SYSTEMATICS OF ENDOMYCHIDAE (COLEOPTERA: CUCUJOIDEA): PHYLOGENETIC AND TAXONOMIC RESEARCH ON A MYCOPHAGOUS BEETLE FAMILY

by

FLOYD WAYNE SHOCKLEY

(Under the Direction of Joseph V. McHugh)

ABSTRACT

Recent interest in the phylogenetic relationships within the family Endomychidae and the association of the family with other Cerylonid Series families, particularly Coccinellidae, has resulted in a number of studies attempting to reconstruct the phylogeny of the family using both morphological and molecular data sources. However, these studies have yielded conflicting hypotheses about the monophyly of the family, reintroducing previous speculation that the family may be a heterogeneous assemblage of taxa rather than a natural group. The work presented herein constitutes significant progress in two different but complementary areas of systematic study on the family Endomychidae. The first part is a family-level phylogenetic analysis based on eight genes utilizing parsimony, likelihood and Bayesian techniques. The second part consists of a taxonomic revision of the genus *Bystus* and a comprehensive morphological study of one exemplar species, *B. piceus*. An updated, annotated checklist for the family and a review of the natural history of the family are also provided.

INDEX WORDS: Systematics, Taxonomy, Entomology, Endomychidae, *Bystus*, Handsome fungus beetles

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I also wish to extend my heartfelt appreciation to my McHugh lab colleagues over the years. Your quest for excellence, camaraderie and passion for our craft was a constant source of inspiration to me even as we shared our distinct and sometimes contrasting perspectives and opinions. This evidence further supports that the family McHughlidae is, in fact, a natural monophyletic group (although a rapidly evolving one). Finally, I would like to acknowledge my loving wife Shannon, my family (including my “adopted” family, the Hagues), and all my friends/colleagues, whose love, support and encouragement over the years were critical to the successful completion of this chapter of my life. This dissertation is dedicated to them and no words can do justice to how thankful I am to have them in my life.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

BACKGROUND

Endomychidae, whose members are collectively known as the Handsome Fungus Beetles, is a moderately speciose family of mycophagous beetles within the Cerylonid Series of the superfamily Cucujoidea (Crowson 1955), with 130 genera and 1782 species and subspecies (Shockley *et al.* 2009). The family is represented worldwide, occurring in all major biogeographical regions; however, the group is predominantly tropical with highest diversity in the Neotropics, equatorial Africa and southeast Asia. Endomychidae is currently arranged into 12 subfamilies (Tomaszewska 2000): Anamorphinae (=Mycotheninae), Danascelinae, Endomychinae, Epipocinae, Eupsilobiinae (=Eidoreinae, Cerasommatidiidae), Leiestinae, Lycoperdininae (=Eumorphinae), Merophysiinae (=Holoparamecinae), Mycetaeinae (=Agaricophilinae), Pleganophorinae (=Trochoideinae), Stenotarsinae and Xenomycetinae.

Most endomychids feed on the fruiting bodies of tough lignicolous basidiomycete fungi, although some species specialize on the softer agarics or on molds, and there are even several species that are facultatively phytophagous or predaceous. They are most often collected directly from the surface of their host fungi. However, they can also be sampled by light traps, pitfall traps, flight intercept traps or by beating/sweeping vegetation in close proximity to their hosts as they often rest on nearby foliage during the day. There are several species that have become stored product pests. Some species, particularly from the subfamily Merophysiinae, are inquilines of social insects. A number of species appear to be involved in mimicry complexes with beetles from other families such as Chrysomelidae, Coccinellidae, Erotylidae and Tenebrionidae, many of which are chemically defended.

In the 50 years since Strohecker's work (1953), very little work has been done to investigate the phylogenetic relationships within Endomychidae, as well as the relationship of the family to other cucujoids. Inclusion of Eupsilobiinae and Anamorphinae in Endomychidae has led some researchers to suggest that the family may be polyphyletic (Ślipiński & Pakaluk 1991, Robertson *et al*. 2008), particularly with respect to the families Coccinellidae and Corylophidae. Historically, Endomychidae was considered to be the sister taxon to the more familiar, predominantly predaceous Coccinellidae. In fact, some older classifications placed these two taxa together under the name "Trimera", based on the shared feature of pseudotrimerous tarsi (Tomaszewska 2000). This condition within Endomychidae is now known to be restricted to the “higher” endomychid subfamilies—Endomychinae, Epipocinae, Lycoperdininae and Stenotarsinae (Tomaszewska 2005).

Because of the potential sister-group relationship with the economically significant Coccinellidae, there has been much interest recently in investigating these relationships more thoroughly. Tomaszewska (2000) performed the first formal phylogenetic analysis of the family. This study, based on morphological characters of the adults, supported the monophyly of the family, but provided no resolution for the relationships of the subfamilies. In a subsequent paper including larval characters, Tomaszewska (2005) obtained better subfamilial resolution. Both studies used Coccinellidae as an outgroup based on its assumed sister group relationship with Endomychidae. Neither study, however, had a broad enough outgroup sampling to rigorously test the monophyly of Endomychidae.

In a broader analysis of Coleoptera families based on three genes (18S, 16S, COI), Hunt *et al*. (2007), recovered a monophyletic Cerylonid Series and a sister group relationship between "higher Endomychidae" and Coccinellidae, but also recovered the Merophysiinae, Leiestinae and Anamorphinae clustered together with Corylophidae, resulting in a polyphyletic Endomychidae. Of course, Endomychidae was not the focus of that ordinal-level study, so the taxon and gene sampling were not ideal to fully resolve the familial and subfamilial relationships of Endomychidae and the other Cerylonid Series families. Nonetheless, the resulting hypotheses about the placement of some endomychid subfamilies raised some interesting and lingering questions about the monophyly of the Endomychidae which warrant further exploration.

Robertson *et al.* (2008), also using molecular sequence data (18S, 28S), conducted the first formal test that was focused on the relationships of the Cerylonid Series and also found that Endomychidae was not monophyletic. While the analysis did recover a monophyletic clade of subfamilies corresponding to Tomaszewska's "higher Endomychidae" as the sister to Coccinellidae, it also recovered Anamorphinae outside of Endomychidae and sister to Corylophidae. Sasaji (1978, 1987, 1990) first proposed that Anamorphinae should be recognized as an independent assemblage ("Mychothenidae") outside of the remaining Endomychidae, but this classification was never widely accepted. Much work is needed still to fully resolve the family and its constituent subfamilies.

ORGANIZATION OF THE DISSERTATION

As is the case with many systematics-based research projects, the research presented here is fairly diverse in topic, addressing relatively independent areas of need and therefore yielding five very distinct "products." The works in this dissertation attempt to provide the following (in order of appearance): (1) a checklist of the endomychid species of the world; (2) a thorough review of the current knowledge of the biology and natural history of Endomychidae; (3) a phylogenetic analysis of sequence data from multiple gene sources using a large and diverse sampling of endomychid exemplars; (4) a comprehensive morphological study of *Bystus piceus* Gorham; and (5) a taxonomic monograph of the New World genus *Bystus*. Chapters 2-6 have been written as journal manuscripts and bear appropriate title pages reflecting their current or future publication status.

Chapter 2 consists of a comprehensive, distributional checklist for the Endomychidae of the world, including new generic and species diversity estimates, all known synonyms including several newly proposed synonymies, and an accompanying bibliography including complete references for all original species descriptions within the family. Chapter 3 consists of an exhaustive review of the ecological associations and natural history of the family Endomychidae. Very little effort has been made by past workers to compile these data in a single document, because they are widely distributed across the scientific literature as scattered notes in many different languages spanning 250+ years. In lieu of the formal “Literature Review” normally required for dissertations including chapters written as journal manuscripts, the combination of Chapters 2 and 3 sufficiently reviews all the known biological and taxonomic information relevant to the family and to the research content of this dissertation so any additional review would be unnecessarily redundant.

Chapter 4 is phylogenetic in nature and has direct implications on the classification of the family. To date, very little work has been done to investigate the phylogenetic relationships of the taxa within the family, as well as the relationship of Endomychidae to other cucujoid families. To compound matters, the few studies that have been done have yielded conflicting results. In the first phylogenetic analysis specifically conducted to examine the relationships of the Cerylonid Series families, Robertson *et al.* (2008), using molecular sequence data (18S, 28S), concluded that Endomychidae was not monophyletic as previously suggested based on analyses of adult or adult+larval morphological characters (Tomaszewska 2000, 2005). Additional analyses with new characters are needed to better resolve the internal relationships of the family.

Chapter 4 addresses these concerns and others while providing a new hypothesis based on molecular data from a variety of sources including nuclear ribosomal (18S, 28S), nuclear protein-coding (Wnt, H3), mitochondrial ribosomal (12S, 16S) and mitochondrial protein-coding (COI, COII) genes. In addition, discrepancies between the new hypotheses generated during this study are compared to previous hypotheses, and differences in the topologies resulting from parsimony vs. Bayesian analyses are noted and discussed. Studies of this type are critical because they provide the necessary phylogenetic framework for clarifying the internal relationships of Endomychidae, as well as the relationship of Endomychidae to other Cerylonid Series families. Phylogenetic studies like this also provide the best context in which to examine the evolution of interesting aspects of endomychid morphology and biology, including their aposematism, involvement in mimicry complexes, and varied feeding strategies (phytophagy, mycophagy, entomophagy).

