losoncz” (Lučenec, 48.333306N 19.666695E, Slovakia). Conspecific with *Cordilura impudica* (Rondani, 1867).

Current name: A junior synonym of *Cordilura impudica* (Rondani, 1867), as currently understood.

***unicolor* Loew, 1864: 17 (*Cordylura*).**

Described from an unspecified number of females from “Andalusien”. A single specimen is mentioned in the “Catalog General Musei Zoologici Berolinensis” as

Cordylura unicolor (No 11373). It has been studied, labelled and is herewith designated as lectotype.

ZMHB material: lectotype female in very good condition, labelled “Spanien Stauding“, “11373“, “Coll. H. Loew“, “*Cordylura unicolor* m.“, “Type“, “*Cordylura umbrosa* Loew LECTOTYPE Designated by J.R. Vockeroth 19“. Type-locality: “Andalusien“ (Spain, Andalusia). Conspecific with *Cordilura albipes* (Fallén, 1819), not with *Parallelomma vittatum* (Meigen, 1826) as considered Šifner (2008: 174).

Current name: A new junior synonym of *Cordilura albipes* (Fallén, 1819), **syn.n.**

vockerothi Ozerov, 2013: 81 (*Norellisoma*).

Described from 8 males and 5 females taken in the Alps of Austria, Switzerland, and Italy.

ZMHB material: holotype male (Ozerov 2013: 81, original designation), in very good condition, labelled “St. Moritz 3/7 10570” [= 3 July 1886], “*Norellisoma* n. sp. 1 det. J.R. Vockeroth 1954“. Type-locality: St. Moritz (Switzerland: ~46.50N, 9.83E).

12 paratypes: 3 males and 4 females same locality as holotype, 28.VI. (9419), 3.VII. (10566, 10567), 4.VII. (10616, 10617, 10642) and 16.VII (11722); 2 males [Italy] “Vallombrosa 54041 V”; 2 males [Switzerland] “Linthal”, 31.5.[19]13 and 6.6.[19]13; 1 female [Austria] “Schneeberg Jul.[18]55“, “coll. H. Loew“. Three of these paratypes are in ZMUM (Ozerov 2013: 83).

Current name: *Norellisoma vockerothi* Ozerov, 2013.

ziegleri Ozerov, 1999: 510 (*Langechristia*).

Described from 3 males and 2 females from Khabarovskiy Kray (Russia).

SDEI material: holotype male (Ozerov 1999: 510, original designation), in very good condition, labelled “RUSSIA: Khabarovskiy Kray Boitsovo 20 km N Bikin Bolsoi Solntsepyok Hill 47.02N 134.21E 250 m, Malaise-falle, 24–27.V.1993 leg. C. Lange & J. Ziegler“. Type-locality: Boitsovo 47.02N 134.21E (Russia, Khabarovskiy Kray). 1 male and 1 female paratypes with the same labels are conspecific with holotype. A further 1 male and 1 female paratypes are in ZMUM (Ozerov 1999: 510).

Current name: *Langechristia ziegleri* Ozerov, 1999.

Nomenclatural summary

Acanthocnema glaucescens (Loew, 1864)

Acanthocnema latipennis Becker, 1894

Cordilura aberrans (Becker, 1894)

rubifrontata Becker, 1894, **syn. n.**

Cordilura albipes (Fallén, 1819)

unicolor Loew, 1864, **syn. n.**

Cordilura bezzii (Sack, 1937)

Cordilura fulvifrons Ozerov, 1997

Cordilura impudica (Rondani, 1867)

umbrosa Loew, 1873

Cordilura picipes (Meigen, 1826)

biseta Loew, 1864

Cordilura picticornis (Loew, 1864)

Cordilura socialis (Becker, 1894)

Cordilura ustulata (Zetterstedt, 1838)

melanacra Loew, 1873

Gimnomera castanipes (Becker, 1894)

Gimnomera lasiostoma (Becker, 1894)

Gonarcticus arcticus (Becker, 1907)

Langechristia amica Ozerov, 1999

Langechristia speciosa Ozerov, 1999

Langechristia ziegleri Ozerov, 1999

Megaphthalma longicornis Hendel, 1913

Nanna armillata (Zetterstedt, 1846)

mensurata Becker, 1894

Nanna articulata (Becker, 1894)

Nanna flavipes (Fallén, 1819)

minuta Becker, 1894

Nanna inermis (Becker, 1894)

Nanna loewi (Becker, 1894)

Nanna tibiella (Zetterstedt, 1838)

nigrifrontata Becker, 1894, **syn. n.**

nutans Becker, 1894

Norellia tipularia (Fabricius, 1794)

melaleuca Loew, 1873

Norellisoma femorale (Loew, 1864)

Norellisoma lesgiae (Becker, 1894)

Norellisoma lituratum (Meigen, 1826)

opaca Loew, 1864

Norellisoma vockerothi Ozerov, 2013

Okeniella dasyprocta (Loew, 1864)

Parallelomma media Becker, 1894

Parallelomma vittatum (Meigen, 1826)

paridis Hering, 1923

Pogonota sahlbergi (Becker, 1900)

Scathophaga alata (Becker, 1914)

Scathophaga albidohirta (Becker, 1907)

Scathophaga dasythrix (Becker, 1894)

Scathophaga incola (Becker, 1900)

Scathophaga litorea (Fallén, 1819)

islandica Becker, 1894

Scathophaga mollis (Becker, 1894)

Scathophaga multisetosa (Holmgren, 1883)

arctica Becker, 1897

Scathophaga obscurinervis (Becker, 1900)

Scathophaga pictipennis (Oldenberg, 1923)

Scathophaga taeniopa (Rondani, 1867)

ordinata Becker, 1894

Scathophaga tinctinervis (Becker, 1894)

Scathophaga varipes (Holmgren, 1883)

septentrionalis Becker, 1897

Spathephilus nigriventris (Loew, 1864)

breviventris Loew, 1873

Spaziphora hydromyzina (Fallén, 1819)

fascipes Becker, 1894

Acknowledgements

It is a pleasure to acknowledge the sustained interest and assistance of Dr. Frank Menzel, Jenny Pohl, and Dr. Joachim Ziegler during my visits to the museums of Müncheberg and Berlin, and in correspondence at all times. My study visit to Berlin and Müncheberg was made possible by a grant from the Deutsche Forschungsgemeinschaft in March 2012.

I am also most grateful for to Dr. Joachim Ziegler and Dr. Adrian Pont who kindly read the manuscript and offered useful comments.

References

- Becker T (1894) Dipterologische Studien. I. Scatomyzidae. Berliner Entomologische Zeitschrift 39(1): 77–196. doi: 10.1002/mmnd.18940390108
- Becker T (1897) Beitrag zur Dipteren-Fauna von Nowaja-Semlja. Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de St. Pétersbourg 2: 396–404.
- Becker T (1900) Beiträge zur Dipteren-Fauna Sibiriens. Northwest-Sibirische Dipteren gesammelt vom Prof. John Sahlberg aus Helsingfors im Jahre 1876 und vom Dr. E. Bergroth aus Tammerfors im Jahre 1877. Acta Societatis Scientiarum Fennicae 26(9): 1–66.
- Becker T (1905) Holometopa. Acalyptera. Scatomyzidae. In: Becker T, Bezzi M, Kertész K, Stein P (Eds) Katalog der paläarktischen Dipteren. Vol. IV. Budapest, 1–21.
- Becker T (1907a) Zur Kenntniss der Dipteren von Central-Asien. I. Cyclorrhapha schizophora holometopa und Orthorrhapha brachycera. Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de St.-Pétersbourg 12: 253–317.
- Becker T (1907b) Beschreibung von 3 neuen Dipteren aus Ost-Grönland. Meddelelser om Grönland 29: 411–414.
- Becker T (1914) Diptères nouveaux récoltés par MM. Ch. Alluaud et R. Jeannel en Afrique orientale 1911–1912. Annales de la Société Entomologique de France 83: 120–130.
- Gorodkov KB (1986) Family Scathophagidae. In: Soós Á, Papp L (Eds) Catalogue of Palaearctic Diptera. Vol. 11. Scathophagidae-Hypodermatidae. Akadémiai Kiadó, Budapest, 11–41.
- Hackman W (1956) The Scathophagidae (Dipt.) of Eastern Fennoscandia. Societas pro Fauna et Flora Fennica. Fauna fennica II. Helsingforsiae, 67 pp.
- Hendel F (1913) Acalyptate Musciden (Dipt.) II. Supplementa Entomologica 2: 77–112.
- Hering M (1923) Minenstudien III. Deutsche Entomologische Zeitschrift 7: 188–206.
- Loew H (1864) Acht neue Cordylura-Arten. Wiener Entomologische Monatschrift 8: 17–26.
- Loew H (1873) Beschreibungen europäischen Dipteren. Dritter Band. Systematische Beschreibung der bekannten europäischen zweiflügeligen Insecten. Von Johann Wilhelm Meigen. Zehnter Theil oder vierter Supplementband. Schmidt, Halle.
- Oldenberg L (1923) Neue Acalyptaten (Diptera) meiner Ausbeute. Deutsche Entomologische Zeitschrift 3: 307–319.
- Ozerov AL (1997) [Five new species of the genus *Cordilura* (Diptera, Scathophagidae) from the Far East of Russia]. Zoologicheskii Zhurnal 76(12): 1424–1429. [in Russian]
- Ozerov AL (1999) [New genus and three new species of Scathophagidae (Diptera) from the Russian Far East]. Zoologicheskii Zhurnal 78(4): 510–512. [in Russian]
- Ozerov AL (2010a) On the Palaearctic fauna of *Norellisoma* Wahlgren, 1917 (Diptera: Scathophagidae). Russian Entomological Journal 18(3) [2009]: 229–234.
- Ozerov AL (2010b) Review of Afrotropical Scathophagidae (Diptera). Russian Entomological Journal 18(4) [2009]: 299–308.
- Ozerov AL (2010c) A Review of Palaearctic species of the genus *Nanna* Strobl, 1894 (Diptera, Scathophagidae) with shining stripes or spots on scutum. Far Eastern Entomologist 214: 1–8.
- Ozerov AL (2010d) Flies of the genus *Parallelomma* Becker in Strobl, 1894 (Diptera, Scathophagidae) in the fauna of Russia. Russian Entomological Journal 18(4) [2009]: 309–317.
- Ozerov AL (2013) Description of five new species and notes on taxonomy of Scathophagidae (Diptera). Russian Entomological Journal 22(1): 81–89.
- Ozerov AL, Krivosheina MG (2011) A revision of the types of two Scathophagidae species (Diptera), described by Becker and deposited in the Zoological Institute, St.-Petersburg, Russia. Russian Entomological Journal 20(1): 105–108.
- Ozerov AL, Krivosheina MG (2013) Types of Scathophagidae (Diptera) at the Zoological Institute of Russian Academy of Sciences, St Petersburg. Zoosystematica Rossica 22(1): 141–149.
- Sack P (1937) 62a. Cordyluridae. (Scatomyzidae). In: Lindner E (Ed) Die Fliegen der palaearktischen Region, Stuttgart, Vol. 7, 103 pp.
- Šifner F (2008) A catalogue of the Scathophagidae (Diptera) of the Palaearctic region, with notes on their taxonomy and faunistics. Acta Entomologica Musei Nationalis Pragae 48(1): 111–196.
- Šifner F (2009) Two new genera of the family Scathophagidae (Diptera). Acta Entomologica Musei Nationalis Pragae 49(1): 287–292.
- Suwa M (1986) The genus *Acanthocnema* in Asia and Europe, with description of three new species from Japan and Nepal (Diptera: Scathophagidae). Insecta Matsumurama. New Series 34: 1–33.
- Vockeroth JR (1977) Family Scathophagidae. In: Delfinado MD, Hardy DE (Eds) A Catalog of the Diptera of the Oriental Region. Vol. 3, Suborder Cyclorrhapha (excluding Division Aschiza). The University Press of Hawaii, Honolulu, 436–438.

Historical aspects of meetings, publication series, and digital resources dedicated to echinoderms

Alexander Ziegler¹, Georgy V. Mirantsev², Michel Jangoux^{3,4} and Andreas Kroh⁵

¹ Ziegler Biosolutions, Fahrgasse 5, 79761 Waldshut-Tiengen, Germany

² A. A. Borisyak Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya Ulitsa 123, 117997 Moskva, CIS

³ Laboratoire de Biologie Marine, Université Libre de Bruxelles, 50 Avenue F. D. Roosevelt, 1050 Bruxelles, Belgium

⁴ Biologie Marine, Université de Mons-Hainaut, 20 Place du Parc, 7000 Mons, Belgium

⁵ Geologisch-Paläontologische Abteilung, Naturhistorisches Museum Wien, Burgring 7, 1010 Wien, Austria

Corresponding author: Alexander Ziegler (alexander_ziegler@gmx.net)

Abstract

Received 9 Sept 2013

Accepted 16 Dec 2013

Published 28 March 2014

Academic editor:

Michael Ohl

Key Words

Echinodermata

history

publication

website

photographs

Half a century after the first scientific meeting dedicated to marine spiny-skinned animals (Deuterostomia: Echinodermata) was held in Washington, DC, we take this opportunity to provide information on a number of historical aspects related to the echinoderm scientific community. Apart from shedding light on the historical origins of modern echinoderm conferences, the present contribution presents photographs taken during the first meeting of echinoderm researchers in 1963 as well as during the first installments of the *International Echinoderm Conference* and the *European Conference on Echinoderms*. Furthermore, we provide background information on publication series dedicated solely to the Echinodermata as well as descriptions of selected digital resources that focus on echinoderms. Finally, we present a number of echinoderm conference logos and flyers in addition to selected information about specific echinoderm meetings.

Introduction

The present article is the third in a series of publications aimed at furthering an understanding of various historical aspects of the echinoderm scientific community. In a first contribution, a concise summary of worldwide echinoderm meetings and associated publications was given (Ziegler and Kroh 2012). The second contribution introduced an online database containing metadata derived from numerous articles and abstracts published in echinoderm conference proceedings since 1963 (Kroh et al. 2013). In order to complement the data provided in these two preceding articles on the history of the echinoderm research community, we here present i) information about the historical origins of echinoderm meetings, ii) photographs taken during the first official echinoderm meeting as well as photographs taken during the inaugural sessions of the *International Echinoderm Conference* (IEC)

and the *European Conference on Echinoderms* (ECE), iii) background information on a number of publication series and digital resources dedicated to echinoderms, and, finally, iv) conference logos and flyers from past echinoderm meetings as well as information on additional echinoderm gatherings. As it is “appropriate that the students in a field be aware of their history” (Lawrence 1998), the present article provides, fifty years after the first-ever echinoderm meeting was held 1963 in Washington, DC, further historical data on meetings and publications that focus on marine spiny-skinned animals.

The historical origins of modern echinoderm meetings

Although our previously published compendium of national, regional, and international echinoderm meetings

might provide the impression that echinoderm scientists started to meet as late as the second half of the 20th century, researchers with a focus on the Echinodermata have convened long before.

The first official echinoderm meeting, the *Symposium on Physiology of Echinodermata* held 1963 in Washington, DC was in fact part of the 16th *International Congress of Zoology* (ICZ). Since the first ICZ, held 1889 in Paris, zoologists from around the world had come together on a regular basis, interrupted only by the two World Wars. However, it was at the conference held in 1963 that multiple parallel symposia were introduced in order to accommodate the ever-growing number of attendees (Romer 1963). The 16th ICZ boasted over 2,500 participants that presented 510 papers and attended 36 sessions as well as 29 special symposia. Although the considerable size of this congress reflected the expansion of zoological sciences during the 20th century, it also exposed the growing disunity of organismic and experimental biology (Johnson 2009). The fragmentation of zoology into different, highly specialized disciplines soon led to a marked decrease in the importance of the ICZ as the representative gathering for zoologists, which in response led to an increase in more focused zoological meetings. The notable increase in national, regional, and international echinoderm conference series from the early 1970s on must be seen in this historical context.

Nonetheless, echinoderm researchers have certainly met and spoken to each other during the fifteen ICZs held prior to the congress in Washington, DC. The programs, participant lists, and selected articles from all these meetings have been published in the form of conference proceedings volumes, and it will be of interest to explore which echinoderm researchers actually came together during these events. The 7th ICZ, held 1907 in Boston, may serve as a good starting point for future historical research, for it was no less a figure than Alexander E. Agassiz who acted as president during the conference (Anonymous 1912).

With the inception of specialized echinoderm conferences from the early 1970s onwards came a transition from meetings intended primarily for established researchers to events that provided a welcoming environment for all academic degrees as well as the occasional echinoderm amateur. Photographs taken during the first echinoderm meeting in 1963 (Fig. 1), group photographs taken during the first gatherings of the IEC in 1972 (Fig. 2) and the ECE in 1979 (Fig. 3), as well as photographs taken during a poster session at the first ECE (Fig. 4) provide an impression of the general atmosphere during these events. This series of photographs also documents that echinoderm science had started to become less and less dominated by male scientists from the 1970s onwards.

Echinoderm publication series

In contrast to several other major invertebrate phyla (e.g. Crustacea, Mollusca), the Echinodermata are not repre-

sented by a journal dedicated solely to their study. Nonetheless, over the years a set of formal and informal publications exclusively aimed at echinoderms has enriched the scientific landscape. These publications include such well-known volumes as *Echinoderms* (Nichols 1962, 1969), *Echinoderm Nutrition* (Jangoux and Lawrence 1982), or *Edible Sea Urchins* (Lawrence 2001, 2006, 2013). However, these books constitute single publication events rather than a continuous series in the form of a journal. Still, there are a few examples for journal-style publication series dedicated exclusively to echinoderms, and in the following we list the most prominent examples in chronological order.

The Echinoderm Newsletter (1968 - today)

Encouraged by the many positive replies to a questionnaire sent out to echinoderm specialists around the world in 1967, Maureen E. Downey and David L. Pawson launched *The Echinoderm Newsletter* in November 1968. The intention of this periodical was to provide an informal means of communication between echinoderm researchers and, in particular, to foster collaboration and minimize duplication of research efforts. With its content arranged around a number of sections such as “Addresses”, “Current Research”, “Job Offers”, “Meetings”, “Mysteries”, “Publications”, or “Requests”, *The Echinoderm Newsletter* relied on active participation and feedback from members within the research community. In fact, the creation of this periodical - in conjunction with the inception of the IEC a few years later - did help considerably to build the present sense of community among echinoderm scientists. The formal publisher of *The Echinoderm Newsletter* was the Department of Invertebrate Zoology of the National Museum of Natural History (NMNH) in Washington, DC. The editors from issue 1 (1968) to issue 11 (1980) were Maureen Downey and Dave Pawson. Having been administered by John M. Lawrence from issue 12 (1982) to issue 18 (1993), responsibility for the periodical eventually returned to the staff at the NMNH. Cynthia G. Ahearn was then in charge of providing the echinoderm community with the latest news from issue 19 (1994) to issue 26 (2001).

In the pioneering pre-digital times, *The Echinoderm Newsletter* was in fact photocopied and then mailed to up to seven hundred subscribers worldwide - at no cost to the reader. Using a state-of-the-art Gestetner mimeograph machine, Maureen Downey, Cindy Ahearn, and Dave Pawson produced up to 56,000 paper sheets per issue, that they laid out in 80 stacks of 700 pages each before manually assembling every single newsletter. Luckily for the editorial team, the NMNH eventually offered to accept *The Echinoderm Newsletter* as an official publication (ISSN 0735-7494), meaning that duplication and collation of each issue would be carried out by the U. S. Government Printing Office. Until issue 22 (1997), *The Echinoderm Newsletter* was available only in printed form, while for issues 23 (1998) and 26 (2001), a digi-

tal version was published in parallel to the print version. Budget cuts at the NMNH eventually led to the omission of hard copies and so, with issue 26, *The Echinoderm Newsletter* became *The Virtual Echinoderm Newsletter*, designed by Susan Hottenrott, but still edited by Cindy Ahearn. In 2004, the responsibility for this now entire-

ly electronical periodical was transferred to the Swedish Museum of Natural History in Stockholm, where it was recreated in reduced form and again named *The Echinoderm Newsletter* (<http://www.nrm.se/echinoderm>).

Of particular interest from a historical perspective are those sections of *The Echinoderm Newsletter* entitled



Figure 1. Impressions from two social gatherings organized during the first official echinoderm meeting, the *Symposium on Physiology of Echinodermata*, held 1963 in Washington, DC as part of the 16th *International Congress of Zoology*. (A) John B. Loefer, Richard A. Boolootian, John M. Anderson, Allahverdi A.-H. Farmanfarmaian. (B) Dennis J. Crisp, W. Randolph Taylor. (C) George P. Wells, Friedrich Krüger. (D) Hans O. Brattström, Wolfgang Wieser, Williamina A. M. Courtney, C. Ladd Prosser, unidentified person. (E) Jeremy D. Woodley, Lary V. Davis, Thomas S. Hopkins, John S. Pearse. (F) John M. Anderson, Aage M. Christensen. Images courtesy Mark Boolootian and Richard A. Boolootian.

“How I Began to Study Echinoderms...”, “Theses & Dissertations”, and “Obituaries”, as they provide a valuable source of information for future historical research on individual echinoderm scientists. We have digitized all back issues of *The Echinoderm Newsletter* and the resulting files have been made accessible through the recently created database *The Echinoderm Files* (<http://tinyurl.com/p2f9d9j>).

Echinoderm Studies (1983–2001)

In parallel to the numerous echinoderm symposium or conference proceedings that have appeared since the mid-1960s - starting with Boolootian (1965) - a short series of echinoderm-related publications entitled *Echinoderm Studies* was issued between 1983 and 2001 (Jangoux and Lawrence 1983, 1987, 1989, 1993, 1996, 2001). The name of the series was inspired by the title of a doctoral thesis published at Uppsala Universitet in the mid-1920s (Gislén 1924). The guiding principle of *Echinoderm Studies* was to cover all aspects of echinoderm research from molecular biology to ecology, paleontology, physiology, and taxonomy. The main goal of the book series (ISSN 0168-6100) was to provide biologists from different backgrounds with a rapid access to the field of echinoderm research and to give direction for future studies in echinoderm science.

The idea for *Echinoderm Studies* emerged between Michel Jangoux and John M. Lawrence at the end of the 1970s and they took the opportunity of the 4th IEC held 1981 in Tampa, Florida to invite the authors of the plenary papers to present their respective field of research in the form of a broad review article. The first issue received critical acclaim (Nichols 1983, Birkeland 1984), as did many of the following volumes (Tyler 1988, Mladenov 1991, Ellers 1997). However, the initial contract that had been signed for six volumes was not renewed by the publisher as a consequence of the purchase of this company by another publishing house, which unfortunately did not judge the series as profitable. For copyright reasons, the content of all six issues of *Echinoderm Studies* is currently only available in printed form through libraries.

SPC Beche-de-mer Information Bulletin (1990 - today)

The *SPC Beche-de-mer Information Bulletin* (BDM) is the only echinoderm-related publication ever issued in true journal format right from its inception (ISSN 1025-4943). As the name suggests, the BDM revolves around sea cucumber fisheries, although its content has expanded considerably over the years. It now includes original research papers and review articles, correspondences, abstracts from publications and conference papers, bibliographies, address lists, spawning observations, market news, information on upcoming meetings and workshops, as well as general data on sea cucumber resource management. The first issue of the BDM was published

in January 1990. Since then, the Secretariat of the Pacific Community (SPC, formerly known as the South Pacific Commission) has published 33 issues of the BDM, all of which are available for download at no charge (<http://tinyurl.com/pr9uzpm>).

The BDM does not constitute a peer-reviewed publication (Conand 2008), as all contributions are sent to the managing editor, who then decides, with the help of specialized colleagues, whether the article is fit for publication. Until issue 27 (2008), Chantal Conand acted as the managing editor, before co-editing issue 28 (2008) together with Igor Eeckhaut, who became the managing editor of the BDM from that issue onwards. Technical and editorial aspects of the BDM have been arranged by SPC staff, in particular by Jean-Paul Gaudechoux for the first issues and Aymeric Desurmont since 1996.

The BDM is a bilingual publication: the original texts are submitted and published in English, but a full French translation of each issue, called *La bêche-de-mer bulletin d'information*, is provided by the SPC in addition to the English version (<http://tinyurl.com/ncg76j9>). In some years, the BDM has been published twice annually (i.e., 1990, 1999, 2001, 2002, and 2004–2008), but budget cuts for translation services at SPC have led to a reduction to one issue per year from 2009 onwards. In addition, the supply with printed copies had to be suspended from issue 24 (2006) on due to environmental reasons and further budget cuts at SPC. However, the total page numbers of BDM issues have steadily increased over time, from 14 pages in issue 1 (1990) to 76 pages in issue 32 (2012). Numerous articles published in the BDM over the last 20 years have been cited in high-ranking research papers, further illustrating the importance of the work presented in the *SPC Beche-de-mer Information Bulletin*.

Perspective

We would like to point out that the notable absence of a central publishing organ for the echinoderm community entails that important biographical data on individual echinoderm researchers (e.g., obituaries) have to be published elsewhere, often leading to difficulties in locating this information. It would therefore be important to discuss, in our eyes, how and where such data could be published in the future to ensure an improved accessibility.

Digital echinoderm resources

In addition to their century-old presence in the print media, echinoderms have since the early 1990s increasingly been featured in the digital domain. More than 20 years later, there are today dozens or probably even hundreds of institutional and private websites that provide echinoderm-related information. Because it would be beyond the scope of this article to list them all, we here present a chronological

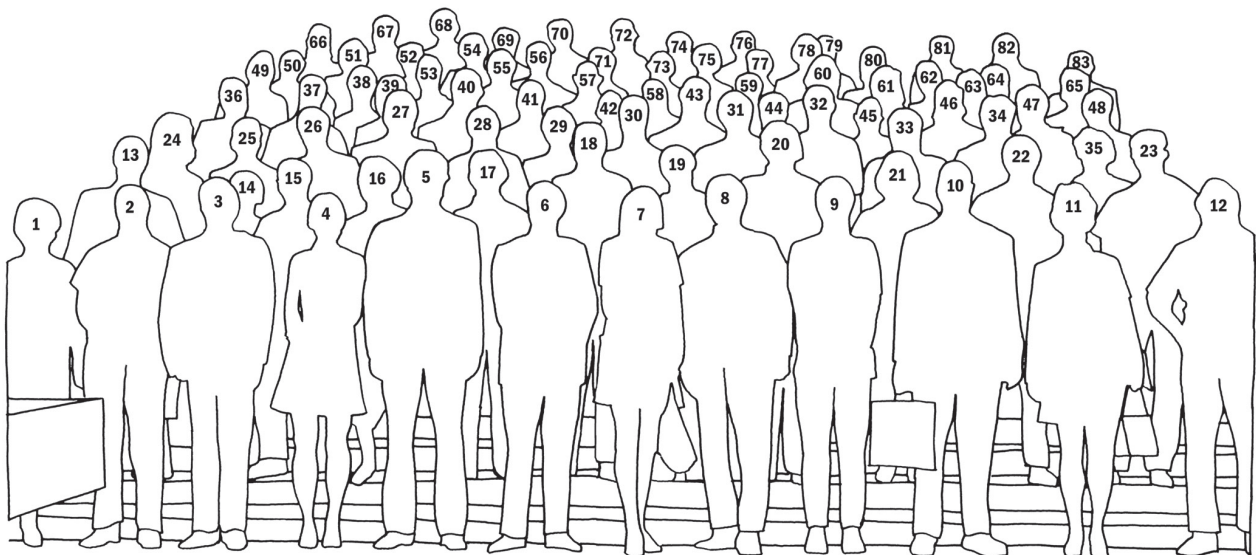


Figure 2. Group photo of the participants of the 1st *International Echinoderm Conference*, held 1972 in Washington, DC. 1 Lucienne Fenaux, 2 Harrell L. Strimple, 3 Thomas A. Ebert, 4 Jacqueline E. Moss, 5 Fu-Shiang Chia, 6 Alfred B. Chaet, 7 Sylvia Broderick, 8 Allahverdi A.-H. Farmanfarmaian, 9 Stanley E. Blake, 10 Michael H. Salazar, 11 Judith Eastwood, 12 Thomas F. Phelan, 13 Albert Breimer, 14 Christina Strimple, 15 John C. Ferguson, 16 Jennifer Nielsen, 17 Charles W. Walker, 18 Porter M. Kier, 19 Richard H. Chesher, 20 William C. Austin, 21 Bertha M. Cutress, 22 Charles Major, 23 Christopher R. C. Paul, 24 Ilana Ferber, 25 David L. Meyer, 26 Donald B. Macurda Jr., 27 Dennis W. Burdick, 28 Gerald J. Bakus, 29 Robert S. Carney, 30 F. Julian Fell, 31 Donald Broom, 32 Robert L. Singletary, 33 A. John Jordan, 34 Lawrence W. Coady, 35 Ailsa M. Clark, 36 Andrew C. Campbell, 37 John M. Lawrence, 38 Jeremy D. Woodley, 39 David G. Atwood, 40 Lowell P. Thomas, 41 John H. Dearborn, 42 Michael A. Kyte, 43 David L. Pawson, 44 Irving Gray, 45 Alan S. Horowitz, 46 David N. Emerson, 47 George D. Sevastopulo, 48 Richard L. Turner, 49 James Sutton, 50 James C. Brower, 51 Frank J. S. Maturo, 52 Edward P. F. Rose, 53 David Nichols, 54 Douglas H. Fenner, 55 W. Ross Ellington, 56 Donald P. Kelso, 57 James Sprinkle, 58 N. Gary Lane, 59 Michael LaBarbera, 60 John P. Eylers, 61 D. Keith Serafy, 62 Elizabeth M. Sides, 63 Dana Scott, 64 Maria Elena Caso, 65 Frank Jeal, 66 Jerald A. Halpern, 67 J. Wyatt Durham, 68 John M. Warn, 69 Dennis R. Kolata, 70 Ronald L. Parsley, 71 Richard U. Gooding, 72 Bruce M. Bell, 73 Gordon Hendler, 74 John S. Pearse, 75 Richard R. Strathmann, 76 Thomas S. Hopkins, 77 Stephen E. Stancyk, 78 John Caldwell, 79 Unidentified person, 80 Frederick H. C. Hotchkiss, 81 Aage M. Christensen, 82 Juan C. Castilla, 83 Fred C. Ziesenhenn. Image courtesy John M. Lawrence.

list of selected digital resources, some of which have already been discontinued. Most of these echinoderm websites - as well as multiple others - have also been featured in the section “Echinoderm Links” of the more recent issues of *The Echinoderm Newsletter*.

Starnet Echinoderm Newsletter (1992–1997)

One of the first, if not *the* first, digital echinoderm projects was the *Starnet Echinoderm Newsletter*, launched in 1992. This resource was created and edited by Winston A. Hide, who at that time was working for Dave Pawson as a postdoctoral student. The *Starnet Echinoderm Newsletter* was originally a stand-alone website, but later came to complement *The Echinoderm Newsletter* (see above). The aim of this electronic resource was to provide the worldwide echinoderm community with instantaneous and up-to-date information about meetings, book reviews, addresses of echinoderm scientists, and even recipes, as well as with a forum for current research. Apart from the main website, the project also included an electronic newsletter sent out to all subscribers via Email. The *Starnet Echinoderm Newsletter* went offline in 1997.

The Tree of Life Web Project (1996 - today)

Since its official release in 1996, the digital resource *The Tree of Life Web Project* (ToL) aims to provide information about the current knowledge of the evolutionary tree of life (<http://tinyurl.com/wz8l>). The contents of ToL are created by a multi-national team of more than five hundred biologists, each of them an expert for a particular group of organisms. The main goal is to document all significant clades and to provide basic information about the diversity and phylogeny of life on Earth. The individual web pages of ToL are arranged according to branching patterns between taxa and permit browsing the hierarchy of life as well as the characteristics of individual groups (Maddison et al. 2007). ToL covers extant and fossil taxa, providing images of characteristic morphology, images of key taxa, bibliographical lists, web links, vernacular names, as well as evidence for morphological and molecular characters.

The prototype of ToL was developed in 1994. Back then, the database underlying ToL was created using the software Mac-Clade and its NEXUS file format. However, in 2004, this program was replaced by TreeGrow, a cross-platform system which would allow all taxonomic experts to edit their web pages directly, thereby resulting in a more dynamic web environment. Despite similar names and foci, ToL is not directly associated with the National Science Foundation’s *Assembling the Tree of Life* (AToL) initiative. Therefore, in order to avoid confusion, ToL’s initial name, *The Tree of Life*, was changed to its current name, *The Tree of Life Web Project*.

Echinoderms are represented in ToL by a number of individual web pages. The first of these to go online was the website on Crinoidea, created in 1998 by William I. Ausich and Charles G. Messing (<http://tolweb.org/Crinoidea>). A

year later, the main page on the Echinodermata, compiled by Gregory A. Wray, was launched (<http://tinyurl.com/q9mka8t>). In 2000, this web page was followed by pages on holothurians (<http://tinyurl.com/p3xs4p7>) written by Alexander M. Kerr. Asteroidea, compiled by Emily Knott, were the next clade of extant echinoderms to follow, going online in 2004 (<http://tinyurl.com/pms4wol>). The last echinoderm-related website in ToL to be published was the page on the fossil clade Somasteroidea, online since 2005 and written by Alexander E. Primus (<http://tolweb.org/Somasteroidea/24272>).

