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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.

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- **Abstract**
- **Introduction**
- **Materials and Methods**
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- **Acknowledgements**
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- **Tables with captions**
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In Focus

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The birth of malacology. When and how?

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Abstract

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 molluscous animals as whole organisms). This process ended in 1825 when the very term “malacology” was finally established by Ducrotay de Blainville.

Key Words

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

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 molluscanous 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”, 1, 6). The first two families correspond approximately to the contemporary taxa, whereas testaceans (Ostracodera) and mollusks (Malakia) are merely two divisions of that large group known today as the phylum Mollusca. Aristotle’s Malakia included mostly cephalopods, while Ostracodera 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 mollusan 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. Linnaeus’ 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 that 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 consideration 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 unenterprising” 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 class 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 class 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-
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 malacozaaires. De Blainville wrote: “A branch of science devoted to this part of zoology [i.e. study of Malacoza] 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 “sudden transformation”. 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 birth 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

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

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Abstract

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 cuspidate, 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 (*Pororchestia luzonensis*) was described by Baker (1915) from the summit of Mt. Maquiling, and in the same paper he described another species (*Pororchestia lagunae*) from the freshwater lake of central Luzon (Bay Lake), Philippines. Still in the early 20th century, another high altitude landhopper species *Pororchestia 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 anomal* (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 Muizium Zoologi with the prefix UKMMZ for museum numbers.

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 samroiyodensis* sp. n.

http://zoobank.org/B4E6BF5F4-A905-47D2-A2E7-9D048913A121

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

(Figures 2-10)

**Type material.** Holotype, female, 10.6 mm, PSU-ZC-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 ⅓ 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 1](image1.png)

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

![Figure 2](image2.png)

Figure 2. Live *Floresorchestia samroiyodensis* 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 dactyls. 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 in 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 anteroproximal 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; subchela- tion strong, dactylus not exceeding palm and slightly obtuse.

Gnathopod 2 of male strongly subchelate, larger than 1; basis, anterior margin smooth, widened distally; ischi- um lobed anteriorly; merus subequal in length with ischi- um; 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 sub- quadrate 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, anteroproxi- mal 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 pos- terior lobe; basis oval; ischium shortest, posteroproximal margin notched; merus shorter to carpus in length, an- terior margin straight, posterior margin slightly convex; carpus both margins parallel; propodus slender; dactylus short.
Figure 3. *Floresorchestia samroiyodensis* 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 samroiyodensis* sp. n., holotype, female, (PSUZC-CR-0275) 10.6 mm. Khao Sam Roi Yod National Park. All scales represent 0.5 mm.
Figure 5. Floresorchestia samroiyodensis sp. n., holotype, female, (PSUZC-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 samroiyodensis* sp. n., holotype, female, (PSUZC-CR-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 samroiyodensis sp. n., allotype, male, (PSUZC-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 samroiyodensis* 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 samroiyodensis* sp. n., allotype, male, (PSUZC-CR-0274) 10.5 mm. Khao Sam Roi Yod National Park. Scales for IMD, rMD and UL represent 0.1 mm; MP and MX1 represent 0.2 mm.
Figure 10. *Floresorchestia samroiyodensis* 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, postero proximal 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, subquadrangle; 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.

Pleon pods well developed, subisimilar 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; maxillipeds 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 samroiyodensis 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.

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Thanks are due to Drs. Jaruwat Nabhitabhata, Pornsilp Pholphunthin and Mr. Kwan Nuicharoen 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 Hongphattharakaree in providing the amphipod photo for this study.

Reference


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**Abstract**

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. millsonii*, 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. millsonii* for Central African populations of these larger arboreal frogs. However, we had neither genetic nor acoustic data from the type locality of *L. millsonii* 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. millsonii* in the future. For populations east of the Cross River, Nigeria, the name *L. guineensis* would be available.

**Key Words**

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

**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.

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Rödel, M.-O. et al.: The taxonomic status of two West African Leptopelis species

(Stohlgren 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 anurans. 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 Tai 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 and DNeasy tissue extraction kits (Qiagen) or High Pure PCR Template Preparation kits (Roche). We used the primers 16S-A-L and 16S-B-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* 4 beta10 (Swofford 2001).

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

<table>
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<th>GenBank #</th>
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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.
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 ± 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 ± 0.22%; N = 36). The intraspecific variation in L. aubryi ranged from 0–2.12% (0.86 ± 0.94%; N = 15). The intraspecific variation in L. spiritusnoctis ranged from 0–0.62% (0.27 ± 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 ± sd: 11.24 ± 0.12%; N = 4). The intraspecific variation in L. macrotis ranged from 0–0.22% (0.11 ± 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.

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 (ZFMB 87708).
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 ± 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.