Extensive morphological studies are necessary components of or precursors to any generic revision. These studies help to define the morphological terminology to be used, identify potentially diagnostic features for descriptions and keys, and lay the foundation for subsequent phylogenetic work. Chapter 5 is a large morphological study which was conducted on one exemplar species, *Bystus piceus* Gorham. Previous descriptions of species of *Bystus* have generally been accompanied by incomplete or inaccurate illustrations, leading to much confusion about the value of morphological features considered to be useful for diagnosing this genus. Chapter 5 attempts to rectify this problem and fill in gaps in the knowledge of the external and internal anatomy of one exemplar species of this genus.

Chapter 6 is a monographic revision of the New World genus *Bystus* Guérin–Méneville. *Bystus* is of particular interest because it is currently the largest anamorphine genus with 18 species, all of which are geographically restricted to the Western Hemisphere with most of the diversity in the tropics. The revision presented in Chapter 6 is an important first step in resolving some of the many taxonomic problems in this genus and will hopefully serve as a benchmark for future taxonomic studies on other anamorphine taxa. In addition to providing thorough redescriptions of the genus and previously described species, descriptions are also given for new species and subimaginal stages, including extensive illustration, digital imaging and scanning electron micrography. Keys are provided for adults and known larvae of *Bystus*.

Finally, in Chapter 7 I will attempt to summarize the major findings and conclusions of works presented in the previous chapters. It should be noted that since all chapters besides this one and Chapter 7 have been written in manuscript format, each comes with its own respective set of acknowledgements, references, tables and figures (at the end and in that order).

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CHAPTER 2

AN ANNOTATED CHECKLIST OF THE HANDSOME FUNGUS BEETLES OF THE WORLD (COLEOPTERA: CUCUJOIDEA: ENDOMYCHIDAE)[1]

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[1] Shockley, F.W., K.W. Tomaszewska and J.V. McHugh. 2009. *Zootaxa* 1999:1-113. Reprinted here with permission of Magnolia Press.

ABSTRACT

A worldwide checklist is provided for the family Endomychidae (Coleoptera: Cucujoidea). An updated subfamilial classification is presented, based on recent higher-level phylogenetic analyses and incorporating many recently described taxa. At present, Endomychidae contains 1782 valid species and subspecies in 130 genera organized into 12 subfamilies. Two new synonyms are recognized: *Symbiotes latus* Redtenbacher, 1849 = *Symbiotes latus* var. *roberti* Falcoz & Roman, 1930 **syn. nov.**; and *Cholovocerida* Belon, 1884 = *Displotera* Reitter, 1887b **syn. nov.** Two new combinations are proposed: *Cholovocerida ecitonis* (Wasmann, 1890) for *Coluocera ecitonis* Wasmann, 1890 **comb. nov.**; and *Cholovocerida maderae* (Wollaston, 1854) for *Cholovocera maderae* Wollaston, 1854 **comb. nov.** *Loeblia ceylanica* Dajoz, 1972a is here designated as the type species for *Loeblia* Dajoz, 1972a, and *Rhymbus hemisphaericus* Gerstaecker, 1858 is designated as the type species for *Rhymbus* Gerstaecker, 1858. *Nomen nudum* status is proposed for *Mycetaea tafilaletica* Smirnoff, 1957. Thirty-two species originally described under *Corynomalus* Chevrolat, 1836 and subsequently transferred to *Amphix* Laporte, 1840, have been returned to *Corynomalus*. Known fossil taxa are summarized.

Key words: Endomychidae, Anamorphinae, Danascelinae, Endomychinae, Epipocinae, Eupsilobiinae, Leiestinae, Lycoperdininae, Merophysiinae, Mycetaeinae, Pleganophorinae, Stenotarsinae, Xenomycetinae, taxonomy, classification.

INTRODUCTION

Endomychidae is a moderately speciose family of mycophagous beetles placed within the Cerylonid Series of the superfamily Cucujoidea (Crowson 1955). Many endomychid species are brightly and attractively colored, garnering their common name, the Handsome Fungus Beetles. The family is represented in all major biogeographical regions, but most diversity is concentrated in the tropical regions. Historically, large treatments of Endomychidae were limited to regional checklists and descriptive papers. This type of "regionalization" led to the creation of numerous synonyms, particularly among cryptic, polymorphic, and cosmopolitan species. This problem was compounded by an inadequate understanding of the phylogenetic relationships of the group.

Gerstaecker (1858) completed the first comprehensive treatment of Endomychidae. Several other large familial treatments were published in the latter part of the 19th century (Gorham 1887–99; Ganglbauer 1899a; Ganglbauer 1899b), although these were all regionally focused. During the early to mid–1900's several large world-wide catalogues were produced for the family (Csiki 1901a; Csiki 1910; Arrow 1920a). Some taxonomic works treated current endomychid taxa that were not historically classified within Endomychidae (*e.g.*, Belon 1902; Hetschko 1926). The last family-level checklist was published by Strohecker (1953a), which included the first and only comprehensive keys to the known endomychid genera of the world. Unfortunately, this treatment lacked the phylogenetic context necessary for establishing a natural classification and in the ~50 years since has become largely outdated due to new descriptions and transfers of taxa between Endomychidae and other families.

Strohecker (1953a) included Sphaerosominae as a subfamily of Endomychidae, which is now recognized as a distinct family, *i.e.* Alexiidae (=Sphaerosomatidae) (Sengupta & Crowson 1973; Lawrence 1982; Ślipiński & Pakaluk 1991; Lawrence & Newton 1995). Similarly, the endomychid subfamilies Merophysiinae and Eupsilobiinae, were formerly placed in Latridiidae and Cerylonidae, respectively, and as such were excluded from Strohecker's checklist. The currently recognized subfamilies Anamorphinae, Leiestinae and Xenomycetinae were considered tribes within the subfamily Mycetaeinae by Strohecker. Since 1953, a few family-level regional checklists have been published for Endomychidae, including a recent checklist of the Endomychidae of Mexico (Arriaga–Varela *et al.* 2007) and the Palaearctic (Rücker & Löbl 2007; Tomaszewska 2007b). There has been no attempt to produce a comprehensive world checklist that incorporates new taxa described since Strohecker (1953a) and that utilizes recently available phylogenetic hypotheses (*e.g.*, Tomaszewska 2000b; Tomaszewska 2005; Robertson *et al.* 2008) to modify the higher-level classification.

Strohecker's monograph (1953a) appears to be the source for endomychid diversity estimates (≈120 genera & 1300 spp.) that are given in recent treatments of the family (*e.g.*, Lawrence 1991; Tomaszewska 2000b; Skelley & Leschen 2002). These figures are now outdated underestimates. This work provides distributional data and current counts of the genera and species for the family and subfamilies, including those taxa known only from the fossil record.

METHODS

This checklist was generated using previously published catalogues to establish a base list and was modified with new taxa and synonymies following an exhaustive search of the Zoological Record (1864–present) and other pertinent literature. In total, 650 references were examined, and 619 were entered into the accompanying bibliography. For simplicity, only the first occurrence of a generic- or species-level name has been included and their use in subsequent catalogues and checklists were only cited if they represented new combinations or spellings. Twelve subfamilies are recognized for Endomychidae following Tomaszewska (2000b): Anamorphinae (=Mychotheninae), Danascelinae, Endomychinae, Epipocinae, Eupsilobiinae

(=Eidoreinae, Cerasommatidiidae), Leiestinae, Lycoperdininae (=Eumorphinae), Merophysiinae (=Holoparamecinae), Mycetaeinae (=Agaricophilinae), Pleganophorinae (=Trochoideinae), Stenotarsinae and Xenomycetinae. The subfamilies, genera and species are arranged in alphabetical order within their respective higher level taxon. To the extent possible, published distributional data were summarized. For species entries from selected regions, distributional data are further subdivided into states, islands and provinces, referenced using either a two- or three-letter abbreviated coden (Supplemental Material 2.1).

RESULTS

Endomychidae is comprised of 1782 species and subspecies in 130 genera organized among 12 subfamilies. For the purposes of this checklist, subspecies are retained as separate entities rather than being treated under the parent species. Of those taxa, 14 species are known only from fossils and represent 12 genera from 6 subfamilies. These taxa are listed separately at the end of the checklist. Among extant taxa, Lycoperdininae and Anamorphinae have the highest generic level diversity, which combined includes ~60% of endomychid genera (Fig. 2.1). Lycoperdininae also has the highest species-level diversity (~40%), with Stenotarsinae a not too distant second (~26%) (Fig. 2.2) due in large part to the speciose genus *Stenotarsus* Perty, 1832, which alone includes 256 species.

One species, *Bystus hirtulus* (Kirsch, 1876), was excluded from the checklist based on its erroneous placement in Endomychidae. One new synonym was proposed for *Symbiotes latus* Redtenbacher, 1849. The merophysiine genus *Cholovocerida* Belon, 1884, previously synonymized erroneously under *Cholovocera* Motschulsky, 1838, is returned to valid status. The genus *Displotera* Reitter, 1887b, is synonomyzed under *Cholovocerida* Belon, 1884, based on priority. Thus, two new combinations are created for *Cholovocerida ecitonis* (Wasmann, 1890) and *Cholovocerida maderae* (Wollaston, 1854). The description by Belon (1884) is consistent with the descriptions of both *Cholovocera* Motschulsky, 1838 and *Displotera* Reitter, 1887b, two similar genera of Merophysiinae. However, no species of *Cholovocera* Motschulsky, 1838 occur in the Western Hemisphere, and *Cholovocerida* Belon, 1884 has priority over *Displotera* Reitter, 1887b as the correct senior synonym.