Although there has not been any major activity over the past several years, the echinoderm section of ToL will expand in the coming years (Greg Wray, pers. comm.). This development will primarily be fueled by the National Science Foundation’s new AToL project, the *Echinoderm Tree of Life* (EToL).

Sea Urchin Embryology (1998 - today)

Likely the first truly interactive website on echinoderms was *Sea Urchin Embryology* (<http://tinyurl.com/noss-wz3>), which went online in 1998. The aim of this electronic publication was to provide high school teachers with a digital resource on sea urchin fertilization and deuterostome development that could be constantly updated by the editors. The website offers advanced high school level laboratory activities with materials to support school lessons. *Sea Urchin Embryology* was inspired by animations of cell development that Chris Patton had created for Daniel Mazia at Stanford University in the mid-1990s. Funded by the National Science Foundation, a team surrounding David Epel, Pamela Miller, and Chris Patton created a first version of the website with 150 pages in 1997, but *Sea Urchin Embryology* was later expanded to well over 300 pages. The site was programmed using Hypertext Markup Language (HTML) and was complemented with animated Graphics Interchange Format (GIF) files, Joint Photographics Expert Group (JPEG) files, and further types of digital data. *Sea Urchin Embryology* received numerous awards, among them the “Bridge Steller Site” award by The Bridge and the “Webivore Featured Site” award by Webivore, Inc. Although the website is still maintained by Chris Patton, new information has not been added for some time. Since 2005, *Sea Urchin Embryology* has been complemented by a further digital resource, the *Virtual Urchin* website (see below).

The Echinoid Directory (1999 - today)

In 1999, another electronic echinoderm project went online, *The Echinoid Directory* (<http://tinyurl.com/p3bkosd>). This website was created by Andrew B. Smith and is aimed at replacing the pages on sea urchins found in *The Treatise on Invertebrate Paleontology* (Moore 1966). In order to complement the data contained within this printed volume, Andrew Smith made use of the advantages of a web-based

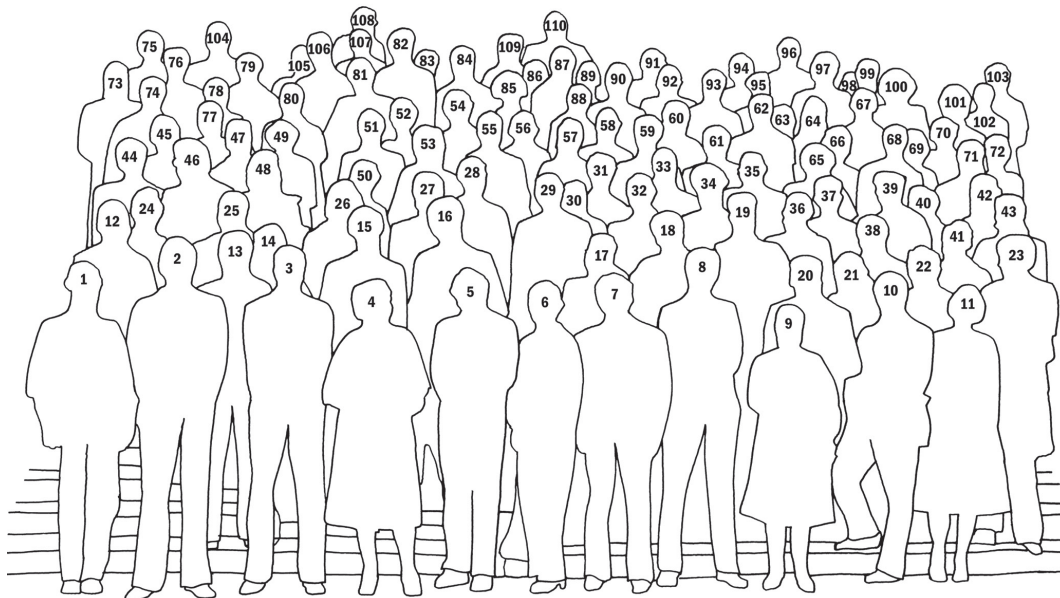


Figure 3. Group photo of the participants of the 1st European Conference on Echinoderms, held 1979 in Brussels. 1 Chantal De Ridder, 2 Michel Jangoux, 3 Claude Massin, 4 Anneliese Strenger, 5 Charles W. Walker, 6 Mrs. Hulbert, 7 Alan W. Hulbert, 8 David Nichols, 9 Mrs. Vasserot, 10 Robert F. O'Brien, 11 Anke Burkhardt, 12 Helge Hilgers, 13 Alfred Goldschmid, 14 Mrs. Goldschmid, 15 Richard M. Pagett, 16 Alan M. Raymond, 17 Raimundo Pidal, 18 Jean Le Menn, 19 Michel Huet, 20 Jean-Michel Vasserot, 21 Maria de Natividade Albuquerque, 22 Konrad Märkel, 23 Sebastian Bachmann, 24 Heinz Splechtna, 25 F. Jensenius Madsen, 26 Mrs. Guille, 27 Alain Guille, 28 Hubert Caspers, 29 Henri Termier, 30 Genevieve Termier, 31 Mrs. Roman, 32 Jean Roman, 33 Edwin Van Impe, 34 Jean-Guy Ferrand, 35 Robert Delavault, 36 Mrs. Huet, 37 Yulin Liao, 38 Jovanka Mitrović, 39 Norman Millott, 40 Mrs. Millott, 41 Ricard Martínez, 42 John E. Binyon, 43 Edward P. F. Rose, 44 Duncan Heddle, 45 Michel Philippe, 46 Jean-Pierre Féral, 47 Daniel Fournier, 48 Solveig Sjögren, 49 Monique Guillou, 50 Ms. Bacallado-Aranega, 51 Jacques Guillou, 52 Mrs. David, 53 Juan Jose Bacallado-Aranega, 54 Bruno David, 55 Celso Rodriguez Babio, 56 Mrs. Monteiro Marques, 57 Myriam Sibuet, 58 Enrico Tortonese, 59 Michel Roux, 60 Peter A. Voogt, 61 Gustave Cherbonnier, 62 Reimund Haude, 63 Mrs. Paterson, 64 Mrs. Durkin, 65 Ailsa M. Clark, 66 Radu Sukarno, 67 Michael K. Durkin, 68 Richard P. S. Jefferies, 69 Lesley I. Messer, 70 Ester Ryberg, 71 David G. Stephenson, 72 Edith Bricourt, 73 Guy Coppois, 74 Michel Demargne, 75 Christopher R. C. Paul, 76 Erhard Höbaus, 77 Pierre Magniez, 78 Alain Bidar, 79 Geoffrey Q. Case, 80 Lydie Dupont, 81 M. De Waal, 82 Wolfram P. Tertschnig, 83 Unidentified person, 84 Gerardo Gustato, 85 Aagje J. Van der Plas, 86 Anna Villari, 87 Derek E. G. Briggs, 88 Vasco M. A. Monteiro Marques, 89 Megumi F. Strathmann, 90 Rob C. H. M. Oudejans, 91 Peter M. Jost, 92 Unidentified person, 93 Gordon L. J. Paterson, 94 Paula F. Dehn, 95 Hussein Kamel Badawi, 96 Roland H. Emson, 97 Paul A. Tyler, 98 Grace S. Y. Lim, 99 John M. Lawrence, 100 Andrew B. Smith, 101 Ilana Ferber, 102 Haruo Kanatani, 103 Desmond B. Johnson, 104 Iain C. Wilkie, 105 Jaume Gallemlé Paulet, 106 Kurt Traer, 107 Bent Hansen, 108 Jan J. S. Broertjes, 109 Richard R. Strathmann, 110 Tine Valentinčič.

approach, in particular the possibility to continuously update and improve the content of the website and to upload an unlimited number of images. The currently more than 2,500 pages of *The Echinoid Directory* are arranged taxonomically, covering both extinct and extant taxa. Dichotomous keys permit sea urchin identification to genus level, while additional sections illustrate various aspects of echinoid biology and systematics. The initial design was carried out by Andrew Smith, while the technical development was accomplished by the information technology department at the Natural History Museum in London. The website has been generated using various Hypertext Transfer Protocol (HTTP) and JavaScript software. *The Echinoid Directory* was edited by Andrew Smith from 1999 to 2011, but he and Andreas Kroh are sharing the editorship since 2011. From 2006 on, the project has been opened to registered contributors, who can add or modify existing pages. An example is provided by the addition of interactive three-dimensional Portable Document Format (PDF) models of several sea urchin species that are available for download and online inspection (<http://tinyurl.com/p2ndfom>). *The Echinoid Directory* was elected “Best Palaeo Website” by The Palaeontological Association, received the “GSIS Outstanding Website” award by the Geoscience Information Society, and is indexed in the ISI Web of Knowledge Current Web Contents. The Natural History Museum is committed to maintaining the website for the coming years.

The Echinoderm-L (2000 - today)

In 2000, *The Echinoderm-L* project (<http://tinyurl.com/pjjenvp>) was introduced to the echinoderm community. This digital resource (the letter “L” stands for the software LISTSERV) was created by Sabine Stöhr following discussions during the 10th IEC held 2000 in Dunedin, New Zealand. Similar to part of the now inactive *Starnet Echinoderm Newsletter* (see above), *The Echinoderm-L* is an electronic mailing list intended to facilitate direct communication and discussion between echinoderm scientists. Like with other electronic mailing lists, each participant can send an Email to the editor, who will then send it on to all registered users. The mail server was configured by Cary Karp at the Swedish Museum of Natural History in Stockholm. The LISTSERV software was used from 2000 to 2010, while the software Mailman was employed from 2011 to 2012. However, since 2012, *The Echinoderm-L* is run using the Google Groups software. Sabine Stöhr plans to keep the mailing list active for the coming years.

Virtual Urchin (2005 - today)

The *Virtual Urchin* website (<http://tinyurl.com/ydyaxrt>), funded by the National Science Foundation, was launched in 2005. It was created by a team surrounding Jason Hodin, Pamela Miller, and David Epel at Stanford University. The aim of *Virtual Urchin* is to augment the materials already available at the *Sea Urchin Embryo-*

logy website (see above), which is primarily intended for high school teachers. In contrast, for *Virtual Urchin* students are the target users, and the intention is to provide them with a “real research lab” experience, albeit online. The website was built using HTML and Cascading Style Sheets (CSS) using multiple Flash animations. The content is arranged around a number of virtual tutorials that provide information about sea urchin fertilization and development as well as sea urchin anatomy and ecology. The website developers are currently planning to expand their concept to sea urchin larvae, but are also open to echinoderm biologists that seek to design high-quality outreach activities based on their research (Jason Hodin, pers. comm.).

The Echinoblog (2008 - today)

In order to engage the public in echinoderm science, Christopher L. Mah started his web log (or blog), *The Echinoblog* (<http://echinoblog.blogspot.com/>), in 2008. Since then, he has added more than 400 entries to his website, which contains numerous exquisite images and many lines of informative text. The aim of this digital project is to raise the public’s awareness about echinoderms and other marine invertebrates. Chris Mah has designed and developed *The Echinoblog* using the Google Blogger software and is currently the acting producer of the website. The content of his blog is primarily a digest of echinoderm research and a presentation of facts about echinoderms which are poorly understood by the public (e.g., the fact that sand dollars are sea urchins). But the website also includes images of other eye-catching invertebrates, including polychaetes, amphipods, or ctenophores. *The Echinoblog* is accompanied by a Twitter feed (<https://twitter.com/echinoblog>), also produced by Chris Mah. This complementary resource constitutes an almost instantaneous way of communicating scientific facts and findings to a wider audience.

The World Register of Marine Species (2008 - today)

The *World Register of Marine Species* (WoRMS) is a large database project aimed at providing an authoritative and comprehensive list of names of extant and extinct marine organisms. The main website (<http://www.marinespecies.org>) was launched in 2008, building on previously available data from the European Register of Marine Species as well as the infrastructure of the Aphia platform of the Vlaams Instituut voor de Zee (VLIZ). The species lists contained in WoRMS are supplemented by additional information on marine organisms, including, but not limited to, species distribution, nomenclatural status, ecological traits, vernacular names, and images. The database is hosted by VLIZ and is curated by more than two hundred taxonomic experts. Some taxa and/or regional lists are covered particularly extensively and are therefore represented by individual websites. Three of these thematic databases are focused on echinoderms:

The World Ophiuroidea Database (<http://tinyurl.com/q9elnbk>), created in 2007 by Sabine Stöhr and Timothy O'Hara; *The World Asteroidea Database* (<http://tinyurl.com/o6dz4qy>), launched in 2009 by Chris Mah; and *The World Echinoidea Database* (<http://tinyurl.com/pcohn6h>), published in 2010 by Andreas Kroh and Richard J. Mooi. Similar projects for holothuroids and crinoids are currently in preparation.

The Echinoderm Files (2013 - today)

The latest addition to the digital world of echinoderms is the website *The Echinoderm Files* (<http://tinyurl.com/nrrrkme>). This website, which went online in 2013, provides bibliographical information and metadata on 2,450 articles and abstracts published in the proceedings of IEC and ECE meetings (Kroh et al. 2013). In addition to these



Figure 4. Impressions from a poster session organized during the 1st *European Conference on Echinoderms*, held 1979 in Brussels. (A) Jan J. S. Broertjes, Haruo Kanatani, Peter A. Voogt. (B) Guy Coppoïs, Chantal De Ridder, Edith Bricourt, Lucie Jangoux, Robert Fenaux, Lucienne Fenaux. (C) Mrs. Monteiro Marques, Vasco M. A. Monteiro Marques, Gustave Cherbonnier, Lucie Jangoux, Solveig Sjögren. (D) Alfred Goldschmid (background), Tim Bowmer, Claude Massin, Jean-Pierre Féral, John Costelloe, Brendan O'Connor. (E) Richard M. Pagett, Iain C. Wilkie, Alan M. Raymond, Roland H. Emson. (F) Raimundo Pidal, Ricard Martínez, Enrico Tortonese, F. Jensenius Madsen, Bent Hansen.

two major echinoderm conference series, publications related to a number of independent echinoderm symposia have been included as well. By making the bibliographical data of these proceedings volumes available in the form of a searchable database, *The Echinoderm Files* aims at facilitating an easier access to the information contained within these often hard-to-locate volumes. In addition, the website supplements the information on echinoderm meetings and symposia compiled in Ziegler and Kroh (2012). The website itself has been programmed using the software Exhibit 3.0, which allows online searching and browsing of the database. Furthermore, the raw data contained within the database can be downloaded in different file formats for convenient data export. *The Echinoderm*

Files has been integrated into the project landscape of *The World Register of Marine Species* (see above).

Perspective

For well over 20 years now, the Internet has been successfully used to document the diversity of echinoderms and to present scientific and popular facts about this group of marine invertebrates to a wider audience. Although websites do not constitute formal publications in the classical sense, their contribution to echinoderm science should not be underestimated. In particular so, because websites facilitate rapid access to pieces of information that previously were hard or even impossible to locate.

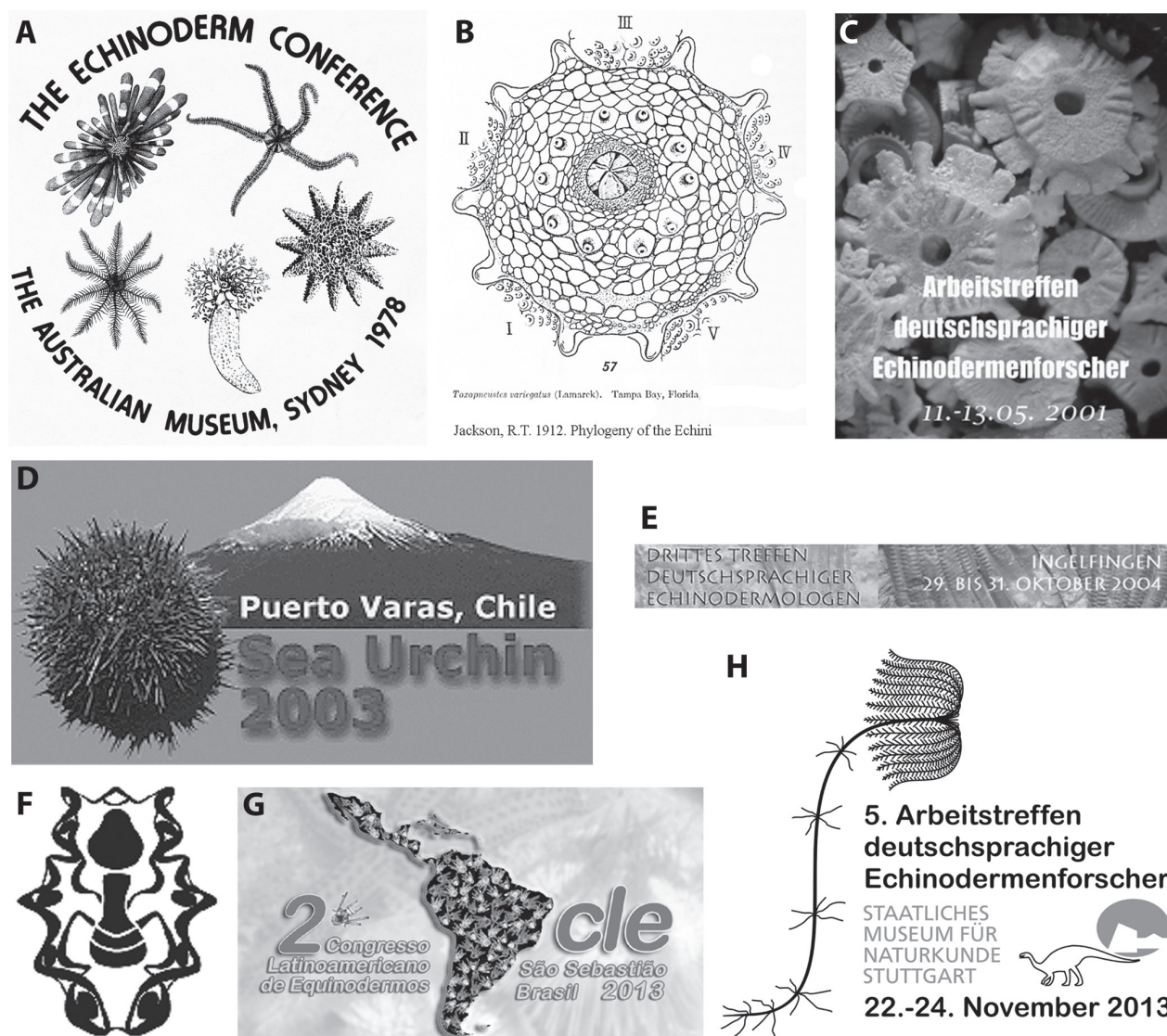


Figure 5. Conference logos from selected national, regional, and international echinoderm meetings held from 1978 to 2013. (A) 3rd International Echinoderm Conference, Sydney, Australia, 1978. (B) 5th Florida Echinoderm Festival, Tampa, Florida, USA, 1999. (C) 1. Arbeitstreffen deutschsprachiger Echinodermenforscher, Greifswald, Germany, 2001. (D) International Conference on Sea-Urchin Fisheries and Aquaculture, Puerto Varas, Chile, 2003. (E) 3. Arbeitstreffen deutschsprachiger Echinodermenforscher, Ingelfingen, Germany, 2004. (F) ACIAR-SPC Asia-Pacific Tropical Sea Cucumber Aquaculture Symposium, Nouméa, New Caledonia, 2011. (G) 2º Congresso Latinoamericano de Equinodermos, São Sebastião, Brazil, 2013. (H) 5. Arbeitstreffen deutschsprachiger Echinodermenforscher, Stuttgart, Germany, 2013.

Conference logos and flyers

In addition to the conference logos previously depicted in our first contribution on the history of echinoderm meetings (Ziegler and Kroh 2012), we are able to present further logos from national, regional, and international echinoderm conferences (Fig. 5).

We are particularly pleased to announce that the logo of the 3rd IEC (1978, Sydney, Australia), which was thought to have been lost, has been retrieved (Fig. 5A). This logo - and many others - can also be found online at *The Echinoderm Files* website (<http://tinyurl.com/o9fzoq8>). Furthermore, Figure 6 shows one of the echinoderm flyers traditionally handed out during the *Meeting of the Geological Society of America*. Such leaflets have been used to announce the informal gatherings of the *Friends of the Echinoderms*. Lane (1997) and Lawrence (1998) provide detailed background information about these events. Finally, the following echinoderm meeting unfortunately went unnoticed in our previous compilations:

Symposium on Biology and Ecology of the Crown-of-thorns starfish, *Acanthaster planci* (L.) (held as part of the Pacific Science Association Second Inter-Congress)

Agana, Guam, USA, 23–24 May 1973

Organized by Lucius G. Eldredge and the Pacific Science Association

Proceedings volume: Biology and Ecology of the Crown-of-thorns starfish, *Acanthaster planci* (L.), *Micronesica*, 9, 1–243, ISSN 0026-279X

Last but not least, we would like to correct a mistake made in our first article on the history of echinoderm meetings: the *Symposium on Echinoderm Development*, held as part of the *Winter Meeting of the American Society of Zoologists* took place in 1973 from December 27–28, instead of December 20–23.

Concluding remarks

Although the Echinodermata have been the focus of scientific study for well over 2,000 years, in particular the last 50 years have witnessed a significant increase in knowledge on all aspects of echinoderm biology. This welcome development must in part be attributed to the improved communication among echinoderm scientists due to meetings and the associated proceedings. Given the impressive tools for data dissemination and direct communication that are available to researchers nowadays, we estimate an even faster knowledge gain to occur in echinoderm science in the coming years.

Acknowledgements

We are grateful to the following members of the echinoderm community for their help in assembling the information presented here:

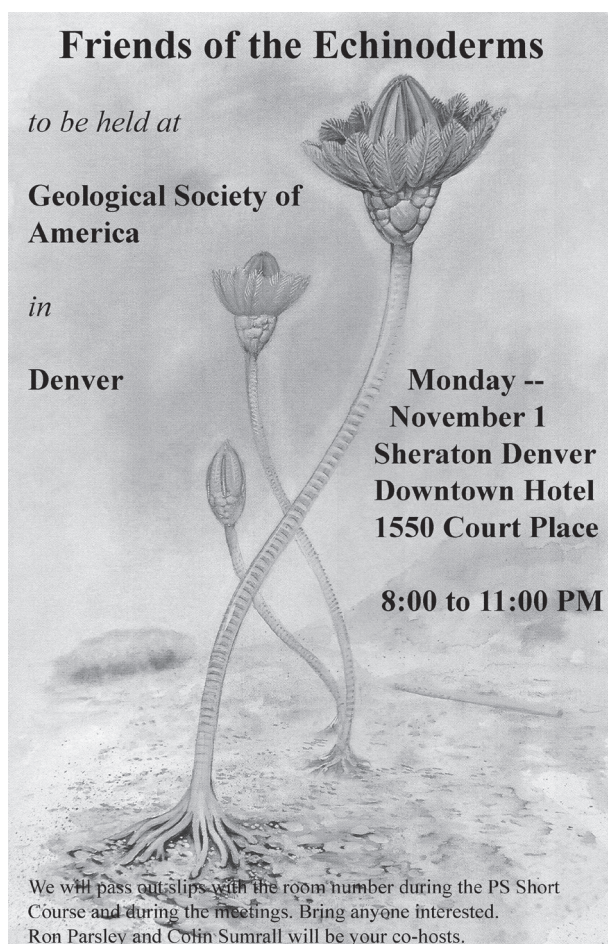


Figure 6. Flyer announcing an informal gathering of the *Friends of the Echinoderms* during the 2010 *Meeting of the Geological Society of America* in Denver, Colorado, USA. Image courtesy Ronald L. Parsley.

Michael F. Barker (Dunedin, New Zealand), Maria Byrne (Sydney, Australia), Chantal Conand (La Réunion, France), Bruno David (Dijon, France), Aymeric Desurmont (Nouméa, New Caledonia), Janina F. Dynowski (Stuttgart, Germany), Winston A. Hide (Cambridge, Massachusetts, USA), Jason Hodin (Pacific Grove, California, USA), Christopher L. Mah (Washington, DC, USA), Claus Nielsen (Copenhagen, Denmark), Ronald L. Parsley (New Orleans, Louisiana, USA), Jaume Gallemlé Paulet (Barcelona, Spain), David L. Pawson (Washington, DC, USA), Doris J. Pawson (Washington, DC, USA), John S. Pearse (Santa Cruz, California, USA), Vicki B. Pearse (Santa Cruz, California, USA), Francis W. E. Rowe (Hoxne, UK), Andrew B. Smith (London, UK), Andrej N. Soloviev (Moscow, Russia), Sabine Stöhr (Stockholm, Sweden), Megumi F. Strathmann (Friday Harbor, Washington, USA), Richard R. Strathmann (Friday Harbor, Washington, USA), Richard L. Turner (Melbourne, Florida, USA), Paul A. Tyler (Southampton, UK), Iain C. Wilkie (Glasgow, UK), and Gregory A. Wray (Durham, North Carolina, USA). Richard A. Booloottian and his son Mark Booloottian (Santa Cruz, California, USA) kindly sent us images from the first echinoderm meeting held in 1963. We would like to thank John M. Lawrence (Tampa, Florida, USA) and Andreas Ziegler (Berlin, Germany) for their helpful comments on earlier versions of our manuscript.

References

- Anonymous (1912) Proceedings of the Seventh International Congress of Zoology. The University Press, Cambridge, 972 pp.
- Birkeland C (1984) Book review: Echinoderm Studies. Volume 1. The Quarterly Review of Biology 59: 342–343.
- Booolootian RA (1965) Physiology of Echinodermata. Interscience, New York, 822 pp.
- Conand C (2008) Editorial. SPC Beche-de-mer Information Bulletin 28: 1.
- Ellers O (1997) Book review: Echinoderm Studies. Volume 5. The Quarterly Review of Biology 72: 340.
- Gislén T (1924) Echinoderm Studies. Zoologiska Bidrag från Uppsala 9: 1–316.
- Jangoux M, Lawrence JM (1982) Echinoderm Nutrition. Balkema, Rotterdam, 654 pp.
- Jangoux M, Lawrence JM (1983) Echinoderm Studies 1. Balkema, Rotterdam, 203 pp.
- Jangoux M, Lawrence JM (1987) Echinoderm Studies 2. Balkema, Rotterdam, 285 pp.
- Jangoux M, Lawrence JM (1989) Echinoderm Studies 3. Balkema, Rotterdam, 382 pp.
- Jangoux M, Lawrence JM (1993) Echinoderm Studies 4. Balkema, Rotterdam, 368 pp.
- Jangoux M, Lawrence JM (1996) Echinoderm Studies 5. Balkema, Rotterdam, 250 pp.
- Jangoux M, Lawrence JM (2001) Echinoderm Studies 6. Balkema, Rotterdam, 347 pp.
- Johnson K (2009) The return of the Phoenix: the 1963 International Congress of Zoology and American zoologists in the twentieth century. Journal of the History of Biology 42: 417–456.
- Kroh A, Jangoux M, Mirantsev GV, Ziegler A (2013) The Echinoderm Files: a database-facilitated access to a hidden treasure trove. Cahiers de Biologie Marine 54: 549–557.
- Lane NG (1997) Introduction to the Paleontological Society short course ‘Geobiology of Echinoderms’. The Paleontological Society Papers 3: 1–2.
- Lawrence JM (1998) A history of meetings on Echinodermata in North America. Gulf of Mexico Science 16: 112–114.
- Lawrence JM (2001) Edible Sea Urchins: Biology and Ecology. First edition. Elsevier, Amsterdam, 419 pp.
- Lawrence JM (2006) Edible Sea Urchins: Biology and Ecology. Second edition. Elsevier, Amsterdam, 529 pp.
- Lawrence JM (2013) Sea Urchins: Biology and Ecology. Third edition. Academic Press, London, 600 pp.
- Maddison DR, Schulz KS, Maddison WP (2007) The Tree of Life Web Project. Zootaxa 1668: 19–40.
- Mladenov P (1991) Book review: Echinoderm Studies. Volume 3. The Quarterly Review of Biology 66: 89–90.
- Moore RC (1966) Treatise on Invertebrate Paleontology, Part U, Echinodermata 3. The University of Kansas Press, Lawrence, 366 pp.
- Nichols D (1962) Echinoderms. First edition. Hutchinson University Library, London, 200 pp.
- Nichols D (1969) Echinoderms. Second edition. Hutchinson University Library, London, 192 pp.
- Nichols D (1983) Talk of echinoderms at Tampa Bay. Nature 306: 296.
- Romer AS (1963) International Congress of Zoology, 20–27 August 1963. Science 140: 1113–1116.
- Tyler PA (1988) Book review: Echinoderm Studies. Volume 2. The Quarterly Review of Biology 63: 468–469.
- Ziegler A, Kroh A (2012) Echinoderm conferences and symposia: a concise history and bibliography. Zoosymposia 7: 1–24.

Trematodes obtained from the thiarid freshwater snail *Melanoides tuberculata* (Müller, 1774) as vector of human infections in Thailand

Duangduen Krailas¹, Suluck Namchote¹, Tunyarut Koonchornboon², Wivitchuta Dechruksa¹ and Dusit Boonmekam¹

¹ Department of Biology, Faculty of Science, Silpakorn University, Nakhonpathom 73000, Thailand

² Department of Anatomy, Pramongkuthklao College of Medicine, Bangkok 10400, Thailand

Corresponding author: Duangduen Krailas (kduang@su.ac.th, kduang@gmail.com)

Abstract

Received 8 Jan 2014
Accepted 18 Feb 2014
Published 28 March 2014

Academic editor:
Matthias Glaubrecht

Key Words

Trematoda
Cercariae
human health
shedding
Thiaridae
Cerithioidea

Larval stages of trematodes obtained from the freshwater snail *Melanoides tuberculata* (Cerithioidea, Thiaridae) as intermediate host were studied by using cercarial emergence and crushing snails. Between December 2004 and September 2009 snails from one hundred twenty locations in Thailand were collected every two months for one year at each sampling site. Counts per unit of time method was used in this study, and the samples of snails were collected every 10 minutes per sampling by five collectors. The cercarial stages were examined using shedding and crushing methods. The infection rate was found to be 18.79%, i.e. 6,019 animals infected in a total of 32,026. Nine different types in eighteen species of cercariae were categorized, viz. are (1) Parapleurophocercous cercariae: *Haplorchis pumilio*, *Haplorchis taichui*, and *Stictodora tridactyla*; (2) Pleurophocercous cercariae: *Centrocestus formosanus*; (3) Xiphidiocercariae: *Acanthatrium hitaense*, *Loxogenoides bicolor*, and *Haematoloechus similis*; (4) Megalurous cercariae: *Cloacitrema philippinum* and *Philophthalmus* sp.; (5) Furcocercous cercariae: *Cardicola alseae*, *Alaria mustelae*, *Transversotrema laruei*, *Apatemon gracilis*, and *Mesostephanus appendiculatus*; (6) Echinostome cercariae: *Echinochasmus pelecani*; (7) Amphistome cercariae: *Gastrothylax crumenifer*; (8) Renicolid cercariae: *Cercaria caribbea* LXVIII; and, (9) Cotylomicrocercous cercariae: *Podocotyle* (*Podocotyle*) *leporis*.

Introduction

The neglected tropical diseases (NTDs) represent the most common parasitic infections affecting the world's poorest people (Hotez et al. 2007). In addition to their detrimental effects on health, NTDs have a chronic debilitating effect by undermining the physical and cognitive development of individuals residing in areas infested with NTDs, especially for children and women of child-bearing age. An especially deleterious effect has been shown on their educational performance and future economic productivity (Hotez et al. 2007, 2009).

It is important to note in this context that trematodes infecting humans, especially liver fluke and intestinal flukes, are highly prevalent in Southeast Asian countries (Wongratnacheewin et al. 2001; Chai et al. 2005). These infections have a major public health impact. It has been

reported that the highest degree of infections with trematodes were discovered in the gastrointestinal tract of humans living in the north region of Thailand (Pungpak et al. 1998, Radomyos et al. 1998) and the most metacercarial species were found in cyprinoid fish in the north and northeastern regions (Srisawangwong et al. 1997b, Sukontason et al. 1999). The liver fluke *Opisthorchis viverrini* can cause cholangiocarcinoma, a kind of cancer in gall bladder (Sripa et al. 2010), while the intestinal fluke *Haplorchis taichui* is a possible agent of irritable bowel syndrome-like symptoms (Wattanakulpanich et al. 2010). However, Thai people have considerably underestimated these trematodes by continually eating Thai traditional food prepared from raw freshwater fish (Chuboon et al. 2005). So the prevalence of trematodes in Thailand has been a continual problem until now.

Life cycle of trematodes

Trematodes need three hosts to complete their life cycles. After their eggs hatch in the water source such as canals and streams, the miracidium, their first larval stage, will swim and find the first intermediate host, namely freshwater snails and terrestrial snails close to water. In particular, snail species of the genus *Bithynia* are known as intermediate hosts of the liver fluke *Opisthorchis viverrini* (Tesana 2002). Some edible mollusks, such as the viviparid *Filopaludina* spp. and the bivalve *Corbicula* spp., are known as the first and second intermediate hosts of echinostome intestinal fluke (Temcharoen 1992a, b, Krailas et al. 2008). Thus, we can call these trematode infections mollusk-transmitted diseases.