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<th>Species and call type</th>
<th>CD (ms)</th>
<th>minF (Hz)</th>
<th>maxF (Hz)</th>
<th>FR (Hz)</th>
<th>DF (Hz)</th>
<th>FF (Hz)</th>
<th>sDF (Hz)</th>
<th>eDF (Hz)</th>
<th>CF (Hz)</th>
<th>PC</th>
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<th>Country</th>
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<td>3143.4 ± 835.5</td>
<td>2726.4 ± 2726.4</td>
<td>2786.1 ± 2660.2</td>
<td>425.9 ± 119.8</td>
<td>Ivory Coast</td>
<td>this paper</td>
<td></td>
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<td>(chuck; N= 13)</td>
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<td>46.3</td>
<td>80.5</td>
<td>62.5</td>
<td>156.7</td>
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<tr>
<td><em>aubryi</em></td>
<td>43.0 ± 8.0</td>
<td>1353.0</td>
<td>2019.0</td>
<td>1540.0 ± 2049.0</td>
<td>162.0 ± 225.0</td>
<td>13.0 ± 2.0</td>
<td>Equatorial Guinea</td>
<td>Bosch et al. (2000)</td>
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<tr>
<td>(chuck; N= 4)</td>
<td>8.0</td>
<td>321.0</td>
<td>461.0</td>
<td>321.0</td>
<td>156.7</td>
<td></td>
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<tr>
<td><em>aubryi</em></td>
<td>10.0 ± 2.0</td>
<td>1512.3 ± 238.4</td>
<td>3771.2 ± 2259.1</td>
<td>2984.6 ± 2984.6</td>
<td>3004.2 ± 3009.8</td>
<td>5.6 ± 0.0</td>
<td>Cameroon</td>
<td>this paper</td>
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<td></td>
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<tr>
<td>(chuck; N= 22)</td>
<td>2.0</td>
<td>238.4</td>
<td>292.3</td>
<td>440.8</td>
<td>238.0</td>
<td>249.3</td>
<td>217.2</td>
<td>159.8</td>
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<tr>
<td><em>aubryi</em></td>
<td>35.0</td>
<td>2547.0</td>
<td>3394.0</td>
<td>847.0</td>
<td>2842.0</td>
<td>3015.0</td>
<td>eastern Nigeria</td>
<td>A. Schiøtz</td>
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<td>(chuck; N= 1)</td>
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<td>847.0</td>
<td>2842.0</td>
<td>2842.0</td>
<td></td>
<td>173.0</td>
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<tr>
<td><em>spiritusnoctis</em></td>
<td>334.5 ± 122.5</td>
<td>2525.0 ± 114.0</td>
<td>3297.9 ± 773.0</td>
<td>2996.9 ± 2996.9</td>
<td>2799.5 ± 2998.9</td>
<td>199.4 ± 15.2</td>
<td>Ivory Coast</td>
<td>this paper</td>
<td></td>
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<tr>
<td>(buzz; N= 22)</td>
<td>122.5</td>
<td>114.0</td>
<td>86.5</td>
<td>122.0</td>
<td>26.2</td>
<td>26.2</td>
<td>43.5</td>
<td>27.5</td>
<td>50.6</td>
<td>5.5</td>
<td>3.43</td>
<td>3.49</td>
<td>1.1</td>
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<tr>
<td><em>aubryi</em></td>
<td>51.0 – 105.0</td>
<td>2191.0</td>
<td>3562.0</td>
<td>1370.7</td>
<td>2906.3</td>
<td>2906.3</td>
<td>2719.0</td>
<td>2906.0</td>
<td>187.0</td>
<td>2.33 ± 0.58</td>
<td>3.97 ± 1.38</td>
<td>46.24 ± 2.22</td>
<td>0.03 ± 0.01</td>
<td>Cameroon</td>
<td>this paper</td>
</tr>
<tr>
<td>(buzz; N= 3)</td>
<td>105.0</td>
<td>2191.0</td>
<td>3562.0</td>
<td>1370.7</td>
<td>2906.3</td>
<td></td>
<td></td>
<td>187.0</td>
<td>2.33 ± 0.58</td>
<td>3.97 ± 1.38</td>
<td>46.24 ± 2.22</td>
<td>0.03 ± 0.01</td>
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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).
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 ± 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...
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 the west 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 africana*, *Conraua crassipes*, *Acanthixalus spinosus*, *Afrixalus paradoradalis*; 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. picatus*; Onadeko and Rödel 2009) or even Cameroon (e.g. *Hyperolius concolor*, *H. guttulatus*, *H. fasciventris*, *Phlyctimantis boulengeri*; Schiøtz 1967, 1999). The latter are farnbush 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 Gvodzík 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. spiritusnoctis* 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 Kühler and Frank Glaw provided helpful critique.

**References**


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.

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Link: http://id.pensoft.net/suppl/70de990-b67d-11e3-be98-ba608e0881c

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.

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Link: http://id.pensoft.net/suppl/f233130-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.

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Link: http://id.pensoft.net/suppl/8233130-b67d-11e3-83b8-f99820085417
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

Explaination 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.

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Link: http://id.pensoft.net/suppl/f9b6f090-b67d-11e3-9eb7-1b2703913844
The Primary Types of Scathophagidae (Diptera) in the Museum für Naturkunde Berlin, and Senckenberg Deutsches Entomologisches Institut, Germany

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Abstract

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 nutans Becker, 1894 (Poland); Cochliarium castanipes Becker, 1894 (Switzerland); Cochliarium lasiostoma Becker, 1894 (Switzerland); Cordylura aberrans Becker, 1894 (Sweden); Cordylura bezii Sack, 1937 (Italy); Cordylura biseita 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 picitornis Loew, 1864 (Russia); Cordylura umbrosa Loew, 1873 (Slovakia); Cordylura unicolor Loew, 1864 (Spain); Parallelomma longicornis Hendel, 1913 (Taiwan); Parallelomma media Becker, 1894 (Poland); Pselaphphila 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).

Key Words

Diptera
Scathophagidae
Museum für Naturkunde Berlin
Senckenberg Deutsches Entomologisches Institut
collection

type specimens

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 scaphophagid 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 Zoologicj 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 14180–38339), 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 depositaries of specimens used or discussed in this paper:

- MNHP – Muséum National d’Histoire Naturelle, Paris, France;
- NMW – Naturhistorisches Museum Wien, Vienna, Austria;
- ZMHB — Museum für Naturkunde, Berlin, Germany;
- ZMUH — Zoological Museum, 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”, “Cordylura rufimana Meig det. F. Šifner s.”. 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 *Cordylura* Fallén, 1810, correctly recognised by recent authors.

**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. Orrogyn (1–8.VII.95), am Fl. Orrogyn 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. Ич — р Орогын с Цайдам, го. Робоклоо 1–3 VII 95”, “Gobi. Asien 51896. VII”, “albidihirta Beck.”, “ZMU Berl.”, “Scatophaga albidohirta Beck. SYNTYPE 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.


**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 *Scatophaga milites-tosa* (Holmgren, 1883).

**ZMHB material:** a male syntype (left mid leg missing), labelled “Novaja Semlja, mons Tschernyschew, G. J.

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

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

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


Current name: Gonarcticus arctica (Becker, 1907).

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

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


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

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

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


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.


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

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

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

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ZMHB material: 2 male and 1 female syntypes, all in excellent condition. The male labelled “St. Moritz 5/7 10777” [= 5 July 1886], Coclhiarium 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”, Coclhiarium castanipes Becker PARALECTOTYPE labelled 1954 by J.R. Vockeroth and the female “St. Moritz 30/6 10132”, Coclhiarium castanipes Becker PARALECTOTYPE labelled 1954 by J.R. Vockeroth have been labelled as paralecotypes.

Current name: Gymnomera 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 Zettersted, 1838.

ZMHB material: 3 males and 1 female syntypes. A male (right mid leg missing, right wing slightly torn) labelled “Cord. caudata Zett. Lapp. 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”.


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 Behryng. 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: Scatophaga 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 Zettersted’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.


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: Khabarovsky 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).

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

Described from an unspecified number of the female sex from “Kreuth; Gerstaekert.”. 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 (*Scathophaga*).

Described from 4 male syntypes from “Kantaika und der Insel Nikander” [river Khantyaya: 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.”, “Scathophaga incola Beck. det. Becker”, “Scathophaga incola Becker PARALECOTYPE labelled 1954 by J.R. Vockerth”. It has been labelled by me as a syntype of *Scathophaga 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”.


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

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

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 litoraea* (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 litoraea* (Fallén, 1819), as currently understood.

**lasiostoma** 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 lasiostoma Becker LECTOTYPE Designated by Vockerth 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 lasiostoma Becker PARALECOTYPE labelled 1954 by J.R. Vockerth”, is conspecific with the lectotype and has been labelled as paralectotype.

**Current name**: *Gimmomera lasiostoma* (Becker, 1894).

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

Described from an unspecified number of the female sex taken “Schlesien. 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 Gorokov (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.