An unpublished, handwritten notation by Strohecker suggests that the genus *Atrichonota* Arrow, 1925 should be moved from Stenotarsinae to Endomychinae and synonymized under *Endomychus* Panzer, 1795. An examination of Arrow's original description and illustration clearly demonstrate this proposed placement is indeed correct. In fact, Arrow's own comments accompanying the description bear out his uncertainty about the status of this genus and its close affiliation with *Endomychus*. However, we have not had the opportunity to examine any specimens of *Atrichonota* so we have chosen to leave it, along with *Polymus* Mulsant, 1846, as *incertae sedis* following Tomaszewska (2000b, 2005). Likewise, *Cyclotomima* Pic, 1925 and *Opetius* Mulsant, 1851 have been listed as *incertae sedis* following Strohecker (1953a).

Loeblia ceylanica Dajoz, 1972a is newly designated as the type species for the anamorphine genus *Loeblia* Dajoz, 1972a. *Rhymbus hemisphaericus* Gerstaecker, 1858 is newly designated as the type species for the anamorphine genus *Rhymbus* Gerstaecker, 1858. *Rhanis* Dejean, 1836 and *Stenotarsus gigante* Nedved, 1996 are listed as *nomina nuda* based on designations in previous works. *Mycetaea tafilaletica* Smirnoff, 1957 (Mycetaeinae), is newly designated as *nomen nudum*. The first use of this name by Smirnoff (1957) is not accompanied by a description or illustration of any kind. The name appears again in a subsequent paper by Smirnoff (1958) and in a recent electronic resource discussing nutrition in arthropod natural enemies (Legner 2008). No additional references clarifying the status of this species or formally describing it could be identified.

Following Bousquet (2004) and Arriaga–Varela *et al.* (2007), the commonly used name *Amphix* Laporte, 1840 is synonymized under *Corynomalus* Chevrolat, 1836. Thirty-two species that were originally described under *Corynomalus* and subsequently transferred to *Amphix* have been returned to *Corynomalus*.

CHECKLIST OF THE ENDOMYCHIDAE OF THE WORLD

ENDOMYCHIDAE Leach, 1815

Endomychides Leach, 1815: 116.

Fungicolae Latreille, 1825: 406.

Endomychidae Stephens, 1831: 398.

Endomycites Newman, 1834: 420.

Lycoperdinae Redtenbacher, 1844: 117.

Sulcicolles Mulsant, 1846: 1.

Endomychidea Costa, 1850: 1.

Endomycici Gorham, 1873: 1.

Endomychoidea Verhoeff, 1895: 272.

ANAMORPHINAE Strohecker, 1953a

Anamorphini Strohecker, 1953a: 15.

Mychotheninae Sasaji, 1978: 8.

Mychothenidae Sasaji, 1987: 44.

Acritosomatinae Pakaluk & Ślipiński, 1995: 328.

***Aclemmysa* Reitter, 1904**

Aclemmysa Reitter, 1904: 41.

Type species: *Aclemmysa solarii* Reitter, 1904.

algirica Capra, 1924: 139. Algeria.

solarii Reitter, 1904: 42. Italy.

***Acritosoma* Pakaluk & Ślipiński, 1995**

Acritosoma Pakaluk & Ślipiński, 1995: 330.

Type species: *Acritosoma elongatum* Pakaluk & Ślipiński, 1995.

elongatum Pakaluk & Ślipiński, 1995: 332. Peru.

ovatum Pakaluk & Ślipiński, 1995: 334. Mexico.

***Afralexia* Strohecker, 1967**

Afralexia Strohecker, 1967: 241.

Type species: *Afralexia rufa* Strohecker, 1967.

nigra Strohecker, 1967: 242. Congo.

rufa Strohecker, 1967: 243. Congo, Ghana.

***Anagaricophilus* Arrow, 1922**

Anagaricophilus Arrow, 1922: 80.

Type species: *Anagaricophilus pulchellus* Arrow, 1922.

concinnus Vinson, 1950: 142. Mauritius.

longus Strohecker, 1974d: 309. Madagascar.

nitidus Strohecker, 1974d: 308. Madagascar.

octospilotus Strohecker, 1974d: 313. Madagascar.

pulchellus Arrow, 1922: 82. Seychelles.

rugosus Strohecker, 1974d: 309. Madagascar.

stigmatus Strohecker, 1974d: 310. Madagascar.

stillifer Strohecker, 1974d: 307. Madagascar.

vinsoni Strohecker, 1979a: 453. Mauritius.

vulneratus Strohecker, 1974d: 313. Madagascar.

***Anamorphus* LeConte, 1878**

Anamorphus LeConte, 1878: 445.

Type species: *Anamorphus pusillus* LeConte, 1878.

Anamorphus LeConte & Horn, 1883: 120.

Trichopsephus Arrow, 1920a: 78.

niger (Arrow), 1920a: 79. Belize.

Trichopsephus niger Arrow, 1920a: 79.

punctipennis (Gorham), 1898: 338. Grenada.

Dialexia punctipennis Gorham, 1898: 338.

pusillus LeConte, 1878: 445. United States (FL, MD, OK)

tenuicornis (Gorham), 1887–99: 146. Guatemala, Nicaragua, Panama, St. Vincent.

Exysma tenuicornis Gorham, 1887–99: 146.

Trichopsephus tenuicornis: Arrow, 1920a: 78.

waltoni Blatchley, 1918: 423. United States (OH).

***Anamycetaea* Strohecker, 1975c**

Anamycetaea Strohecker, 1975c: 628.

Type species: *Anamycetaea keralae* Strohecker, 1975c.

keralae Strohecker, 1975c: 628. India.

Asymbius **Gorham, 1896**

Asymbius Gorham, 1896: 299.

Type species: *Asymbius crinipes* Gorham, 1896.

claviger Arrow, 1925: 400. Myanmar.

crinipes Gorham, 1896: 299. Myanmar.

formosanus Csiki, 1937: 173. Taiwan.

foveicollis Chûjô & Kiuchi, 1974: 1. Japan.

gigas Strohecker, 1979e: 81. Borneo.

hamulatus Arrow, 1926a: 251. India, Sumatra.

indicus Strohecker, 1982b: 308. India.

marginatus Arrow, 1927: 113. Sumatra.

minutus Arrow, 1926a: 250. Sumatra.

rufus Arrow, 1925: 401. India.

sinensis Strohecker, 1982b: 308. China.

Austroclemmus **Strohecker, 1953a**

Austroclemmus Strohecker, 1953a: 18.

Type species: *Rhymbus saltensis* Weise, 1906.

bonariensis (Steinheil), 1869: 257. Argentina.

Symbiotes bonariensis Steinheil, 1869: 257.

bruchi (Weise), 1906: 231. Argentina.

Rhymbus bruchi Weise, 1906: 231.

Bystus bruchi: Strohecker, 1953a: 21.

saltensis (Weise), 1922: 40. Argentina.

Rhymbus saltensis Weise, 1922: 40.

Baeochelys Strohecker, 1974b

Baeochelys Strohecker, 1974b: 539.

Type species: *Baeochelys umbrosus* Strohecker, 1974b.

humicola Strohecker, 1974b: 540. D.R. Congo.

plagiatus Strohecker, 1980b: 47. Kenya.

umbrosus Strohecker, 1974b: 539. D.R. Congo, Uganda.

Bryodryas Strohecker, 1974d

Bryodryas Strohecker, 1974d: 312.

Type species: *Bryodryas lunidorsum* Strohecker, 1974d.

lunidorsum Strohecker, 1974d: 312. Madagascar.

Bystodes Strohecker, 1953a

Bystodes Strohecker, 1953a: 19.

Type species: *Bystodes paulus* Strohecker, 1953a.

africanus Strohecker, 1962a: 54. Congo, D.R. Congo.

angustus Strohecker, 1974a: 150. Sri Lanka.

ceylonicus (Arrow), 1925: 397. India, Sri Lanka.

Exysma ceylonica Arrow, 1925: 397.

felix Strohecker, 1974a: 150. Sri Lanka.

flavoapicalis Sasaji, 1990: 70. Japan.

hesperus (Strohecker), 1959c: 186. Cameroon, Ghana.

Geoendomychus hesperus Strohecker, 1959c: 186.

kidoi Sasaji, 1990: 71. Japan.

lugubris Strohecker, 1974a: 150. Sri Lanka.

orbicularis (Gorham), 1887: 652. China, Japan.

Symbiotes orbicularis Gorham, 1887: 652.

Idiophyes orbicularis: Strohecker, 1953a: 25.

paulus Strohecker, 1953a: 19. Philippines (MDO).

taiwanensis Sasaji, 1970: 1. Taiwan, Vietnam.

yaeyamensis Sasaji, 1990: 72. Japan.

***Bystus* Guérin–Méneville, 1857c**

Bystus Guérin–Méneville, 1857c: 270.

Type species: *Bystus coccinelloides* Guérin–Méneville, 1857c.

Rhymbus Gerstaecker, 1858: 347.

Type species: *Rhymbus hemisphaericus* Gerstaecker, 1858. [new designation]

Rymbus Costa, Vanin & Casari-Chen, 1988. Misspelling.

apicalis (Gerstaecker), 1858: 350. Colombia, Guatemala, Mexico.