In the snails, they will develop from miracidium to sporocyst to redia and finally to cercaria. Cercaria will leave the snails, head to the second intermediate host, e.g. freshwater fish, and develop to be metacercaria, the infective stage. At least 18 species of cyprinoid fish act as the second intermediate hosts. If the vertebrates, like animals and humans, eat the infected raw fish, they will receive the metacercaria, which will not be digested by digestive enzymes. Instead, the trematodes will become adult and lay eggs, which are then emitted to the water again with the hosts' stool.

Survey of freshwater snails as the first intermediate hosts in Thailand

Several studies have been conducted on the fauna of mollusks with focus on their trematode infections (Wegeberg et al. 1999, Abdul-Salam et al. 2004). Not only in Asia but also Africa and Australia, these trematodes have been widely studied (Diaz et al. 2008, Derraik 2008). In Thailand, medically-important freshwater snails have been investigated since 1980 (Upatham et al. 1980, 1981, Nithiuthai et al. 2002, Krailas et al. 2003, Sri-aroon et al. 2005, Ukong et al. 2007, Dechruksa et al. 2007, Krailas et al. 2008). It was found that because of their life cycle and host specificity, the distribution of trematodes depends on the presence of the first and second intermediate hosts, as well as the eating habit of local people (Radomyos et al. 1998).

Freshwater Snails of the Thiaridae in Thailand

Many of the trematode infected freshwater snails are from the Cerithioidea, a large, essentially marine, group of caenogastropods with approximately 200 genera and with mainly pan-tropical distributions, which have been used also as model for evolutionary systematic studies (Glaubrecht 1996, 1999, 2000, 2011, Glaubrecht et al. 2009). To focus on the family Thiaridae, this group rep-

resents, as became evident in recent studies (Glaubrecht 1996, 1999, 2011, Lydeard et al. 2002, Strong et al. 2008, 2011), one of the two (or three) independent invasions into and colonizations of freshwater habitats. Mainly distributed in Southeast Asia, they are to be considered, together with the Pachychilidae as most significant intermediate hosts for infections in humans. For instance, the thiarids *Tarebia granifera* and *Thiara toucheana*, as well as the pachychilid *Brotia asperata*, *Brotia costula episcopalis* and *Brotia c. peninsularis* were found to be the first intermediate hosts for lung flukes (Tang 1940, Tubangui et al. 1950, Davis 1971, Brandt 1974). In addition, the thiarids *Tarebia granifera* and *Melanooides tuberculata* are the first intermediate hosts for intestinal fluke and blood flukes (Malek and Cheng 1974, Pointier and Jourdan 2000). In Thailand, *T. granifera* and *M. tuberculata* have been reported as the first intermediate host for lung and intestinal flukes (Upatham et al. 1995, Ukong et al. 2007, Dechruksa et al. 2007).

Melanooides tuberculata (Müller, 1774)

This taxon is common to freshwaters within its native distributional range that covers much of tropical Africa, Asia and the Oceania. It is now also present in much of the tropical and subtropical New World as a consequence of introductions that started during the last century (Madsen and Frandsen 1989). They were described as alien species around the world. Moreover, the species exhibits considerable polymorphism in shell ornamentation across its geographical range; however, at the same time among sites discrete lineages or 'morphs' of *M. tuberculata* can be separated by shell characters, such as coloration and ornamentation, apparently due to the predominantly parthenogenetic reproduction resulting from negligible intrapopulation variability in these traits (Samadi et al. 1999). For example, on Martinique Islands, each morph of *M. tuberculata* is different in terms of juveniles, growth rate and even parasite infection rate.

M. tuberculata is considered to be of medical significance, as most of the above cited parasites can affect humans. Although there can be considerable seasonal variation in the intensity of parasitism in these snails, the incidence of *M. tuberculata* with trematode parasites has been recorded to be as high as 92% (Derraik 2008). A checklist from 136 scientific published studies revealed that *M. tuberculata* could be host for flukes, identified as belonging to 17 families, 25 genera, and 37 species (Pinto and De Melo 2011). These trematodes are both animals and human parasites. Nevertheless, in Thailand there are only very few reports about *Melanooides* infection in certain specific areas of the country to date. However, investigations around Thailand have never been conducted. So, in the present study we have surveyed now the trematode infections of *M. tuberculata* all over Thailand.

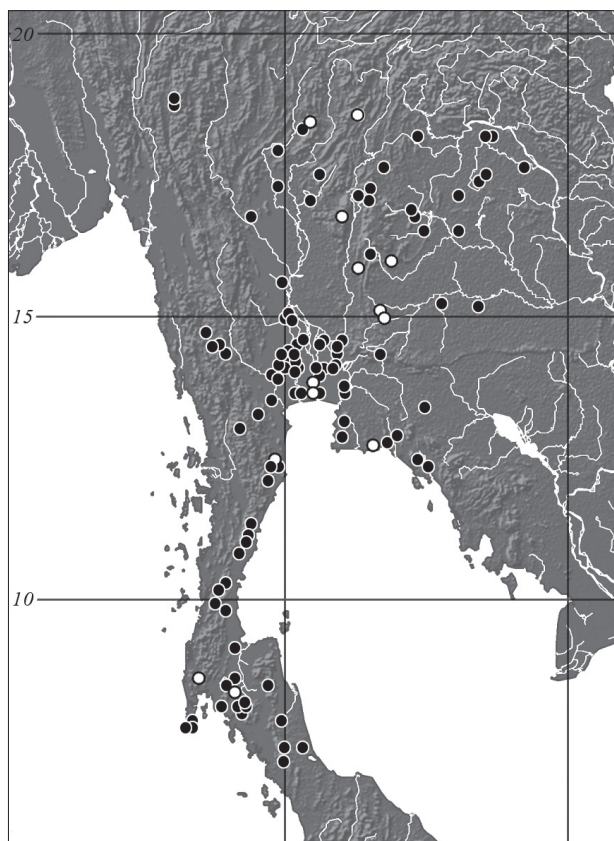


Figure 1. Occurrence of *Melanoides tuberculata* in Thailand. Closed symbol – *M. tuberculata* with infection; open symbol – *M. tuberculata* without infection.

Materials and methods

Sampling sites

One hundred twenty locations in Thailand, which are used by humans as sources of water, were examined (snail collection sites). For the exact data, please refer to the first section of the Result section in this report. The positions of collection sites were recorded by GPS (Garmin PLUS III, Taiwan). The localities of the relevant samples were mapped on a dot-by-dot basis to a digitally reduced version of the drainage pattern map of Thailand, as developed in Dechruksa et al. (2013). This map was created using a Reliefkarte on the basis of the Global 30-Arc-Second Elevation Data (GTOPO30) from the U.S. Geological Survey and a river map from the Map/server Aquarius Geomar, and then compiled using Adobe Photoshop CS3 and Adobe Illustrator.

Collection of snails

Between December 2004 and September 2009, snails were collected every two months for one year from each localities, using the counts per unit of time sampling method (Olivier and Schneiderman 1956). Five researchers collected samples by handpicking and scooping ev-

ery 10 minutes at each sampling site. The snail samples were then categorized into species according to their shell morphology. They were later examined for trematode infections.

Examination for parasitic infections

Parasitic infections were investigated by using snail shedding and crushing methods. Emerged cercariae were collected in dechlorinated water and observed for their swimming behavior (Krailas et al. 2003). Sporocysts and rediae were examined under a dissecting microscope.

Study of cercarial morphology

The cercariae were studied unstained or vitally stained with 0.5% neutral red and Semichon's acetic carmine & fast green. Descriptions of the morphology and anatomy of cercariae were based on the study of living cercariae that had escaped from the snails. Sample measurements (average size) in micrometers were taken from 20 specimens fixed in 10% formalin. Measurements in micrometers with averages in parentheses were taken from 20 specimens. Details of the cercariae were drawn using a camera lucida, and all their species were identified (Schell 1962, 1970, Nasir 1974, Yamaguti 1975; Ito 1980). For scanning electron microscopy, cercariae were fixed in 2.5% glutaraldehyde phosphate buffer (0.1 mol/l, pH 7.4) at 4 °C for at least 2 hours and post-fixed in 1% osmium tetroxide in the same buffer for 2 hours at 4 °C. They were dehydrated through a graded series of ethanol, and then dried in a critical point dryer using liquid carbon dioxide as a transition medium. The specimens were coated with gold-palladium in an ion-sputtering apparatus (Polaron CPD 7501, UK), and then examined in a scanning electron microscope (Camscan mx 2000, UK or JEOL, JSM-5410 LV, Japan).

Results

Melanoides tuberculata in Thailand

The thiarid *Melanoides tuberculata* was found in and sampled from study sites in five regions in Thailand, as shown in Table 1, Fig. 1. These include the following:

The North: N1 = Sakunotayan Waterfall, Wangtong District, Phitsanulok Province (SUT0109001) (N 16°50'20.6", E 100°32'15.6", Altitude 40 m); N2 = Kaeng Sopha Waterfall, Wangtong District, Phitsanulok Province (SUT0109002) (N 16°52'22.3", E 100°50'29.6", Altitude 398 m); N3 = Thung Salaeng Luang Stream, Wangtong District, Phitsanulok Province (SUT0109003) (N 16°50'50.0", E 100°51'57.2", Altitude 452 m); N4 = Pha Laht Waterfall, Nakhon Thai District, Phitsanulok Province (SUT0109004) (N 17°01'69.1", E 100°56'77.8", Altitude 267 m); N5 = Thum Pla Stream, Muang District, Mae Hong Son Province (SUT0109005)

Table 1. Locations in Thailand with *Melanooides tuberculata* found, the number of collected snails and infection rates.

No. (no. specimen)	Name	GPS	No. of collected snails	No. of infected snails	Infection rates (%)
North					
N1 (SUT0109001)	Sakunotayan Waterfall, Wangtong District, Phitsanulok	N 16° 50' 20.6" E 100° 32' 15.6" Altitude 40 m	13	3	23.08
N2 (SUT0109002)	Kaeng Sopha Waterfall, Wangtong District, Phitsanulok	N 16° 52' 22.3" E 100° 50' 29.6" Altitude 398 m	3	1	33.33
N3 (SUT0109003)	Thung Salaeng Luang Stream, Wangtong District, Phitsanulok	N 16° 50' 50.0" E 100° 51' 57.2" Altitude 452 m	3	0	0
N4 (SUT0109004)	Pha Laht Waterfall, Nakhon Thai District, Phitsanulok	N 17° 01' 69.1" E 100° 56' 77.8" Altitude 267 m	5	4	80
N5 (SUT0109005)	Thum Pla Stream, Muang District, Mae Hong Son	N 19° 25' 31.7" E 97° 59' 24.9" Altitude 343 m	60	38	63.33
N6 (SUT0109006)	Huay Sua Thao Stream, Muang District, Mae Hong Son	N 19° 15' 32.0" E 97° 54' 43.7" Altitude 237 m	51	9	17.65
N7 (SUT0109007)	Klong Nam Lai Waterfall, Klong Lan District, Kam Phaeng Phet	N 16° 11' 32.7" E 99° 15' 51.0" Altitude 241 m	63	28	44.44
N8 (SUT0109008)	Tad Duen Waterfall, Sri Satchanalai District, Sukhothai	(N 17° 33' 23.2" E 99° 29' 76.8" Altitude 414 m)	161	38	23.60
N9 (SUT0109009)	Sri Satchanalai Stream, Sri Satchanalai National Park, Sukhothai	N 17° 33' 5.9" E 99° 29' 24.8" Altitude 182 m	113	24	21.24
N10 (SUT0109010)	Mae Pool Waterfall, Lub Lae District, Ut-taradit	N 17° 43' 45.0" E 99° 58' 50.6" Altitude 164 m	70	9	12.86
N11 (SUT0109011)	Chueng Thong Waterfall, Muang District, Prae	N 18° 01' 54.2" E 100° 15' 52.8" Altitude 298 m	7	3	42.85
N12 (SUT0109012)	Huay Sa Nien Stream, Muang district, Nan	N 18° 51' 1.3" E 100° 39' 16.2" Altitude 280 m	60	0	0
N13 (SUT0109013)	Huay Ton Phueng Waterfall, Doi Pu Nang National Park, Chiang Muon District, Phayao	N 18° 55' 5.3" E 100° 12' 15.7" Altitude 379 m	131	1	0.76
N14 (SUT0109014)	Tansawan Waterfall, Doi Pu Nang National Park, Chiang Muon District, Phayao	N 18° 51' 22.7" E 100° 11' 9.6" Altitude 420 m	368	16	4.35
N15 (SUT0109015)	Mae Mine Stream, Mae Ta District, Lampang	N 18° 07' 1.8" E 99° 37' 35.1" Altitude 269 m	201	5	2.49
Northeast					
NE16 (SUT0109016)	Huay Lum Po Dang Stream, Thepsathit District, Chaiyapoom	N 15° 33' 42.8" E 101° 24' 56.9" Altitude 471 m	311	0	0
NE17 (SUT0109017)	Sai Thong Waterfall, Sai Thong National Park, Nong Bua Ra Hoew District, Chaiyapoom	N 15° 52' 34.7" E 101° 30' 34.7" Altitude 397 m	275	14	5.09
NE18 (SUT0109018)	Tad Tone Waterfall, Muang District, Chaiyaphom	N 15° 58' 42.5" E 102° 02' 24.9" Altitude 384 m	70	0	0
NE19 (SUT0109019)	Kongkaew Waterfall, Khao Yai National Park, Pak Chong District, Nakhon Ratchasima	N 14° 26' 14.8" E 101° 22' 37.6" Altitude 713 m	15	0	0
NE20 (SUT0109020)	Lam Takhong Stream, Khao Yai National Park, Pak Chong district, Nakhon Ratchasima	N 14° 25' 19.6" E 101° 23' 26.3" Altitude 700 m	344	0	0
NE21 (SUT0109021)	Ban Cha Rut Reservoir, Bua Ched District, Surin	N 14° 25' 50.4" E 103° 57' 47.7" Altitude 201 m	441	150	34.01
NE22 (SUT0109022)	Nong Bua Rai Reservoir, Khao Panomroong, Pra Kone Chai District, Buriram	N 14° 32' 51.2" E 102° 58' 9.4" Altitude 202 m	48	22	45.83
NE23 (SUT0109023)	Pla Ba Waterfall, Pu Rua District, Loei	N 17° 23' 24.3" E 101° 22' 27.4" Altitude 640 m	19	0	0
NE24 (SUT0109024)	Than Thong Waterfall, Sung Kom District, Nong Khai	N 18° 01' 34.7" E 102° 22' 8.7" Altitude 195 m	678	102	15.04
NE25 (SUT0109025)	Huay Hor Water Gate, Muang District, Nakhon Panom	N 17° 21' 8.4" E 104° 47' 2.1" Altitude 145 m	215	70	32.56
NE26 (SUT0109026)	Tad Kham Waterfall, Pu Lung Ga National Park, Ban Pang District, Nakhon Panom	N 17° 57' 1.4" E 104° 09' 39.9" Altitude 148 m	1,257	887	70.56
NE27 (SUT0109027)	Tad Po waterfall, Pu Lung Ga National Park, Ban Pang district, Nakhon Panom	N 17° 59' 0.9" E 104° 08' 34.3" Altitude 148 m	654	167	25.54

No. (no. specimen)	Name	GPS	No. of collected snails	No. of Infected snails	Infection rates (%)
NE28 (SUT0109028)	Nong Haan, Muang Distrcit, Sakol Nakhon	N 17° 09' 50.1" E 104° 09' 43.7" Altitude 161 m	68	3	4.41
NE29 (SUT0109029)	Nam Poong Dam, Gud Bak Distrcit, Sakol Nakhon	N 16° 58' 11.8" E 103° 59' 13.4" Altitude 290 m	260	57	21.92
NE30 (SUT0109030)	Lam Pow Dam, Muang District, Sri Sa Ket	N 16° 36' 22.3" E 103° 26' 27.5" Altitude 165 m	329	9	2.74
NE31 (SUT0109031)	Ban Nong Wang Wong Reservior, Sri Som Det District, Roi-Et	N 15° 56' 53.5" E 103° 31' 27.8" Altitude 178 m	1,281	126	9.84
NE32 (SUT0109032)	Bung Toong Sang, Muang District, Khon Kaen	N 16° 26' 27.8" E 102° 51' 28.1" Altitude 154 m	173	3	1.73
NE33 (SUT0109033)	Bung Kaen Nakhon, Muang District, Khon Kaen	N 16° 24' 46.6" E 102° 50' 21.9" Altitude 143 m	218	18	8.26
NE34 (SUT0109034)	Nong Sa Ad Bamroong Reservoir, Kosum Pisai District, Mahasarkham	N 16° 18' 0.5" E 102° 54' 38.5" Altitude 169 m	552	31	5.62
NE35 (SUT0109035)	Tad Tone Waterfall, Nong Soong District, Muk-daharn	N 16° 29' 34.9" E 104° 19' 1.1" Altitude 219 m	427	81	18.97
East					
E36 (SUT0109036)	Khao Khaew National Park, Sriracha District, Chonburi	N 13° 12' 45.0" E 101° 03' 50.2" Altitude 128 m	613	93	15.17
E37 (SUT0109037)	Ban Nong Pla Lai, Bang lamung District, Chonburi	N 12° 57' 54.3" E 100° 56' 47.8" Altitude 17 m	610	80	13.11
E38 (SUT0109038)	Rayong River, Muang District, Rayong	N 12° 39' 52.6" E 101° 14' 48.5" Altitude 6 m	51	0	0
E39 (SUT0109039)	Hin Khao Canal, Muang District, Rayong	N 12° 36' 31.7" E 101° 23' 22.4" Altitude 1 m	252	2	0.79
E40 (SUT0109040)	Pung rad Canal, Klang District, Rayong	N 12° 42' 49.5" E 101° 46' 23.4" Altitude 15 m	827	42	5.08
E41 (SUT0109041)	Chantaburi River, Muang District, Chantaburi	N 12° 36' 13.8" E 102° 07' 11.6" Altitude 8 m	278	18	6.47
E42 (SUT0109042)	Nam Tok Plew Stream, Plew District, Chantaburi	N 12° 31' 14.3" E 102° 10' 35.4" Altitude 39 m	223	14	6.28
E43 (SUT0109043)	Pa Tong Canal, Soi Dao District, Chantaburi	N 13° 07' 5.9" E 102° 13' 13.6" Altitude 231 m	206	20	9.71
E44 (SUT0109044)	Klong Kaew Waterfall, Bo Rai District, Trad	N 12° 37' 3.0" E 102° 34' 52.0" Altitude 81 m	347	83	23.92
E45 (SUT0109045)	Sra Kaew, Muang District, Sra Kaew	N 13° 49' 7.0" E 102° 03' 37.9" Altitude 43 m	480	188	39.17
E46 (SUT0109046)	Eto Waterfall, Muang District, Prachinburi	N 14° 08' 58.9" E 101° 24' 45.4" Altitude 39 m	810	317	39.14
Central					
C47 (SUT0109047)	Dusit Zoo Pond, Dusit, Bangkok	N 13° 46' 17.4" E 100° 31' 14.8" Altitude 2 m	26	9	34.62
C48 (SUT0109048)	Drainage at Kasetsart University, Bang Khen campus, Bangkok	N 13° 50' 40.7" E 100° 34' 33.5" Altitude 5 m	199	5	2.51
C49 (SUT0109049)	Pond at Kasetsart University, Bang Khen Campus, Bangkok	N 13° 50' 22.6" E 100° 34' 43.4" Altitude 1 m	92	1	1.09
C50 (SUT0109050)	Hin Dad Waterfall, Thong Pa Poom District, Kanchanaburi	N 14° 37' 29.8" E 98° 43' 40.2" Altitude 186 m	13	0	0
C51 (SUT0109051)	Pha Tad Waterfall, Sri Sa wat District, Kanchanaburi	N 14° 38' 54.9" E 98° 46' 41.6" Altitude 196 m	14	2	14.29
C52 (SUT0109052)	Sai Yok Noi Waterfall, Sai Yok District, Kanchanaburi	N 14° 14' 27.6" E 99° 03' 55.9" Altitude 166 m	158	35	22.15
C53 (SUT0109053)	Sai Yok Yai Waterfall, Sai Yok District, Kanchanaburi	N 14° 26' 03.0" E 98° 51' 14.7" Altitude 140 m	91	3	3.30
C54 (SUT0109054)	Wans Soong Canal, Bang Kla District, Chachuengsaio	N 13° 39' 46.2" E 101° 10' 48.2" Altitude 18 m	161	19	11.80

No. (no. specimen)	Name	GPS	No. of collected snails	No. of Infected snails	Infection rates (%)
C55 (SUT0109055)	Sua Noi Canal, Bnag pa Kong District, Cha-chuengsao	N 13° 34' 31.0" E 100° 57' 13.8" Altitude 2 m	239	8	3.35
C56 (SUT0109056)	Bung Sam Pao, Muang District, Chainat	N 15° 16' 5.9" E 100° 05' 11.1" Altitude 41 m	482	39	8.09
C57 (SUT0109057)	Bird park Pond, Muang District, Chainat	N 15° 12' 26.5" E 100° 09' 21.9" Altitude 31 m	433	242	55.89
C58 (SUT0109058)	Fish Pond at Bird Park, Muang District, Chainat	N 15° 12' 18.8" E 100° 09' 20.0" Altitude 39 m	885	41	4.63
C59 (SUT0109059)	Khun Daan Prakarnchon Dam, Muang District, Nakhonnayok	N 14° 18' 36.5" E 101° 19' 14.3" Altitude 25m	501	130	25.95
C60 (SUT0109060)	Ban mai Phai Chedi, Kampangsaen District, Nakhonpathom	N 14° 02' 10.5" E 100° 03' 27.3" Altitude 10 m	361	21	5.82
C61 (SUT0109061)	Rice paddy, Banglen District, Nakhonpathom	N 14° 01' 57.1" E 100° 10' 24.0" Altitude 5m	260	38	14.62
C62 (SUT0109062)	Rice Field at Nong Kra Done, Muang District, Nakhonpathom	N 13° 52' 41.6" E 99° 55' 50.0" Altitude 14 m	276	22	7.97
C63 (SUT0109063)	Pond at Silpakorn University, Muang District, Nakhonpathom	N 13° 48' 84.2" E 100° 02' 64.5" Altitude 11 m	272	27	9.93
C64 (SUT0109064)	Bung Bo Ra Ped Lake, Muang District, Nakhon Sawan	N 15° 42' 3.06" E 100° 10' 28.1" Altitude 17 m	274	23	8.39
C65 (SUT0109065)	Klong bang Ta nai, Pak Kred District, Nontaburi	N 13° 57' 10.1" E 100° 29' 05.4" Altitude 15 m	380	41	10.79
C66 (SUT0109066)	Ratniyom Canal, Sai Noi District, Nontaburi	N 14° 04' 17.8" E 100° 19' 23.7" Altitude 9 m	568	139	24.47
C67 (SUT0109067)	Pra Udom Canal, Lad Loom Kaew District, Pathumtani	N 14° 01' 31.0" E 100° 22' 01.1" Altitude 14 m	49	12	24.49
C68 (SUT0109068)	Na Mai Canal, Lad Loom Kaew District, Pathumtani	N 14° 03' 32.7" E 100° 26' 54.6" Altitude 22 m	95	9	9.47
C69 (SUT0109069)	Wat Ko Phai, Bang Ban District, Ayutthaya	N 14° 24' 40.9" E 100° 26' 44.6" Altitude 9 m	4	2	50
C70 (SUT0109070)	Pond at Ban Ta Woong, Ta Woong District, Lopburi	N 14° 50' 24.4" E 100° 28' 21.4" Altitude 13 m	161	11	6.83
C71 (SUT0109071)	Suan Ma Dua waterfall, Pattana Nikom District, Lopburi	N 14° 55' 06.0" E 101° 13' 09.2" Altitude 125 m	233	16	6.87
C72 (SUT0109072)	Pasak Chonlasit Reservior, Pattana Nikom District, Lopburi	N 14° 56' 22.2" E 101° 04' 47.4" Altitude 44 m	15	1	6.67
C73 (SUT0109073)	Tam Ru Canal, Muang District, Samut Prakan	N 13° 30' 54.7" E 100° 41' 12.0" Altitude 1 m	99	0	0
C74 (SUT0109074)	Prachachomchuen Canal, Ampawa District, Samut Songkram	N 13° 25' 06.7" E 99° 57' 17.8" Altitude 4 m	29	5	17.24
C75 (SUT0109075)	Don Ko Canal, Ban Phaew District, Samut Sakhon	N 13° 38' 08.0" E 100° 05' 03.0" Altitude 7 m	42	6	14.29
C76 (SUT0109076)	Ta Pa Canal, Ban Phaew District, Samut Sakhon	N 13° 38' 07.3" E 100° 06' 20.1" Altitude 30 m	85	1	1.18
C77 (SUT0109077)	Muak Lek Waterfall, Muak Lek District, Saraburi	N 14° 43' 13.2" E 101° 11' 19.4" Altitude 156 m	199	2	1.01
C78 (SUT0109078)	Dong Phya Yen Waterfall, Muak Lek District, Saraburi	N 14° 44' 0.6" E 101° 11' 44.6" Altitude 162 m	180	5	2.78
C79 (SUT0109079)	Site1 at Ched Kot Waterfall, Kaeng Koi District, Saraburi	N 14° 28' 48.5" E 101° 10' 22.3" Altitude 185 m	118	39	33.05
C80 (SUT0109080)	Site2 at Ched Kot waterfall, Kaeng Koi District, Saraburi	N 14° 28' 34.6" E 101° 10' 16.4" Altitude 157 m	37	12	32.43
C81 (SUT0109081)	Reservoir at Sam Lan Waterfall, Muang District, Saraburi	N 14° 25' 52.2" E 100° 57' 49.6" Altitude 88 m	315	8	2.54
C82 (SUT0109082)	Muang Moo pond, Muang District, Singhaburi	N 14° 52' 09.1" E 100° 24' 59.1" Altitude 16 m	282	29	10.28

No. (no. specimen)	Name	GPS	No. of collected snails	No. of Infected snails	Infection rates (%)
C83 (SUT0109083)	Ban Bang Mae Mai Pond, Bang Pla Ma District, Suphanburi	N 14° 20' 32.2" E 100° 09' 04.9" Altitude 8 m	349	85	24.36
C84 (SUT0109084)	Wat bang Yai Pond, Bang Pla Ma District, Suphanburi	N 14° 18' 41.2" E 100° 09' 03.7" Altitude 5 m	956	46	4.81
C85 (SUT0109085)	Bung Cha Wak Pond, Derm Bang Nang Buad District, Supahanburi	N 14° 54' 04.4" E 100° 03' 48.0" Altitude 26 m	176	30	17.05
C86 (SUT0109086)	Huay Po Canal, Muang District, Angthong	N 14° 36' 08.3" E 100° 24' 12.9" Altitude 14 m	65	10	15.38
South					
S87 (SUT0109087)	Water Gate km. 19+500, Cha-Am District, Petchaburi	N 12° 51' 15.1" E 99° 59' 48.5" Altitude 17 m	95	4	4.21
S88 (SUT0109088)	Emergency Water Gate, Cha-Am District, Petchaburi	N 12° 57.4' 26.0" E 100° 02' 07.5" Altitude 14 m	3	0	0
S89 (SUT0109089)	Petchaburi Dam, Tayang District, Petchaburi	N 12° 54' 58.6" E 99° 51' 34.4" Altitude 20 m	137	5	3.65
S90 (SUT0109090)	Pond at Silpakorn University Petchaburi Campus, Cha-Am District, Petchaburi	N 11° 26' 04.6" E 99° 26' 56.9" Altitude 90 m	1,074	1,051	97.86
S91 (SUT0109091)	Huai Yang stream, Huai Yang District, Prachuab-kirikhun	N 11° 36' 47.0" E 99° 40' 08.4" Altitude 18 m	211	30	14.22
S92 (SUT0109092)	Thap sakae stream, Tuap sakae District, Prachuab-kirikhun	N 11° 29' 40.1" E 99° 36' 20.3" Altitude 13 m	124	8	6.45
S93 (SUT0109093)	Kha On waterfall, Bangsapan District, Prachuab-kirikhun	N 11° 26' 04.6" E 99° 26' 56.9" Altitude 90 m	32	4	12.50
S94 (SUT0109094)	Sai Khu waterfall, Bangsapan District, Prachuab-kirikhun	N 11° 14' 21.8" E 99° 21' 36.1" Altitude 83 m	429	25	5.83
S95 (SUT0109095)	Kapoh Waterfall, Ta Sae District, Chumporn	N 10° 44' 28.7" E 99° 12' 53.9" Altitude 69 m	133	5	3.76
S96 (SUT0109096)	Ra Canal, Lungsuan District, Chumporn	N 09° 59' 04.3" E 99° 00' 59.8" Altitude 44 m	739	97	13.13
S97 (SUT0109097)	Si Kheed Waterfall, Sichon District, Nakhon Sri Thammarat	N 09° 00' 40.8" E 99° 46' 30.1" Altitude 45 m	9	1	11.11
S98 (SUT0109098)	Krung Ching Waterfall, Noppitum District, Nakhon Sri Thammarat	N 08° 43' 14.0" E 99° 40' 15.2" Altitude 45 m	18	5	27.78
S99 (SUT0109099)	Yod Leung Stream, Noppitum District, Nakhon Sri Thammarat	N 08° 38' 10.5" E 99° 45' 11.6" Altitude 68 m	872	343	0.39
S100 (SUT0109100)	Palien River, Yan Ta Khao District, Trang	N 07° 22' 11.5" E 99° 40' 51.6" Altitude 12 m	205	22	10.73
S101 (SUT0109101)	Palien Dam, Palien District, Trang	N 07° 19' 13.2" E 99° 48' 28.8" Altitude 43 m	506	46	9.09
S102 (SUT0109102)	Tone Tok Waterfall, Palien District, Trang	N 07° 16' 44.2" E 99° 53' 10.6" Altitude 41 m	301	78	25.91
S103 (SUT0109103)	Tone Plew Waterfall, Nayong District, Trang	N 07° 32' 48.2" E 99° 47' 17.0" Altitude 63 m	1,049	97	0.09
S104 (SUT0109104)	Ang Thong Waterfall, Sikao District, Trang	N 07° 33' 01.2" E 99° 24' 56.9" Altitude 37 m	311	107	34.41
S105 (SUT0109105)	Falan Waterfall, Srinakarin District, Pattaloong	N 07° 36' 25.9" E 99° 54' 39.0" Altitude 80 m	1	0	0
S106 (SUT0109106)	Ban Au Rua Stream, Muang District, Ratchaburi	N 13° 31' 21.9" E 99° 50' 57.3" Altitude 152 m	9	2	22.22
S107 (SUT0109107)	Huay Haeng Stream, Suanphueng District, Ratchaburi	N 13° 31' 03.9" E 99° 20' 29.2" Altitude 113 m	213	18	8.45
S108 (SUT0109108)	Huay Nuang Stream, Suanphueng District, Ratchaburi	N 13° 31' 21.9" E 99° 17' 36.5" Altitude 151m	234	23	9.83
S109 (SUT0109109)	Bangborn Stream, Kraburi District, Ranong	N 10° 20' 10.8" E 98° 46' 48.7" Altitude 18 m	34	2	5.88

No. (no. specimen)	Name	GPS	No. of collected snails	No. of Infected snails	Infection rates (%)
S110 (SUT0109110)	Na Ca Stream, Wild Life Sanctuary, Muang District, Ranong	N 9° 27' 26.6" E 98° 30' 36.9" Altitude 3 m	56	1	1.79
S111 (SUT0109111)	Wiphawadee Waterfall, Donsak District, Surat Thani	N 9° 8' 9.6" E 99° 40' 31.2" Altitude 10 m	70	2	2.86
S112 (SUT0109112)	Yan Canal, Wipawadee District, Surathani	N 9° 12' 12.8" E 98° 57' 20.3" Altitude 66 m	292	21	7.19
S113 (SUT0109113)	Ton Sai Waterfall, Tha Lang District, Phuket	N 8° 1' 32.4" E 98° 21' 58.8" Altitude 45 m	222	27	12.16
S114 (SUT0109114)	Bang Pae waterfall, Tha Lang District, Phuket	N 8° 2' 20.5" E 98° 23' 49.3" Altitude 50 m	76	13	17.11
S115 (SUT0109115)	Kathu Waterfall, Kathu District, Phuket	N 7° 55' 49.4" E 98° 19' 34" Altitude 43 m	385	5	1.30
S116 (SUT0109116)	Raman Waterfall, Ta Kua Tung District, Phang Nga	N 8° 27' 8.5" E 98° 28' 0.9" Altitude 33 m	3	0	0
S117 (SUT0309117)	Sa Morakot Stream, Klong Tom District, Krabi	N 7° 55' 14.9" E 99° 15' 47.1" Altitude 24 m	356	4	1.12
S118 (SUT0109118)	Panan Waterfall, Kuan galung District, Satoon	N 6° 51' 22.8" E 100° 9' 48.6" Altitude 47 m	170	6	3.53
S119 (SUT0109119)	Tha Phae Dam, Kuan Done District, Satoon	N 6° 49' 26" E 100° 2' 2.3" Altitude 41 m	760	8	1.05
S120 (SUT0109120)	Klong Muang, Kuan Niang District, Songkhla	N 7° 12' 24.5" E 100° 22' 43.1" Altitude 13 m	82	9	10.98

(N 19°25'31.7", E 97°59'24.9", Altitude 343 m); N6 = Huay Sua Thao Stream, Muang District, Mae Hong Son Province (SUT0109006) (N 19°15'32.0", E 97°54'43.7", Altitude 237 m); N7 = Klong Nam Lai Waterfall, Klong Lan District, Kam Phaeng Phet Province (SUT0109007) (N 16°11'32.7", E 99°15'51.0", Altitude 241 m); N8 = Tad Duen Waterfall, Sri Satchanalai District, Sukhothai Province (SUT0109008) (N 17°33'23.2" E 99°29'76.8", Altitude 414 m); N9 = Sri Satchanalai Stream, Sri Satchanalai National Park, Sukhothai Province (SUT0109009) (N 17°33'5.9", E 99°29'24.8", Altitude 182 m); N10 = Mae Pool Waterfall, Lub Lae District, Ut-taradit Province (SUT0109010) (N 17°43'45.0", E 99°58'50.6", Altitude 164 m); N11 = Chueng Thong Waterfall, Muang District, Prae Province (SUT0109011) (N 18°01'54.2", E 100°15'52.8", Altitude 298 m); N12 = Huay Sa Nien Stream, Muang District, Nan Province (SUT0109012) (N 18°51'1.3", E 100°39'16.2", Altitude 280 m); N13 = Huay Ton Phueng Waterfall, Doi Pu Nang National Park, Chiang Muon District, Phayao Province (SUT0109013) (N 18°55'5.3", E 100°12'15.7", Altitude 379); N14 = Tansawan Waterfall, Doi Pu Nang National Park, Chiang Muon District, Phayao Province (SUT0109014) (N 18°51'22.7", E 100°11'9.6", Altitude 420 m); N15 = Mae Mine Stream, Mae Ta District, Lampang Province (SUT0109015) (N 18°07'1.8", E 99°37'35.1", Altitude 269 m).