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

Described from 2 males “vom Kaukasus aus Lesgia”.

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

media Becker, 1894: 96 (Parallelomma).
Described from an unspecified number of the male sex from “Aus Schlesien, Umgegend von Liegnitz”.
Current name: Parallelomma medium Becker, 1894.

melaleuca Loew, 1873: 245 (Cordylyra).
Described from an unspecified number of females from “Griechenland”. A single specimen is mentioned in the “Catalog General Musei Zoologi Berolinenis” as Cordylyra 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”, “Cordylyra melaleuca Lw.”, “Type”, “Cordylyra 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 Różanka, part of Międzyzdroje, near Kłodzko (Poland)]. It is conspecific with Cordylura ustulata (Zetterstedt, 1838).
Current name: According by Šifner (2008: 151) it is a junior synonym of Nanna armillata (Zetterstedt, 1846).

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).

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

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”.

All other syntypes have been labelled as paralectotypes: 2 males, both in good condition and labelled “Sibiriia Schnabl”, “Coll. H. Loew”, “Scatophaga mollis Becker PARALECTOTYPE labelled 1954 by J.R. Vockeroth”; female (right wing damaged), labelled “Sibiriia 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 Scatophaga Meigen, 1803.

nigriventris Loew, 1864: 19 (Cordylura).
Described from an unspecified number of both sexes from “Sibirien”.

ZMHB material: There is one male, near the box label “naturae Becker”, 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.

nutans Becker, 1894: 120 (Amaurosoma).
Described from an unspecified number of both sexes from “Sibirien”.

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: “Südtirol 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.

nigrifrontata Becker, 1894: 120 (Amaurosoma).
Described from “Ein Pärchen aus Süd-Tirol vom Lusier Pass”.

ZMHB material: 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: “Südtirol 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).
obscurinervis Becker, 1900: 55 (Scathophaga).

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. Sahlh.”, “Ins. Nikandr.”, “42482”, “obscurinervis Beck.”, “Scathophaga obscurnervis Becker PARALECTOTYPE labelled 1954 by J.R. Vockeroth”. It has been labelled as a syntype.

Current name: Scathophaga obscurnervis (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 Designed 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 synonymised 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 Designed by J.R. Vockeroth 19”, “Scoppeuma 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 taeoniopa Rond. det. 1962 J.R. Vockeroth”, and has been labelled as paralectotype; Vockeroth’s determination is correct.

Current name: A junior synonym of Scathophaga taeoniopa (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”.


Current name: A junior synonym of Parallelomma vitattum (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 picticor- nis m.”, “Type”, “Cordylura picticornis Lw. LECTOTYPE Designed by J.R. Vockeroth 19” and provided with a small black label. Type-locality: “Sibirien” (Russia).

Current name: Cordilura 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“.


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. praecc.”, “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.


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-Semljja. 5. Aug. 1896”. 3 syntypes (Ozerov and Krivosheina 2013: 146).


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

socialis Becker, 1894: 90 (Cordylura).

Described from an unspecified number of both sexes [“C. pudica. Zett. Dpt. Sc. V. 1998, 3 [“Sucia meridionali... in Scania... ad Hafniam” (Sweden, Denmark)]; Rond., Prodr. VII, 14, 4.[ «unicem 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 Cordylura, 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 Chuguyeva, 44.05 N, 134.12 E 650 m, Malaisefalle 31.V.–03.VI.1993 leg. C. Lange & J. Ziegler”. Type-locality: 30 km SE Chuguyeva (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 Seitenstein [Austria]”, “8/5 88”, “tinctinervis Beck”, “Conios sternum 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 Borelinensis” as Cordylura umbrosa (No 11398). It has been studied, labelled and is herewith designated as lectotype.


Current name: A junior synonym of Cordylura 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 Borelinensis” as
Cordylura unicolor (No 11373). It has been studied, labelled and is herewith designated as lectotype.


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).


Current name: Norellisoma vockerothi Ozerov, 2013.

ziegleri Ozerov, 1999: 510 (Langechristia).

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

SDEI material: holotype male (Ozerov 1999: 510, original designation), in very good condition, labelled “RUSSIA: Khabarovskiy Krai Boitsovo 20 km N Bikin Bolsoi Solntsepyok Hill 47.02N 134.21E 250 m, Malaisefalle, 24–27.V.1993 leg. C. Lange & J. Ziegler”. Type-locality: Boitsovo 47.02N 134.21E (Russia, Khabarovskiy Krai), 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
Gimmnera castanipes (Becker, 1894)
Gimmmera lasiofora (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)
imuta Becker, 1894
Nanna inermis (Becker, 1894)
Nanna loewi (Becker, 1894)
Nanna tiibialis (Zetterstedt, 1838)
nigrifrontata Becker, 1894, syn. n.
nutans Becker, 1894
Norellia tipulata (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 dasyspota (Loew, 1864)
Parallelomma media Becker, 1894
Parallelomma vittatum (Meigen, 1826)
paridis Hering, 1923
Pogonota sahlbergi (Becker, 1900)
Scathophaga alata (Becker, 1914)
Scathophaga albidohirta (Becker, 1894)
Scathophaga dasythrix (Becker, 1894)
Scathophaga incola (Becker, 1900)
Scathophaga litorea (Fallén, 1819)
 islandica Becker, 1894
Scathophaga mollis (Becker, 1894)
Scathophaga multiseta (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

zse.pensoft.net
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Historical aspects of meetings, publication series, and digital resources dedicated to echinoderms

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Abstract

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.

Key Words

Echinodermata
history
publication
website
photographs

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

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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 represented 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 entirely 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

“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 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/pr9uzrpm).

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...
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.


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...
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 Embryology* 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 Echinoderm Files (2013 - today)

The latest addition to the digital world of echinoderms is the website The Echinoderm Files (http://tinyurl.com/mnrrkme). 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

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.

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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

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.

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

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Abstract

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. (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 alsaea*, *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*) *lepis*.

Key Words

Trematoda
Cercariae
human health
shedding
Thiaridae
Cerithioidea

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 (Wongratanacheewin 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 (Watthanakulpanich 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 (*Trematocera* spp. and *Tuculluca* spp.). 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 cyprinid fish act as the second intermediate hosts. If the vertebrates, like animals and humans, eat the infected raw fish, they will receive *Opisthorchis viverrini*. Thus, we can call these trematode infections mollusk-transmitted diseases.

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 in 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). 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 represents, 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 episopalisis* 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 *Melanoides tuberculata* are the first intermediate hosts for intestinal fluke and blood flukes (Malek and Cheng 1974, Pointier and Jourdane 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).

*Melanoides 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 *Melanoides* 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.
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 every 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, Nakhonthai 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 *Melanoides tuberculata* found, the number of collected snails and infection rates.