Rhymbus apicalis Gerstaecker, 1858: 350.

coccinelloides Guérin–Méneville, 1857c: 270. Colombia.

decipiens (Gorham), 1875a: 21. Brasil.

Rhymbus decipiens Gorham, 1875a: 21.

decorator Leschen & Carlton, 1993: 37. Peru.

drakei (Weise), 1903: 206. Paraguay.

Rhymbus drakei Weise, 1903: 206.

fibulatus (Gorham), 1887–99: 144. Mexico.

Rhymbus fibulatus Gorham, 1887–99: 144.

foveatus Strohecker, 1957a: 259. Venezuela.

globosus (Gorham), 1898: 337. Colombia, Grenada.

Rhymbus globosus Gorham, 1898: 337.

hemisphaericus (Gerstaecker), 1858: 349. Belize, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama.

Rhymbus hemisphaericus Gerstaecker, 1858: 349.

limbatus (Gorham), 1873a: 63. Mexico.

Rhymbus limbatus Gorham, 1873a: 63.

pallidulus (Gerstaecker), 1858: 351. Belize, Brasil.

Rhymbus pallidulus Gerstaecker, 1858: 351.

Rhymbus pallidus Costa, Vanin & Casari–Chen, 1988: 201.

Rymbus pallidus Costa, Vanin & Casari–Chen, 1988: pl. 96.

piceus (Gorham), 1887–99: 143. Panama.

Rhymbus piceus Gorham, 1887–99: 143.

rhizobioides (Gorham), 1875a: 20. Brasil.

Rhymbus rhizobioides Gorham, 1875a: 20.

rufus (Weise), 1903: 206. Argentina, Paraguay.

Rhymbus rufus Weise, 1903: 206.

seminulum (Gorham), 1873a: 56. French Guiana.

Rhymbus seminulum Gorham, 1873a: 56.

ulkei (Crotch), 1873: 362. United States (AL, AR, DC, FL, GA, IN, KS, KY, MO, PA, SC, TN).

Alexia ulkei Crotch, 1873: 362.

Rhymbus ulkei: Horn, 1875: 132.

Symbiotes ulkei: LeConte & Horn, 1883: 121.

Parexysma ulkei: Csiki, 1905: 573.

Rhymbus ulkei granulatus Blatchley, 1910: 535.

Exysma ulkei: Arrow, 1920a: 78.

Rhymbus granulatus: Poole & Gentili, 1996: 266.

unicolor (Gorham), 1898: 338. St. Vincent.

Rhymbus unicolor Gorham, 1898: 338.

vestitus (Gorham), 1887–99: 144. Panama.

Rhymbus vestitus Gorham, 1887–99: 144.

***Catapotia* Thomson, 1860**

Catapotia Thomson, 1860: 13.

Type species: *Catapotia laevissima* Thomson, 1860.

Cremnodes Gerstaecker, 1858: 412.

Type species: *Cremnodes glabra* Gerstaecker, 1858.

glabra (Gerstaecker), 1858: 414. Brasil.

Cremnodes glabra Gerstaecker, 1858: 414.

kuhneli (Mader), 1935: 297. Peru.

Cremnodes kuhneli Mader, 1935: 297.

laevissima Thomson, 1860: 14. Costa Rica, Ecuador, Guatemala, Mexico, Nicaragua, Panama, Peru.

pilifer (Mader), 1936a: 26. Peru.

Cremnodes pilifer Mader, 1936a: 26.

schwabi (Mader), 1936a: 25. Peru.

Cremnodes schwabi Mader, 1936a: 25.

***Clemmus* Hampe, 1850**

Clemmus Hampe, 1850: 353.

Type species: *Clemmus troglodytes* Hampe, 1850.

Clemnus Redtenbacher, 1858: 975.

Clemmys Seidlitz, 1887–91: 62.

abbreviatus (Reitter), 1889a: 277. Japan.

Clemnus abbreviatus Reitter, 1889a: 277.

humeralis (Lea), 1921a: 368. Australia (QLD).

Idiophyes humeralis Lea, 1921a: 368.

minor (Crotch), 1873: 362. United States (AL, AR, DC, GA, IL, IN, KS, KY, LA, MO, OK, VA).

Alexia minor Crotch, 1873: 362.

Rhymbus minutus Gorham, 1873a: 56.

Rhymbus minor: Csiki, 1901a: 42.

troglodytes Hampe, 1850: 353. Austria, Bulgaria, Croatia, Czech Republic, Hungary, Italy, Romania, Slovakia, Slovenia.

***Coryphus* Csiki, 1902b**

Coryphus Csiki, 1902b: 352.

Type species: *Coryphus biroi* Csiki, 1902b.

biroi Csiki, 1902b: 352. Papua–New Guinea.

clavatus Strohecker, 1979e: 81. Papua–New Guinea.

irianus Strohecker, 1979e: 82. Papua–New Guinea.

niger Strohecker, 1979e: 82. Papua–New Guinea.

***Cyrtomychus* Kolbe, 1910**

Cyrtomychus Kolbe, 1910: 35.

Type species: *Cyrtomychus coccinelloides* Kolbe, 1910.

coccinelloides Kolbe, 1910: 35. Seychelles.

minor Arrow, 1922: 78. Seychelles.

***Cysalemma* Dajoz, 1970b**

Cysalemma Dajoz, 1970b: 706.

Type species: *Cysalemma africana* Dajoz, 1970b.

africana Dajoz, 1970b: 707. South Africa.

***Dexialia* Sasaji, 1970**

Dexialia Sasaji, 1970: 4.

Type species: *Dexialia ovalis* Sasaji, 1970.

minor (Chûjô), 1941: 82. Japan, Russia (FET), Taiwan.

Symbiotes minor Chûjô, 1941: 82.

Exysma minor: Nakane, 1958: 35.

mirabilis Sasaji, 1995: 22. Japan.

ovalis Sasaji, 1970: 4. Taiwan. Vietnam.

spectabilis Sasaji, 1984: 32. Japan.

***Dialexia* Gorham, 1887-99**

Dialexia Gorham, 1887–99: 146.

Type species: *Dialexia setulosa* Gorham, 1887–99.

globosa Arrow, 1926a: 252. Sumatra.

hisanoi Sasaji, 1978: 12. Japan.

setulosa Gorham, 1887–99: 147. Guatemala.

testudo Arrow, 1926a: 253. Sumatra.

thoracica (Weise), 1903: 205. Tanzania.

Rhymbus thoracicus Weise, 1903: 205.

Bystus thoracicus: Strohecker, 1953a: 22.

Pararhymbus thoracicus: Strohecker, 1953a: 20.

***Endocoelus* Gorham, 1886**

Endocoelus Gorham, 1886: 162.

Type species: *Endocoelus orbicularis* Gorham, 1886.

contractus (Gorham), 1896: 298. India, Myanmar.

Stenotarsus contractus Gorham, 1896: 298.

idius Strohecker, 1983a: 338. India.

minor Strohecker, 1974a: 153. Sri Lanka.

orbicularis Gorham, 1886: 162. Sri Lanka.

***Erotendomychus* Lea, 1922**

Erotendomychus Lea, 1922: 302.

Type species: *Erotendomychus bimaculatus* Lea, 1922.

bimaculatus Lea, 1922: 303. Australia (NSW, VIC).

dentatus Tomaszewska 2004b: 399. Australia (QLD).

dorrigo Tomaszewska 2004b: 400. Australia (NSW).

elongatus Tomaszewska 2004b: 402. Australia (QLD).

emarginatus Tomaszewska 2004b: 403. Australia (NSW).

erectus Tomaszewska 2004b: 404. Australia (QLD).

joalah Tomaszewska 2004b: 405. Australia (NSW, QLD).

kirrama Tomaszewska 2004b: 407. Australia (QLD).

lawrencei Tomaszewska 2004b: 407. Australia (QLD).

leai Tomaszewska 2004b: 409. Australia (QLD).

micropunctatus Tomaszewska 2004b: 411. Australia (QLD).

micrus Tomaszewska 2004b: 412. Australia (NSW).

ovatus Tomaszewska 2004b: 412. Australia (QLD).

peckorum Tomaszewska 2004b: 414. Australia (NSW).

yeatesi Tomaszewska 2004b: 417. Australia (QLD).

***Exysma* Gorham, 1887-99**

Exysma Gorham, 1887–99: 145.

Type species: *Exysma laevigata* Gorham, 1887–99.

Parexysma Csiki, 1905: 573.

Type species: *Exysma parvula* Gorham, 1887–99.

laevigata Gorham, 1887–99: 145. Mexico, Panama.

orbicularis Gorham, 1887–99: 146. Guatemala.

Exysma spherica Arrow, 1920a: 77.

parvula Gorham, 1887–99: 145. Costa Rica, Guatemala.

Parexysma parvula: Csiki, 1905: 573.

***Exysmodes* Dajoz, 1970a**

Exysmodes Dajoz, 1970a: 245.

Type species: *Exysmodes pubescens* Dajoz, 1970a.

pubescens Dajoz, 1970a: 246. South Africa.

Geoendomychus Lea, 1922

Geoendomychus Lea, 1922: 304.

Type species: *Geoendomychus pubescens* Lea, 1922.

assamensis Strohecker, 1983a. 336. India.

contusus Strohecker, 1974d: 314. Madagascar.

csikii (Weise), 1903: 204. Tanzania.