The Northeast: NE 16 = Huay Lum Po Dang Stream, Thepsathit District, Chaiyapoom Province (SUT0109016) (N 15°33'42.8", E 101°24'56.9", Altitude 471 m); NE 17 = Sai Thong Waterfall, Sai Thong Nation-

al Park, Nong Bua Ra Hoew District, Chaiyapoom Province (SUT0109017) (N 15°52'34.7", E 101°30'34.7", Altitude 397 m); NE18 = Tad Tone Waterfall, Muang District, Chaiyapoom Province (SUT0109018) (N 15°58'42.5", E 102°02'24.9", Altitude 384 m); NE19 = Kongkaew Waterfall, Khao Yai National Park, Pak Chong District, Nakhon Ratchasima Province (SUT0109019) (N 14°26'14.8", E 101°22'37.6", Altitude 713 m); NE20 = Lam Takhong Stream, Khao Yai National Park, Pak Chong District, Nakhon Ratchasima Province (SUT0109020) (N 14°25'19.6", E 101°23'26.3", Altitude 700 m); NE21 = Ban Cha Rut Reservoir, Bua Ched District, Surin Province (SUT0109021) (N 14°25'50.4", E 103°57'47.7", Altitude 201 m); NE22 = Nong Bua Rai Reservoir, Khao Panomroong, Pra Kone Chai District, Buriram Province (SUT0109022) (N 14°32'51.2", E 102°58'9.4", Altitude 202 m); NE23 = Pla Ba Waterfall, Pu Rua District, Loei Province (SUT0109023) (N 17°23'24.3", E 101°22'27.4", Altitude 640 m); NE24 = Than Thong Waterfall, Sung Kom District, Nong Khai Province (SUT0109024) (N 18°01'34.7", E 102°22'8.7", Altitude 195 m); NE25 = Huay Hor Water Gate, Muang District, Nakhon Panom Province (SUT0109025) (N 17°21'8.4", E 104°47'2.1", Altitude 145 m); NE26 = Tad Kham Waterfall, Pu Lung Ga National Park, Ban Pang District, Nakhon Panom Province (SUT0109026) (N 17°57'1.4", E 104°09'39.9", Altitude 148 m); NE27 = Tad Po Waterfall, Pu Lung Ga National Park, Ban Pang District, Nakhon Panom Province (SUT0109027) (N 17°59'0.9", E 104°08'34.3", Altitude 148 m); NE28 = Nong Han, Muang District, Sakol Nakhon Prov-

ince (SUT0109028) (N 17°09'50.1", E 104°09'43.7", Altitude 161 m); NE29 = Nam Poong Dam, Gud Bak District, Sakol Nakhon Province (SUT0109029) (N 16°58'11.8", E 103°59'13.4", Altitude 290 m); NE30 = Lam Pow Dam, Muang District, Sri Sa Ket Province (SUT0109030) (N 16°36'22.3", E 103°26'27.5", Altitude 165 m); NE31 = Ban Nong Wang Wong Reservoir, Sri Som Det District, Roi-Et Province (SUT0109031) (N 15°56'53.5", E 103°31'27.8", Altitude 178 m); NE32 = Bung Toong Sang, Muang District, Khon Kaen Province (SUT0109032) (N 16°26'27.8", E 102°51'28.1", Altitude 154 m); NE33 = Bung Kaen Nakhon, Muang District, Khon Kaen Province (SUT0109033) (N 16°24'46.6", E 102°50'21.9", Altitude 143 m); NE34 = Nong Sa Ard Bamroong Reservoir, Kosum Pisai District, Mahasarakham Province (SUT0109034) (N 16°18'0.5", E 102°54'38.5", Altitude 169 m); NE35 = Tad Tone Waterfall, Nong Soong District, Mukdaharn Province (SUT0109035) (N 16°29'34.9", E 104°19'1.1", Altitude 219 m)

The East: E36 = Khao Khaew National Park, Sri-racha District, Chonburi Province (SUT0109036) (N 13°12'45.0", E 101°03'50.2", Altitude 128 m); E37 = Ban Nong Pla Lai, Bang lamung District, Chonburi Province (SUT0109037) (N 12°57'54.3", E 100°56'47.8", Altitude 17 m); E38 = Rayong River, Muang District, Rayong Province (SUT0109038) (N 12°39'52.6", E 101°14'48.5", Altitude 6 m); E39 = Hin Khao Canal, Muang District, Rayong Province (SUT0109039) (N 12°36'31.7", E 101°23'22.4", Altitude 1 m); E40 = Pung rad Canal, Klang District, Rayong Province (SUT0109040) (N 12°42'49.5", E 101°46'23.4", Altitude 15 m); E41 = Chantaburi River, Muang District, Chantaburi Province (SUT0109041) (N 12°36'13.8", E 102°07'11.6", Altitude 8 m); E42 = Nam Tok Plew Stream, Plew District, Chantaburi Province (SUT0109042) (N 12°31'14.3", E 102°10'35.4", Altitude 39 m); E43 = Pa Tong Canal, Soi Dao District, Chantaburi Province (SUT0109043) (N 13°07'5.9", E 102°13'13.6", Altitude 231 m); E44 = Klong Kaew Waterfall, Bo Rai District, Trad Province (SUT0109044) (N 12°37'3.0", E 102°34'52.0", Altitude 81 m); E45 = Sra Kaew, Muang District, Srakaew Province (SUT0109045) (N 13°49'7.0", E 102°03'37.9", Altitude 43 m); E46 = Eto Waterfall, Muang District, Prachinburi Province (SUT0109046) (N 14°08'58.9", E 101°24'45.4", Altitude 39 m).

The Central: C47 = Dusit Zoo Pond, Dusit, Bangkok (SUT0109047) (N 13°46'17.4", E 100°31'14.8", Altitude 2 m); C48 = Drainage at Kasetsart University, Bang Khen Campus, Bangkok (SUT0109048) (N 13°50'40.7", E 100°34'33.5", Altitude 5 m); C49 = Pond at Kasetsart University, Bang Khen Campus, Bangkok (SUT0109049) (N 13°50'22.6", E 100°34'43.4", Altitude 1 m); C50 = Hin Dad Waterfall, Thong Pa Poom District, Kanchanaburi Province (SUT0109050) (N 14°37'29.8", E 98°43'40.2", 186 m); C51 = Pha Tad Waterfall, Sri Sa wat District, Kanchanaburi Province

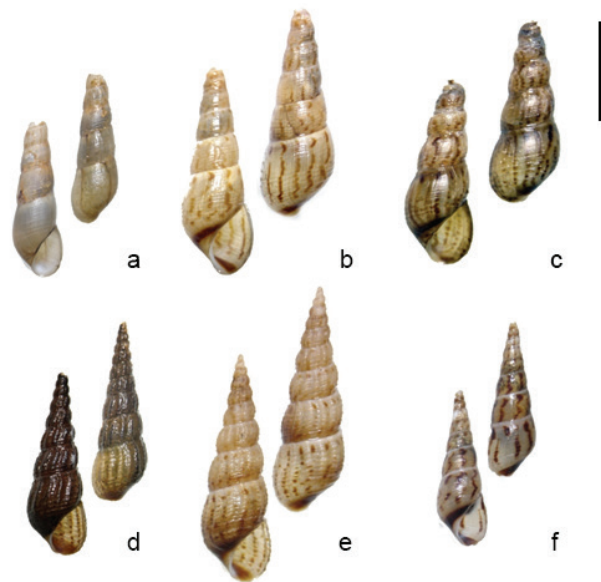


Figure 2. Shell Morphology of *Melanoides tuberculata* in Thailand

- Sri Satchanalai Stream, Sri Satchanalai National Park, Sri Satchanalai District, Sukhothai Province (SUT0109009)
- Lam Takhong Stream, Khao Yai National Park, Pak Chong District, Nakhon, Ratchasima Province (SUT0109020)
- Rice Field at Nong Kra Done, Muang District, Nakhon Pathom Province (SUT0109062)
- Pond in Silpakorn University, Muang District, Nakhon Pathom Province (SUT0109063)
- Bang Ta-nai Canal, Pak Kred District, Nontaburi Province (SUT0109065)
- Huay Nuang Stream, Suanphuang District, Ratchaburi Province (SUT0109108)

Scale bar = 1.0 mm.

(SUT0109051) (N 14°38'54.9", E 98°46'41.6", Altitude 196 m); C52 = Sai Yok Noi Waterfall, Sai Yok District, Kanchanaburi Province (SUT0109051) (N 14°14'27.6", E 99°03'55.9", Altitude 166 m); C53 = Sai Yok Yai Waterfall, Sai Yok District, Kanchanaburi Province (SUT0109053) (N 14°26'03.0", E 98°51'14.7", Altitude 140 m); C54 = Wans Soong Canal, Bang Kla District, Chachuengsao Province (SUT0109054) (N 13°39'46.2", E 101°10'48.2", Altitude 18 m); C55 = Sua Noi Canal, Bnag pa Kong District, Chachuengsao Province (SUT0109055) (N 13°34'31.0", E 100°57'13.8", Altitude 2 m); C56 = Bung Sam Pao, Muang District, Chainat Province (SUT0109056) (N 15°16'5.9", E 100°05'11.1", Altitude 41 m); C57 = Bird Park Pond, Muang District, Chainat Province (SUT0109057) (N 15°12'26.5", E 100°09'21.9", Altitude 31 m); C58 = Fish Pond at Bird Park, Muang District, Chainat Province (SUT0109058) (N 15°12'18.8", E 100°09'20.0", Altitude 39 m); C59 = Khun Daan Prakarnchon Dam, Muang District, Nakhonnayok Province (SUT0109059) (N 14°18'36.5", E 101°19'14.3", Altitude 25m); C60 = Ban mai Phai Chedi, Kampangsaen District, Nakhonpathom Province (SUT0109060) (N 14°02'10.5", E 100°03'27.3", Altitude 10 m); C61 = Rice paddy, Ban-

glen District, Nakhonpathom Province (SUT0109061) (N 14°01'57.1", E 100°10'24.0", Altitude 5 m); C62 = Rice Field at Nong Kra Done, Muang District, Nakhon Pathom Province (SUT0109062) (N 13°52'41.6", E 99°55'50.0", Altitude 14 m); C63 = Pond at Silpakorn University, Muang District, Nakhonpathom Province (SUT0109063) (N 13°48'84.2", E 100°02'64.5", Altitude 11 m); C64 = Bung Bo Ra Ped Lake, Muang District, Nakhon Sawan province (SUT0109064) (N 15°42'3.06", E 100°10'28.1", Altitude 17 m); C65 = Bang Ta nai Canal, Pak Kred District, Nontaburi Province (SUT0109065) (N 13°57'10.1", E 100°29'05.4", Altitude 15 m); C66 = Ratniyom Canal, Sai Noi District, Nontaburi Province (SUT0109066) (N 14°04'17.8", E 100°19'23.7", Altitude 9 m); C67 = Pra Udom Canal, Lad Loom Kaew District, Pathumtani Province (SUT0109067) (N 14°01'31.0", E 100°22'01.1", Altitude 14 m); C68 = Na Mai Canal, Lad Loom Kaew District, Pathumtani Province (SUT0109068) (N 14°03'32.7", E 100°26'54.6", Altitude 22 m); C69 = Wat Ko Phai, Bang Ban District, Ayutthaya Province (SUT0109069) (N 14°24'40.9", E 100°26'44.6", Altitude 9 m); C70 = Pond at Ban Ta Woong, Ta Woong District, Lopburi Province (SUT0109070) (N 14°50'24.4", E 100°28'21.4", Altitude 13 m); C71 = Suan Ma Dua Waterfall, Pattana Nikom District, Lopburi Province (SUT0109071) (N 14°55'06.0", E 101°13'09.2", Altitude 125 m); C72 = Pasak Chonlasit Reservoir, Pattana Nikom District, Lopburi Province (SUT0109072) (N 14°56'22.2", E 101°04'47.4", Altitude 44 m); C73 = Tam Ru Canal, Muang District, Samut Prakan Province (SUT0109073) (N 13°30'54.7", E 100°41'12.0", Altitude 1 m); C74 = Prachachomchuen Canal, Ampawa District, Sanut Songkram Province (SUT0109074) (N 13°25'06.7", E 99°57'17.8", Altitude 4 m); C75 = Don Ko Canal, Ban Phaew District, Samut Sakhon Province (SUT0109075) (N 13°38'08.0", E 100°05'03.0", Altitude 7 m); C76 = Ta Pa Canal, Ban Phaew District, Samut Sakhon Province (SUT0109076) (N 13°38'07.3", E 100°06'20.1", Altitude 30 m); C77 = Muak Lek Waterfall, Muak Lek District, Saraburi Province (SUT0109077) (N 14°43'13.2", E 101°11'19.4", Altitude 156 m); C78 = Dong Phya Yen Waterfall, Muak Lek District, Saraburi Province (SUT0109078) (N 14°44'0.6", E 101°11'44.6", Altitude 162 m); C79 = Site1 at Ched Kot Waterfall, Kaeng Koi District, Saraburi Province (SUT0109079) (N 14°28'48.5", E 101°10'22.3", Altitude 185 m); C80 = Site2 at Ched Kot Waterfall, Kaeng Koi District, Saraburi Province (SUT0109080) (N 14°28'34.6", E 101°10'16.4", Altitude 157 m); C81 = Reservoir at Sam Lan Waterfall, Muang District, Saraburi Province (SUT0109081) (N 14°25'52.2", E 100°57'49.6", Altitude 88 m); C82 = Muang Moo Pond, Muang District, Singhaburi Province (SUT0109082) (N 14°52'09.1", E 100°24'59.1", Altitude 16 m); C83 = Ban Bang Mae Mai Pond, Bang Pla Ma District, Suphanburi Province (SUT0109083) (N 14°20'32.2", E 100°09'04.9", Altitude 8 m); C84 = Wat

bang Yai Pond, Bang Pla Ma District, Suphanburi Province (SUT0109084) (N 14°18'41.2", E 100°09'03.7", Altitude 5 m); C85 = Bung Cha Wak, Derm Bang Nang Buad District, Suphanburi Province (SUT0109085) (N 14°54'04.4", E 100°03'48.0", Altitude 26 m); C86 = Huay Po Canal, Muang District, Angthong Province (SUT0109086) (N 14°36'08.3", E 100°24'12.9", Altitude 14 m).

The South: S87 = Water Gate km. 19+500, Cha-Am District, Petchaburi Province (SUT0109087) (N 12°51'15.1", E 99°59'48.5", Altitude 17 m); S88 = Emergency Water Gate, Cha-Am District, Petchaburi Province (SUT0109088) (N 12°57.4'26.0", E 100°02'07.5", Altitude 14 m); S89 = Petchaburi Dam, Tayang District, Petchaburi Province (SUT0109089) (N 12°54'58.6", E 99°51'34.4", Altitude 20 m); S90 = Pond at Silpakorn University Petchaburi Campus, Cha-Am district, Petchaburi Province (SUT0109090) (N 11°26'04.6", E 99°26'56.9", Altitude 90 m); S91 = Huai Yang stream, Huai Yang District, Prachuabkirikhun Province (SUT0109091) (N 11°36'47.0", E 99°40'08.4", Altitude 18 m); S92 = Thap Sakae Stream, Tuap Sakae District, Prachuabkirikhun Province (SUT0109092) (N 11°29'40.1", E 99°36'20.3", Altitude 13 m); S93 = Kha On Waterfall, Bangsapan District, Prachuabkirikhun Province (SUT0109093) (N 11°26'04.6"E 99°26'56.9", Altitude 90 m); S94 = Sai Khu Waterfall, Bangsapan District, Prachuabkirikhun Province (SUT0109094) (N 11°14'21.8", E 99°21'36.1", Altitude 83 m); S95 = Kapoh Waterfall, Ta Sae District, Chumporn Province (SUT0109095) (N 10°44'28.7", E 99°12'53.9", Altitude 69 m); S96 = Ra Canal, Lungsuan District, Chumporn Province (SUT0109096) (N 09°59'04.3", E 99°00'59.8", Altitude 44 m); S97 = Si Kheed Waterfall, Sichon District, Nakhon Sri Thammarat Province (SUT0109097) (N 09°00'40.8", E 99°46'30.1", Altitude 45 m); S98 = Krung Ching Waterfall, Noppitum District, Nakhon Sri Thammarat Province (SUT0109098) (N 08°43'14.0", E 99°40'15.2", Altitude 45 m); S99 = Yod Leung Stream, Noppitum District, Nakhon Sri Thammarat Province (SUT0109099) (N 08°38'10.5", E 99°45'11.6", Altitude 68 m); S100 = Palian River, Yan Ta Khao District, Trang Province (SUT0109100) (N 07°22'11.5", E 99°40'51.6", Altitude 12 m); S101 = Palian Dam, Palien District, Trang Province (SUT0109101) (N 07°19'13.2", E 99°48'28.8", Altitude 43 m); S102 = Tone Tok Waterfall, Palien District, Trang Province (SUT0109102) (N 07°16'44.2"E 99°53'10.6", Altitude 41 m); S103 = Tone Plew Waterfall, Nayong District, Trang Province (SUT0109103) (N 07°32'48.2"E 99°47'17.0", Altitude 63 m); S104 = Ang Thong Waterfall, Sikao District, Trang Province (SUT0109104) (N 07°33'01.2", E 99°24'56.9", Altitude 37 m); S105 = Falan Waterfall, Srinakarin District, Pattaloong Province (SUT0109105) (N 07°36'25.9", E 99°54'39.0", Altitude 80 m); S106 = Ban Au Rua Stream, Muang District, Ratchaburi Province (SUT0109106) (N

13°31'21.9", E 99°50'57.3", Altitude 152 m); S107 = Huay Haeng Stream, Suanphueng District, Ratchaburi Province (SUT0109107) (N 13°31'03.9", E 99°20'29.2", Altitude 113 m); S108 = Huay Nuang Stream, Suanphueng District, Ratchaburi Province (SUT0109108) (N 13°31'21.9", E 99°17'36.5", Altitude 151m); S109 = Bangborn Stream, Kraburi District, Ranong Province (SUT0109109) (N 10°20'10.8", E 98°46'48.7", Altitude 18 m); S110 = Na Ca Stream, Wild Life Sanctuary, Muang District, Ranong Province (SUT0109110) (N 9°27'26.6"E 98°30'36.9", Altitude 3 m); S111 = Wiphawadee Waterfall, Donsak District, Surat Thani Province (SUT0109111) (N 9°8'9.6", E 99°40'31.2", Altitude 10 m); S112 = Yan Canal, Wipawadee District, Surathani Province (SUT0109112) (N 9°12'12.8", E 98°57'20.3"Altitude 66 m); S113 = Ton Sai Waterfall, Tha Lang District, Phuket Province (SUT0109113) (N 8°1'32.4", E 98°21'58.8", Altitude 45 m); S114 = Bang Pae Waterfall, Tha Lang District, Phuket Province (SUT0109114) (N 8°2'20.5", E 98°23'49.3", Altitude 50 m); S115 = Kathu Waterfall, Kathu District, Phuket Province (SUT0109115) (N 7°55'49.4", E 98°19'34", Altitude 43 m); S116 = Raman Waterfall, Ta Kua Tung District, Phang Nga

Province (SUT0109116) (N 8°27'8.5", E 98°28'0.9", Altitude 33 m); S117 = Sa Morakot Stream, Klong Tom District, Krabi Province (SUT0309117) (N 7°55'14.9", E 99°15'47.1", Altitude 24 m); S118 = Panan Waterfall, Kuan galung District, Satoon Province (SUT0109118) (N 6°51'22.8", E 100°9'48.6", Altitude 47 m); S119 = Tha Phae Dam, Kuan Done District, Satoon Province (SUT0109119) (N 6°49'26", E 100°2'2.3", Altitude 41 m); S120 = Klong Muang, Kuan Niang District, Songkhla Province (SUT0109120) (N 7°12'24.5", E 100°22'43.1", Altitude 13 m).

Habitat at the study sites in Thailand

The study sites were usually found to be covered with big and medium trees that allow the sunlight to pass through to the stream. The average light intensity was >10,000 lux at noon. The current was swift in the rainy season, and water temperature was 21–28 °C. There were small to medium sized rocks all over the streams. The collected snails were found on the rocks, rough sand, and on aquatic plants. The physico-chemical quality of the environment and the water changed with the seasons and affected the study areas during the dry and flood season.

Table 2. Distribution of cercariae obtained from *Melanoides tuberculata* (32,026 snails) in Thailand. Abbreviations: N - North; NE - Northeast; E - East; C - Central; S - South.

Cercaria species	No. infected snails distribution					Total	Infection rates (%)
	N = 15	NE = 20	E = 11	C = 39	S = 35		
Type 1. Parapleurophocercous cercariae:							
1. <i>Haplorchis pumilio</i>	23	0	58	265	25	371	1.16
2. <i>Haplorchis taichui</i>	1	2	0	0	89	92	0.29
3. <i>Stictodora tridactyla</i>	0	582	75	210	1,315	2,182	6.81
Type 2. Pleurophocercous cercariae:							
4. <i>Centrocestus formosanus</i>	55	0	3	10	6	74	0.23
Type 3. Xiphidiocercariae:							
5. <i>Acanthatrium hitaense</i>	9	14	54	1	10	88	0.27
6. <i>Loxogenoides bicolor</i>	29	802	485	573	484	2,373	7.41
7. <i>Haematoloechus similis</i>	53	314	92	1	8	468	1.46
Type 4. Megalurous cercariae:							
8. <i>Cloacitrema philippinum</i>	1	0	11	0	0	12	0.04
9. <i>Philophthalmus</i> sp.	0	0	0	52	5	57	0.18
Type 5. Furcocercous cercariae:							
10. <i>Cardicola alseae</i>	0	2	0	2	22	33	0.1
11. <i>Alaria mustelae</i>	0	1	2	22	22	47	0.15
12. <i>Transversotrema laruei</i>	8	0	21	2	58	89	0.28
13. <i>Apatemon gracilis</i>	0	20	0	4	31	55	0.17
14. <i>Mesostephanus appendiculatus</i>	0	3	0	0	0	3	0.009
Type 6. Echinostome cercariae:							
15. <i>Echinochasmus pelecani</i>	0	0	19	0	0	19	0.06
Type 7. Amphistome cercariae:							
16. <i>Gastrothylax crumenifer</i>	0	0	4	0	4	8	0.02
Type 8. Renicolid cercariae:							
17. <i>Cercaria caribbea</i> LXVIII	0	0	33	12	0	45	0.14
Type 9. Cotylomicrocercous cercariae:							
18. <i>Podocotyle (Podocotyle) lepomis</i>	0	0	0	3	0	3	0.009
No. infected snails	179	1,740	857	1,164	2,079	6,019	18.79
No. of cercaria species	8	9	12	13	13	18	

Table 3. Size range and average size (in micrometers, calculated from 20 cercariae) of eighteen species of cercariae were measured and obtained from *Melanooides tuberculata* in Thailand.

Trematodes species																		
	H. pumilio	H. taichui	S. tridactyla	C. formosanus	A. hitaense	L. bicolor	H. similis	C. philippinum	Philophthalmus sp.	C. disease	A. mustelae	T. laruei	A. gracilis	M. appendiculatus	E. pelecani	G. crumenifer	C. caribbea LXVIII	P (Podocotyle) lepomis
Body	85-128 (av. 108) ×168-295 (av. 257)	93-135 (av. 132) ×156-276 (av. 242)	69-149 (av. 112) ×255-309 (av. 275)	45-72 (av. 64) ×82-120 (av. 117)	53-92 (av. 78) ×80-110 (av. 100)	54-82 (av. 75) ×90-120 (av. 110)	87-104 (av. 95) ×130-164 (av. 148)	122-184 (av. 169) ×280-450 (av. 396)	120-125 (av. 122) ×525-595 (av. 570)	18-39 (av. 28) ×72-110 (av. 95)	105-154 (av. 138) ×185-280 (av. 255)	425-670 (av. 574) ×280-510 (av. 370)	41.5-90.0 (av. 72) ×115-140 (av. 126)	92-120 (av. 109) ×160-250 (av. 225)	68-87 (av. 85) ×100-125 (av. 118)	190-250 (av. 220) ×350-415 (av. 370)	128-140 (av. 129) ×390-435 (av. 420)	65-93 (av. 73) ×103-145 (av. 123)
Genital pore	12-18 (av. 15) ×12-18 (av. 15)
Oral sucker	27-48 (av. 36) ×27-48 (av. 36)	24-45 (av. 38) ×27-45 (av. 38)	36-48 (av. 38) ×33-52 (av. 41)	16-26 (av. 24) ×17-28 (av. 25)	25-32 (av. 30) ×34-40 (av. 37)	24-30 (av. 28) ×24-30 (av. 28)	34-42 (av. 38) ×37-46 (av. 42)	50-60 (av. 56) ×50-60 (av. 56)	50-57 (av. 55) ×55-62.5 (av. 60)	.	28-40 (av. 36) ×28-40 (av. 36)	.	15-25 (av.21.45) ×20-30 (av. 23)	20-45 (av. 35) ×35-48 (av. 39)	21-30 (av. 23) ×24-30 (av. 25)	45-65 (av. 52) ×45-65 (av. 52)	28-33 (av. 26.) ×28-33 (av. 26)	30-38 (av. 32) ×25-38 (av. 30)
Anterior organ	11-15 (av. 13) ×14-20 (av. 17)
Stylet	8-13 (av. 10) ×11-13 (av. 12)	5-8 (av. 7) ×14-20 (av. 18)	20-34 (av. 30) ×20-34 (av. 32)	4-6 (av. 5) ×6-10 (av. 8)
Eye spots	.	.	6-12 (av. 8) ×12-17 (av. 14)	14-20 (av. 18) ×14-20 (av. 18)
Pharynx	8-10 (av. 9) ×12-19 (av. 15)	8-10 (av. 10) ×12-18 (av. 15)	11-19 (av. 16) ×14-21 (av. 17)	7-9 (av. 8) ×8-10 (av. 9)	10-15 (av. 13) ×12-24 (av. 20)	4-6 (av. 5) ×4-10 (av. 8)	11-13 (av. 12) ×15-17 (av. 16)	23-38 (av. 35) ×25-40 (av. 35)	20-25 (av. 23) ×20-25 (av. 23)	.	10-15 (av. 13) ×14-17 (av. 15)	25-57 (av. 574) ×280-510 (av. 370)	6-10 (av. 8) ×7-13 (av. 9)	8-10 (av. 9) ×11-18 (av. 15)	8-15 (av. 12) ×9-15 (av. 12)	8-10 (av. 10) ×8-12 (av. 11)	8-14 (av. 12) ×10-14 (av. 12)	13-18 (av. 14) ×10-13 (av. 11)
Ventral sucker	14-24 (av. 18) ×14-24 (av. 18)	15-25 (av. 20) ×15-25 (av. 20)	10-25 (av. 19) ×10-25 (av. 19)	12-16 (av. 14) ×12-16 (av. 14)	15-16 (av. 16) ×15-18 (av. 17)	12-18 (av. 15) ×13-20 (av. 17)	10-20 (av. 16) ×12-20 (av. 18)	60-70 (av. 68) ×60-75 (av. 70)	62.5-67.5 (av. 64) ×55-70 (av. 64)	.	15-30 (av. 22) ×15-30 (av. 22)	85-105 (av. 95) ×85-105 (av. 95)	16-25 (av. 23) ×20-30 (av. 25)	15-24 (av. 20) ×15-24 (av. 20)	20-31 (av. 25) ×22-30 (av. 25)	48-68 (av. 55) ×48-68 (av. 55)	29-36 (av. 30) ×29-36 (av. 30)	28-40 (av. 35) ×28-40 (av. 35)
Excretory bladder	28-40 (av. 34) ×28-40 (av. 34)	30-42 (av. 37) ×30-42 (av. 37)	87-119 (av. 98) ×52-98 (av. 76)	24-30 (av. 28) ×38-52 (av. 45)	8-12 (av. 10) ×20-46 (av. 38)	8-10 (av. 9) ×10-30 (av. 25)	20-22 (av. 21) ×20-24 (av. 22)	15-20 (av. 18) ×14-21 (av. 18)	37.5-45 (av. 41) ×35-50 (av. 41)	3-8 (av. 5) ×10-35 (av. 21)	11-23 (av. 15) ×11-21 (av. 15)	.	15-25 (av. 18) ×15-30 (av. 20)	20-40 (av. 35) ×20-40 (av. 35)	21-35 (av. 33) ×23-36 (av. 33)	80-140 (av. 125) ×80-140 (av. 125)	15-20 (av. 17) ×15-20 (av. 17)	20-30 (av. 26) ×18-25 (av. 21)

Trematodes species																		
	H. pumilio	H. taichui	S. tridactyla	C. formosanus	A. hitense	L. bicolor	H. similis	C. philippinum	Philophthalmus sp.	C. alseae	A. mustelae	T. laruei	A. gracilis	M. appendiculatus	E. pelecani	G. crumenifer	C. caribbea LXVIII	P (Podocotyle) leporinis
Penetration gland	.	.	20-30 (av. 26) ×25-30 (av. 26)
	10-36 (av. 30) ×465-528 (av. 490)	15-42 (av. 35) ×378-514 (av. 485)	37-55 (av. 45) ×486-595 (av. 546)	14-17 (av. 15) ×69-92 (av. 82)	19-25 (av. 23) ×26-75 (av. 68)	20-30 (av. 27) ×35-80 (av. 75)	27-34 (av. 30) ×90-120 (av. 115)	25-38 (av. 34) ×230-547 (av. 480)	30-32.5 (av. 31) ×425-512.5 (av. 454)	23-38 (av. 35) ×95-130 (av. 115)	65-95 (av. 82) ×328-450 (av. 410)	34-38 (av. 35) ×395-480 (av. 450)	43-65 (av. 52) ×50-75 (av. 61)
Tail Tail stem	15-30 (av. 26) ×154-197 (av. 185)	48-60 (av. 55) ×220-300 (av. 260)	50-185 (av. 98) ×254-570 (av. 360)	30-45 (av. 39) ×240-312 (av. 286)	25-40 (av. 35) ×425-525 (av. 495)
Tail furcal	7-11 (av. 9) ×28-54 (av. 51)	38-65 (av. 60) ×245-320 (av. 280)	45-110 (av. 66) ×145-310 (av. 204)	10-25 (av. 18) ×130-160 (av. 146)	15-25 (av. 20) ×160-170 (av. 165)
Lateral finfold	.	.	9-15 (av. 13) ×88-100 (av. 95)
Dorso-median finfold	5-12 (av. 8)
Append-ages	18-72 (av. 47) ×120-250 (av. 160)

Parasitic infections

A total of 32,026 *Melanoides tuberculata* were collected and examined for trematode infections (Fig. 2). The cercarial infections were examined using shedding and crushing methods. The infection rate was 18.79% (6,019/32,026). Nine types and eighteen species of cercariae were categorized. They were (1) Parapleurophocercous cercariae: *Haplorchis pumilio*, *Haplorchis tai-chui* and *Stictodora tridactyla*; (2) Pleurophocercous cercariae: *Centrocestus formosanus*; (3) Xiphidiocercariae: *Acanthatrium hitaense*, *Loxogenoides bicolor* and *Haematoloechus similis*; (4) Megalurous cercariae: *Cloacitrema philippinum* and *Philophthalmus* sp.; (5) Furcocercous cercariae: *Cardicola alseae*, *Alaria mustelae*, *Transversotrema laruei*, *Apatemon gracilis* and *Mesostephanus appendiculatus*; (6) Echinostome cercariae: *Echinochasmus pelecani*; (7) Amphistome cercariae: *Gastrothylax crumenifer*; (8) Renicolid cercariae: *Cercaria caribbea* LXVIII; and, (9) Cotylomicrocercous cercariae: *Podocotyle (Podocotyle) lepomis* (Table 2).