<table>
<thead>
<tr>
<th>No. (no. specimen)</th>
<th>Name</th>
<th>GPS</th>
<th>No. of collected snails</th>
<th>No. of infected snails</th>
<th>Infection rates (%)</th>
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<td>N1 (SUT0109001)</td>
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<td>1</td>
<td>33.33</td>
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<td>Pha Laht Waterfall, Nakhtonthai District, Phitsanulok</td>
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<td>4</td>
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<td>N5 (SUT0109005)</td>
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<td>No. of Infected snails</td>
<td>Infection rates (%)</td>
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<td>Nong Haan, Muang District, Sakol Nakhon</td>
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<td>81</td>
<td>18.97</td>
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**East**

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<th>No. of collected snails</th>
<th>No. of Infected snails</th>
<th>Infection rates (%)</th>
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<td>Khao Kхаew National Park, Sriracha District, Chonburi</td>
<td>N 13° 12' 45.0&quot; E 101° 03' 50.2&quot; 50.2° Altitude 128 m</td>
<td>613</td>
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<td>E37 (SUT0109037)</td>
<td>Ban Nong Pia Lai, Bang lamung District, Chonburi</td>
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<td>80</td>
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<td>Rayong River, Muang District, Rayong</td>
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<td>Nam Tok Plew Stream, Plew District, Chantaburi</td>
<td>N 12° 31' 14.3&quot; E 102° 10' 35.4&quot; 35.4° Altitude 39 m</td>
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<td>E43 (SUT0109043)</td>
<td>Pa Tong Canal, Soi Dao District, Chantaburi</td>
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<td>Sra Kaew, Muang District, Sra Kaew</td>
<td>N 13° 49’ 7.0” E 102° 03’ 37.9” 37.9° Altitude 43 m</td>
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<td>Eto Waterfall, Muang District, Prachinburi</td>
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<td>C47 (SUT0109047)</td>
<td>Dusit Zoo Pond, Dusit, Bangkok</td>
<td>N 13° 46’ 17.4” E 100° 31’ 14.8” 14.8° Altitude 2 m</td>
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<td>C48 (SUT0109048)</td>
<td>Drainage at Kasetsart University, Bang Khen campus, Bangkok</td>
<td>N 13° 50’ 40.7” E 100° 34’ 33.5” 33.5° Altitude 5 m</td>
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<td>Pond at Kasetsart University, Bang Khen Campus, Bangkok</td>
<td>N 13° 50’ 22.6” E 100° 34’ 43.4” 43.4° Altitude 1 m</td>
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<td>Hin Dad Waterfall, Thong Pa Poom District, Kanchanaburi</td>
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<td>Sai Yok Noi Waterfall, Sai Yok District, Kanchanaburi</td>
<td>N 14° 14’ 27.6” E 99° 03’ 55.9” 55.9° Altitude 166 m</td>
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<td>Fish Pond at Bird Park, Muang District, Chainat</td>
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<td>C59 (SUT0109059)</td>
<td>Khun Daan Prakarnchon Dam, Muang District, Nakhornayok</td>
<td>N 14° 18' 36.5&quot; E 101° 19' 14.3&quot;</td>
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<td>Ban mai Phai Chedi, Kampangsaen District, Nakhonpathom</td>
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<td>C61 (SUT0109061)</td>
<td>Rice paddy, Banglen District, Nakhonpathom</td>
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<td>Rice Field at Nong Kra Done, Muang District, Nakhonpathom</td>
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<td>C71 (SUT0109071)</td>
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<td>C78 (SUT0109078)</td>
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<td>Site1 at Ched Kot Waterfall, Kaeng Koi District, Saraburi</td>
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<td>C80 (SUT0109080)</td>
<td>Site2 at Ched Kot waterfall, Kaeng Koi District, Saraburi</td>
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<td>Muang Moo pond, Muang District, Singhaburi</td>
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**South**

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<td>Water Gate km. 19+500, Cha-Am District, Petchaburi</td>
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<td>Petchaburi Dam, Tayang District, Petchaburi</td>
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<td>N 11° 36' 47.0&quot; E 99° 40' 08.4&quot; Altitude 18 m</td>
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<td>Pailan River, Yan Ta Khao District, Trang</td>
<td>N 07° 22' 11.5&quot; E 99° 40' 51.6&quot; Altitude 12 m</td>
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<td>Tone Tok Waterfall, Palien District, Trang</td>
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<td>Ang Thong Waterfall, Sikao District, Trang</td>
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<td>Falan Waterfall, Srinarin District, Pattaloong</td>
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<td>S109 (SUT0109109)</td>
<td>Bangborn Stream, Kraburi District, Ranong</td>
<td>N 10° 20' 10.8&quot; E 98° 46' 48.7&quot; Altitude 18 m</td>
<td>34</td>
<td>2</td>
<td>5.88</td>
</tr>
</tbody>
</table>
Kraiias, D. et al.: Trematodes in the freshwater Snail Melanoides tuberculata in Thailand

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

(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°33'3.9", E 99°29'24.8", Altitude 182 m); N10 = Mae Pool Waterfall, Luab Rae Province, 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 Muang District, Phraya Province (SUT0109013) (N 18°55'5.3", E 100°12'15.7", Altitude 379); N14 = Tansawan Waterfall, Doi Pu Nang National Park, Chiang Muang District, Phraya 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 National Park, Nong Bua Ra Hoew District, Chaiyapoom Province (SUT010917) (N 15°52'34.7", E 101°30'34.7", Altitude 397 m); NE18 = Tad Tone Waterfall, Muang District, Chaiyapoom Province (SUT010918) (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, Burirum 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 Province...
The East: E36 = Khao Khaew National Park, Sriracha District, Chonburi Province (SUT0109036) (N 13°12'45.0", E 101°03'50.2", Altitude 128 m); E37 = Ban Wong 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 Pla Lai, Bang lamung District, Chonburi Province (SUT0109042) (N 12°31'14.3", E 102°10'35.4", Altitude 39 m); E43 = Pa Tong Canal, Sao 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, Sarakaew 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 (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, Nang 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, Chai nat Province (SUT0109056) (N 15°16'5.9", E 100°05'11.1", Altitude 41 m); C57 = Bird Park Pond, Muang District, Chai nat Province (SUT0109057) (N 15°12'26.5", E 100°09'21.9", Altitude 31 m); C58 = Fish Pond at Bird Park, Muang District, Chai nat Province (SUT0109058) (N 15°12'18.8", E 100°09'20.0", Altitude 39 m); C59 = Khun Daan Prakarnchon Dam, Muang District, Nak honnayok Province (SUT0109059) (N 14°18'36.5", E 101°19'14.3", Altitude 25m); C60 = Ban mai Phai Chedi, Kampangsaen District, Nak honpathom Province (SUT0109060) (N 14°02'10.5", E 100°03'27.3", Altitude 10 m); C61 = Rice paddy, Ban-