Rhymbus csikii Weise, 1903: 204.

Bystus csikii: Strohecker, 1953a: 22.

Pararhymbus csikii: Strohecker, 1953a: 20.

flavinodis Arrow, 1926a: 252. Sumatra.

glaber Lea, 1922: 304. Australia (QLD).

mus Arrow, 1927: 113. Sumatra.

oculatus Arrow, 1922: 80. Seychelles.

partitus (Weise), 1903: 205. Tanzania.

Rhymbus partitus Weise, 1903: 205.

Bystus partitus: Strohecker, 1953a: 22.

Pararhymbus partitus: Strohecker, 1953a: 20.

pubescens Lea, 1922: 304. Australia (LHI).

punctatus Arrow, 1926a: 251. Sumatra.

Idiophyes Blackburn, 1895

Idiophyes Blackburn, 1895: 234.

Type species: *Idiophyes brevis* Blackburn, 1895.

boninensis Sasaji, 1978: 19. Japan.

brevis Blackburn, 1895: 235. Australia.

ceylonica (Arrow), 1925: 397. Sri Lanka.

Exysma ceylonica Arrow, 1925: 397.

duplicata (Fauvel), 1903: 345. New Caledonia.

Sphaerosoma duplicatum Fauvel, 1903: 345.

eumetopus Strohecker, 1974a: 152. Sri Lanka.

garambae Strohecker, 1962a: 53. Congo, D.R. Congo.

indicus (Arrow), 1925: 398. India.

Exysma indica Arrow, 1925: 398.

niponensis (Gorham), 1874b: 225. China, Japan, Philippines (MDO).

Symbiotes niponensis Gorham, 1874b: 225.

Exysma niponensis: Arrow, 1920a: 77.

novabritanniae Strohecker, 1981a: 345. Papua–New Guinea.

rotundus Strohecker, 1977a: 840. Reunion.

satoi Sasaji, 2003: 299. Japan.

uenoi Sasaji, 1990: 73. Japan.

virescens (Fauvel), 1903: 346. New Caledonia.

Sphaerosoma virescens Fauvel, 1903: 346.

viridis Lea, 1921a: 367. Australia.

***Loeblia* Dajoz, 1972a**

Loeblia Dajoz, 1972a: 212.

Type species: *Loeblia ceylanica* Dajoz, 1972a. [new designation]

ceylanica Dajoz, 1972a: 214. Sri Lanka.

nigra Dajoz, 1972a: 215. Sri Lanka.

***Malagaricophilus* Strohecker, 1974d**

Malagaricophilus Strohecker, 1974d: 311.

Type species: *Malagaricophilus spilotus* Strohecker, 1974d.

spilotus Strohecker, 1974d: 311. Madagascar.

***Micropsephodes* Champion, 1913**

Micropsephodes Champion, 1913: 119.

Type species: *Micropsephodes serraticornis* Champion, 1913.

lundgreni Leschen & Carlton, 2000: 233. United States (FL, GA, LA, SC, TN).

serraticornis Champion, 1913: 119. Guatemala.

***Micropsephus* Gorham, 1887-99**

Micropsephus Gorham, 1887–99: 149.

Type species: *Micropsephus mniophilinus* Gorham, 1887–99.

mniophilinus Gorham, 1887–99: 149. Guatemala, Mexico.

***Mychothenus* Strohecker, 1953a**

Mychothenus Strohecker, 1953a: 24. Replacement for *Mychophilus* Frivaldszky, 1877.

Mychophilus Frivaldszky, 1877: 19.

Type species: *Mychophilus minutus* Frivaldszky, 1877.

asiaticus Sasaji, 1978: 2. Japan.

caspicus (Reitter), 1883: 113. Armenia, Azerbaijan, Georgia, Russia.

Mychophilus caspicus Reitter, 1883: 113.

hirashimai Sasaji, 1990: 68. Japan.

japonica (Reitter), 1889a: 277. Japan, Taiwan.

Alexia japonica Reitter, 1889a: 277.

Mychophilus japonicus: Chûjô, 1938: 406.

minutus (Frivaldszky), 1877: 20. Austria, Croatia, Hungary, Italy, Serbia & Montenegro, Slovakia, Slovenia.

Mychophilus minutus Frivaldszky, 1877: 20.

tropicalis Strohecker, 1962a: 55. Congo, D.R. Congo, Ghana.

***Papuella* Strohecker, 1956a**

Papuella Strohecker, 1956a: 69.

Type species: *Papuella birolecta* Strohecker, 1956a.

birolecta Strohecker, 1956a: 70. Papua–New Guinea.

globosa (Arrow), 1926a: 252. Sumatra.

Dialexia globosa Arrow, 1926a: 252.

***Pararhymbus* Arrow, 1920b**

Pararhymbus Arrow, 1920b: 335.

Type species: *Pararhymbus longicornis* Arrow, 1920b.

longicornis Arrow, 1920b: 335. Vietnam.

***Parasymbius* Arrow, 1920a**

Parasymbius Arrow, 1920a: 80.

Type species: *Parasymbius philippinensis* Arrow, 1920a.

macrocerus Strohecker, 1943: 390. Philippines (LZN).

philippinensis Arrow, 1920a: 80. Philippines (ISB).

Rhymbillus Reichensperger, 1915

Rhymbillus Reichensperger, 1915: 12.

Type species: *Rhymbillus hospes* Reichensperger, 1915.

hospes Reichensperger, 1915: 13. South Africa.

Rhymbomicrus Casey, 1916

Rhymbomicrus Casey, 1916: 139.

Type species: *Alexia lobata* LeConte & Horn, 1883.

Micropsephellus Arrow, 1920a: 79.

Type species: *Micropsephus hemisphaericus* Champion, 1913.

caseyi Pakaluk, 1987: 458. United States (KS, OK).

hemisphaericus (Champion), 1913: 118. Guatemala, Mexico, Nicaragua.

Micropsephus hemisphaericus Champion, 1913: 118.

Micropsephellus hemisphaericus: Arrow, 1920a: 80.

lobatus (LeConte & Horn), 1883: 121. United States (DC, DE, KS, MD, NC, OH, OK, VA)

Alexia lobata LeConte & Horn, 1883: 121.

Rhymbomicrus lobatus: Casey, 1916: 139.

nigripennis (Arrow), 1920a: 80. Grenada, St. Vincent.

Micropsephellus nigripennis Arrow, 1920a: 80.

stephani Pakaluk, 1987: 460. United States (OK).

Symbiotes Redtenbacher, 1849

Symbiotes Redtenbacher, 1849: 198.

Type species: *Symbiotes latus* Redtenbacher, 1849.

Microchondrus Wollaston, 1854: 196.

Type species: *Microchondrus domuum* Wollaston, 1854.

Eponomastus Buysson, 1891: 95.

armatus Reitter, 1881b: 227. Austria, Croatia, Greece, Italy, Slovenia, Switzerland.

dury Blatchley, 1910: 536. Canada (ON), United States (IN, MI, NY, OH, PA, WI).

Symbiotes waltoni Dury, 1912: 103.

Symbiotes oblongus Casey, 1916: 142.

Symbiotes lacustris Casey, 1916: 141.

Symbiotes pilosus Casey, 1916: 143.

gibberosus (Lucas), 1846: 222. Algeria, Austria, Belgium, Canada (AB, BC, ON), Canary Islands, Czech Republic, Denmark, France, Germany, Greece, Hungary, Italy, Liechtenstein, Luxembourg, Madeira, Morocco, Netherlands, Poland, Serbia & Montenegro, Slovakia, Slovenia, Spain, United States (CA, CO, FL, ID, KS, MT, NY, OH, UT, WI).

Cryptophagus gibberosus Lucas, 1846: 222.

Symbiotes pygmaeus Hampe, 1850: 353.

Microchondrus domuum Wollaston, 1854: 197.

Symbiotes minutus Schaufuss, 1882: 544.

Symbiotes duryi Walton, 1912: 461.

Symbiotes montanus Casey, 1916: 140.

impressus Dury, 1912: 102. United States (OH).

latus Redtenbacher, 1849: 198. Austria, Belgium, Denmark, France, Germany, Great Britain, Italy, Liechtenstein, Luxembourg, Netherlands, Serbia & Montenegro.

Symbiotes rubiginosus Reitter, 1880a: 95.

Symbiotes latus var. *roberti* Falcoz & Roman, 1930: 30. [new synonym]

DANASCELINAE Tomaszewska, 2000b

Danascelinae Tomaszewska, 2000b: 494.

***Danascelis* Tomaszewska, 1999**

Danascelis Tomaszewska, 1999: 279.

Type species: *Danascelis elongata* Tomaszewska, 1999.

elongata Tomaszewska 1999: 282. Pakistan.

***Hadromychus* Bousquet & Leschen, 2002**

Hadromychus Bousquet & Leschen, 2002: 293.

Type species: *Hadromychus chandleri* Bousquet & Leschen, 2002.

chandleri Bousquet & Leschen, 2002: 296. Canada (NS, ON, QB), United States (NH).

ENDOMYCHINAE Gerstaecker, 1857

Endomychini Gerstaecker, 1857: 239.

Endomychina Thomson, 1863: 300.

Endomycidae Gorham, 1873a: 28.

Endomychites Chapuis, 1876: 130.

***Bolbomorphus* Gorham, 1887**

Bolbomorphus Gorham, 1887: 647.