Characteristics of cercariae were described from living cercariae, fixed cercariae and cercarial images from scanning microscope. Sizes of cercariae were measured for identification of cercarial species (Table 3). The behavior of cercariae was studied and reported for the physiological data of trematodes.

Type 1. Parapleurophocercous cercariae

1. *Haplorchis pumilio* Looss, 1899 (Yamaguti, 1975)

Haplorchis pumilio (Fig. 3) were found from 371 *M. tuberculata*. The infection rate was 1.16% (371/32,026) (Table 2). The body shape is oval, and its surface is covered with fine spines and sensory hairs. The pigment eyespots and pharynx are present. There are seven pairs of penetration glands, which are arranged in two longitudinal series with a ventral sucker and genital primordia. Their ducts are arranged in two bundles. Four of them were open through the dorsal wall, and four through the ventral wall of the oral sucker in two oblique symmetrical rows. The mouth aperture has transverse rows of spines. The ventral sucker and genital primordia are prevesicular. The excretory bladder has a rounded shape and is composed of fine pigments. No flame cells were found in the tail stem. The tail is long, attached to the dorsal end of the body, with lateral finfolds nearby and a dorso-ventral finfold for the greater distal portion. Cercariae were produced within rediae.

Size range and average size (in micrometers, calculated from 20 cercariae):

Body: 85-128 μm (av. 108 μm) \times 168-295 μm (av. 257 μm)
 Oral sucker: 27-48 μm (av. 36 μm) \times 27-48 μm (av. 36 μm)

Ventral sucker: 14-24 μm (av. 18 μm) \times 14-24 μm (av. 18 μm)
 Pharynx: 8-10 μm (av. 9 μm) \times 12-19 μm (av. 15 μm)
 Excretory bladder: 28-40 μm (av. 34 μm) \times 28-40 μm (av. 34 μm)
 Tail: 10-36 μm (av. 30 μm) \times 465-528 μm (av. 490 μm)

Movement behavior: The cercaria moved by rolling up and springing the body back to move forward in a screwing motion for 2–4 seconds and then rested for 15–20 seconds on the surface of water. It survived up to 2–3 hours in the water after emergence.

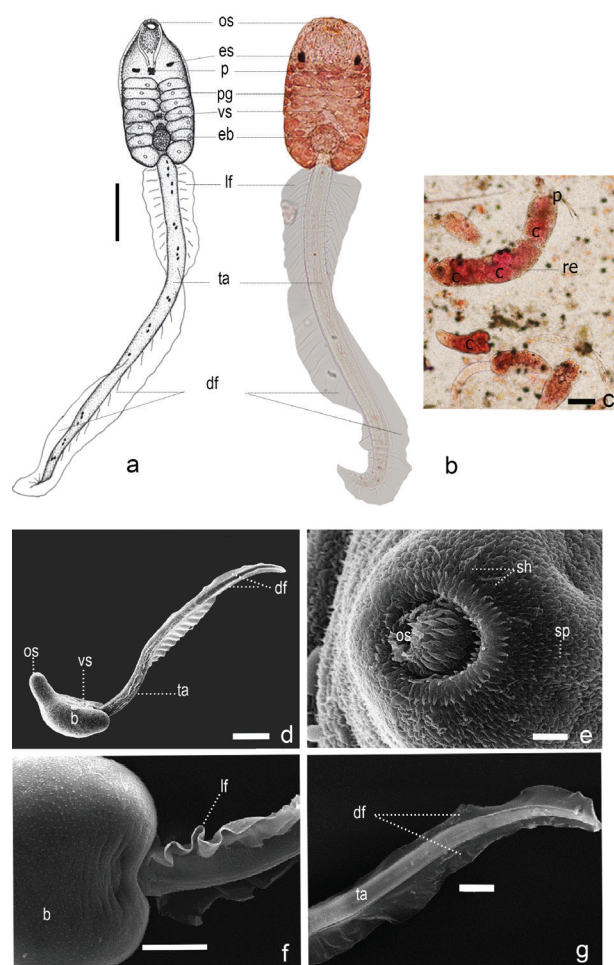


Figure 3. Image of *Haplorchis pumilio*;

- a. Drawing of cercaria structure
- b. Cercaria stained with 0.5% neutral red
- c. Redia stained with 0.5 % neutral red
- d.- g. Images of Scanning Electronmicroscope

Abbreviations: os - oral sucker, es - eye spot, p - pharynx, pg - penetration gland, vs - ventral sucker, eb - excretory bladder, lf - lateral finfold, ta - tail, df - dorso-ventral finfold, re - redia, c - cercaria, b - body, sp - spine, sh - sensory hair (scale a, b = 100 μm , c = 10 μm).

2. *Haplorchis taichui* Nishigori, 1924 (Yamaguti, 1975)

Haplorchis taichui (Fig. 4) were found from 92 *M. tuberculata*, the infection rate was 0.29% (92/32,026) (Table 2). Cercarial body is oval in shape, colored with orange yellow, and entirely covered with minute spines and sensory hairs. The oral sucker is situated ventrally in the head region. There are transverse rows of spines at the mouth aperture. The pigment eyespots and a pharynx are present. Seven pairs of penetration glands extend from the pharynx to the end of the body. There are two longitudinal rows with a ventral sucker and genital primordia; their ducts open on the anterior end of the body. The excretory bladder has a round shape and was composed of fine pigments. A long tail is attached to the dorsal end of

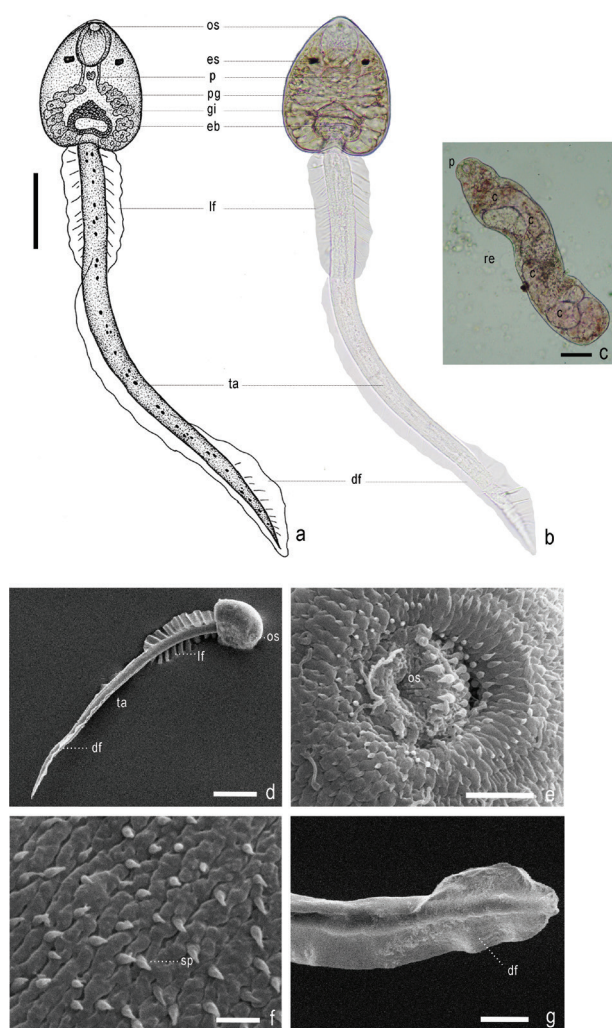


Figure 4. Image of *Haplorchis taichui*;

- a. Drawing of cercaria structure
- b. Cercaria without staining
- c. Redia without staining
- d.- g. Images of Scanning Electronmicroscope

Abbreviations: os - oral sucker, es - eye spot, p - pharynx, pg - penetration gland, gi - genital primordia, eb - excretory bladder, lf - lateral finfold, ta - tail, df - dorsal finfold, re - redia, c - cercaria, sp - spine (scale a, b = 100 μ m, c = 20 μ m).

the body, with lateral finfolds nearby and a dorso-ventral finfold for the greater distal portion. No flame cells are found in the tail stem. Cercariae were produced within the rediae.

Size range and average size (in micrometers, calculated from 20 cercariae):

Body:	93-135 μ m (av. 132 μ m) \times 156-276 μ m (av. 242 μ m)
Oral sucker:	24-45 μ m (av. 38 μ m) \times 27-45 μ m (av. 38 μ m)
Ventral sucker:	15-25 μ m (av. 20 μ m) \times 15-25 μ m (av. 20 μ m)
Pharynx:	8-10 μ m (av. 10 μ m) \times 12-18 μ m (av. 15 μ m)
Excretory bladder:	30-42 μ m (av. 37 μ m) \times 30-42 μ m (av. 37 μ m)
Tail:	15-42 μ m (av. 35 μ m) \times 378-514 μ m (av. 485 μ m)

Movement behavior: Cercariae were escaped from the rediae. In the water, they floated on the surface or in the middle. The body part sank lower than the tail. The movement rolled around fast on the water, about 8 to 12 seconds, then rested for 5-10 seconds. It survived up to 2-3 hours in the water after emergence.

3. *Stictodora tridactyla* Martin & Kuntz, 1955 (Yamaguti, 1975)

Stictodora tridactyla (Fig. 5) were found from 2,182 *M. tuberculata*. The infection rate was 6.81% (2,182/32,026) (Table 2). The body is oval in shape and yellowish brown in color. There are 3 rows of oral spines (4-6, 12-14, 22-24), and 7 pairs of penetration glands in 4 groups of 3:4:4:3. The penetration ducts are open near the oral sucker. The eight ducts are arranged in two bundles, four open through the dorsal wall, and four through the ventral wall. The ventral sucker is small. There is one pair of eye spots with coarse granules, with a small globular pharynx between the eye spots. The excretory bladder in the flattened V-shaped is situated at the end of the body. The tail is longer than the body with a bilateral finfold and a dorso-ventral finfold. Both the dorsal and ventral finfolds arose at a short distance from the anterior and the posterior end of the lateral finfold. There is no flame cell, but 3-5 groups of pigment, an opening duct of the excretory bladder at the tip of the tail. Cercariae were produced within the rediae.

Size range and average size (in micrometers, calculated from 20 cercariae):

Body:	69-149 μ m (av. 112 μ m) \times 255-309 μ m (av. 275 μ m)
Oral sucker:	36-48 μ m (av. 38 μ m) \times 33-52 μ m (av. 41 μ m)
Eye spots:	6-12 μ m (av. 8 μ m) \times 12-17 μ m (av. 14 μ m)

Pharynx:	11-19 μm (av. 16 μm) \times 14-21 μm (av. 17 μm)
Ventral sucker:	10-25 μm (av. 19 μm) \times 10-25 μm (av. 19 μm)
Excretory bladder:	87-119 μm (av. 98 μm) \times 52-98 μm (av. 76 μm)
Penetration gland:	20-30 μm (av. 26 μm) \times 25-30 μm (av. 26 μm)
Tail:	37-55 μm (av. 45 μm) \times 486-595 μm (av. 546 μm)
Lateral finfold:	9-15 μm (av. 13 μm) \times 88-100 μm (av. 95)

Movement behavior: The cercaria floated on the surface or in the middle of the water.

The body sank lower than the tail. The body moves by turning over left and right. The rolling movement is fast on the water, about 5-7 seconds, and rests for about 25-27 seconds. The body sinks on the surface of the water and then moves upside down.

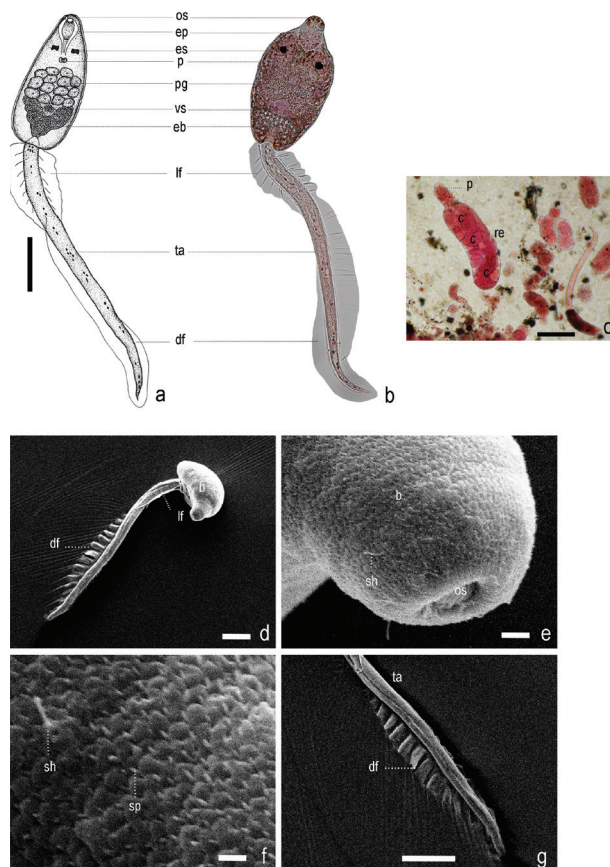


Figure 5. Image of *Stictodora tridactyla*;

- Drawing of cercaria structure
- Cercaria stained with 0.5% neutral red
- Redia stained with 0.5 % neutral red
- d.- g. Images of Scanning Electronmicroscope

Abbreviations: os - oral sucker, ep - esophagus, es - eye spot, p - pharynx, pg - penetration gland, vs - ventral sucker, eb - excretory bladder, lf - lateral finfold, ta - tail, df - dorsal finfold, re - redia, c - cercaria, b - body, sp - spine, sh - sensory hair (scale a, b = 100 μm , c = 10 μm).

Type 2. Pleurophocercous cercariae

4. *Centrocestus formosanus* Nishigori, 1924 (Yamaguti, 1975)

This parasite (Fig. 6) was found in 74 *M. tuberculata*. The infection rate was 0.23% (74/32,026) (Table 2). Cercarial body is oval in shape. A pair of eyespots lay at the level of the pharynx. The oral sucker has two rows of oral spines similar to hooks of the tapeworm (rostellar hooks, four in the anterior and five in the posterior) on the dorsal wall of the mouth aperture. Short esophagus, the parenchymal body is spinulate, and yellowish brown in color. Acetabulum is found between the intestinal bifurcation and the excretory vesical. The bladder is a flattened V-shape. Seven pairs of penetration glands lay anterolateral to the acetabulum in front of an inverted V-shape. Cystogenous cells are distributed in the posterior part. The genital primordial part is somewhat elongated and triangular, between the acetabulum and the excretory vesicle. The tail is slender, with a very indistinct dorsal and ventral finfolds, both of which are more conspicuous in the distal half, with a tiny spike on the tip. Cercariae were produced within the rediae.

Size range and average size (in micrometers, calculated from 20 cercariae):

Body:	45-72 μm (av. 64 μm) \times 82-120 μm (av. 117 μm)
Oral sucker:	16-26 μm (av. 24 μm) \times 17-28 μm (av. 25 μm)
Ventral sucker:	12-16 μm (av. 14 μm) \times 12-16 μm (av. 14 μm)
Pharynx:	7-9 μm (av. 8 μm) \times 8-10 μm (av. 9 μm)
Excretory bladder:	24-30 μm (av. 28 μm) \times 38-52 μm (av. 45 μm)
Tail:	14-17 μm (av. 15 μm) \times 69-92 μm (av. 82 μm)

Movement behavior: The cercaria moved by rolling up and springing the body back to move forward in a screwing motion for 8-10 seconds and then rested for about 45-50 seconds. It survived up to 3-4 hours in the water after emergence.

Type 3. Xiphidiocercariae

5. *Acanthatrium hitaense* Koga, 1953 (Yamaguti, 1975)

This parasite (Fig. 7) was found in 88 *M. tuberculata*. The infection rate was 0.27% (88/32,026) (Table 2). The parasite is virgulate xiphidiocercaria. The body is oval in shape and white in color. There are stylet and virgulate glands in the oral sucker, and 2 pairs of penetration glands in each side of the body. The pharynx is round and short, the ventral sucker is smaller than the oral sucker, and, the small excretory bladder is located at the end of the body. The tail

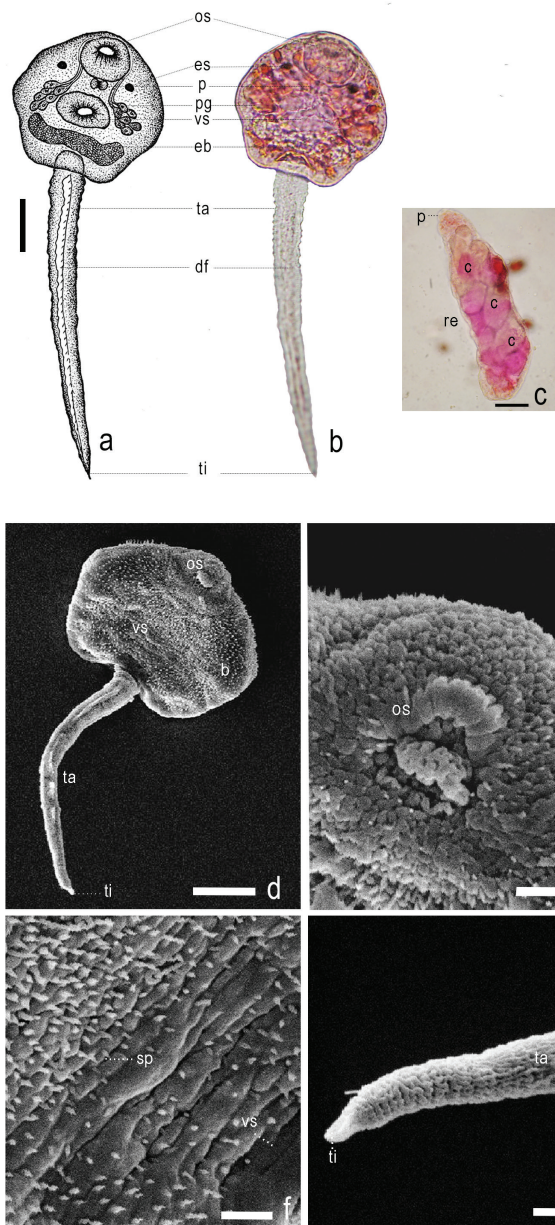


Figure 6. Image of *Centrocestus formosanus*;

- a. Drawing of cercaria structure
- b. Cercaria stained with 0.5% neutral red
- c. Redia stained with 0.5 % neutral red
- d.- g. Images of Scanning Electronmicroscope

Abbreviations: os - oral sucker, es - eye spot, p - pharynx, pg - penetration gland, vs - ventral sucker, eb - excretory bladder, ta - tail, df - dorsal finfold, ti - tip, re - redia, c - cercaria, b - body, sp - spine (scale a, b = 100 μ m, c = 10 μ m).

is shorter than the body, inserted to the posterior end of the body. Cercariae were produced within the sporocyst.

Size range and average size (in micrometers, calculated from 20 cercariae):

Body: 53-92 μ m (av. 78 μ m) \times 80-110 μ m (av. 100 μ m)

Oral sucker:	25-32 μ m (av. 30 μ m) \times 34-40 μ m (av. 37 μ m)
Stylet:	8-13 μ m (av. 10 μ m) \times 11-13 μ m (av. 12 μ m)
Ventral sucker:	15-16 μ m (av. 16 μ m) \times 15-18 μ m (av. 17 μ m)
Pharynx:	10-15 μ m (av. 13 μ m) \times 12-24 μ m (av. 20 μ m)
Excretory bladder:	8-12 μ m (av. 10 μ m) \times 20-46 μ m (av. 38 μ m)
Tail:	19-25 μ m (av. 23 μ m) \times 26-75 μ m (av. 68 μ m)

Movement behavior: The cercaria floated on the surface or in the middle of the water. They moved by rolling up and springing the body back to move forward in a screwing motion for 45-60 seconds, and then rested for 2-5 seconds at the water surface. Some cercariae were stuck on the surface of the container, and moved by the oral sucker and ventral sucker. It survived up to 2-4 hours in the water after emergence.

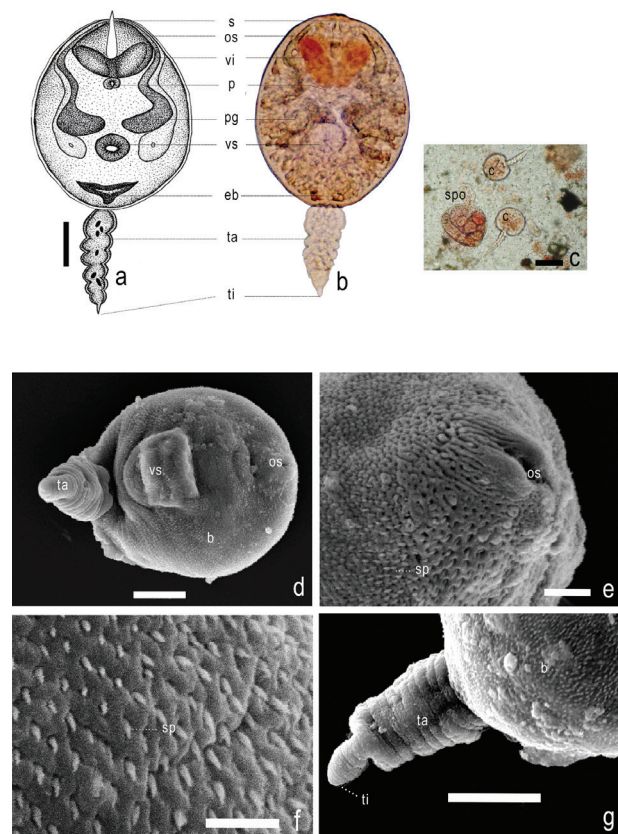


Figure 7. Image of *Acanthatrium hitaense*;

- a. Drawing of cercaria structure
- b. Cercaria stained with 0.5% neutral red
- c. Sporocyst stained with 0.5 % neutral red
- d.- g. Images of Scanning Electronmicroscope

Abbreviations: s - stylet, os - oral sucker, vi - vigulate gland, p - pharynx, pg - penetration gland, vs - ventral sucker, eb - excretory bladder, ta - tail, ti - tip, spo : sporocyst, c - cercaria, b - body, sp - spine (scale a, b = 25 μ m, c = 50 μ m).

6. *Loxogenoides bicolor* Kaw, 1945 (Yamaguti, 1975)

Loxogenoides bicolor (Fig. 8) was found from 2,373 *M. tuberculata*. The infection rate was 7.41% (2,373/32,026) (Table 2). The body of cercaria is spinose and oval in shape. Its entire body is dotted with granules. The ventral sucker is smaller than the oral sucker. A virgular organ is located in the region of the oral sucker. A stylet is present. Three pairs of penetration glands exist: two anterior pairs and a posterior pair. The penetration glands had granules and ducts. The ducts opened near the tip of the stylet. There is a C-shaped genital primordium and a U-shaped excretory bladder. The tail is spinose, with slightly longer spines at the tip. Cercariae were produced within the sporocyst.

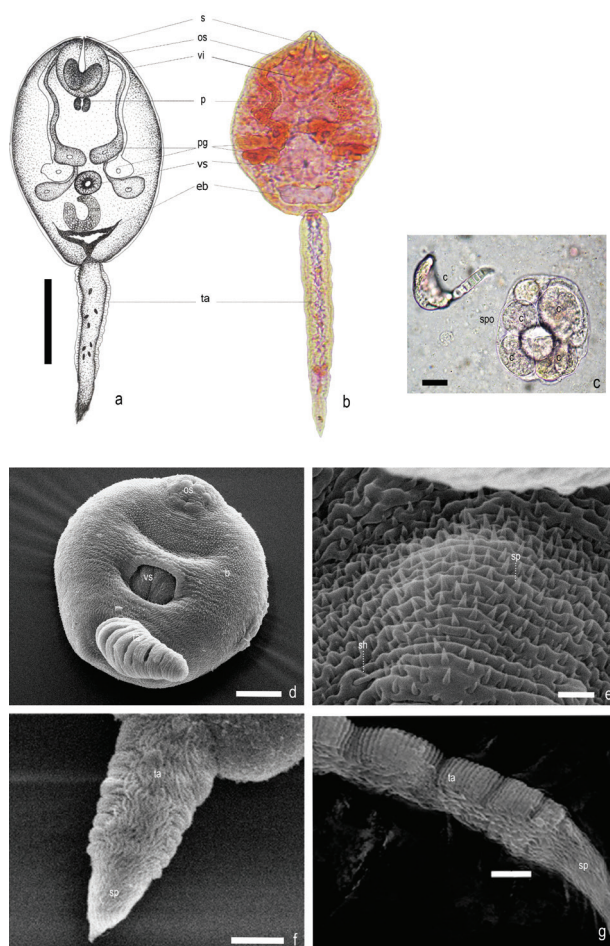


Figure 8. Image of *Loxogenoides bicolor*;

- a. Drawing of cercaria structure
- b. Cercaria stained with 0.5% neutral red
- c. Sporocyst stained with 0.5 % neutral red
- d.- g. Images of Scanning Electronmicroscope

Abbreviations: s - stylet, os - oral sucker, vi - virgular gland, p - pharynx, pg - penetration gland, vs - ventral sucker, eb - excretory bladder, ta - tail, spo : sporocyst, c - cercaria, b - body, sp - spine (scale a, b = 50 μ m, c = 20 μ m).

Size range and average size (in micrometers, calculated from 20 cercariae):

Body:	54-82 μ m (av. 75 μ m) \times 90-120 μ m (av. 110 μ m)
Oral sucker:	24-30 μ m (av. 28 μ m) \times 24-30 μ m (av. 28 μ m)
Stylet:	5-8 μ m (av. 7 μ m) \times 14-20 μ m (av. 18 μ m)
Ventral sucker:	12-18 μ m (av. 15 μ m) \times 13-20 μ m (av. 17 μ m)
Pharynx:	4-6 μ m (av. 5 μ m) \times 4-10 μ m (av. 8 μ m)
Excretory bladder:	8-10 μ m (av. 9 μ m) \times 10-30 μ m (av. 25 μ m)
Tail:	20-30 μ m (av. 27 μ m) \times 35-80 μ m (av. 75 μ m)

Movement behavior: The cercaria moved by folding its tail and rolling up the body and moved from left to right quickly. In resting position, they floated on the surface or in the middle of the water. The body sank lower than the tail. The cercaria moved about 60-75 seconds, and rested for about 2-5 seconds. It survived up to 2-3 hours in the water after emergence.

7. *Haematoloechus similis* Looss, 1899 (Yamaguti, 1975)

Haematoloechus similis (Fig. 9) was found in 468 *M. tuberculata*. The infection rate was 1.46% (468/32,026) (Table 2). This parasite was classified into Xiphidiocercariae. The body is ovate, and the surface is covered with spines. Cytogenous cell is not observed. A stylet is 30-32 μ m long, with no virgulate gland. Six pairs of penetration glands of irregular shape are present, extending from the middle of the body to near the posterior end of body, each with large nuclei and fine granules. Their ducts are bundled, one on each side, opening near the tip of the stylet. Prepharynx is short, and pharynx poorly differentiated. Esophagus, ceca and genitalia are not developed. The excretory vesicle is Y shape. The flame cell formula is $2[(3+3+3)+(3+3+3)]=36$. The tail is not finflod. Cercariae were produced within the sporocyst.

Size range and average size (in micrometers, calculated from 20 cercariae):

Body:	87-104 μ m (av. 95 μ m) \times 130-164 μ m (av. 148 μ m)
Oral sucker:	34-42 μ m (av. 38 μ m) \times 37-46 μ m (av. 42 μ m)
Stylet:	20-34 μ m (av. 30 μ m) \times 20-34 μ m (av. 32 μ m)
Ventral sucker:	10-20 μ m (av. 16 μ m) \times 12-20 μ m (av. 18 μ m)
Pharynx:	11-13 μ m (av. 12 μ m) \times 15-17 μ m (av. 16 μ m)
Excretory bladder:	20-22 μ m (av. 21 μ m) \times 20-24 μ m (av. 22 μ m)

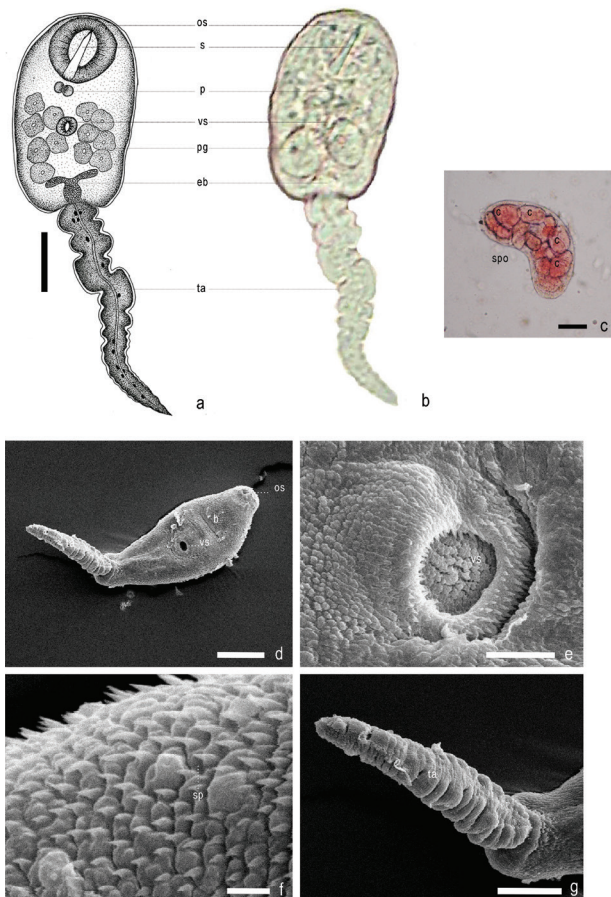


Figure 9. Image of *Haematoloechus similis*;

- a. Drawing of cercaria structure
- b. Cercaria without staining
- c. Sporocyst stained with 0.5 % neutral red
- d.- g. Images of Scanning Electronmicroscope

Abbreviations: s - stylet, os - oral sucker, p - pharynx, pg - penetration gland, vs - ventral sucker, eb - excretory bladder, ta - tail, spo : sporocyst, c - cercaria, b - body, sp - spine (scale a, b = 50 μ m, c = 50 μ m).

Tail: 27-34 μ m (av. 30 μ m) \times 90-120 μ m (av. 115 μ m)

Movement behavior: The cercaria floated on the surface or in the middle of the water. The body sank lower than the tail. It moved by folding its tail back to the body and turning its body to roll quickly from left to right, darting forward for about 15-20 seconds, and resting for about 10-15 seconds. It survived up to 1-2 hours in the water after emergence.

Type 4. Megalurous cercariae

8. *Cloacitrema philippinum* Velasquez, 1969 (Yamaguti, 1975)

Cloacitrema philippinum (Fig. 10) was found in 12 *M. tuberculosis*. The infection rate was 0.04% (12/32,026) (Table 2). The body is elongate and muscular. There is no eye

spot, and no spine on the body surface. There are long pre-pharynx and pharynx. The long ceca runs almost to the end of the body. There are numerous sensory papillae on the surface of body. The oral sucker has 12 opening ducts. The cystogenous cells were found all over the body. The thin wall of the excretory vesicle extends when moving, and the ventral sucker is bigger than the oral sucker. The long tail is inserted to the posterior end of the body. The clear vacuoles distributed along the tail, containing granules. There is an adhesive organ at the tip of the tail, with no lateral finfolds. Cercariae were produced within the rediae.