Figure 2. Shell Morphology of Melanoides tuberculata in Thailand

a. Sri Satchanalai Stream, Sri Satchanalai National Park, Sri Satchanalai District, Sukhothai Province (SUT0109009)
b. Lam Takkhong Stream, Khao Yai National Park, Pak Chong District, Nakorn, Ratchasima Province (SUT0109020)
c. Rice Field at Nong Kra Done, Muang District, Nakorn Pathom Province (SUT0109062)
d. Pond in Silpakorn University, Muang District, Nakorn Pathom Province (SUT0109063)
e. Bang Ta-nai Canal, Pak Kred District, Nontaburi Province (SUT0109065)
f. Huay Nuang Stream, Suankhuang District, Ratburi Prov inc e (SUT0109108)

Scale bar = 1.0 mm.
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°57’42.6", 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, Prachabkirikhun Province (SUT0109091) (N 11°36’47.0", E 99°40’08.4", Altitude 18 m); S92 = Thap Sakae Stream, Tuap Sake 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, Chumphon Province (SUT0109095) (N 10°44’28.7", E 99°12’53.9", Altitude 69 m); S96 = Ra Canal, Lungsuan District, Chumphon Province (SUT0109096) (N 09°59’04.3", E 99°00’59.8", Altitude 44 m); S97 = Si Kheed Waterfall, Sichon District, Nakorn Sri Thammarat Province (SUT0109097) (N 09°00’40.8", E 99°46’30.1", Altitude 45 m); S98 = Krung Ching Waterfall, Noppitum District, Nakorn Sri Thammarat Province (SUT0109098) (N 08°43’14.0", E 99°40’15.2", Altitude 45 m); S99 = Yod Leung Stream, Noppitum District, Nakorn Sri Thammarat Province (SUT0109099) (N 08°38’10.5", E 99°45’11.6", Altitude 68 m); S100 = Paliian River, Yan Ta Khaio District, Trang Province (SUT0109100) (N 07°22’11.5", E 99°40’51.6", Altitude 12 m); S101 = Paliian 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, Pattalung Province (SUT0109105) (N 07°36’25.9", E 99°54’39.0", Altitude 80 m); S106 = Ban Au Rua Stream, Muang District, Rachaburi Province (SUT0109106) (N
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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 151 m); 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°12’12.8”, E 99°40’31.2”, Altitude 10 m); S112 = Yan Canal, Wiwawadee District, Surat Thani Province (SUT0109112) (N 9°12’12.8”, E 98°50’57.3”, Altitude 113 m); S113 = Ton Sai Waterfall, Tha Lang District, Phuket Province (SUT0109113) (N 8°2’20.5”, E 98°23’49.3”, Altitude 50 m); S114 = Bang Pae Waterfall, Tha Lang District, Phuket Province (SUT0109114) (N 8°1’32.4”, E 98°21’58.8”, Altitude 45 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, Satoon 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.

<table>
<thead>
<tr>
<th>Cercaria species</th>
<th>No. infected snails</th>
<th>Total Infection rates (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type 1. Parapleurophocercous cercariae:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Haplorchis pumilio</td>
<td>23 0 58 265 25</td>
<td>371 1.16</td>
</tr>
<tr>
<td>2. Haplorchis taichui</td>
<td>1 2 0 0 89</td>
<td>92 0.29</td>
</tr>
<tr>
<td>3. Stictodora tridactyla</td>
<td>0 582 75 210 1,315</td>
<td>2,182 6.81</td>
</tr>
<tr>
<td>Type 2. Pleurophocercous cercariae:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4. Centrocestus formosanus</td>
<td>55 0 3 10 6</td>
<td>74 0.23</td>
</tr>
<tr>
<td>Type 3. Xiphidiocercariae:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5. Acanthotrema hitaense</td>
<td>9 14 54 1 10</td>
<td>88 0.27</td>
</tr>
<tr>
<td>6. Loxogenoides bicolor</td>
<td>29 802 485 573 484</td>
<td>2,373 7.41</td>
</tr>
<tr>
<td>7. Haematoloechus similis</td>
<td>53 314 92 1 8</td>
<td>468 1.46</td>
</tr>
<tr>
<td>Type 4. Megalurous cercariae:</td>
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<td></td>
</tr>
<tr>
<td>8. Cibacrona philippinum</td>
<td>1 0 11 0 0</td>
<td>12 0.04</td>
</tr>
<tr>
<td>9. Phosphothrix sp.</td>
<td>0 0 0 52 5</td>
<td>57 0.18</td>
</tr>
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<td>Type 5. Furcocercous cercariae:</td>
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<tr>
<td>10. Cardiochasmus philippinum</td>
<td>0 2 0 2 22</td>
<td>33 0.1</td>
</tr>
<tr>
<td>11. Ariaia mustelae</td>
<td>0 1 2 22 22</td>
<td>47 0.15</td>
</tr>
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<td>12. Transversotrema laruei</td>
<td>8 0 21 2 58</td>
<td>89 0.28</td>
</tr>
<tr>
<td>13. Apateon gracilis</td>
<td>0 20 0 4 31</td>
<td>55 0.17</td>
</tr>
<tr>
<td>14. Metostrum appendiculatus</td>
<td>0 3 0 0 0</td>
<td>3 0.009</td>
</tr>
<tr>
<td>Type 6. Echinostome cercariae:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>15. Echinochasmus pelecani</td>
<td>0 0 19 0 0</td>
<td>19 0.06</td>
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<tr>
<td>Type 7. Amphistome cercariae:</td>
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</tr>
<tr>
<td>16. Gastrothylax crumenifer</td>
<td>0 0 4 0 4</td>
<td>8 0.02</td>
</tr>
<tr>
<td>Type 8. Renicolid cercariae:</td>
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<tr>
<td>17. Cercaria caribbea LXVIII</td>
<td>0 0 33 12 0</td>
<td>45 0.14</td>
</tr>
<tr>
<td>Type 9. Cotylomicrocercous cercariae:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>18. Podocotyle (Podocotyle) lepomis</td>
<td>0 0 0 3 0</td>
<td>3 0.009</td>
</tr>
</tbody>
</table>