Type species: *Bolbomorphus gibbosus* Gorham, 1887.

chinensis Mader, 1955: 69. China.

flavofasciatus Chûjô, 1940: 216. Taiwan.

gibbosus Gorham, 1887: 647. Japan, Taiwan.

mediojunctus (Pic), 1921: 1. China, Vietnam.

Encymon mediojunctus Pic, 1921: 1.

Eucteanus mediojunctus: Mader, 1936b: 64.

Eucteanus mediojunctus var. *disjunctus* Mader, 1936b: 65.

Bolbomorphus undulatus Pic, 1925: 2.

sexpunctatus Arrow, 1920a: 69. China, Vietnam.

Bolbomorphus quadriguttatus Mader, 1938: 48.

theryi Gorham, 1897: 461. China.

Cyclotoma Mulsant, 1851

Cyclotoma Mulsant, 1851: 71.

Type species: *Cyclotoma testudinaria* Mulsant, 1851.

Panomoea Gerstaecker, 1857: 241.

Type species: *Panomoea coccinellina* Gerstaecker, 1857.

Niteta Weise, 1890: 21.

Type species: *Niteta quatuordecimpunctata* Weise, 1890.

acleta Strohecker, 1958a: 44. Philippines (PWN).

alleni Tomaszewska, 2003a: 204. India.

borneensis (Gorham), 1875a: 21. Borneo.

Panamoea borneensis Gorham, 1875a: 21.

Niteta duodecimpunctata Weise, 1890: 22.

cingalensis (Gorham), 1886: 162. Sri Lanka.

Panamoea cingalensis Gorham, 1886: 162.

coccinellina (Gerstaecker), 1857: 242. Philippines (LZ, MDO).

Panomoea coccinellina Gerstaecker, 1857: 242.

Cyclotoma testudinaria var. Mulsant, 1851: 72.

Niteta quatuordecimpunctata Weise, 1890: 22.

conica Tomaszewska, 2000a: 354. Taiwan.

formosana Chûjô, 1938: 403. Taiwan.

indiana (Gorham), 1897: 462. Cambodia, India, Laos, Myanmar, Taiwan, Vietnam.

Panomoea indiana Gorham, 1897: 462.

merkli Tomaszewska, 2000a: 361. Laos.

monticola Arrow, 1923: 490. India.

nicoleae Tomaszewska, 2000a: 355. Vietnam.

nigra Tomaszewska, 2002d: 204. India.

octomaculata Tomaszewska, 2002d: 206. Myanmar.

quinquepunctata Arrow, 1928: 356. Laos.

sumatrensis (Gorham), 1888: 152. Sumatra.

Panomoea sumatrensis Gorham, 1888: 152.

testudinaria Mulsant, 1851: 71. Java.

Panomoea pardalina Gerstaecker, 1858: 366.

undecimnotata (Frivaldszky), 1883: 133. Borneo.

Panomoea undecimnotata Frivaldszky, 1883: 133.

***Endomychus* Panzer, 1795**

Endomychus Panzer, 1795: 175.

Type species: *Chrysomela coccinea* Linnaeus, 1758.

Cyanauges Gorham [in Gorham & Lewis], 1874: 54.

Type species: *Cyanauges gorhami* Lewis [in Gorham & Lewis], 1874.

Caenomychus Lewis, 1893: 153.

agatae Tomaszewska, 1997a: 240. India.

armeniacus Motschulsky, 1835: 321. Armenia, Georgia, Russia (SET), Ukraine, Iran.

Endomychus scovitzi Falderman, 1837: 411.

atriceps Pic, 1932: 25. Cambodia, China.

atricornis Tomaszewska, 1998: 301. Myanmar.

atripes Pic, 1921: 2. China, Vietnam.

Endomychus curtus Pic, 1927a: 10.

bicolor Gorham, 1875a: 22. India, Nepal.

biguttatus Say, 1824: 96. Canada (NB, NF, NS, ON), United States (AL, AR, AZ, CT, DC, FL, GA, IA, IL, IN, KS, LA, MA, MD, MI, MO, MS, NC, NH, NJ, NY, OH, PA, RI, TN, TX, WI, VA).

chinensis Csiki, 1937: 174. China, Taiwan

coccineus (Linnaeus), 1758: 371. Albania, Austria, Belarus, Belgium, Bosnia, Bulgaria, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Germany, Great Britain, Greece, Hungary, Ireland, Italy, Latvia, Liechtenstein, Luxembourg, Macedonia, Moldavia, Netherlands, Norway, Poland, Romania, Russia (NET), Serbia & Montenegro, Slovakia, Slovenia, Spain, Sweden, Switzerland, Ukraine.

Chrysomela coccinea Linnaeus, 1758: 371.

Chrysomela quadrimaculata deGeer, 1775: 301.

Galleruca coccinea: Fabricius, 1792: 20.

Endomychus coccineus var. *biehli* Reitter, 1888: 424.

Endomychus coccineus var. *krynickii* Ganglbauer, 1899b: 940.

Endomychus quadripunctatus Gorham, 1873a: 64.

Cyanauges quadripunctatus: Gorham, 1887: 650.

divisus Arrow, 1920b: 334. Cambodia, Laos, Myanmar, Vietnam.

Endomychus bicolor Gorham, 1896: 302.

flavus Strohecker, 1943: 390. China.

foveolatus Tomaszewska, 2002b: 151. China, Myanmar.

gorhami (Lewis)[in Gorham & Lewis], 1874: 55. China, Japan.

Cyanauges gorhami Lewis [in Gorham & Lewis], 1874: 55.

Caenomychus gorhami: Mader, 1936d: 100.

Caenomychus violaceipennis Mader, 1941a: 170.

Endomychus gorhami kyushuensis Sasaji, 1978: 25.

humeralis (Pic), 1922b: 10. China, India, Pakistan.

Caenomychus humeralis Pic, 1922b: 10.

jureceki Mader, 1936c: 69. Russia (FET).

limbatus (Horn), 1870: 96. Canada (BC), United States (CA, ID, NV, OR, WA).

Mycetina limbata Horn, 1870: 96.

Mycetina endomychoides Fall, 1901: 304.

Aphorista limbata Csiki, 1910: 39.

micrus Tomaszewska, 1997a: 231. Pakistan.

mroczkowskii Tomaszewska, 1997a: 227. Nepal.

nigricapitatus Tomaszewska, 2002b: 152. China.

nigriceps Chûjô, 1938: 404. China, Taiwan.

Caenomychus muelleri Mader, 1955: 71.

nigricornis Chûjô, 1938: 405. Taiwan.

nigripes Mader, 1955: 70. China.

nigropiceus (Gorham), 1887: 651. Japan.

Cyanauges nigropiceus Gorham, 1887: 651.

Caenomychus nigropiceus: Ohta, 1931: 234.

Endomychus hiranoi Sasaji, 1978: 27.

pakistanicus Tomaszewska, 1997a: 231. Pakistan.

plagiatus (Gorham), 1887: 650. Japan.

Cyanauges plagiatus Gorham, 1887: 650.

Caenomychus plagiatus: Ohta, 1931: 235.

Endomychus plagiatus interruptus Nakane, 1994: 82.

punctatus Arrow, 1928: 355. China, Vietnam.

Endomychus divisus punctatus Arrow, 1928: 355.

quadra (Gorham), 1887: 651. Japan.

Cyanauges quadra Gorham, 1887: 651.

Caenomychus quadratus Ohta, 1931: 235.

Endomychus ohbayashii Nakane, 1951: 116.

Endomychus ohbayashii shirahatai Nakane, 1951: 117.

Endomychus ohbayashii kojimai Nakane, 1994: 83.

rogeri Tomaszewska, 1997a: 238. Vietnam.

rufipes Pic, 1946a: 80. Kenya.

sasajii Tomaszewska, 1998: 301. Taiwan.

sauteri Chûjô, 1938: 405. Taiwan.

slipinskii Tomaszewska, 1997a: 237. Myanmar.

thoracicus Charpentier, 1825: 245. Austria, Italy, Romania.

tomishimai Nakane, 1994: 82. Japan.

tonkineus Pic, 1922b: 9. Vietnam.

yunnani Tomaszewska, 1997a: 227. China.

***Eucteanus* Gerstaecker, 1857**

Eucteanus Gerstaecker, 1857: 240.

Type species: *Eucteanus coelestinus* Gerstaecker, 1857.

Homalosternus Guérin–Méneville, 1857b: 581.

Type species: *Eumorphus hardwickei* Hope, 1831.

coelestinus Gerstaecker, 1857: 240. India.

Eucteanus hardwickei Csiki, 1910: 54.

cruciger Gorham, 1897: 460. India.

dohertyi Gorham, 1897: 461. China, Myanmar.

elegans Arrow, 1937: 110. China, Myanmar.

eucerus Arrow, 1920a: 68. India.

hardwickei (Hope), 1831: 22. Nepal, Taiwan.

Eumorphus hardwickei Hope, 1831: 22.

humeralis Arrow, 1920a: 67. Myanmar.

latipennis Arrow, 1937: 110. Myanmar.

marseuli Gorham, 1873a: 56. India.

mussuricus Arrow, 1925: 352. India.

subovatus (Pic), 1925: 2. China.

Bolbomorphus subovatus Pic, 1925: 2.

vicinus Arrow, 1920a: 67. India.

***Meilichius* Gerstaecker, 1857**

Meilichius Gerstaecker, 1857: 240.