Size range and average size (in micrometers, calculated from 20 cercariae):

Body: 122-184 μ m (av. 169 μ m) \times 280-450 μ m (av. 396 μ m)
 Oral sucker: 50-60 μ m (av. 56 μ m) \times 50-60 μ m (av. 56 μ m)

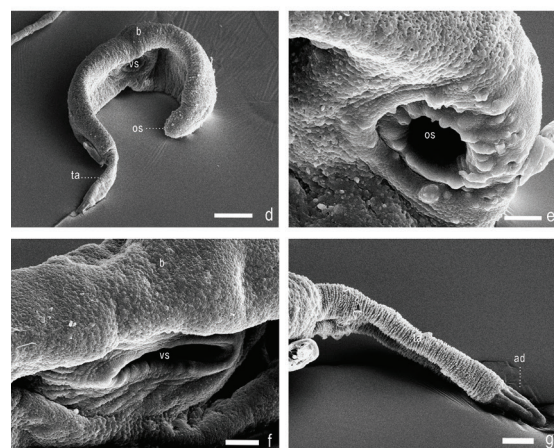
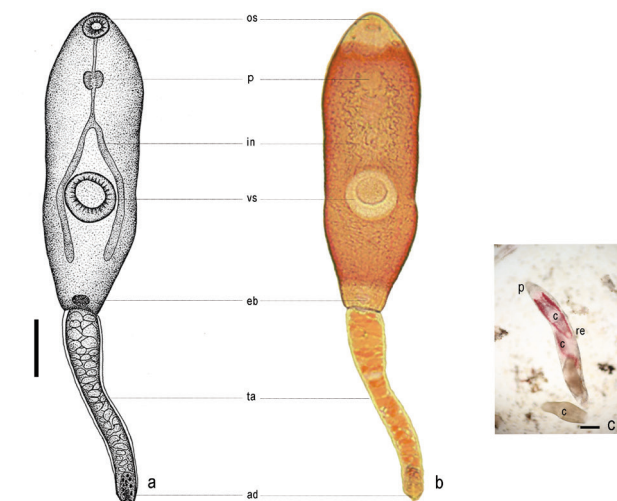


Figure 10. Image of *Cloacitrema philippinum*;

- a. Drawing of cercaria structure
- b. Cercaria stained with 0.5% neutral red
- c. Redia stained with 0.5 % neutral red
- d.- g. Images of Scanning Electronmicroscope

Abbreviations: os - oral sucker, p - pharynx, in - intestine, vs - ventral sucker, eb - excretory bladder, ta - tail, ad - adhesive gland, re - redia, c - cercaria, b - body (scale a, b = 100 μ m, c = 50 μ m).

Ventral sucker:	60-70 μ m (av. 68 μ m) \times 60-75 μ m (av. 70 μ m)
Pharynx:	23-38 μ m (av. 35 μ m) \times 25-40 μ m (av. 35 μ m)
Excretory bladder:	15-20 μ m (av. 18 μ m) \times 14-21 μ m (av. 18 μ m)
Tail:	25-38 μ m (av. 34 μ m) \times 230-547 μ m (av. 480 μ m)

Movement behavior: The cercaria floated on the surface or in the middle of the water. It moved by stretching the body and rolling on the water surface around 20-28 seconds and resting for about 2-4 seconds. The adhesive gland anchored on the container surface. It survived up to 2-4 hours in the water after emergence.

9. *Philophthalmus* sp. Looss, 1899 (Urabe, 2005)

Philophthalmus sp. (Fig. 11) was found in 57 *M. tuberculata*. The infection rate was 0.18% (57/32,026) (Table 2).

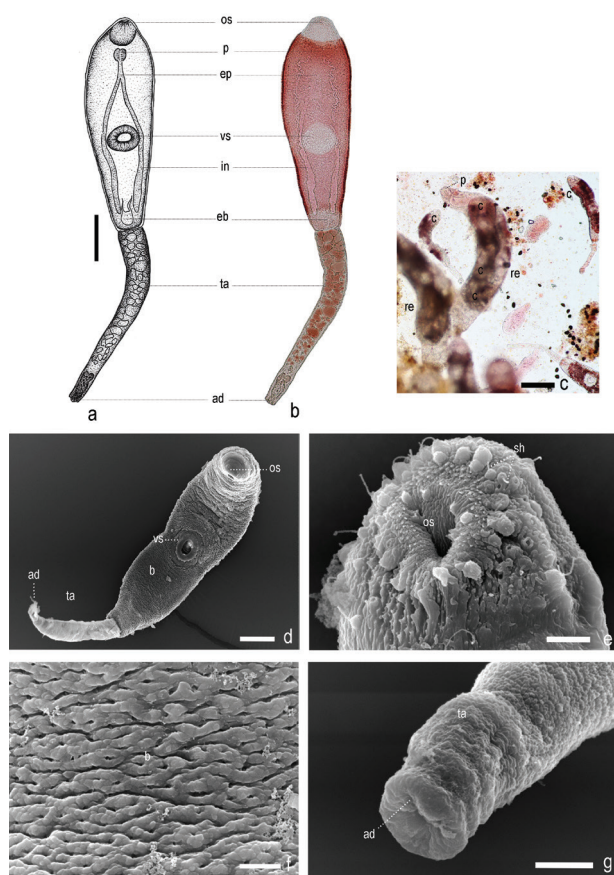


Figure 11. Image of *Philophthalmus* sp.;

- a. Drawing of cercaria structure
- b. Cercaria stained with 0.5% neutral red
- c. Redia stained with 0.5 % neutral red
- d.- g. Images of Scanning Electronmicroscope

Abbreviations: os - oral sucker, p - pharynx, ep - esophagus, vs - ventral sucker, in - intestine, eb - excretory bladder, ta - tail, ad - adhesive gland, re - redia, c - cercaria, b - body (scale a, b = 100 μ m, c = 50 μ m).

The body is elongated and white in color, with numerous minute spines on the half body at the posterior end. It has a muscular body, no eye spot, long prepharynx and pharynx, Y-shaped esophagus, and a large ventral sucker. The intestine runs almost to the end of the body. There are plenty of cyst glands along their bodies. The tail is the same length as the body but flexible, with various sizes of vacuole and granules along the tail. The adhesive gland cells were found. Cercariae were produced within the rediae.

Size range and average size (in micrometers, calculated from 20 cercariae):

Body:	120-125 μ m (av. 122 μ m) \times 525-595 μ m (av. 570 μ m)
Oral sucker:	50-57 μ m (av. 55 μ m) \times 55-62.5 μ m (av. 60 μ m)
Ventral sucker:	62.5-67.5 μ m (av. 64 μ m) \times 55-70 μ m (av. 64 μ m)
Pharynx:	20-25 μ m (av. 23 μ m) \times 20-25 μ m (av. 23 μ m)
Excretory bladder:	37.5-45 μ m (av. 41 μ m) \times 35-50 μ m (av. 41 μ m)
Tail:	30-32.5 μ m (av. 31 μ m) \times 425-512.5 μ m (av. 454 μ m)

Movement behavior: The cercaria floated on the surface or in the middle of the water. It moved by stretching and floating on the surface of the water, and moved forward. Adhesive gland are stuck on the container for cercarial moving. The cercariae became metacercarial cyst immediately in the container.

Type 5. Furcocercous cercariae

10. *Cardicola alseae* Meade & Pratt, 1965 (Yamaguti, 1975)

Cardicola alseae (Fig. 12) were found from 47 *M. tuberculata* which is equivalent to an infection rate of 0.1% (33/32,026) of the total number of the collected snails (Table 2). The small hook-like body had an anterior organ, and was covered with minute spines. The longer spines were found in some parts of the body, the dorsal and ventral of the posterior end. The dorso-median finfold was observed in the middle part of the body. Many large granules were observed, with a penetration gland located at the middle part of the body. The excretory bladder was small. The tail is furcocercous; its furcae are shorter than the beginning of the tail, and sharp like animal crawls. Minute spines and sensory hairs were observed. A caudal body, longitudinal muscle, no flame cell, and furcal finfold were observed, with the opening duct of excretory bladder at the fork tail tip. Cercariae were produced within the sporocyst.

Size range and average size (in micrometers, calculated from 20 cercariae):

Body:	18-39 μ m (av. 28 μ m) \times 72-110 μ m (av. 95 μ m)
-------	---

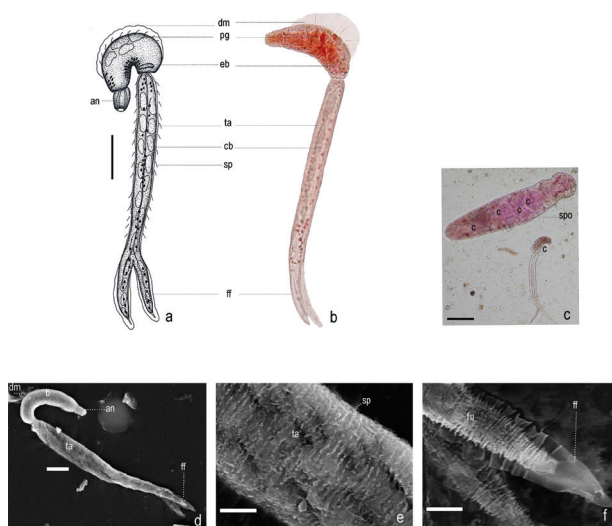


Figure 12. Image of *Cardicola alseae*;

- Drawing of cercaria structure
- Cercaria stained with Semichon's acetic carmine & fast green
- Sporocyst stained with 0.5 % neutral red
- f. Images of Scanning Electronmicroscope

Abbreviations: dm - dorso-median finfold, pg - penetration gland, eb - excretory bladder, an - anterior organ, ta - tail, cb - caudal body, sp - spine, fu - furca, spo : sporocyst, c - cercaria (scale a, b = 50 μ m, c = 20 μ m).

Anterior organ:	11-15 μ m (av. 13 μ m) \times 14-20 μ m (av. 17 μ m)
Excretory bladder:	3-8 μ m (av. 5 μ m) \times 10-35 μ m (av. 21 μ m)
Tail stem:	15-30 μ m (av. 26 μ m) \times 154-197 μ m (av. 185 μ m)
Tail furcal:	7-11 μ m (av. 9 μ m) \times 28-54 μ m (av. 51 μ m)
Dorso-median finfold:	5-12 μ m (av. 8 μ m)

Movement behavior: The cercaria floated on the surface of the water. The body and tail hanged rolling. It moved by folding its tail back to the body, moving forward around 6-10 seconds, and resting for 3-4 seconds. When at rest the body hangs upwards and rolls back slowly downwards with the tail stem and furcae moved upwards. It survived up to 2-3 hours in the water after emergence.

11. *Alaria mustelae* Bosma, 1899 (Yamaguti, 1975)

Alaria mustelae (Fig. 13) were found from 47 *M. tuberculata* which is equivalent to an infection rate of 0.15% (47/32,026) of the total number of the collected snails (Table 2). Cercarial body has a long shape. Unpigmented eyespots lay on the midway between two suckers in lateral fields, prepharynx short, pharynx small and muscular, esophagus rather long, ceca extending a short distance

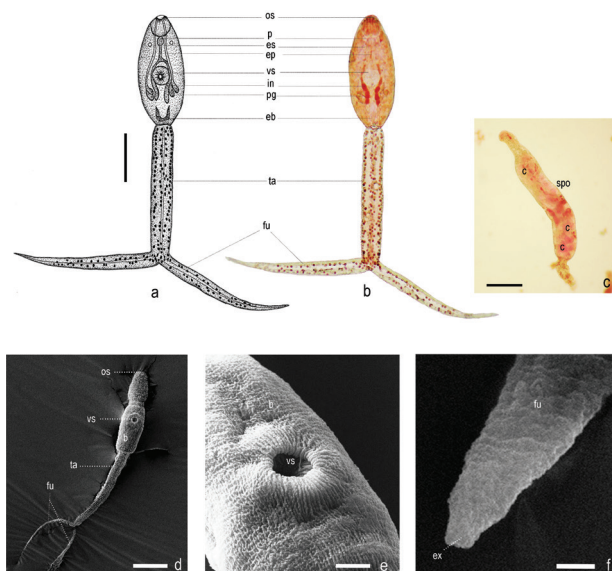


Figure 13. Image of *Alaria mustelae*;

- Drawing of cercaria structure
- Cercaria stained with 0.5% neutral red
- Sporocyst stained with 0.5 % neutral red
- f. Images of Scanning Electronmicroscope

Abbreviations: os - oral sucker, p - pharynx, es - eye spot, ep - esophagus, vs - ventral sucker, in - intestine, pg - penetration gland, eb - excretory bladder, ta - tail, fu - furca, spo : sporocyst, c - cercaria (scale a, b = 50 μ m, c = 10 μ m).

posterior to acetabulum. The oral sucker is slightly larger than the postequatorial acetabulum. There are two pairs of penetration glands, filled with fine granules. The duct openings on each side of the mouth are in spineless circumoral area. The body is covered entirely with spines and two irregular spines around the aperture of the ventral sucker. Genital primordium is a small mass of cells anterior to the excretory vesicle. Cercaria developed within the sporocyst. The tail stem was without spines; the furcae was irregularly spinose (long hair like), with no caudal bodies. The excretory pore was found at the fork tail tip.

Size range and average size (in micrometers, calculated from 20 cercariae):

Body:	105-154 μ m (av. 138 μ m) \times 185-280 μ m (av. 255 μ m)
Oral sucker:	28-40 μ m (av. 36 μ m) \times 28-40 μ m (av. 36 μ m)
Ventral sucker:	15-30 μ m (av. 22 μ m) \times 15-30 μ m (av. 22 μ m)
Pharynx:	10-15 μ m (av. 13 μ m) \times 14-17 μ m (av. 15 μ m)
Tail stem:	48-60 μ m (av. 55 μ m) \times 220-300 μ m (av. 260 μ m)
Tail furcae:	38-65 μ m (av. 60 μ m) \times 245-320 μ m (av. 280 μ m)

Movement behavior: The cercariae moved by rolling up and springing back the body to swiftly move forward

in a quick semi-circular motion. It then rested by floating with its head on top for a long time about 20-30 seconds then moved quickly about 7-15 seconds and rested by floating again. It survived up to 2-3 hours in the water after emergence.

12. *Transversotrema laruei* Velasquez, 1958 (Yamaguti, 1975)

Transversotrema laruei (Fig. 14) were found from 89 *M. tuberculata*, which is equivalent to an infection rate of 0.28% (89/32,026) of the total number of the collected snails (Table 2). The body is in a bowl-like shape and light brownish in color, with numerous spines like fish scales on the body surface. Many granules are observed. The genital pore of the seminal vesicle is at the anterior end of the body. There are very big round eye spots, and the ventral sucker is globular. There is a mouth on the ventral sucker. The esophagus is narrow and long, attached to the intestine. There are 1 pair of testes, with an ovary on the left side of the testes. A small excretory bladder is at the posterior end. The tail is longer than the body length with a fork tip, and one pair of appendage at the base of the tail. An adhesive pad was observed at the end of the tail. The furcal tails are spatulate. There are 4 flame cells, and an opening duct of the excretory bladder is on the furcal tail. Cercariae were produced within the rediae.

Size range and average size (in micrometers, calculated from 20 cercariae):

Body:	425-670 μm (av. 574 μm) \times 280-510 μm (av. 370 μm)
Genital pore:	12 - 18 μm (av. 15 μm) \times 12 - 18 μm (av. 15 μm)
Pharynx:	25 – 57 μm (av. 574 μm) \times 280- 510 μm (av. 370 μm)
Eye spot:	14 –20 μm (av. 18 μm) \times 14 - 20 μm (av. 18 μm)
Excretory bladder:	11-23 μm (av. 15 μm) \times 11-21 μm (av. 15 μm)
Ventral sucker:	85 -105 μm (av. 95 μm) \times 85 - 105 μm (av. 95 μm)
Tail stem:	50 -185 μm (av. 98 μm) \times 254-570 μm (av. 360 μm)
Tail furcae:	45-110 μm (av. 66 μm) \times 145-310 μm (av. 204 μm)
Appendages:	18 -72 μm (av. 47 μm) \times 120-250 μm (av. 160 μm)

Movement behavior: The cercaria floated on the surface or in the middle of the water. The body sank lower than the tail. It moved very fast by turning from left to right, and moving forward in a screwing motion for about 5-8 seconds, and resting about 2-3 minutes by floating with its head and tail folded together. The furcae floated upwards, moving by wavering on the container surface.

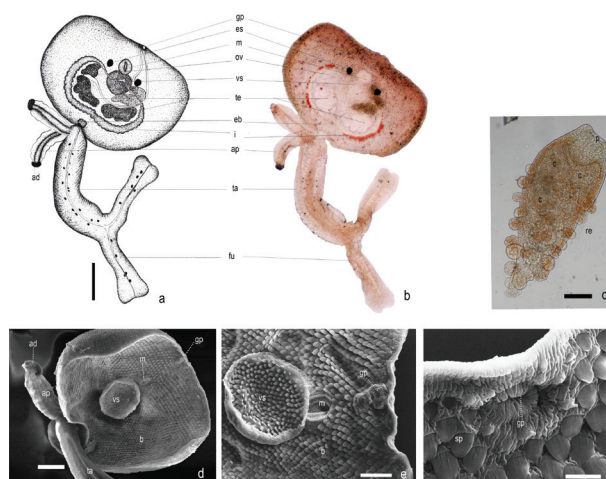


Figure 14. Image of *Transversotrema laruei*;

- Drawing of cercaria structure
- Cercaria stained with 0.5% neutral red
- Redia stained with 0.5 % neutral red
- f. Images of Scanning Electronmicroscope

Abbreviations: gp - genital pore, es - eye spot, m - mouth, ov - ovary, vs - ventral sucker, te - testes, eb - excretory bladder, i - intestine, ap - appendages, ta - tail, fu - furca, p - pharynx, re - redia, c - cercaria (scale a, b = 100 μm , c = 20 μm).

13. *Apatemon gracilis* Szidat, 1928 (Yamaguti, 1975)

Apatemon gracilis (Fig. 15) were found from 55 *M. tuberculata*, which is equivalent to an infection rate of 0.17% (55/32,026) of the total number of the collected snails (Table 2). The cercarial body is oval in shape, and the prepharynx is practically absent. The anterior region has a cuticle spine. It has unpigmented eyespots. The tail stem contains about 16 caudal bodies. There are 4 pairs of penetration glands which lie between the acetabulum and genital primordia. The excretory bladder is very small. Cercariae were produced within the sporocyst.

Size range and average size (in micrometers, calculated from 20 cercariae):

Body:	41.5-90.0 μm (av. 72 μm) \times 115-140 μm (av. 126 μm)
Oral sucker:	15-25 μm (av. 21.45 μm) \times 20-30 μm (av. 23.25 μm)
Ventral sucker:	16-25 μm (av. 23 μm) \times 20-30 μm (av. 25 μm)
Excretory bladder:	15-25 μm (av. 18 μm) \times 15-30 μm (av. 20 μm)
Pharynx:	6-10 μm (av. 8 μm) \times 7-13 μm (av. 9 μm)
Tail stem:	30-45 μm (av. 39 μm) \times 240-312 μm (av. 286 μm)
Tail furcae:	10-25 μm (av. 18 μm) \times 130-160 μm (av. 146 μm)

Movement behavior: The cercariae floated on the surface or in the water. The body sank lower than the spread-

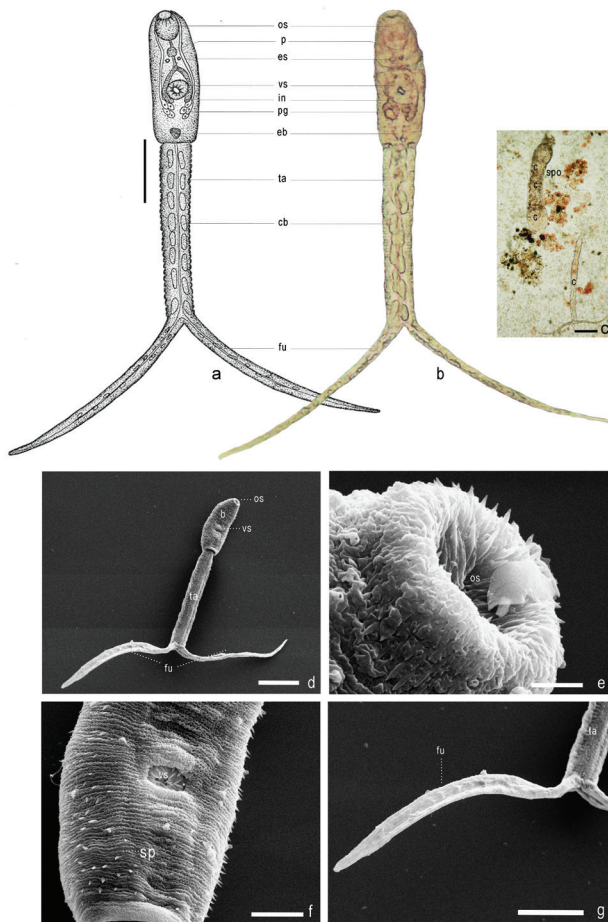


Figure 15. Image of *Apatemon gracilis*;
a. Drawing of cercaria structure
b. Cercaria stained with 0.5% neutral red
c. Sporocyst stained with 0.5 % neutral red
d.- g. Images of Scanning Electronmicroscope

Abbreviations: os - oral sucker, p - pharynx, es - eye spot, vs - ventral sucker, in - intestine, pg - penetration gland, eb - excretory bladder, ta - tail, cb - caudal body, fu - furca, b - body, sp - spine, spo - sporocyst, c - cercaria (scale a, b = 100 μ m, c = 20 μ m).

ing fork tail. It moved by rolling up and springing back the body to swiftly move forward in a semi-circular motion. It then rested by floating with its head on top for about 12-15 seconds, then moved quickly about 3-6 seconds and rested by floating again.

14. *Mesostephanus appendiculatus* (Cicrea, 1916) Lutz, 1935 (Yamaguti, 1975)

Mesostephanus appendiculatus (Fig. 16) were found from 3 *M. tuberculata*, which is equivalent to an infection rate of 0.009% (3/32,026) of the total number of the collected snails (Table 2). The cercarial body is oval in shape and spinose. There are many spines on the surface and the oral sucker. Coarse granules and cytogenous gland are scattered inside the body. The pharynx is small and round. The pre-pharynx and esophagus are almost as long as the pharynx.

A large intestine, composed of two cecae, is terminated near a small excretory bladder. A ventral sucker vestigial is found to be in small groups. The tail is forked and longer than the body and the tail surface is covered with many spines. The tail stem is longer than the furca. The tail tubule opens at the tip of each tail furca in which no flame cell is found. Cercariae were produced within the sporocyst.

Size range and average size (in micrometers, calculated from 20 cercariae):

Body:	92-120 μ m (av. 109 μ m) \times 160-250 μ m (av. 225 μ m)
Oral sucker:	20-45 μ m (av. 35 μ m) \times 35-48 μ m (av. 39 μ m)
Ventral sucker:	15-24 μ m (av. 20 μ m) \times 15-24 μ m (av. 20 μ m)
Excretory bladder:	20-40 μ m (av. 35 μ m) \times 20-40 μ m (av. 35 μ m)
Pharynx:	8-10 μ m (av. 9 μ m) \times 11-18 μ m (av. 15 μ m)

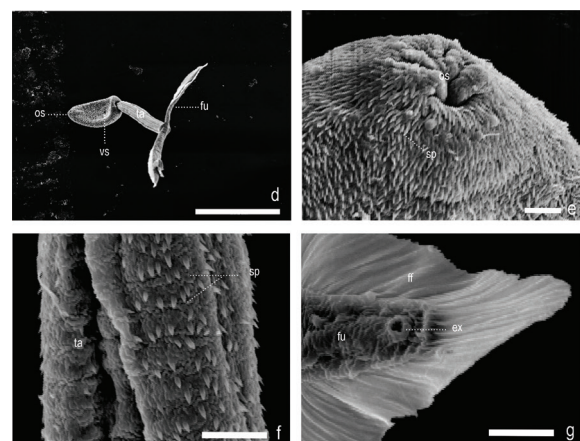
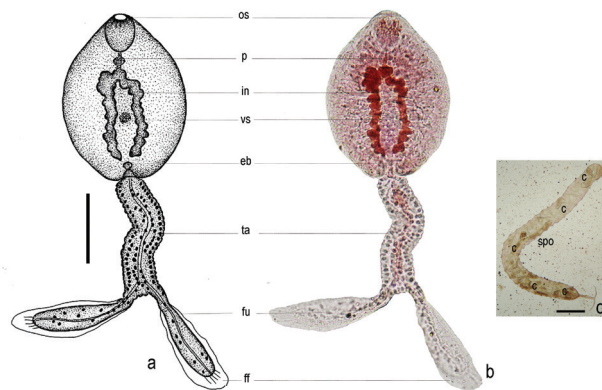


Figure 16. Image of *Mesostephanus appendiculatus*;
a. Drawing of cercaria structure
b. Cercaria stained with 0.5% neutral red
c. Sporocyst stained with 0.5 % neutral red
d.- g. Images of Scanning Electronmicroscope

Abbreviations: os - oral sucker, p - pharynx, in - intestine, vs - ventral sucker, eb - excretory bladder, ta - tail, fu - furca, ff - furcal finfold b - body, sp - spine, ex - excretory pore, spo - sporocyst, c - cercaria (scale a, b = 100 μ m, c = 20 μ m).

Tail stem:	25-40 μm (av. 35 μm) \times 425-525 μm (av. 495 μm)
Tail furcae:	15-25 μm (av. 20 μm) \times 160-170 μm (av. 165 μm)

Movement behavior: The cercaria floated on the surface or in the water. The body sank lower than the spreading fork tail. It moved by rolling up and springing back the body to swiftly move forward in a semi-circular motion for about 2-4 seconds. It then rested by floating with its head on top of the tail and slowly rotated its body to the bottom while lifting up its spreading fork tail. It rested for about 20-30 seconds and survived up to 2-3 hours in the water.

Type 6. Echinostome cercariae

15. *Echinochasmus pelecani* Johnston & Simpson, 1944 (Yamaguti, 1975)

Echinochasmus pelecani (Fig. 17) were found from 19 *M. tuberculata* which is equivalent to an infection rate of 0.06% (19/32,026) of the total number of the collected snails (Table 2). Cercarial body is elongate, white in

color, no eye spot, oral sucker with 3 opening of duct (1 median, 2 submedian), cystogenous cell containing rhabdites. Collar spine is not appearance. Esophagus was between pharynx and ventral sucker, ceca reaching to bladder, two main excretory tubes meet together before entering bladder, Genital primordia are two mass behind ventral sucker, no penetration gland, flame cell pattern not determine. Tail is the same length as body, flexible, vacuole appearance along the tail. Cercariae were produced within rediae.

Size range and average size (in micrometers, calculated from 20 cercariae):

Body:	68-87 μm (av. 85 μm) \times 100-125 μm (av. 118 μm)
Oral sucker:	21-30 μm (av. 23 μm) \times 24-30 μm (av. 25 μm)
Ventral sucker:	20-31 μm (av. 25 μm) \times 22-30 μm (av. 25 μm)
Pharynx:	8-15 μm (av. 12 μm) \times 9-15 μm (av. 12 μm)
Excretory bladder:	21-35 μm (av. 33 μm) \times 23-36 μm (av. 33 μm)
Tail:	23-38 μm (av. 35 μm) \times 95-130 μm (av. 115 μm)

Movement behavior: The cercaria floated on the surface or in the water. It moved very fast by rolling up and springing back about 5-10 seconds. It survived up to 3-4 hours in the water after emergence.

Type 7. Amphistome cercariae

16. *Gastrothylax crumenifer* (Creplin, 1847) Otto, 1896 (Yamaguti, 1975)

Gastrothylax crumenifer (Fig. 18) were found from 8 *M. tuberculata* which is equivalent to an infection rate of 0.02% (8/32,026) of the total number of the collected snails (Table 2). Cercariae were liberated from the rediae. The body shape is ovate and large. The eye spots have conical lens with yellow pigment through the body with a smooth surface. The ceca ended 0.14-0.17 mm away from the posterior end of the body, with symmetrical testes at the level of the ceca end. The oral sucker is equal to the ventral sucker. The tail inserted to the posterior end of the body. There are various sizes of vacuole through the tail.

Size range and average size (in micrometers, calculated from 20 cercariae):

Body:	190-250 μm (av. 220 μm) \times 350-415 μm (av. 370 μm)
Oral sucker:	45-65 μm (av. 52 μm) \times 45-65 μm (av. 52 μm)
Ventral sucker:	48-68 μm (av. 55 μm) \times 48-68 μm (av. 55 μm)
Pharynx:	8-10 μm (av. 10 μm) \times 8-12 μm (av. 11 μm)

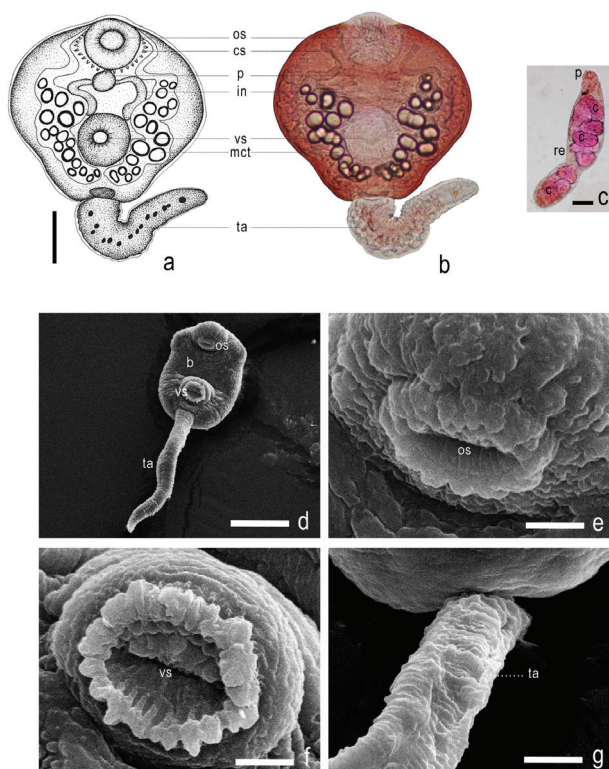


Figure 17. Image of *Echinochasmus pelecani*;

- a. Drawing of cercaria structure
- b. Cercaria stained with 0.5% neutral red
- c. Redia stained with 0.5 % neutral red
- d.- g. Images of Scanning Electronmicroscope

Abbreviations: os - oral sucker, cs - collar spine, p - pharynx, in - intestine, vs - ventral sucker, mct - main collecting tube, ta - tail, re - redia, c - cercaria (scale a, b = 50 μm , c = 10 μm).

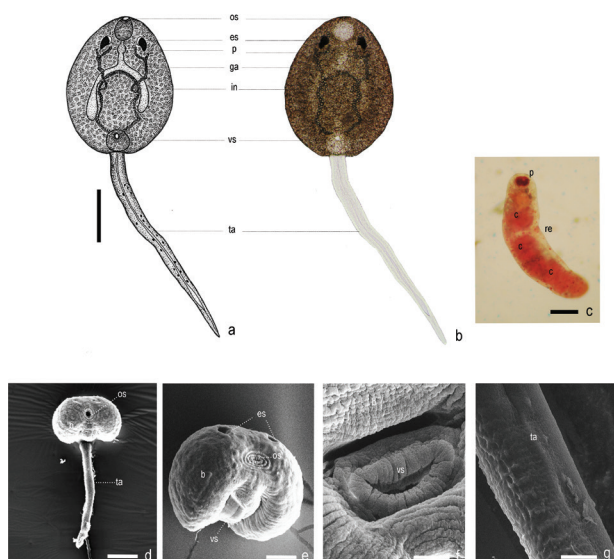


Figure 18. Image of *Gastrothylax crumenifer*;

- a. Drawing of cercaria structure
- b. Cercaria stained with 0.5% neutral red
- c. Redia stained with 0.5 % neutral red
- d.- g. Images of Scanning Electronmicroscope

Abbreviations: os - oral sucker, p - pharynx, es - eye spot, vs - ventral sucker, ga - genital atrium, in - intestine, vs - ventral sucker, ta - tail, re - redia, c - cercaria (scale a, b = 100 μ m, c = 10 μ m).

Esophagous: 80-140 μ m (av. 125 μ m) \times 80-140 μ m (av. 125 μ m)
 Tail: 65-95 μ m (av. 82 μ m) \times 328-450 μ m (av. 410 μ m)

Movement behavior: The cercaria floated on the surface or in the water. It moved by wavering on the surface of the water for around 8-10 seconds, and then rolling up and springing back for about 5-10 seconds. It survived up to 3-4 hours in the water after emergence. The cercariae were photo-sensitive. They shrank rapidly in changing light conditions.

Type 8. *Renicolid cercariae*

17. *Cercaria caribbea* LXVIII (Cable, 1963) (Yamaguti, 1975)

Cercaria caribbea LXVIII (Fig. 19) were found from 45 *M. tuberculata* which is equivalent to an infection rate of 0.14% (45/32,026) of the total number of the collected snails (Table 2). Cercariae developed in the sporocyst. Its body is flat with yellow pigment and numerous minute spines on the surface of the body, with no eye spot, a small sucker of 28-36 μ m, a short prepharynx, a pharynx of 12-14 μ m, plenty of small cephalic glands in the middle of the body, a short excretory vesicle split into two since the upper of the acetabulum. The tail is straight, and is longer than the length of the body, with no lateral fin-fold, and no flame cells.