No. infected snails

<p>| No. of cercaria species | 179 1,740 857 1,164 2,079 6,019 18.79 |
| No. of cercaria species | 8 9 12 13 13 18 |</p>
<table>
<thead>
<tr>
<th>Trematodes species</th>
<th>C. philophthalmus</th>
<th>C. similis</th>
<th>C. philippinum</th>
<th>C. caribbea</th>
<th>C. pseudo</th>
<th>C. carinata</th>
<th>C. m. gracilis</th>
<th>C. appendiculatus</th>
<th>C. pelecani</th>
<th>C. crumenifer</th>
<th>C. philippinum</th>
<th>C. philippinum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body</td>
<td>85-128</td>
<td>87.59</td>
<td>82.40</td>
<td>85-120</td>
<td>87.59</td>
<td>38-50</td>
<td>125</td>
<td>41.5-90.0</td>
<td>92.5-120</td>
<td>68-128</td>
<td>125</td>
<td>41.5-90.0</td>
</tr>
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<td>Genital pore</td>
<td>85-128</td>
<td>87.59</td>
<td>82.40</td>
<td>85-120</td>
<td>87.59</td>
<td>38-50</td>
<td>125</td>
<td>41.5-90.0</td>
<td>92.5-120</td>
<td>68-128</td>
<td>125</td>
<td>41.5-90.0</td>
</tr>
<tr>
<td>Oral sucker</td>
<td>85-128</td>
<td>87.59</td>
<td>82.40</td>
<td>85-120</td>
<td>87.59</td>
<td>38-50</td>
<td>125</td>
<td>41.5-90.0</td>
<td>92.5-120</td>
<td>68-128</td>
<td>125</td>
<td>41.5-90.0</td>
</tr>
<tr>
<td>Anterior organ</td>
<td>85-128</td>
<td>87.59</td>
<td>82.40</td>
<td>85-120</td>
<td>87.59</td>
<td>38-50</td>
<td>125</td>
<td>41.5-90.0</td>
<td>92.5-120</td>
<td>68-128</td>
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<td>41.5-90.0</td>
</tr>
<tr>
<td>Pharynx</td>
<td>85-128</td>
<td>87.59</td>
<td>82.40</td>
<td>85-120</td>
<td>87.59</td>
<td>38-50</td>
<td>125</td>
<td>41.5-90.0</td>
<td>92.5-120</td>
<td>68-128</td>
<td>125</td>
<td>41.5-90.0</td>
</tr>
<tr>
<td>Ventral sucker</td>
<td>85-128</td>
<td>87.59</td>
<td>82.40</td>
<td>85-120</td>
<td>87.59</td>
<td>38-50</td>
<td>125</td>
<td>41.5-90.0</td>
<td>92.5-120</td>
<td>68-128</td>
<td>125</td>
<td>41.5-90.0</td>
</tr>
<tr>
<td>Excretory bladder</td>
<td>85-128</td>
<td>87.59</td>
<td>82.40</td>
<td>85-120</td>
<td>87.59</td>
<td>38-50</td>
<td>125</td>
<td>41.5-90.0</td>
<td>92.5-120</td>
<td>68-128</td>
<td>125</td>
<td>41.5-90.0</td>
</tr>
</tbody>
</table>

**Table 3:** Size range and average size (in micrometres, calculated from 20 cercariae) of eighteen species of cercariae were measured and obtained from *Melanoides tuberculata* in Thailand.
<table>
<thead>
<tr>
<th></th>
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</thead>
<tbody>
<tr>
<td>Penetration gland</td>
<td>-</td>
<td>-</td>
<td>20:30 (av. 26)</td>
<td>-</td>
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<td>-</td>
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<tr>
<td>Tail</td>
<td>10:36 (av. 30)</td>
<td>15:42 (av. 35)</td>
<td>37:55 (av. 45)</td>
<td>19:25 (av. 15)</td>
<td>20:30 (av. 27)</td>
<td>27:34 (av. 30)</td>
<td>25:38 (av. 34)</td>
<td>30:32.5 (av. 31)</td>
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<td>Tail stem</td>
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<tr>
<td>Tail furcal</td>
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<tr>
<td>Lateral finfold</td>
<td>-</td>
<td>-</td>
<td>9:15 (av. 1)</td>
<td>-</td>
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<td>-</td>
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<tr>
<td>Dorso-median finfold</td>
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<tr>
<td>Appendages</td>
<td>-</td>
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<td>-</td>
<td>-</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>18:72 (av. 47)</td>
<td>-</td>
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</tr>
</tbody>
</table>
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 tachui and Stictodora tridactyla; (2) Pleurophocercous cercariae: Centrocestus formosanus; (3) Xiphidiocercariae: Acanthatrium hitaense, Loxogenoides bicolor and Haematoloechus similis; (4) Megalurous cercariae: Cloacitremum 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) Cotylomiocercous 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):

<table>
<thead>
<tr>
<th>Structure</th>
<th>Size Range</th>
<th>Average Size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body</td>
<td>85-128 µm (av. 108 µm) × 168-295 µm (av. 257 µm)</td>
<td></td>
</tr>
<tr>
<td>Oral sucker</td>
<td>27-48 µm (av. 36 µm) × 27-48 µm (av. 36 µm)</td>
<td></td>
</tr>
<tr>
<td>Ventral sucker</td>
<td>14-24 µm (av. 18 µm) × 14-24 µm (av. 18 µm)</td>
<td></td>
</tr>
<tr>
<td>Pharynx</td>
<td>8-10 µm (av. 9 µm) × 12-19 µm (av. 15 µm)</td>
<td></td>
</tr>
<tr>
<td>Excretory bladder</td>
<td>28-40 µm (av. 34 µm) × 28-40 µm (av. 34 µm)</td>
<td></td>
</tr>
<tr>
<td>Tail</td>
<td>10-36 µm (av. 30 µm) × 465-528 µm (av. 490 µm)</td>
<td></td>
</tr>
</tbody>
</table>

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.
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 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 µm (av. 132 µm) × 156-276 µm (av. 242 µm)
- **Oral sucker**: 24-45 µm (av. 38 µm) × 27-45 µm (av. 38 µm)
- **Ventral sucker**: 15-25 µm (av. 20 µm) × 15-25 µm (av. 20 µm)
- **Pharynx**: 8-10 µm (av. 10 µm) × 12-18 µm (av. 15 µm)
- **Excretory bladder**: 30-42 µm (av. 37 µm) × 30-42 µm (av. 37 µm)
- **Tail**: 15-42 µm (av. 35 µm) × 378-514 µm (av. 485 µm)

**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.


*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 yelloowish 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 µm (av. 112 µm) × 255-309 µm (av. 275 µm)
- **Oral sucker**: 36-48 µm (av. 38 µm) × 33-52 µm (av. 41 µm)
- **Eye spots**: 6-12 µm (av. 8 µm) × 12-17 µm (av. 14 µm)
Pharynx: 11-19 μm (av. 16 μm) × 14-21 μm (av. 17 μm)
Ventral sucker: 10-25 μm (av. 19 μm) × 10-25 μm (av. 19 μm)
Excretory bladder: 87-119 μm (av. 98 μm) × 52-98 μm (av. 76 μm)
Penetration gland: 20-30 μm (av. 26 μm) × 25-30 μm (av. 26 μm)
Tail: 37-55 μm (av. 45 μm) × 486-595 μm (av. 546 μm)
Lateral finfold: 9-15 μm (av. 13 μm) × 88-100 μm (av. 95 μm)

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.