Type species: *Meilichius nigricollis* Gerstaecker, 1857.

Thelgetrum Gorham, 1875b: 314.

Type species: *Thelgetrum ampliatum* Gorham, 1875b.

Milichius Gemminger & Harold, 1876: 3737.

Gibbiger Csiki, 1900b: 375.

Type species: *Milichius fasciatus* Heller, 1898.

aeneoniger Strohecker, 1944: 141. India.

ampliatus (Gorham), 1875b: 314. Philippines (LZN, MDO).

Thelgetrum ampliatum Gorham, 1875b: 314.

apicicornis Arrow, 1920a: 72. Borneo.

biplagiatus Arrow, 1920a: 73. Borneo.

brevicollis Arrow, 1920a: 72. Borneo.

callosus Pic, 1930c: 19. Borneo.

erotyloides Strohecker, 1951a: 166. China.

expetitus Gorham, 1885: 523. Sumatra.

fasciatus (Heller), 1898: 40. Celebes.

Milichius fasciatus Heller, 1898: 40.

ferrugineus Frivaldszky, 1883: 132. Borneo.

fuscipes Arrow, 1920a: 70. Sumatra.

geminatus Strohecker, 1958a: 45. Philippines (LZN).

impressicollis Strohecker, 1943: 389. Philippines (LZN).

javanicus Csiki, 1900b: 376. Java.

klapperichi Mader, 1941b: 938. China, Taiwan.

multimaculatus Sasaji, 1970: 15. Taiwan.

nigricollis Gerstaecker, 1857: 241. Borneo, Malaysia, Sumatra.

ornatus Arrow, 1920b: 332. Laos.

pachycerus Strohecker, 1951a: 166. Borneo.

politus Arrow, 1920a: 71. Sumatra.

EPIPOCINAE Gorham, 1873a

Epipocinae Gorham, 1873a: 20.

Epipocini Csiki, 1901a: 31.

Epipocites Chapuis, 1876: 87.

Anidrytus Gerstaecker, 1858

Anidrytus Gerstaecker, 1858: 256.

Type species: *Anidrytus bipunctatus* Gerstaecker, 1858.

angustulus Gerstaecker, 1858: 269. Colombia.

Anidrytus bisignatus Gerstaecker, 1858: 268.

amazonicus Gorham, 1873a: 46. Brasil, Colombia, Paraguay, Peru.

arrowi Strohecker, 1957a: 269. Brasil.

atratulus Gerstaecker, 1858: 273. Bolivia, Brasil, Panama, Paraguay.

batesi Strohecker, 1997: 175. Brasil.

bechyneorum Strohecker, 1997: 175. Venezuela.

bipunctatus Gerstaecker, 1858: 257. Brasil.

cardisoma Strohecker, 1997: 179. Bolivia.

championi (Gorham), 1887–99: 133. Panama.

Systaechea championi Gorham, 1887–99: 133.

cinctipennis (Guérin–Méneville), 1857c: 267. French Guiana.

Epipocus cinctipennis Guérin–Méneville, 1857c: 267.

circumcinctus Strohecker, 1997: 175. Guatemala.

compactus Strohecker, 1997: 173. Colombia, Peru.

concolor Kirsch, 1876: 112. Brasil, Colombia, Ecuador, Peru.

consobrinus Strohecker, 1957a: 270. Brasil.

contractus Gerstaecker, 1858: 263. Costa Rica, Panama.

Anidrytus dolosus Gorham, 1887–99: 127.

cupreatus Strohecker, 1957a: 269. Peru.

decoratus Arrow, 1920a: 46. Guatemala.

Anidrytus depressus Gorham, 1887–99: 128.

ephippium Gerstaecker, 1858: 264. French Guiana, Panama, Suriname.

Anidrytus fallaciosus Gorham, 1873a: 47.

fuliginosus (Guérin–Méneville), 1857c: 266. Colombia, Mexico.

Epipocus fuliginosus Guérin–Méneville, 1857c: 266.

fuscus Arrow, 1920a: 47. Brasil.

gerstaeckeri Kirsch, 1876: 112. Peru.

gibbosus Strohecker, 1997: 173. Colombia.

glaber Kirsch, 1876: 113. Brasil, Peru.

grandis Strohecker, 1997: 179. French Guiana.

guatemalae Arrow, 1920a: 46. Guatemala, Honduras.

Anidrytus liquefactus Gorham, 1887–99: 126.

helvolus Gerstaecker, 1858: 272. French Guiana, Guyana, Suriname, Venezuela.

Ephebus ignobilis Gorham, 1875a: 17.

hilaris Gerstaecker, 1858: 271. Brasil.

humeralis Arrow, 1920a: 46. Colombia, Ecuador, Peru.

humerosus Strohecker, 1997: 178. Bolivia, Peru.

humilis Gorham, 1873a: 48. Costa Rica, Nicaragua, Panama.

juvencus (Guérin–Méneville), 1857c: 266. Colombia.

Epipocus juvencus Guérin–Méneville, 1857c: 266.

kirschi Strohecker, 1957a: 269. Peru.

latus (Chevrolat), 1844: 317. Brasil.

Lycoperdina lata Chevrolat, 1844: 317.

liquefactus Gorham, 1873a: 47. Bolivia, Colombia, Costa Rica, French Guiana, Guatemala, Panama, Peru.

lugubris Gerstaecker, 1858: 270. Colombia, Venezuela.

major Strohecker, 1997: 177. Brasil.

marginatus (Fabricius), 1801: 504. Brasil, French Guiana.

Endomychus marginatus Fabricius, 1801: 504.

Epipocus cinctipennis Guérin–Méneville, 1857c: 267.

mexicanus Strohecker, 1997: 176. Mexico.

nigricans (Guérin–Méneville), 1857c: 265. Argentina, Brasil, Paraguay.

Epipocus nigricans Guérin–Méneville, 1857c: 265.

nigropiceus Gorham, 1887–99: 126. Costa Rica, Panama.

nimbiferus Strohecker, 1997: 170. Brasil, Colombia.

nitidularius Gerstaecker, 1858: 262. Mexico.

ovatulus Gerstaecker, 1858: 262. Colombia, Venezuela.

pantherinus (Gorham), 1887–99: 131. Panama.

Epopterus pantherinus Gorham, 1887–99: 131.

parallelus Gerstaecker, 1858: 256. Brasil.

Ephebus depressus Gorham, 1875a: 17.

Anidrytus depressus: Arrow, 1920a: 46.

pardalinus Strohecker, 1943: 388. Costa Rica.

parki Strohecker, 1997: 171. Panama.

pilosus Arrow, 1920a: 47. Brasil.

plagiatus Gerstaecker, 1858: 259. French Guiana.

porcus Strohecker, 1957a: 269. Colombia.

quadripunctatus Gorham, 1886: 159. Brasil.

scalaris (Gorham), 1887–99: 130. Nicaragua, Panama.

Epopterus scalaris Gorham, 1887–99: 130.

spadiceus (Guérin–Méneville), 1857c: 266. Colombia.

Epipocus spadiceus Guérin–Méneville, 1857c: 266.

stenus Strohecker, 1979c: 716. Brasil.

tenuipes Strohecker, 1957a: 271. Bolivia.

trinitatis Strohecker, 1997: 177. Trinidad and Tobago, Venezuela.

unicolor Kirsch, 1876: 111. Peru.

variegatus (Guérin–Méneville), 1857c: 266. Brasil.

Epipocus variegatus Guérin–Méneville, 1857c: 266.

Anidrytus singularis Gerstaecker, 1858: 260.

***Ephebus* Gerstaecker, 1858**

Ephebus Gerstaecker, 1858: 293.

Type species: *Ephebus cardinalis* Gerstaecker, 1858.

cardinalis Gerstaecker, 1858: 294. Colombia, Venezuela.

chontalesianus Gorham, 1887–99: 132. Costa Rica, Guatemala, Guyana, Honduras, Nicaragua, Panama.

convexiusculus Gerstaecker, 1858: 296. Brasil.

exclusus Strohecker, 1975d: 335. Guatemala.

hirtulus Gerstaecker, 1858: 297. Bolivia, Brasil.

longulus Stroheckjer, 1975d: 336. Brasil.

piceus Gorham, 1887–99: 131. Colombia, Guatemala, Nicaragua.

pumilus Gerstaecker, 1858: 297. Colombia.

sulcatus Strohecker, 1975d: 336. Colombia, El Salvador, Mexico.

terminatus Gerstaecker, 1858: 295. Colombia, Venezuela.

***Epipocus* Germar, 1843**

Epipocus Germar, 1843: 86.

Type species: *Endomychus tibialis* Chevrolat, 1834.

alvaradi Strohecker, 1977c: 311. Guatemala.

aztecus Strohecker, 1977c: 307. Mexico.

balli Strohecker, 1977c: 311. Guatemala, Mexico.

bifidus Gerstaecker, 1858: 248. Costa Rica, Guatemala, Honduras, Nicaragua.

brunneus Gorham, 1887–99: 124. Mexico.

Epipocus mollicomus Arrow, 1920a: 45.

caribanus Strohecker, 1977c: 322. Honduras.

cinctus LeConte, 1853: 358. Guatemala, Mexico, United States (AZ, TX).