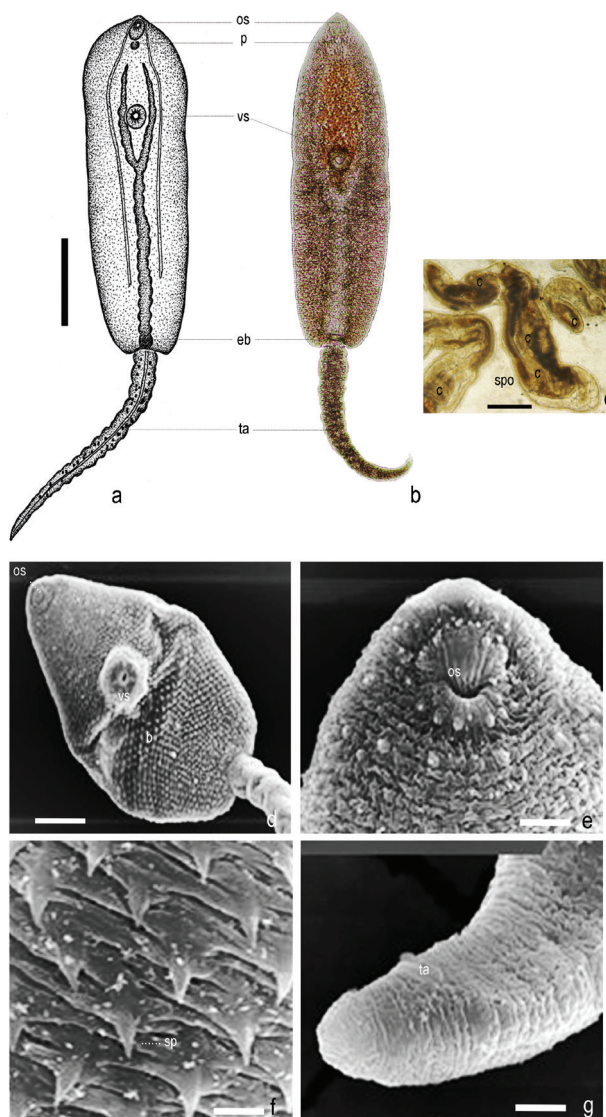


Figure 19. Image of *Cercaria caribbea* LXVIII;

- a. Drawing of cercaria structure
- b. Cercaria stained with 0.5% neutral red
- c. Sporocyst stained with 0.5 % neutral red
- d.- g. Images of Scanning Electronmicroscope

Abbreviations: os - oral sucker, p - pharynx, vs - ventral sucker, eb - excretory bladder, ta - tail, spo - sporocyst (scale a, b = 100 μ m, c = 10 μ m).

Size range and average size (in micrometers, calculated from 20 cercariae):

Body: 128-140 μ m (av. 129 μ m) \times 390-435 μ m (av. 420 μ m)
 Oral sucker: 28-33 μ m (av. 26 μ m) \times 28-33 μ m (av. 26 μ m)
 Ventral sucker: 29-36 μ m (av. 30 μ m) \times 29-36 μ m (av. 30 μ m)
 Pharynx: 8-14 μ m (av. 12 μ m) \times 10-14 μ m (av. 12 μ m)
 Excretory bladder: 15-20 μ m (av. 17 μ m) \times 15-20 μ m (av. 17 μ m)

Tail: 34-38 μm (av. 35 μm) \times 395-480 μm (av. 450 μm)

Movement behavior: The cercaria moved slowly on the bottom of the container, and swam continuously. It survived up to 2-3 hours in the water after emergence.

Type 9. *Cotylomicrocercous cercariae*

18. *Podocotyle (Podocotyle) lepomis* Dobrovolny, 1939 (Yamaguti, 1975)

Podocotyle lepomis (Fig. 20) were found from 3 *M. tuberculata* which is equivalent to an infection rate of 0.009% (3/32,026) of the total number of the collected snails (Table 2). Cercariae developed in the sporocyst. The body is cylindrical in shape, clear white in color, with no sensory hair, spine, 6 papillae on the head, and rough granules present on the body. The stylet is present in oral sucker. There were 2 rows of sensory papillae around the oral sucker, with a long prepharynx. Pharynx is round. The ceca extended to the posterior end, with 5 pairs of penetration glands. 2 of them were not stained with 0.5% neutral red while 3 of them were stained with 0.5% neutral red. Excretory vesicle had a thick wall and open dorsally at the tail, the flame cell formula is $2[(2+2)+(2+2)]$. The tail is short, only half the length of the body, cup-shaped, with an adhesive gland present at the end of the tail for attaching.

Size range and average size (in micrometers, calculated from 20 cercariae):

Body: 65-93 μm (av. 73 μm) \times 103-145 μm (av. 123 μm)

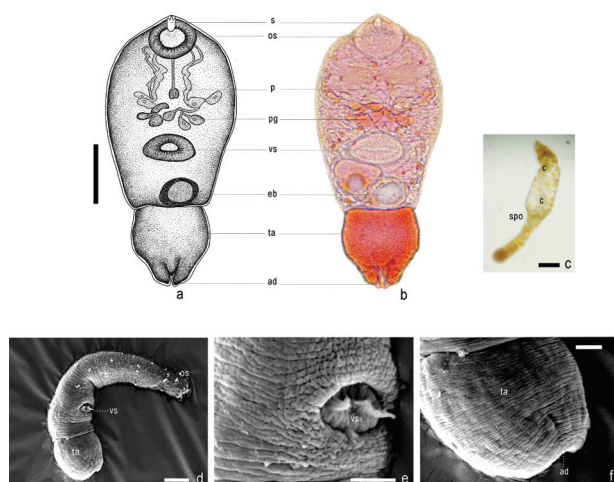


Figure 20. Image of *Podocotyle (Podocotyle) lepomis*;

- a. Drawing of cercaria structure
- b. Cercaria stained with 0.5% neutral red
- c. Sporocyst stained with 0.5 % neutral red
- d.- f. Images of Scanning Electronmicroscope

Abbreviations: s - stylet, os - oral sucker, p - pharynx, penetration gland, vs - ventral sucker, eb - excretory bladder, ta - tail, ad - adhesive organ, spo - sporocyst, c - cercaria (scale a, b = 100 μm , c = 10 μm).

Stylet: 4-6 μm (av. 5 μm) \times 6-10 μm (av. 8 μm)

Oral sucker: 30-38 μm (av. 32 μm) \times 25-38 μm (av. 30 μm)

Ventral sucker: 28-40 μm (av. 35 μm) \times 28-40 μm (av. 35 μm)

Pharynx: 13-18 μm (av. 14 μm) \times 10-13 μm (av. 11 μm)

Excretory bladder: 20-30 μm (av. 26 μm) \times 18-25 μm (av. 21 μm)

Tail: 43-65 μm (av. 52 μm) \times 50-75 μm (av. 61 μm)

Movement behavior: The cercaria floated with the ventral upside. It moved by floating with its head and tail folded together, and then sprang up. Normally it creeps on the surface of the container using the oral and ventral sucker. The cercaria floated for about 15-20 seconds, and rested for about 10-15 seconds. It survived up to 2-3 hours in the water.

Discussion

Melanoides tuberculata Müller, 1774 is a benthic freshwater thiarid native to Africa and Asia. Its original native range seemed uncertain but nonetheless wide, including parts of Africa, the Mediterranean, Asia and the Pacific Islands (Pace 1973, Clench 1969). Glaubrecht (1996) hypothesized that its origin lies rather in Asia than Africa, given its natural occurrences and the history of Thiaridae; see also Glaubrecht et al. (2009) and Glaubrecht (2011). It had also become established in several other countries. (Facon et al. 2004, Derraik 2008). Aquarium plants exchange by humans caused the brake down of natural dispersal barriers to these snails (Kolar and Lodge 2001). Moreover, *Melanoides* had also adapted well to new environments. For example, on Martinique Island *M. tuberculata* was surveyed in 1979 and 2003. While there were only two morphs found in 1979, in 2003 there were nine morphs. Population dynamics and distribution of *M. tuberculata* were studied in many areas, where they dominated the streams, ponds, and lakes (e.g. Supian and Ikhwanuddin 2002, Eldblom and Kristensen 2003, Facon et al. 2003).

Melanoides tuberculata was found to be intermediate host for a number of trematode parasites (e.g. Pinto and De Melo 2011, Ukong et al. 2007). As a consequence, the introduction of *M. tuberculata* leads to new parasitic cycles in humans in the invaded area. However, there are also reports that show the efficacy of *M. tuberculata* as a biocontrol agent against the schistosome (blood fluke) vector snails *Biomphalaria glabrata* (Pointier and Jourdan 2000).

In Thailand, Brandt (1974) reported that thiarid snails were found in lakes, ponds, marshes, canals, streams, rivers, and other sources of river such as waterfalls. In the present work, we did a smaller scale of investigation than Brandt's. More than thirty thousand of *M. tubercu-*

lata snails were collected from rice paddies, drainages, ponds, canals, water reservoirs, marshes, streams, waterfalls, and rivers in Thailand. The classification of *M. tuberculata* was performed as reported by Brandt (1974). It was quite clear to distinguish *M. tuberculata* from other thiarids, although among these snails there were quite different shell morphologies in terms of ribs, color, pigmentation and even size. Although, based on the shell, the distinction of discrete several morphs was possible (see e.g. Pointier 1989, 1993, Samadi et al. 1999), all of these morphs were still considered to be conspecific within *M. tuberculata*. It is hoped that molecular techniques will help us to eventually solve this question of intraspecific versus intraspecific variation.

In this study, the recovery of adult trematode stages are not completely recorded, but the morphological distinction of cercariae are quite clear from the unstained, stained and electronmicroscopic images, allowing to classify the eighteen species of cercariae from this thiarid snail species into nine types of cercarial morphology, as compiled in the Result section.

In the present study, we also found human trematodes, viz. *Haplorchis taichui*, *Haplorchis pumilio*, *Centrocestus formosanus* and *Cercaria caribbea* LXVIII. Especially the *H. pumilio* human minute intestinal fluke (371/6,019 = 6.16%) showed a high level of prevalence in Thailand. As they complete their complex life cycle not only in humans but also in other vertebrates, it is difficult to control their infection. *H. taichui* is another important minute intestinal fluke. Three cases of humans were reported with mucosal ulceration, mucosal and submucosal haemorrhages, fusion and shortening villi, chronic inflammation and fibrosis of submucosa; in addition, there was a report of the pathology in the small intestine of patients caused by *H. taichui* (Sukontason et al. 2005). In earlier reports, *Haplorchis* spp. were found to be of high prevalence of infection in the north of Thailand (Chontanarith and Wongsawad 2010). In the present report, we now found *Haplorchis* infections in every region of Thailand.

The minute intestinal flukes were reported not only in Asia but also in South America. The life cycle of *H. pumilio* was studied from redia to adult under natural and

experimental conditions in the digestive gland of *Melanoides tuberculata*, collected from Agasanta, Venezuela (Diaz et al. 2008). It seems that *M. tuberculata* was one of the important intermediate host snails of humans and animal trematodes in the world.

For animal parasites, the cercariae with the highest prevalence were *L. bicolor* (2,373/6,019 = 39.43%), an amphibian trematode. However, the other animal parasites were also very important for public health. For example, the eye fluke *Philophthalmus* spp. are parasites of birds, using a snail intermediate host and birds as the definitive host. However, they also occurred in human and other animals. Human infection by these eye flukes occur via direct contact with the eye by cercariae in the water or by ingestion of cercariae in contaminated water (Alicata 1962, Waikagul et al. 2006, Derrai 2008).

One of heterophyid trematodes, *Stictodora tridactyla* was reported that they occasionally infested brackish water and marine snails, while metacercariae encyst in fish, with the definitive hosts being birds and mammals including humans (Chai et al. 1988, Abdul-Salam et al. 2000). *S. tridactyla* also infected *M. tuberculata* with other cercariae as well. The infection rate of *S. tridactyla* is 6.81% (2,182/6,019). In our previous study, we found *S. tridactyla* in *M. tuberculata* and even more in *M. jugicostis* (Ukong et al. 2007).

The highest infection rate of parasite is 7.41% (2,373/6,019) with *Loxogenoides bicolor* being the most common parasite found in the present study. This parasite is one of the Xiphidiocercariae, being produced by trematodes from the superfamily Plagiorchioidea (Schell 1962, Malek and Cheng 1974). They were found in other thiarid snails, such as *Thiara* (i.e. *Plotia*) *scraba* at Erawan Waterfall, Kanchanaburi, Thailand (Ukong et al. 2007).

Interestingly, it can cause double infection or even triple infection in *M. tuberculata* together with other trematodes. We found a total of 326 double infections and 13 triple infections in *M. tuberculata* (Table 4). *S. tridactyla* and *L. bicolor* were found to be common in double infections, while *S. tridactyla*, *L. bicolor* and *C. alseae* were commonly found triple infections. *C. alseae* is a blood-dwelling trematode.

Table 4. Double trematode infections and triple trematode infections of collected *Melanoides tuberculata*.

Infections	Type	No. of infected snails
Double	<i>Loxogenoides bicolor</i> + <i>Stictodora tridactyla</i>	135
	<i>Cardicola alseae</i> + <i>Stictodora tridactyla</i>	162
	<i>Apatemon gracilis</i> + <i>Stictodora tridactyla</i>	3
	<i>Loxogenoides bicolor</i> + <i>Cercaria caribbea</i> LXVIII	3
	<i>Loxogenoides bicolor</i> + <i>Philophthalmus</i> sp.	7
	<i>Loxogenoides bicolor</i> + <i>Haplorchis pumilio</i>	10
	<i>Alaria mustelae</i> + <i>Haplorchis pumilio</i>	1
	<i>Haplorchis taichui</i> + <i>Alaria mustelae</i>	1
	<i>Haplorchis taichui</i> + <i>Loxogenoides bicolor</i>	2
	<i>Haplorchis taichui</i> + <i>Acanthatrium hitaense</i>	2
	<i>Loxogenoides bicolor</i> + <i>Stictodora tridactyla</i> + <i>Podocotyle lepomis</i>	1
Triple	<i>Loxogenoides bicolor</i> + <i>Stictodora tridactyla</i> + <i>Cardicola alseae</i>	12
	Total	339

This parasite is furcocercous cercariae. It is produced by trematodes from the family Sanguinicolidae. Found in freshwater fishes they were reported to have sporocysts that developed in the visceral mass of the snail *Oxytrema silicula* from Alsae River, Oregon, USA (Meade 1967). In Thailand, *C. alseae* was also found in the thiarid snail *Tarebia granifera* at Erawan Waterfall (Ukong et al. 2007). The others furcocercous cercariae *Alaria mustelae*, *Transversotrema laruei*, *Apatemon gracilis*, and *Mesostephanus appendiculatus*, can also be found in *M. tuberculata*. These parasites, such as *Transversotrema laruei* and *Apatemon gracilis*, were found with metacercariae in brackish and freshwater fishes. The adult stages of these flukes inhibit the small intestine of their bird hosts (Smith and Hickman 1983).

Although the counts per unit of time method (Olivier and Schneiderman 1956) used to measure the density of the snail population in the marked areas does not represent the total population, our observations were performed all year round. That way we were able to document seasonal variation in the intensity of parasitism in *M. tuberculata*. Thus, we consider our data of cercariae infection rates from this research to be reliable. Since most of the above cited intestinal flukes affect humans and animals alike (Derraik 2008), in conclusion we can state that the thiarid snail *Melanooides tuberculata* can doubtlessly be considered as of considerable medical significance in Thailand and elsewhere.

Acknowledgements

This research was supported by the Research and Development Institute, Silpakorn University, Thailand. We also thank Department of Biology, and Faculty of Science, Silpakorn University. We would like to especially thank Assist. Prof. Dr. Chalerm Sri Chantasingh and PD. Dr. Matthias Glaubrecht for valuable suggestions and editing the manuscript.

References

- Abdul-Salam J, Sreelatha BS, Ashkanani H (2000) Surface ultrastructure of *Stictodora tridactyla* (Trematoda: Heterophyidae) from Kuwait Bay. *Parasitology International* 49: 1-7.
- Abdul-Salam J, Sreelatha BS, Ashkanani H (2004) The eye fluke *Philophthalmus hegeneri* (Digenea: Philophthalmidae) in Kuwait Bay. *Kuwait Journal of Science & Engineering* 31: 119-133.
- Alicata JE (1962) Life cycle and developmental stages of *Philophthalmus gralli* in the intermediate and final hosts. *Journal of Parasitology* 48: 47-54.
- Brandt AM (1974) The non-marine aquatic mollusca of Thailand. *Archiv für Molluskenkunde* 105 (1/4): 1-423.
- Chai JY, Hong SJ, Lee SH, Seo BS (1988) *Stictodora* sp. (Trematoda: Heterophyidae) recovered from a man in Korea. *The Korean Journal of Parasitology* 26: 127-132.
- Chai JY, Murrell KD, Lymbery AJ (2005) Fish-borne parasitic zoonoses: status and issues. *International Journal of Parasitology* 35: 1233-1254.
- Chontanarath C, Wongsawad C (2010) Prevalence of *Haplorchis taichui* in field collected snails: A molecular approach. *The Korean Journal of Parasitology* 48 (4): 343-346.
- Chuboon S, Wongsawad C, Ruamsuk A, Nithikathkul C (2005) Survival of *Haplorchis taichui* metacercariae in Lab-pla, Thai traditional food preparation. *The Southeast Asian Journal of Tropical Medicine and Public Health* 36 (suppl 4): 110-111.
- Clench WJ (1969) *Melanooides tuberculata* (Müller) in Florida. *Nautilus* 83: 72.
- Davis GM (1971) Systematic studies of *Brotia costula episcopalis*, first intermediate host of *Paragonimus westermani* in Malaysia. *Proceedings of the Academy of Natural Sciences of Philadelphia* 123: 53-66.
- Dechruksa W, Krailas D, Ukong S, Inkapananakul W, Koonchornboon T (2007) Trematode infections of the freshwater snail family Thiaridae in the Khek river, Thailand. *The Southeast Asian Journal of Tropical Medicine and Public Health* 38 (6): 1016-1028.
- Dechruksa W, Krailas D, Glaubrecht M (2013) Evaluating the status and identity of "*Melania*" *jugicostis* Hanley & Theobald, 1876 – an enigmatic thiarid gastropod in Thailand (Caenogastropoda, Cerithioidea). *Zoosystematics and Evolution* 89 (2): 293-309.
- Derraik JGB (2008) The potential significance to human health associated with the establishment of the snail *Melanooides tuberculata* in New Zealand. *The New Zealand Medical Journal* 121: 25-32.
- Diaz MT, Hernandez LE, Bashirullah AK (2008) Studies on the life cycle of *Haplorchis pumilio* (Looss, 1896) (Trematoda: Heterophidae) in Venezuela. *Revista Científica FCV-LUZ* 18(1): 35-42.
- Eldblom C, Kristensen TK (2003) A revision of the genus *Melanooides* (Gastropoda: Thiaridae) in Lake Malawi. *African Zoology* 38(2): 357-369.
- Facon B, Machline E, Pointier JP, David P (2004) Variation in desiccation tolerance in freshwater snails and its consequences for invasion ability. *Biological Invasions* 6: 283-293.
- Facon B, Pointier JP, Glaubrecht M, Poux C, Jarne P, David P (2003) A molecular phylogeography approach to biological invasion of the new world by parthenogenetic thiarid snails. *Molecular Ecology* 12: 3027-3039.
- Glaubrecht M (1996) Evolutionsökologie und Systematik am Beispiel von Süß- und Brackwasserschnecken (Mollusca: Caenogastropoda: Cerithioidea): Ontogenese-Strategien, paläontologische Befunde und Historische Zoogeographie. Backhuys Publishers. Leiden. [in German with extended English abstract]
- Glaubrecht M (1999) Systematics and the evolution of viviparity in tropical freshwater gastropods (Cerithioidea: Thiaridae sensu lato) – an overview. *Courier Forschungs-Institut Senckenberg* 215: 91-96.
- Glaubrecht M (2000) A look back in time: Toward an historical biogeography as synthesis of systematic and geologic patterns outlined with limnic gastropods. *Zoology* 102: 127-147.
- Glaubrecht M (2011) Towards solving Darwin's "mystery": Speciation and radiation in lacustrine and riverine freshwater gastropods. *The American Malacological Society* 29: 187-216.
- Glaubrecht M, Brinkmann N, Pöppe J (2009) Diversity and disparity 'down under': Systematics, biogeography and reproductive modes of the 'marsupial' freshwater Thiaridae (Caenogastropoda, Cerithioidea) in Australia. *Zoosystematics and Evolution* 85(2): 199-275.

- Hotez PJ, Molyneux DH, Fenwick A, Kumaresan J, Ehrlich Sachs S, Sachs JD, Savioli L (2007) Control of neglected tropical diseases. *New England Journal of Medicine* 357: 1018–1027.
- Hotez PJ, Fenwick A, Savioli L, Molyneux DH (2009) Rescuing the “bottom billion” through neglected tropical disease control. *The Lancet* 373: 1570–1574.
- Ito J (1980) Studies on cercariae in Japan. Shizuoka University. Oya, Surugaku, Shizuoka.
- Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* 19: 199–204.
- Krailas D, Dechruksa W, Ukong S, Janecharut T (2003) Cercarial infection in *Paludomus petrosus*, Freshwater snail in Pa La-U Waterfall. *The Southeast Asian Journal of Tropical Medicine and Public Health* 34: 286–290.
- Krailas D, Chotesaengsri S, Pattaradussadee N, Notesiri N, Dechruksa W (2008) Bucephalid (Gasterostome) cercariae obtained from freshwater clams in Thailand. *The Journal of Tropical Medicine and Parasitology* 31: 70–76.
- Lydeard C, Holznagel WE, Glaubrecht M, Ponder WF (2002) Molecular phylogeny of a circum-global, diverse gastropod superfamily (Cerithioidea: Mollusca: Caenogastropoda): pushing the deepest phylogenetic limits of mitochondrial LSU rDNA sequences. *Molecular Phylogenetics and Evolution* 22 (3): 399–406.
- Madsen H, Frandsen F (1989) The spread of fresh water snails including those of medical and veterinary importance. *Acta Tropica* 46: 139–149.
- Malek EA, Cheng TC (1974) Medical and Economic malacology. Academic Press, New York.
- Meade TG (1967) Life history studies on *Cardicola klamathensis* (Wales, 1958)
- Meade, Pratt (1965) (Trematoda: Sanguinicolidae). *Proceedings of the Helminthological Society of Washington* 34 (2): 210–212.
- Nasir P (1974) British freshwater cercariae. The British Museum, London.
- Nithiuthai S, Suwansaksri J, Wiwanitkit V, Chaengphukeaw P (2002) A survey of metacercariae in cyprinoid fish in Nakhon Ratchasima, northeast Thailand. *The Southeast Asian Journal of Tropical Medicine and Public Health* 33 (3): 103–105.
- Olivier LC, Schneiderman M (1956) Method for estimating the density of aquatic snail population. *Experimental Parasitology* 5: 109–117.
- Pace GL (1973) Freshwater snails of Taiwan. *Malacological Review* 1(suppl): 24–31.
- Pinto HA, De Melo AL (2011) A checklist of trematodes (Platyhelminthes) transmitted by *Melanoides tuberculata* (Mollusca: Thiaridae). *Zootaxa* 2799: 15–28.
- Pointier JP (1989) Conchological studies of *Thiara (Melanoides) tuberculata* (Mollusca: Gastropoda: Thiaridae) in the French West Indies. *Walkerana* 3: 203–209.
- Pointier JP (1993) The introduction of *Melanoides tuberculata* (Mollusca: Thiaridae) to the island of Saint Lucia (West Indies) and its role in the decline of *Biomphalaria glabrata*, the snail intermediate hosts of *Schistosoma mansoni*. *Acta Tropica* 54: 13–18.
- Pointier JP, Jourdan J (2000) Biological control of the snail hosts of Schistosomiasis in areas of low transmission: the example of the Caribbean area. *Acta Tropica* 77: 53–60.
- Pungpak S, Radomyos P, Radomyos B, Schelp FP, Jongsuksuntigul P, Bunnag D (1998) Treatment of *Opisthorchis viverrini* and intestinal fluke infections with praziquantel. *The Southeast Asian Journal of Tropical Medicine and Public Health* 29: 246–9.
- Radomyos B, Wongsaroj T, Wilairatana P, Radomyos P, Praevanich R, Meesomboon V, Jongsuksuntikul P (1998) Opisthorchiasis and intestinal fluke infections in northern Thailand. *The Southeast Asian Journal of Tropical Medicine and Public Health* 29: 123–127.
- Samadi S, Mavárez J, Pointier JP, Delay B, Jarne P (1999) Microsatellite and morphological analysis of population structure in the parthenogenetic freshwater snail *Melanoides tuberculata*: insights into creation of clonal variability. *Molecular Ecology* 8: 1141–1153.
- Schell SC (1962) Parasitology laboratory manual. Wiley. New York.
- Schell SC (1970) How to know the Trematode. W. C. Brown Publishers, Iowa.
- Smith SJ, Hickman JL (1983) Two strigeoid trematodes, *Apatemon (Apatemon) gracilis* (Rudolphi, 1819) and *Diploetomum (Dolichorchis) galaxiae* n. sp., which encyst in the freshwater fish *Galaxias auratus* Johnston in Lake Crescent, Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* 117: 21–39.
- Sri-aroon P, Lohachit C, Harada M (2005) Brackish-water Mollusks of Surat Thani Province, Southern Thailand. *The Southeast Asian Journal of Tropical Medicine and Public Health* 36 (suppl 4): 180–188.
- Sripa B, Kaewkes S, Intapan PM, Maleewong W, Brindley PJ (2010) Food-borne trematodiasis in Southeast Asia: epidemiology, pathology, clinical manifestation and control. *Advances in Parasitology* 72: 305–50.
- Srisawangwong T, Sithithaworn P, Tesana S (1997b) Metacercariae isolated from cyprinoid fishes in Khon Kaen district by digestion technique. *The Southeast Asian Journal of Tropical Medicine and Public Health* 28 (suppl 1): 224–226.
- Strong EE, Gargominy O, Ponder WF, Bouchet P (2008) Global diversity of gastropods (Gastropoda; Mollusca) in freshwater. *Hydrobiologia* 595: 149–166.
- Strong EE, Colgan DJ, Healy JM, Lydeard C, Ponder WF, Glaubrecht M (2011) Phylogeny of the gastropod superfamily Cerithioidea using morphology and molecules. *Zoological Journal of the Linnean Society* 162: 43–89.
- Sukontason K, Piangjai S, Muangyimpong Y, Sukontason K, Methanitikorn R, Chaithong U (1999) Prevalence of trematode metacercariae in cyprinoid fish of Ban Pao district, Chiang Mai Province, northern Thailand. *The Southeast Asian Journal of Tropical Medicine and Public Health* 30: 365–70.
- Sukontason K, Unpunyo P, Sukontason KL, Piangjai S (2005) Evidence of *Haplorchis taichui* infection as pathogenic parasite: Three case reports. Case report. *Scandinavian Journal of Infection Diseases* 37: 388–390.
- Supian Z, Ikhwannuddin AM (2002) Population dynamics of freshwater mollusks (Gastropod: *Melanoides tuberculata*) in Crocker Range Park, Sabah. *Asean Review of Biodiversity and Environmental Conservation*. <http://www.Arbec.com.my/pdf/art13julysep02.pdf>
- Tubangui MA, Cabrera BD, Yogore MG (1950) Studies on the human lung fluk (*Paragonimus*) in the Philippines. A preliminary report. *Acta Medica Philippina* 6: 371.
- Tang AA (1940) A comparative study of two types of *Paragonimus* occurring in Fukien, south China. *Clinical Medicine Journal (Suppl 3)*: 267.
- Temcharoen P (1992a) Malacological survey in the Bhumibol Reservoir, the first dam in Thailand. *The Southeast Asian Journal of Tropical Medicine and Public Health* 23: 103–110.

- Temcharoen P (1992b) Malacological survey in the Sirikit Reservoir, the largest Earth filled dam in Thailand. *The Southeast Asian Journal of Tropical Medicine and Public Health* 23: 332-335.
- Tesana S (2002) Diversity of mollusks in the Lam Ta Khong Reservoir, Nakhon Ratchasima, Thailand. *The Southeast Asian Journal of Tropical Medicine and Public Health* 33: 733-738.
- Ukong S, Krailas D, Dangprasert T, Channagarm P (2007) Studies on the morphology of cercariae obtained from freshwater snails at Erawan Waterfall, Erawan National Park, Thailand. *The Southeast Asian Journal of Tropical Medicine and Public Health* 38 (2): 302-312.
- Upatham ES, Sornmai S, Thirachantra S, Sitaputra P (1980) Field studies on the bionomics of alpha and gamma races of *Tricula aperta* in the Mekong River at Khemmarat, Ubol Ratchathani Province, Thailand. In: Bruce JI, Sornmani S, Asch HL, Crawford KA (Eds) *The Mekong Schistosome*. Malacological Review (suppl 2): 239-261.
- Upatham ES, Koura M, Ahmed MD, Awad AH (1981) Studies on the transmission of *Schistosoma haematobium* and the bionomics of *Bulinus* (Ph.) *abyssinicus* in the Somali Democratic Republic. *Annals of Tropical Medicine and Parasitology* 75: 63-69.
- Upatham ES, Kruatrachue M, Chitramwong Y, Jantataemae S (1995) *Malacology*. Suksopa Publishing, Bangkok.
- Waikagul J, Dekumyoy P, Yoonuan T, Praevanit R (2006) The American Society of Tropical Medicine and Hygiene 74: 848-849.
- Wattanakulpanich D, Waikagul J, Maipanich W, Nuamtanong S, Sanguanthiat S, Pubampen S, Praevanit R, Mongkhonmu S, Nawa Y (2010) *Haplorchis taichui* as a possible etiologic agent of irritable bowel syndrome-like symptoms. *The Korean Journal of Parasitology* 48 (3): 225-229.
- Wegeberg AM, Montaudouin XD, Jensen KT (1999) Effect of intermediate host size (*Cerastoderma edule*) on infectivity of cercariae of three *Himasthla* species (Echinostomatidae, Trematoda). *Journal of Experimental Marine Biology and Ecology* 238: 259-269.
- Wongratanacheewin S, Pumidonming W, Sermswan RW, Maleewong W (2001) Development of a PCR-based method for the detection of *Opisthorchis viverrini* in experimentally infected hamsters. *Parasitology* 122: 175-180.
- Urabe M (2005) Cercariae of a species of *Philophthalmus* detected in a freshwater snail, *Semisulcospira libertina*, in Japan. *Parasitology International* 54: 55-7.
- Yamaguti S (1975) A synoptical review of life histories of digenetic Trematodes of vertebrates. Keigaku Publishing, Kyoto.

On the invalidity of *Halitherium schinzii* Kaup, 1838 (Mammalia, Sirenia), with comments on systematic consequences

Manja Voss¹

¹ Museum für Naturkunde - Leibniz Institute for Evolution and Biodiversity Science, Invalidenstraße 43, 10115 Berlin, Germany

Corresponding author: Manja Voss (manja.voss@mfn-berlin.de)

Abstract

Received 25 February 2014

Accepted 4 March 2014

Published 28 March 2014

Academic editor:

Matthias Glaubrecht

Key Words

Holotype

early Oligocene

taxonomy

nomenclature

nomen dubium

paraphyly

The holotype of the sirenian species *Halitherium schinzii* Kaup, 1838 from the Alzey Formation (early Oligocene) of the Mainz Basin, western Germany, is reviewed in detail and revised. It is concluded that the type specimen, an isolated premolar, is non-diagnostic, because it reveals no characters of taxonomic value. Therefore, the taxon name *H. schinzii* is regarded as a *nomen dubium*, thus cannot be applied to any currently proposed sirenian species. The name of the genus “*Halitherium*”, which is based on the type species “*H. schinzii*”, cannot be applied to other species previously assigned to congeneric taxa. Consequently, taxonomic and systematic re-assessment is required. Due to the fact that “*Halitherium*” is the taxonomical basis of the Halitheriinae, conclusions are drawn on the inappropriateness of this subfamily.

Introduction

The genus *Halitherium* includes a number of fossil sirenian species, or sea cows, ranging from the late Eocene to early Miocene. Its type species *H. schinzii* Kaup, 1838 is considered as a widespread Central European taxon that inhabited the early Oligocene coastal waters, especially from Germany (e.g., Voss 2008). The morphological basis for the establishment of this species is a single premolar from the Mainz Basin in western Germany (Kaup 1838; Domning 1996). This premolar forms the focus of the present paper as a first step into a revision of the *Halitherium*-species complex.

Historical Review

In 1834, Kaup and Scholl mentioned a not otherwise specified tooth of an extinct sea cow from the early Oligocene of Germany near Flonheim (Mainz Basin; Fig. 1) as *Pugmeodon schinzii*. As Domning (1996) already recognised, both, the genus and species name, have to be considered

as *nomina nuda*, because Kaup and Scholl (1834) neither provided a description nor a figure of the respective tooth. However, a description and figure of another premolar (HLMD-WT Az 48) under the same species name was given by Kaup (1838), who subsequently transferred it to the genus *Halitherium*, which seemingly is the correct generic name for the species as indicated by later studies (e.g., Kaup 1855; Lepsius 1882; Sickenberg 1934).

Therefore, Domning (1987) opened the nomenclatural case no. 2569 to apply for a proper designation of the holotype of *Pugmeodon schinzii*. By Opinion 1535 of the Bulletin of Zoological Nomenclature Volume 46 (ICZN 1999), all previous designations of type species for the nominal genus *Halitherium* Kaup, 1838 are set aside and *Pugmeodon schinzii* Kaup, 1838 is designated as type species under the plenary powers. Furthermore, the names “*Halitherium*” and “*schinzii*” are ruled to be placed on the official lists and indexes of names and works in Zoology by the International Commission on Zoological Nomenclature (2001).