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) × 82-120 μm (av. 117 μm)
Oral sucker: 16-26 μm (av. 24 μm) × 17-28 μm (av. 25 μm)
Ventral sucker: 12-16 μm (av. 14 μm) × 12-16 μm (av. 14 μm)
Pharynx: 7-9 μm (av. 8 μm) × 8-10 μm (av. 9 μm)
Excretory bladder: 24-30 μm (av. 28 μm) × 38-52 μm (av. 45 μm)
Tail: 14-17 μm (av. 15 μm) × 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
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 µm (av. 78 µm) × 80-110 µm (av. 100 µm)

Oral sucker: 25-32 µm (av. 30 µm) × 34-40 µm (av. 37 µm)

Stylet: 8-13 µm (av. 10 µm) × 11-13 µm (av. 12 µm)

Ventral sucker: 15-16 µm (av. 16 µm) × 15-18 µm (av. 17 µm)

Pharynx: 10-15 µm (av. 13 µm) × 12-24 µm (av. 20 µm)

Excretory bladder: 8-12 µm (av. 10 µm) × 20-46 µm (av. 38 µm)

Tail: 19-25 µm (av. 23 µm) × 26-75 µm (av. 68 µm)

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 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 µm, c = 10 µm).

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 µm, c = 50 µm).

*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.png)

**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 - virgulate 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 µm, c = 20 µm).

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

<table>
<thead>
<tr>
<th>Structure</th>
<th>Size Range</th>
<th>Average Size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body</td>
<td>54-82 µm (av. 75 µm)</td>
<td>90-120 µm (av. 110 µm)</td>
</tr>
<tr>
<td>Oral sucker</td>
<td>24-30 µm (av. 28 µm)</td>
<td>24-30 µm (av. 28 µm)</td>
</tr>
<tr>
<td>Stylet</td>
<td>5-8 µm (av. 7 µm)</td>
<td>14-20 µm (av. 18 µm)</td>
</tr>
<tr>
<td>Ventral sucker</td>
<td>12-18 µm (av. 15 µm)</td>
<td>13-20 µm (av. 17 µm)</td>
</tr>
<tr>
<td>Pharynx</td>
<td>4-6 µm (av. 5 µm)</td>
<td>4-10 µm (av. 8 µm)</td>
</tr>
<tr>
<td>Excretory bladder</td>
<td>8-10 µm (av. 9 µm)</td>
<td>10-30 µm (av. 25 µm)</td>
</tr>
<tr>
<td>Tail</td>
<td>20-30 µm (av. 27 µm)</td>
<td>35-80 µm (av. 75 µm)</td>
</tr>
</tbody>
</table>

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 Xiphidiocercarieae. The body is ovate, and the surface is covered with spines. Cytogenous cell is not observed. A stylet is 30-32 µm 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 finfolded. Cercariae were produced within the sporocyst.

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

<table>
<thead>
<tr>
<th>Structure</th>
<th>Size Range</th>
<th>Average Size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body</td>
<td>87-104 µm (av. 95 µm)</td>
<td>130-164 µm (av. 148 µm)</td>
</tr>
<tr>
<td>Oral sucker</td>
<td>34-42 µm (av. 38 µm)</td>
<td>37-46 µm (av. 42 µm)</td>
</tr>
<tr>
<td>Stylet</td>
<td>20-34 µm (av. 30 µm)</td>
<td>20-34 µm (av. 32 µm)</td>
</tr>
<tr>
<td>Ventral sucker</td>
<td>10-20 µm (av. 16 µm)</td>
<td>12-20 µm (av. 18 µm)</td>
</tr>
<tr>
<td>Pharynx</td>
<td>11-13 µm (av. 12 µm)</td>
<td>15-17 µm (av. 16 µm)</td>
</tr>
<tr>
<td>Excretory bladder</td>
<td>20-22 µm (av. 21 µm)</td>
<td>20-24 µm (av. 22 µm)</td>
</tr>
</tbody>
</table>

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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


Cloacitrema philippinum (Fig. 10) was found in 12 M. tuberculata. 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 prepharynx 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: 122-184µm (av. 169 µm) × 280-450 µm (av. 396 µm)

Oral sucker: 50-60 µm (av. 56 µm) × 50-60 µm (av. 56 µm)
Ventral sucker: 60-70 μm (av. 68 μm) × 60-75 μm (av. 70 μm)
Pharynx: 23-38 μm (av. 35 μm) × 25-40 μm (av. 35 μm)
Excretory bladder: 15-20 μm (av. 18 μm) × 14-21 μm (av. 18 μm)
Tail: 25-38 μm (av. 34 μm) × 230-547 μm (av. 480 μm)

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.

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

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

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

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-liked 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 μm (av. 28 μm) × 72-110 μm (av. 95 μm)
Anterior organ: 11-15 \( \mu m \) (av. 13 \( \mu m \)) \( \times \) 14-20 \( \mu m \) (av. 17 \( \mu m \))

Excretory bladder: 3-8 \( \mu m \) (av. 5 \( \mu m \)) \( \times \) 10-35 \( \mu m \) (av. 21 \( \mu m \))

Tail stem: 15-30 \( \mu m \) (av. 26 \( \mu m \)) \( \times \) 154-197 \( \mu m \) (av. 185 \( \mu m \))

Tail furcal: 7-11 \( \mu m \) (av. 9 \( \mu m \)) \( \times \) 28-54 \( \mu m \) (av. 51 \( \mu m \))

Dorso-median finfold: 5-12 \( \mu m \) (av. 8 \( \mu m \))

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 lateroal fields, prepharynx short, pharynx small and muscular, esophagus rather long, ceca extending a short distance 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 \( \mu m \) (av. 138 \( \mu m \)) \( \times \) 185-280 \( \mu m \) (av. 255 \( \mu m \))
- **Oral sucker:** 28-40 \( \mu m \) (av. 36 \( \mu m \)) \( \times \) 28-40 \( \mu m \) (av. 36 \( \mu m \))
- **Ventral sucker:** 15-30 \( \mu m \) (av. 22 \( \mu m \)) \( \times \) 15-30 \( \mu m \) (av. 22 \( \mu m \))
- **Pharynx:** 10-15 \( \mu m \) (av. 13 \( \mu m \)) \( \times \) 14-17 \( \mu m \) (av. 15 \( \mu m \))
- **Tail stem:** 48-60 \( \mu m \) (av. 55 \( \mu m \)) \( \times \) 220-300 \( \mu m \) (av. 260 \( \mu m \))
- **Tail furcae:** 38-65 \( \mu m \) (av. 60 \( \mu m \)) \( \times \) 245-320 \( \mu m \) (av. 280 \( \mu m \))

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.


*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 brown 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, and the ventral sucker is globular. There is a mouth on the end of the body. There are very big round eye spots, and the ventral sucker of the intestine. There are 1 pair of testes, with an ovary on the left side of the testes. An adhesive pad was observed at the base of the tail. An excretory bladder is at the posterior end. The tail is longer than the body length with a fork tip, and one pair of appendage scales on the body surface. Many granules are observed.