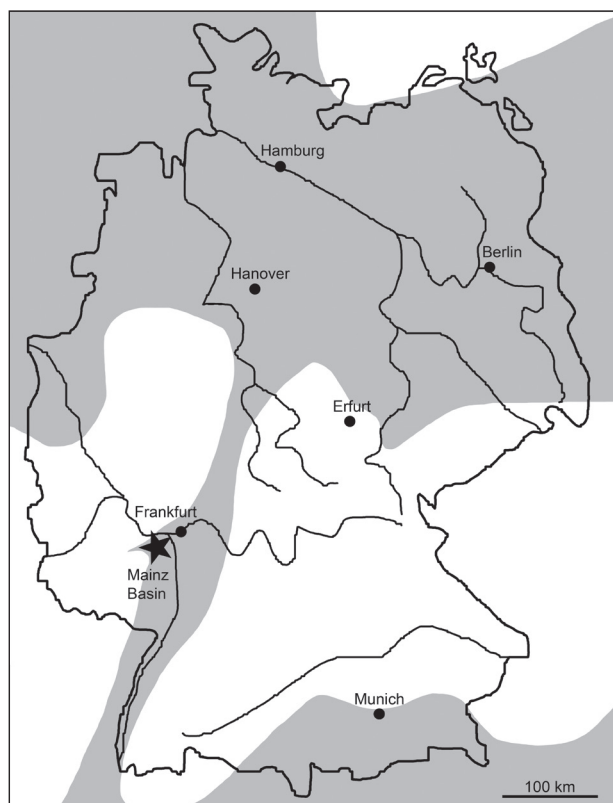


Figure 1. Geographic setting and palaeogeography of the Mainz Basin (black star) in western Germany during the early Oligocene (~ 32 Ma). White areas indicate land, grey areas represent marine conditions (modified after Probst 1986).

In the subsequent decades, early Oligocene sirenian finds from the Mainz Basin comprising cranial and post-cranial elements, and occasionally partial skeletons with nearly complete skulls and mandibles, were generally assigned to *H. schinzii*. Thus, this taxon has become firmly established in the literature as the only sea cow species that had evolved in this specific region to that time (e.g., Krauss 1858; Barthel 1962; Bahlo and Tobien 1982). Apart from its type locality, *H. schinzii* is also known from the Lower Rhine area in western Germany (Voss 2008) and from the Bay of Leipzig in eastern Germany (Fischer and Krumbiegel 1982). Sirenian finds from the Paris Basin (Bizzarini 1995; Bizzarini and Reggiani 2010), the Antwerp and East Flanders Provinces in North Belgium (Sickenberg 1934), Switzerland (Pilleri 1987) and Hungary (pers. obs.) that are referred to *H. schinzii* indicate the widespread distribution of this taxon in Central Europe.

However, considerable intraspecific morphological variations have been postulated for *H. schinzii* since the middle of the 19th century (e.g., Kaup 1855; Lepsius 1882; Sickenberg 1934; Fischer and Krumbiegel 1982). Attempted revisions of *H. schinzii* consequently resulted in the description of numerous specimens forming the basis of new species, as are, respectively, the skull roofs of *H. kaupi* and *H. bronni* (for both taxa see Krauss 1858). However, those are considered to be not valid and synonymous with *H. schinzii* by Domning (1996). Hartlaub (1886) described another species, *Manatherium delheidi*,

based on cranial remains from the lower Oligocene of Antwerp (North Belgium) in comparison with *H. schinzii* from the Mainz Basin (Germany). However, Sickenberg (1934) revised Hartlaub's (1886) species, focussing on aspects of juvenile stages and intraspecific variability. Sickenberg (1934), who already mentioned that a revision of *Halitherium* and *H. schinzii* was necessary, provided a comprehensive and critical review of the Belgian material, but without considering a separation on species level. According to his investigations, all known Belgian records belong exclusively to smaller animals. Therefore, Sickenberg (1934: 271) defined separate morphological groups, "*forma typica*" for the German and "*forma delheidi*" for the Belgian one, and assigned both to *H. schinzii* (see also Domning 1996). The most recent new combination for *H. schinzii* refers to skeletal material from the lower Oligocene of France known as *H. schinzii lareolensis* (Pilleri 1987; Domning 1996).

This review documents that the attempts of different authors to identify morphological distinctions on species level remain ambiguous until today. The debate on splitting and lumping of species currently referred to *H. schinzii* was recently revived by Voss (2012). This author stated that morphological variations within German and Belgian early Oligocene Sirenia might be related to the species level and postulated the presence of an additional species.

The hypothesis of two morphospecies necessitates the examination of the holotype of *H. schinzii* as a target for a revision of this type species. However, the preservation and nature of the holotype material pose major problems. Voss (2010) already postulated that no significant taxonomic definition for *H. schinzii* can be deduced from the premolar HLMD-WT Az 48 and, consequently, this species and the thereon based genus lack a diagnosis.

The present paper aims to clarify this issue by elucidating the morphology and taxonomic value of the premolar and provides perspectives for new taxonomic and systematic approaches.

Abbreviations

BSPG – Bayerische Staatssammlung für Paläontologie und Geologie München (Germany); HLMD – Hessisches Landesmuseum Darmstadt (Germany); M3 – upper molar 3; P2–4 – upper premolar 2–4.

The holotype and validity of *Halitherium schinzii*

Holotype. Premolar HLMD-WT Az 48.

Type horizon and locality. Alzey Formation of the Selztal Group (lower Oligocene) from Flonheim in the Mainz Basin, western Germany.

Description. The tooth (Fig. 2) represents a premolar. However, its exact position within the tooth arcade cannot be certainly determined due to incomplete preservation and

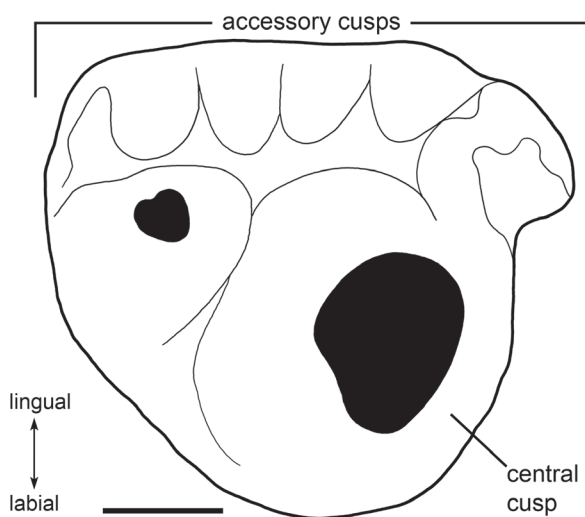


Figure 2. Isolated premolar and holotype specimen of *Halitherium schinzii* HLMD-WT Az 48 in occlusal view. Scale bar equals 0.25 cm.

wear. A single root was present, but is no more preserved. The crown measures 11 mm in maximum diameters with the lingual side being broader mesiodistally than the labial one. Though worn, the central cusp shows a smooth and convex side facing labially. Lingually, five accessory cusps are present. A further, medium sized cusp being also in wear is present mesially or distally depending on the side and locus the premolar inhabits within the jaw. The overall shape of the crown resembles a clenched fist, which tempted Kaup (1838: 319) to introduce for this specimen the new genus *Pugmeodon* (“Faustzahn”), which he transferred into *Halitherium* (Kaup 1838: 536) in the same volume.

Remarks. As it can be inferred from the description above, the taxonomic value of the holotype of *H. schinzii* is doubtful and its assignment to a certain species remains ambiguous. This is additionally corroborated by comparative morphological investigations with species lumped under the genus *Halitherium*.

Compared to *Halitherium taulannense* (Sagne 2001), known by upper and lower premolars, and the *H. schinzii* specimen BSPG 1956 I 540 (see also Barthel 1962), comprising the right P2 and left P3–P4, HLMD-WT Az 48 most likely represents an upper posterior premolar. Using the preserved teeth of both species as reference points, HLMD-WT Az 48 could have occupied either the third or the fourth locus based on its complex cusp pattern. However, a clear assignment of HLMD-WT Az 48 to P3 or P4 of BSPG 1956 I 540 or any upper premolars observable in *H. taulannense* is not possible. On the one hand, this is related to the high degree of wear that precludes comparisons of this tooth with a number of nearly unworn premolars of *H. taulannense* (Sagne 2001), for example. On the other hand, the special crown morphology of HLMD-WT Az 48 described above is considered to hamper a proper identification. The specific arrangement of cusps is found neither in isolated nor associated premolars even of a comparable degree of wear of any known sirenian species.

Apart from BSPG 1956 I 540, complete series of upper premolars are not known in specimens hitherto assigned to *H. schinzii* making further comparative studies difficult. Additionally, other fossil sirenian taxa like *H. cristolii* (Spillmann 1959) have no premolars preserved and only reveal the root alveoli in the bone. Thus, it remains unresolved whether HLMD-WT Az 48 belongs to the left or the right quadrant of the jaw and the identification of its exact position within the tooth arcade is still an open question.

In conclusion, the relation of premolar HLMD-WT Az 48 to the nominal species *H. schinzii* is doubtful or at least cannot be established, because this tooth does not yield any significant characters to diagnose both, the genus and the species. Consequently, the name “*H. schinzii*” is considered a *nomen dubium* as is the genus “*Halitherium*” since “*H. schinzii*” is the type species of that genus. Both terms can be applied to the premolar specimen only and are therefore rejected for further nomenclatural purposes.

Following the principle of priority, article 23.3.5 (ICZN 1999) states that an invalid taxon name must be replaced by the oldest available junior synonym. In this case, three nominal synonyms exist, which however are each considered as inappropriate replacement for “*Halitherium*” due to their poor material basis, uncertain taxonomic assignment and juvenile status or a combination of these factors.

The oldest genus is *Trachitherium* (Gervais 1849; Domning 1996) and is based on a single, isolated lower M3. According to Domning (1988) and Domning and Pervesler (2001) sirenian molars are often characterised by a high degree of intraspecific variation. Beside the fact that this tooth represents the only known specimen, it is therefore emphasised here that the establishment of a new sirenian genus on a molar alone is not sufficient.

The next older genus *Crassitherium* (Van Beneden 1871; Sickenberg 1934; Domning 1996) was established on the basis of a skull fragment and eight vertebrae. While the vertebrae are clearly identified as belonging to a sirenian, there are serious doubts on the taxonomic assignment of the skull fragment, which might be referable to a reptile (Sickenberg 1934: 207). This is also supported by personal investigations of the material in question hence *Crassitherium* is not considered as a useful or valid replacement name.

The third genus *Manatherium* (Hartlaub 1886; Domning 1996) is based on skull fragments of a juvenile. On the basis of personal investigations these fragments are identified as belonging to the frontal, the sphenoid and the right maxilla. Beside the juvenile status of this specimen that already tempted Sickenberg (1934) to declare this genus to be invalid, the preserved material is not considered to reveal diagnostic features for a reliable taxonomic assignment on the species level.

Article 23.3.5 (ICZN 1999) also states that if the rejected name has no valid synonym a new substitute name must be established in its place. Therefore, all taxa originally assigned to “*Halitherium*” require a new designation. A taxonomic and systematic revision of the “*Ha-*

litherium”-species complex is in progress to be published and beyond the scope of the present paper.

It is refrained here to designate a neotype, because the conditions specified in article 75.3 (ICZN 1999) do not apply. Most importantly, the name-bearing type specimen of “*H. schinzii*” is neither lost nor destroyed, but still extant and represented by the premolar HLMD-WT Az 48. Additionally, there has never been designated a paratype or paralectotype, which could be chosen as neotype according to recommendation 75A (ICZN 1999). The choice of a neotype originating from the type locality or even the same geological horizon is difficult for several reasons. An obvious potential neotype could be an incomplete skull cap representing the holotype and only specimen of “*Halitherium*” *kaupi* (Krauss 1858), which was assigned as junior synonym of “*H. schinzii*” by Domning (1996). Presenting mainly indistinctive features, which are typical for a juvenile, this specimen is just fragmentarily preserved including only the supraoccipital and parietal in addition to remnants of the frontal. This incompleteness and poor preservation, but mainly the juvenile status prevents a designation of this specimen as a neotype with sufficient diagnostic characters distinguishing this taxon from other sirenian genera. Another reason for the difficulty finding a neotype is the hypothesis by Voss (2012) that a second sirenian species, viz. “*H. bronni*”, might have been present in the early Oligocene of Germany, and therefore the respective type specimen is also not an available choice. Due to the presumed presence of two sympatric species, suitable material deriving from a host species for the potential neotype is not determinable unambiguously. Therefore, the replacement of an unidentifiable name-bearing type by a neotype (article 75.5; ICZN 1999), which would be possible considering “*H. schinzii*” as a *nomen dubium*, is not performed.

Discussion

Present systematic framework

The hitherto only cladistic approach with the attempt to consider the entire order Sirenia is represented by Domning’s phylogeny published in 1994. Domning’s (1994, 1996) suprageneric classification maintains the traditional taxonomic concept of Simpson (1945). Accordingly, four sirenian families are distinguished (Fig. 3): the Prorastomidae Cope, 1889, the Protosirenidae Sickenberg, 1934, the Dugongidae Gray, 1821 (including the three subfamilies Halitheriinae, Hydrodamalinae and Dugonginae) and the Trichechidae Gill, 1872 (1821) (comprising the two subfamilies Miosireninae and Trichechinae).

The Prorastomidae and Protosirenidae, both representing semiaquatic quadrupeds, are confined to the Eocene and considered paraphyletic (Domning 1994; 2001a, b). The Dugongidae and Trichechidae represent fully aquatic animals and also include the few extant members belonging to the genera *Dugong* and *Trichechus* (Domning 2001a). According to Domning (1994), trichechids are

monophyletic and nested within the Dugongidae. Consequently, the Dugongidae are paraphyletic. Within dugongids only two monophyletic groups are distinguished, the Dugonginae and Hydrodamalinae (Fig. 3). The most diverse dugongid subfamily and largest group within sirenians at all is represented by the Halitheriinae comprising the genera *Caribosiren* Reinhart, 1959, *Eosiren* Andrews, 1902, *Eotheroides* Palmer, 1899, *Halitherium* Kaup, 1838, *Metaxytherium* De Christol, 1840, and *Prototherium* De Zigno, 1887. However, this exclusively extinct group is paraphyletic indicating that higher-level phylogeny and systematics of the whole order Sirenia is paraphyly-based. Moreover, Domning’s phylogenetic analysis (1994) points out that “halitheriines” itself mainly comprise genera that are invariably paraphyletic and in addition the type genus of this subfamily, “*Halitherium*”, is also not monophyletic (Fig. 3).

Domning (1994: 187) stated that his phylogenetic analysis is a preliminary work and in need of systematic revisions in many parts. Nevertheless, the traditional classification concept of four sirenian families is unrevised subject of systematic studies up to now (e.g., Velez-Juarbe et al. 2012). This causes many systematic problems due to missing diagnoses and hampers a reliable taxonomic assignment of new sirenian finds. According to Domning (1994), the most controversial groups refer to the Eocene dugongids and Eocene sirenian taxa in general, the incompletely resolved clade of the dugongines and the inter- and intrageneric relationships of *Metaxytherium*. The need of revision of these groups is beyond doubt. Additionally, the present study emphasises that the “Halitheriinae”, comprising amongst others the Eocene dugongids and the genus *Metaxytherium*, constitute one of the most questionable sirenian groups, which is the focus of the following discussion.

The invalidity of *Halitherium* and its effects on sirenian systematics

According to article 11.7.1.1 (ICZN 1999) a family or subfamily, respectively, should be based on a valid genus. However, as outlined above this does not apply here, because the genus “*Halitherium*” is considered a *nomen dubium* and therefore is rejected. Since the “Halitheriinae” comprise a number of genera this problem could be solved by the designation of a new type genus. This taxonomic practise would be reasonable if the group in question represents a clade. However, the subfamily “Halitheriinae” has never been shown to form a monophyletic group in phylogenetic analyses considering Sirenia as a whole (Domning 1994; Fig. 3) as well as on subsets of the order (e.g., Bajpai and Domning 1997; Domning and Pervesler 2001; Domning and Aguilera 2008; Velez-Juarbe et al. 2012). Doubts on the “halitheriine” monophyly are reinforced by the most up to date phylogenetic analysis on Sirenia recently performed by Voss (2013) in her doctoral thesis, which will be published at a later date.

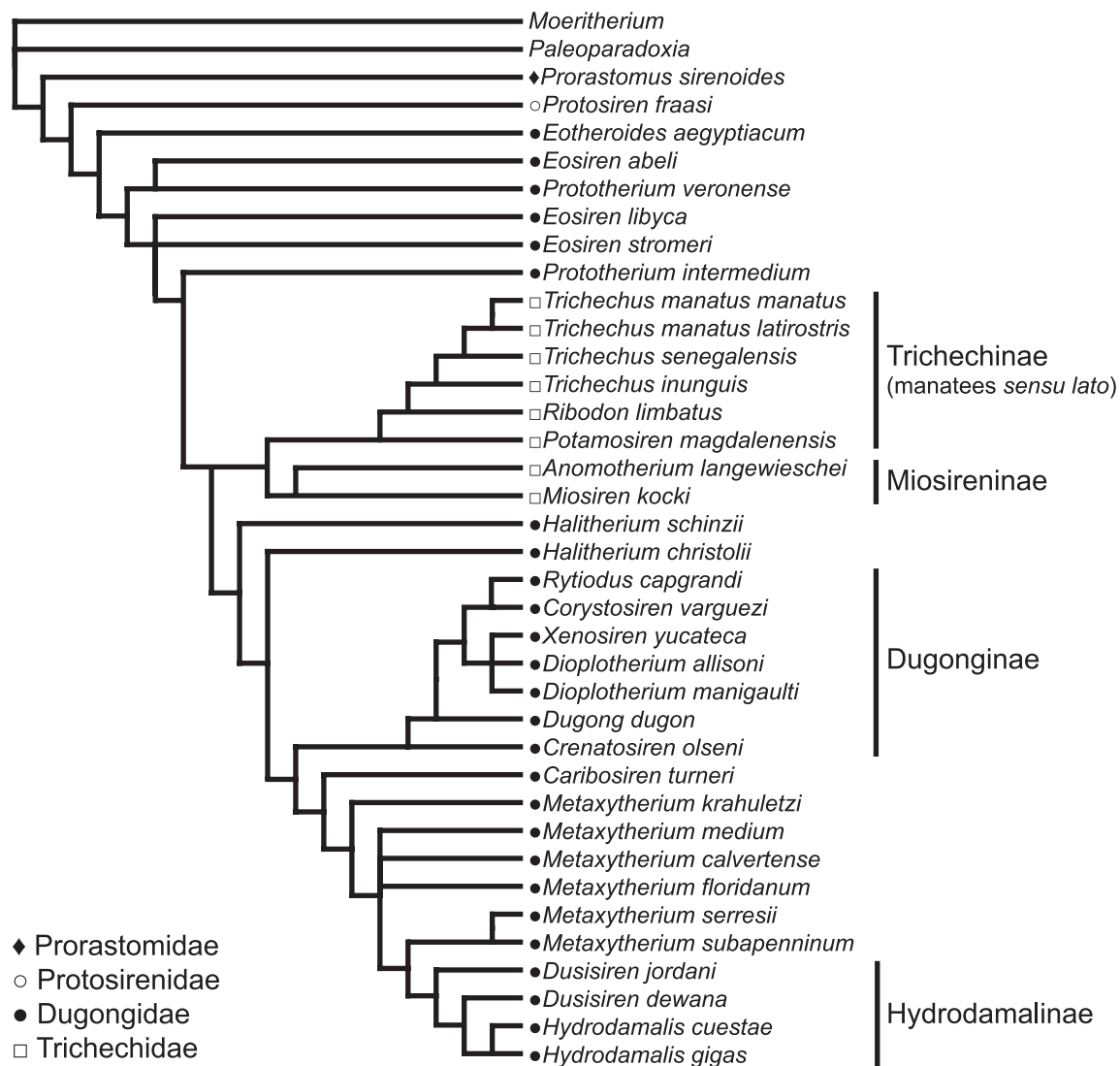


Figure 3. Phylogeny of the Sirenia including 36 species and subspecies based on 62 informative cranial and dental characters (modified after Domning 1994). TL = 162, CI = 0.76, RI = 0.91.

In fact, Simpson (1945) and Domning (1996) demonstrate that the “Halitheriinae” rather represent a historically grown assemblage of taxa characterised by morphological features that neither substantiate a monophyletic grouping nor distinguish it from other subfamilies. The latter is amongst others corroborated by the overlap of characters such as “cheek teeth enamelled, closed roots” that were provided by Simpson (1932: 423–424) to define the “Halitheriinae”, Miosireninae and Rytiodontinae. Consequently, the designation of a new type genus is not possible.

Likewise, the type genus “*Halitherium*” is traditionally considered to be monophyletic, because this has never been substantiated with sufficient evidence from any phylogenetic analysis up to now. The “*Halitherium*”-species complex regarded as valid within the European Palaeogene includes “*H. schinzii*” Kaup, 1838 (early Oligocene of Europe), “*H. cristolii*” Fitzinger, 1842 (late Oligocene of Upper Austria) and “*H. taulannense*” Sagne, 2001 (late Eocene of France). As indicated above, none of these taxa form a clade. Instead, each species represents individual

branches in phylogenetic studies (e.g., Domning 1994; Domning and Aguilera 2008).

This paraphyly of “*Halitherium*” is the main reason for the conclusion drawn herein to question the current use of the subfamily “Halitheriinae”. Based on the fact that “*Halitherium*” is the type genus of the “Halitheriinae”, this subfamily is to be reduced to a single species, the type species “*H. schinzii*”, when all hitherto known phylogenies (e.g., Domning 1994; Domning and Aguilera 2008) are considered. Even if a new substitute name would be established for the genus “*Halitherium*” and the respective taxa of the former “*Halitherium*”-species complex receive a new designation, the taxonomic content of this subfamily will still comprise a single species. Therefore, the use of the “Halitheriinae” is not considered essential, because it does not contribute to a better understanding of sirenian diversity, but would rather lead to confusion. Instead, the rejection of the “Halitheriinae” is considered as a target-oriented solution into a more rigid taxonomic framework.

Conclusions

In the course of the revision of the genus “*Halitherium*”, it is concluded that the premolar holotype of the type species “*H. schinzi*” neither can be clearly identified nor is assignable to a certain species or genus, and therefore it is non-diagnostic. Accordingly, these taxonomic terms are considered as *nomina dubia*. A neotype for “*H. schinzi*” is not designated here due, among other things, to the fact that the presence of two sympatric species in the German early Oligocene is hypothesised (Voss 2012), which makes it difficult to unambiguously define a suitable neotype. As a further consequence, the extinct subfamily “Halitheriinae” is refuted here. On the one hand, this is substantiated by the status of the type genus “*Halitherium*” as *nomen dubium* and, on the other hand, by the paraphyly of “halitheriines” and “*Halitherium*”. Considering all previous phylogenies, especially the order-based analysis by Domning (1994), this subfamily consequently includes a single species only, viz. “*H. schinzi*”. This situation would remain unchanged even though a substitute name would be erected for “*Halitherium*” and “*H. schinzi*”, respectively. Therefore, the use of the “Halitheriinae” is not considered practicable in this study.

As there have been made very few changes to the traditional paraphyly-based classification (see Domning 1994), a first step towards a revised taxonomic concept for the entire sirenian order is suggested here by rejecting the subfamily “Halitheriinae”. Following this recommendation, not only one of the main sources of sirenian paraphyla is resolved, but also new approaches are provided to interpret the taxa originally lumped in this category.

Acknowledgements

I would like to thank Oliver Hampe (Berlin) for supporting this project. Gabriele Gruber, Norbert Micklich, Eric Milsom and Oliver Sandrock (Darmstadt) are acknowledged for their assistance during my visit to the Hessisches Landesmuseum Darmstadt. Additionally, I am grateful to S. Klug (Bristol), who kindly provided assistance in checking the spelling and grammar, and to Michael Ohl and Matthias Glaubrecht for helpful comments on the manuscript.

References

Andrews CW (1902) Preliminary note on some recently discovered extinct vertebrates from Egypt. Part III. Geological Magazine 9: 291–295. doi: 10.1017/S0016756800181178

Bahlo E, Tobien H (1982) Bestandsaufnahme der Säugetiere im “prä-aquitane” Tertiär des Mainzer Beckens. Mainzer geowissenschaftliche Mitteilungen 10: 131–137.

Bajpai S, Domning DP (1997) A new dugongine sirenian from the early Miocene of India. Journal of Vertebrate Paleontology 17: 219–228. doi: 10.1080/02724634.1997.10010965

Barthel W (1962) Über ein neues montiertes Skelett von *Halitherium schinzi* Kaup (Sirenia). Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie 2: 65–68.

Bizzarini F (1995) Osservazioni sull’*Halitherium schinzi* Kaup, 1838 (Sirenia, Mammalia) conservato presso il Museo Civico di Storia Naturale di Venezia. Bollettino del Museo Civico di Storia Naturale di Venezia 44: 163–171.

Bizzarini F, Reggiani P (2010) *Halitherium schinzi* nel nuovo allestimento del Museo di Storia Naturale di Venezia. Bollettino del Museo Civico di Storia Naturale di Venezia 61: 131–137.

Cope ED (1889) Synopsis of the families of Vertebrata. American Naturalist 23: 849–877. doi: 10.1086/275018

De Christol J (1840) Recherches sur divers ossements fossiles attribués par Cuvier à deux phoques, au lamantin, et à deux espèces d’hippopotames, et rapportés au *Metaxytherium*, nouveau genre de cétacé de la famille des dugongs. L’Institut annaires 8: 322–323.

De Zigno A (1887) Quelques observations sur les siréniens fossiles. Bulletin de la Société Géologique de France 15: 728–732.

Domning DP (1987) *Halianassa studeri* von Meyer, 1838 (Mammalia, Sirenia): proposed designation of a neotype and proposed conservation of *Halitherium* Kaup, 1838 by designation of a type species. The Bulletin of Zoological Nomenclature 44: 122–125.

Domning DP (1988) Fossil Sirenia of the West Atlantic and Caribbean region I. *Metaxytherium floridanum* Hay, 1922. Journal of Vertebrate Paleontology 8: 395–426. doi: 10.1080/02724634.1988.10011728

Domning DP (1994) A phylogenetic analysis of the Sirenia. In: Berta A, Deméré T (Eds) Contributions in marine mammal paleontology honoring Frank C. Whitmore Jr. Proceedings of the San Diego Society of Natural History 29: 177–189.

Domning DP (1996) Bibliography and Index of the Sirenia and Desmostylia. Smithsonian Contributions to Paleobiology 80: 1–611.

Domning DP (2001a) Evolution of the Sirenia and Desmostylia. In: Mazin JM, Buffrénil V de (Eds) Secondary adaptation of tetrapods to life in water. Proceedings of the international meeting Poitiers 1996. Verlag Dr. Friedrich Pfeil, Munich, 151–168.

Domning DP (2001b) The earliest known fully quadrupedal sirenian. Nature 413: 625–627. doi: 10.1038/35098072

Domning DP, Aguilera OA (2008) Fossil Sirenia of the West Atlantic and Caribbean Region. VIII. *Nanosiren garciae*, gen. et sp. nov. and *Nanosiren sanchezi*, sp. nov. Journal of Vertebrate Paleontology 28: 479–500. doi: 10.1671/0272-4634(2008)28[479:FSOTWA]2.0.CO;2

Domning DP, Pervesler P (2001) The Osteology and Relationship of *Metaxytherium krahuletzii* Depéret, 1895 (Mammalia: Sirenia). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft Frankfurt am Main 553: 1–89.

Fischer K, Krumbiegel G (1982) *Halitherium schinzi* Kaup, 1838 (Sirenia, Mammalia) aus dem marinen Mitteloligozän des Weißelsterbeckens (Bezirk Leipzig, DDR). Hallesches Jahrbuch für Geowissenschaften 7: 73–95.

Fitzinger LJ (1842) Bericht über die in den Sandlagern von Linz aufgefundenen fossilen Reste eines urweltlichen Säugers (*Halitherium cristolii*). Bericht über das Museum Francisco-Carolinum Linz 6: 61–72.

Gervais FLP (1849) Sur la repartition des mammifères fossils entre les différents Stages tertiaires qui concourent à former le sol de la France. Académie des Sciences et Lettres de Montpellier. Mémoires de la Section des Sciences 1: 203–219.

- Gill T (1872) Arrangement of the families of mammals. Smithsonian Miscellaneous Collections 230: 1–98.
- Gray JE (1821) On the natural arrangement of vertebrate animals. London Medical Repository 15: 296–310.
- Hartlaub C (1886) Ueber *Manatherium delheidi*, eine Sirene aus dem Oligocän Belgiens. Zoologische Jahrbücher 1: 369–378.
- International Commission on Zoological Nomenclature (ICZN) (1989) Opinion 1535. *Halianassa studeri* von Meyer, 1838 (Mammalia, Sirenia): neotype designated; and *Halitherium* Kaup, 1838 (Mammalia, Sirenia): *Pugmeodon schinzii* Kaup, 1838 designated as the type species. The Bulletin of Zoological Nomenclature 46: 83–84.
- International Commission on Zoological Nomenclature (ICZN) (2001) Official lists and indexes of names and works in zoology. Supplement 1986–2000. The International Trust for Zoological Nomenclature. The Natural History Museum, London.
- International Commission on Zoological Nomenclature (ICZN) (1999) International code of Zoological Nomenclature. Fourth edition. The International Trust for Zoological Nomenclature, The Natural History Museum, London.
- Kaup JJ (1838) *Halitherium* und *Pugmeodon* im Maynzer Becken. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 1838: 318–320.
- Kaup JJ (1855) Beiträge zur näheren Kenntnis der urweltlichen Säugethiere. Zweites Heft. Leske, Darmstadt.
- Kaup JJ, Scholl JB (1834) Verzeichnis der Gypsabgüsse von den ausgezeichnetsten urweltlichen Thierresten des Grossherzoglichen Museum zu Darmstadt. Diehl, Darmstadt.
- Krauss CFF (1858) Beiträge zur Kenntnis des Schädel-Baues von *Halitherium*. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 1858: 519–531.
- Lepsius GR (1882) *Halitherium Schinzi*, die fossile Sirene des Mainzer Beckens. I. Band. Abhandlungen des Mittelrheinischen geologischen Vereins, Darmstadt.
- Palmer TS (1899) [Review of Dr. E. L. Trouessart's Catalogus Mammalium tam viventium quam fossilium]. Science 10: 491–495. doi: 10.1126/science.10.249.491
- Pilleri G (1987) The Sirenia of the Swiss Molasse. With a descriptive catalogue of the fossil Sirenia preserved in Swiss collections. Brain Anatomy Institute, Ostermundigen, Bern.
- Probst E (1986) Deutschland in der Urzeit. Von der Entstehung des Lebens bis zum Ende der Eiszeit. C. Bertelsmann Verlag, Munich.
- Reinhart RH (1959) A review of the Sirenia and Desmostylia. University of California Publications in Geological Sciences 36: 1–146.
- Sagne C (2001) *Halitherium taulanense*, nouveau sirénien (Sirenia, Mammalia) de l'Éocène supérieur provenant du domaine Nord-Téthysien (Alpes-de-Haute-Provence, France). Comptes rendus de l'Académie des Sciences de la Terre et des Planètes 333: 471–476.
- Sickenberg O (1934) Beiträge zur Kenntnis Tertiärer Sirenen. I. Die Eozänen Sirenen des Mittelmeergebietes. II. Die Sirenen des Belgischen Tertiärs. Mémoires du Musée Royal d'Histoire Naturelle de Belgique 63: 1–352.
- Simpson GG (1932) Fossil Sirenia of Florida and the evolution of the Sirenia. Bulletin of the American Museum of Natural History 59: 419–503.
- Simpson GG (1945) The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History 85: 1–350.
- Spillmann F (1959) Die Sirenen aus dem Oligozän des Linzer Beckens (Oberösterreich) mit Ausführungen über “Osteosklerose” und “Pachyostose”. Denkschriften der mathematisch-naturwissenschaftlichen Klasse der Österreichischen Akademie der Wissenschaften 110: 1–68.
- Van Beneden PJ (1871) Un sirénien nouveau du terrain rupélien. Bulletins de l'Académie Royale des Sciences de Belgique (2) 32(9/10): 164–178.
- Velez-Juarbe J, Domning DP, Pyenson ND (2012) Iterative Evolution of Sympatric Seacow (Dugongidae, Sirenia) Assemblages during the Past ~26 Million Years. PLoS ONE 7(2): e31294. doi: 10.1371/journal.pone.0031294
- Voss M (2008) New finds of *Halitherium* (Sirenia, Mammalia) from the lower Oligocene of the Rhine area (Germany). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 249: 257–269. doi: 10.1127/0077-7749/2008/0249-0257
- Voss M (2010) Character evolution, homoplasy and interrelationships of Sirenia. Zitteliana B 29: 103.
- Voss M (2012) A new sea cow record from the lower Oligocene of western Germany: new indications on the skeletal morphology of *Halitherium schinzii* (Mammalia: Sirenia). Paläontologische Zeitschrift 86: 205–217. doi: 10.1007/s12542-011-0125-x
- Voss M (2013) Revision of the *Halitherium*-species complex (Mammalia, Sirenia) from the late Eocene to early Miocene of Central Europe and North America. Unpublished Ph.D. thesis, Humboldt-Universität zu Berlin, Germany, 298 pp. <http://edoc.hu-berlin.de/browsing/dissertationen/>