The cercariae produced within the rediae.

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

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

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) × 115-140 μm (av. 126 μm)
- **Oral sucker:** 15-25 μm (av. 21.45 μm) × 20-30 μm (av. 23.25 μm)
- **Ventral sucker:** 16-25 μm (av. 23 μm) × 20-30 μm (av. 25 μm)
- **Excretory bladder:** 15-25 μm (av. 18 μm) × 15-30 μm (av. 20 μm)
- **Pharynx:** 6-10 μm (av. 8 μm) × 7-13 μm (av. 9 μm)
- **Tail stem:** 30-45μm (av. 39 μm) × 240-312 μm (av. 286 μm)
- **Tail furcae:** 10-25μm (av. 18 μm) × 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-
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):

<table>
<thead>
<tr>
<th>Body</th>
<th>92-120 µm (av. 109 µm) × 160-250 µm (av. 225 µm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oral sucker</td>
<td>20-45 µm (av. 35 µm) × 35-48 µm (av. 39 µm)</td>
</tr>
<tr>
<td>Ventral sucker</td>
<td>15-24 µm (av. 20 µm) × 15-24 µm (av. 20 µm)</td>
</tr>
<tr>
<td>Excretory bladder</td>
<td>20-40 µm (av. 35 µm) × 20-40 µm (av. 35 µm)</td>
</tr>
<tr>
<td>Pharynx</td>
<td>8-10 µm (av. 9 µm) × 11-18 µm (av. 15 µm)</td>
</tr>
</tbody>
</table>


*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 spinnose. 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.
Tail stem: 25-40 μm (av. 35 μm) × 425-525 μm (av. 495 μm)
Tail furcae: 15-25 μm (av. 20 μm) × 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


*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) × 100-125 μm (av. 118 μm)
- Oral sucker: 21-30 μm (av. 23 μm) × 24-30 μm (av. 25 μm)
- Ventral sucker: 20-31 μm (av. 25 μm) × 22-30 μm (av. 25 μm)
- Pharynx: 8-15 μm (av. 12 μm) × 9-15 μm (av. 12 μm)
- Excretory bladder: 21-35 μm (av. 33 μm) × 23-36 μm (av. 33 μm)
- Tail: 23-38 μm (av. 35 μm) × 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


*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) × 350-415 μm (av. 370 μm)
- Oral sucker: 45-65 μm (av. 52 μm) × 45-65 μm (av. 52 μm)
- Ventral sucker: 48-68 μm (av. 55 μm) × 48-68 μm (av. 55 μm)
- Pharynx: 8-10 μm (av. 10 μm) × 8-12 μm (av. 11 μm)
Esophagus: 80-140 \( \mu m \) (av. 125 \( \mu m \)) \( \times \) 80-140 \( \mu m \) (av. 125\( \mu m \))

Tail: 65-95 \( \mu m \) (av. 82 \( \mu m \)) \( \times \) 328-450 \( \mu m \) (av. 410 \( \mu m \))

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 \( \mu m \), a short prepharynx, a pharynx of 12-14 \( \mu m \), 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 finfold, and no flame cells.

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

- Body: 128-140 \( \mu m \) (av. 129 \( \mu m \)) \( \times \) 390-435 \( \mu m \) (av. 420 \( \mu m \))
- Oral sucker: 28-33 \( \mu m \) (av. 26 \( \mu m \)) \( \times \) 28-33 \( \mu m \) (av. 26 \( \mu m \))
- Ventral sucker: 29-36 \( \mu m \) (av. 30 \( \mu m \)) \( \times \) 29-36 \( \mu m \) (av. 30 \( \mu m \))
- Pharynx: 8-14 \( \mu m \) (av. 12 \( \mu m \)) \( \times \) 10-14 \( \mu m \) (av. 12 \( \mu m \))
- Excretory bladder: 15-20 \( \mu m \) (av. 17 \( \mu m \)) \( \times \) 15-20 \( \mu m \) (av. 17 \( \mu m \))
Tail:  34-38 μm (av. 35 μm) × 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) × 103-145 μm (av. 123 μm)

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

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

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

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

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

Tail:  43-65 μm (av. 52 μm) × 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 Jourdane 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. tubercul-
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 destination 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 (Chontananarth and Wongssawad 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, Derraik 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 Loxogonoides 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) scabra 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>
<thead>
<tr>
<th>Infections</th>
<th>Type</th>
<th>No. of infected snails</th>
</tr>
</thead>
<tbody>
<tr>
<td>Double</td>
<td>Loxogonoides bicolor + Stictodora tridactyla</td>
<td>135</td>
</tr>
<tr>
<td></td>
<td>Cardicola alseae + Stictodora tridactyla</td>
<td>162</td>
</tr>
<tr>
<td></td>
<td>Apatemon gracilis + Stictodora tridactyla</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Loxogonoides bicolor + Cercaria caribbea LXVIII</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Loxogonoides bicolor + Philophthalmus sp.</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>Loxogonoides bicolor + Haplorchis pumilio</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Alaria mustelae + Haplorchis pumilio</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Haplorchis taichui + Alaria mustelae</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Haplorchis taichui + Loxogonoides bicolor</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Haplorchis taichui + Acanthatrium hitaense</td>
<td>2</td>
</tr>
<tr>
<td>Triple</td>
<td>Loxogonoides bicolor + Stictodora tridactyla + Podocotyle lepomis</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Loxogonoides bicolor + Stictodora tridactyla + Cardicola alseae</td>
<td>12</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>339</td>
</tr>
</tbody>
</table>
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 mus- telae*, *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 as of considerable medical significance in Thailand.

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**References**


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

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Abstract

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.

Key Words

Holotype
early Oligocene
taxonomy
nomenclature
*nomen dubium*
paraphyly

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).
In the subsequent decades, early Oligocene sirenian finds from the Mainz Basin comprising cranial and postcranial 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 Staatsammlung 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
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. cristoli (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 Trachytherium (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 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 Manatherium is not considered as a useful or valid replacement name.

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

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.
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 paralotype, 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 Dugongi- nae) 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 emphasizes 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 “Halitheri-inae” 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 Pervoleser 2001; Domning and Aguiler A 2008; Velez-Juarbe et al. 2012). Doubts on the “halitherine” 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.
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.” cristoli 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 Aguiler 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 Aguiler 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.

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**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.
Conclusions

In the course of the revision of the genus “Halitherium”, it is concluded that the premolar holotype of the type species “H. schinzii” 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. schinzii” 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 “halitherines” and “Halitherium”. Considering all previous phylogenies, especially the order-based analysis by Domning (1994), this subfamily consequently includes a single species only, viz. “H. schinzii”. This situation would remain unchanged even though a substitute name would be erected for “Halitherium” and “H. schinzii”, 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 paraphily-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 paraphyly is resolved, but also new approaches are provided to interpret the taxa originally lumped in this category.

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