Epipocus mutilatus Gerstaecker, 1858: 249.

cryptus Strohecker, 1977c: 320. Mexico.

figuratus Gerstaecker, 1858: 247. Belize, Costa Rica, Guatemala, Honduras, Mexico.

flavipes Strohecker, 1977c: 322. Mexico.

funeralis Strohecker, 1977c: 323. Colombia.

gorhami Strohecker, 1977c: 308. Mexico, United States (AZ).

guatemalae Strohecker, 1977c: 321. Guatemala.

guatemoc Strohecker, 1977c: 324. Mexico.

itzanus Strohecker, 1977c: 320. Guatemala.

longicornis Gerstaecker, 1858: 255. Mexico.

Epipocus binotatus Gorham, 1887–99: 124.

manni Strohecker, 1977c: 321. Costa Rica, Guatemala.

mixtecus Strohecker, 1977c: 323. Mexico.

nanus Strohecker, 1977c: 306. United States (AZ).

opacus Strohecker, 1977c: 306. United States (AZ, CA).

politus politus Guérin–Méneville, 1857c: 265. Colombia.

Epipocus politus Guérin–Méneville, 1857c: 265.

politus gerstaeckeri Strohecker, 1977c: 317. Colombia.

Epipocus politus Gerstaecker, 1858: 242.

punctatus LeConte, 1853: 358. Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Panama, United States (AL, AR, AZ, FL, GA, IL, LA, MS, NC, TN, TX, VA).

Epipocus bivittatus Gerstaecker, 1858: 243.

Epipocus discoidalis LeConte, 1853: 358.

rufitarsus (Chevrolat), 1835: 123. Costa Rica, Guatemala, Honduras, Mexico.

Endomychus rufitarsus Chevrolat, 1835: 123.

sallaei Gorham, 1887–99: 125. Mexico.

similis Strohecker, 1977c: 315. Guatemala.

subcostatus Gorham, 1887–99: 123. Mexico.

tibialis (Chevrolat), 1834: 94. Belize, Guatemala, Mexico.

Endomychus tibialis Chevrolat, 1834: 94.

Endomychus (*Epipocus*) *tibialis* Chevrolat, 1844: 317.

Epipocus mollicomus Gorham, 1875a: 15.

Epipocus simplicipes Casey, 1916: 146.

toltecus Strohecker, 1977c: 308. Mexico.

tristinoctis Strohecker, 1977c: 321. Mexico.

tristis costaricensis Strohecker, 1977c: 317. Costa Rica.

tristis tristis Guérin–Méneville, 1857c: 265. Colombia, Costa Rica, Panama.

Epipocius tristis Guérin–Méneville, 1857c: 265.

unicolor Horn, 1870: 96. Mexico, United States (AZ, CO, NM).

Epipocus punctipennis Casey, 1916: 145.

Epipocus parvus Arrow, 1920a: 45.

verapacis Strohecker, 1977c: 323. Guatemala.

***Epopterus* Chevrolat, 1844**

Epopterus Chevrolat, 1844: 380.

Type species: *Erotylus ocellatus* Olivier, 1791–92.

annulatus Guérin–Méneville, 1857c: 268. Brasil, Guyana.

anomalus Strohecker, 1997: 164. Colombia, Ecuador.

aravacus Strohecker, 1997: 165. Venezuela.

atriventris Strohecker, 1997: 165. Bolivia, Brasil.

batesi Strohecker, 1957a: 268. Brasil.

bioculatus Strohecker, 1997: 162. French Guiana.

callerianus Strohecker, 1997: 168. Ecuador.

clara Gorham, 1874a: 443. Brasil, Colombia, Peru.

comptus Gorham, 1887–99: 130. Nicaragua.

confusus Strohecker, 1997: 163. Brasil.

Epopterus cucullinus Strohecker 1957a: 267.

cordatus Strohecker, 1957a: 266. Brasil, Venezuela.

crypticus Strohecker, 1997: 166. Brasil.

cucullinus Gorham, 1873a: 49. Brasil, Colombia, Peru.

cyclicus Strohecker, 1957a: 268. Peru.

decempunctatus Gerstaecker, 1858: 290. Colombia, Trinidad and Tobago, Venezuela.

Epopterus bifasciatus Pic, 1931: 9.

deltoideus Strohecker, 1957a: 266. Brasil.

dilectus Gorham, 1875a: 16. Ecuador.

dives Gorham, 1874a: 443. Brasil, Colombia, Peru.

eganus Gorham, 1886: 160. Brasil, Colombia, Peru.

ephippiger Gorham, 1886: 160. Brasil, Colombia, Peru.

fallax Gerstaecker, 1858: 287. Brasil.

fasciatus angustatus Strohecker, 1997: 166. Brasil.

Epopterus angustatus Strohecker, 1957a: 268.

fasciatus fasciatus (Fabricius), 1801: 570. Brasil.

Tritoma fasciatum Fabricius, 1801: 570.

Epopterus fasciatus: Gerstaecker, 1858: 288.

flavolineatus Strohecker, 1957a: 266. Brasil.

flavonotatus Strohecker, 1997: 168. Brasil, French Guiana.

geminus Gerstaecker, 1858: 288. Colombia, Venezuela.

geniculatus Pic, 1931: 9. Bolivia.

gracilis Strohecker, 1997: 164. Peru.

histrio Gerstaecker, 1858: 292. Brasil, French Guiana, Guyana.

lineoguttatus Gorham, 1886: 161. Brasil, Colombia, Peru.

longus Strohecker, 1957a: 268. Brasil.

loretensis Strohecker, 1997: 164. Peru.

mimeticus Strohecker, 1959c: 181. Brasil, Colombia, Peru, Venezuela.

myops Guérin–Méneville, 1857c: 268. Brasil, Colombia.

Epopterus ocellatus myops Csiki, 1901a: 47.

nigerrimus Strohecker, 1957a: 268. Argentina, Brasil.

nigrocinctus Strohecker, 1957a: 264. Brasil, Colombia, Peru, Venezuela.

notatus Strohecker, 1957a: 266. Colombia.

obliquus Strohecker, 1957a: 265. Brasil, Ecuador, Peru.

ocellatus (Olivier), 1791–92: 437. Belize, Bolivia, Brasil, Colombia, French Guiana, Guatemala, Mexico, Nicaragua, Panama.

Erotylus ocellatus Olivier, 1791–92: 437.

Eumorphus ocellatus: Olivier, 1808: 1067.

Epopterus ocellatus var. *annulatus* Guérin–Méneville, 1857c: 268.

Epopterus ocellatus var. *myops* Guérin–Méneville, 1857c: 268.

Epopterus ocellatus var. *differens* Pic, 1932: 20.

partitus kirschi Strohecker, 1997: 160. Colombia, Ecuador.

Epopterus kirschi Strohecker, 1959c: 181.

partitus maculosus (Gorham), 1887–99: 129. Belize, Guatemala, Mexico, Nicaragua.

Epopterus ocellatus maculosus Gorham 1887–99: 129.

partitus partitus Gerstaecker, 1858: 277. Mexico.

Epopterus partitus Gerstaecker, 1858: 277.

parvus Strohecker, 1997: 169. Brasil.

picticollis Strohecker, 1997: 162. Peru.

pictus (Perty), 1832: 111. Brasil.

Endomychus pictus Perty, 1832: 111.

quaesitus Gorham, 1873a: 51. Brasil, Colombia, Peru.

quechuanus Strohecker, 1997: 167. Peru.

reticulatus Strohecker, 1997: 165. Bolivia.

rubiginosus Gerstaecker, 1858: 291. Brasil, French Guiana.

ryei Gorham, 1873a: 50. Brasil, Colombia, Peru.

signaticollis Gerstaecker, 1858: 291. Colombia, Panama, Venezuela.

Epopterus scalaris (in part) Gorham, 1887–99: 130.

similis Strohecker, 1957a: 265. Brasil, Ecuador, Peru.

submaculatus Strohecker, 1997: 169. Bolivia.

testudinarius Gorham, 1873a: 48. Brasil, Colombia, Peru.

tigrinus Gerstaecker, 1858: 278. Brasil.

tomentosus (Guérin–Méneville), 1857c: 266. Brasil.

Epipocus tomentosus Guérin–Méneville, 1857c: 266.

transversus Strohecker, 1957a: 264. Bolivia.

trimaculatus Guérin–Méneville, 1857c: 268. Colombia.

undulatus Guérin–Méneville, 1857c: 269. Argentina, Bolivia, Brasil, Paraguay.

vacuus Gerstaecker, 1857: 283. French Guiana, Panama.

Epopterus scalaris (in part) Gorham 1887–99: 130.

variegatus Erichson, 1847: 184. Bolivia, Peru.

Epopterus decoratus Kirsch, 1876: 114.

Epopterus peruvianus Pic, inedit.

vernicatus Gerstaecker, 1858: 285. Brasil.

vicinus Pic, 1931: 9. Bolivia.

zebra Strohecker, 1957a: 269. Peru.

EUPSILOBIINAE Casey, 1895

Eupsilobiini Casey, 1895: 454.

Euspilobiini Sasaji, 1986: 229.

Eidoreinae Sasaji, 1986: 235.

Cerasommatidiidae Brèthes, 1925: 199.

***Cerasommatidia* Brèthes, 1925**

Cerasommatidia Brèthes, 1925: 199.

Type species: *Cerasommatidia arrowi* Brèthes, 1925.

arrowi Brèthes, 1925: 201. Brasil.

***Chileolobius* Pakaluk & Ślipiński, 1990**

Chileolobius Pakaluk & Ślipiński, 1990: 708.

Type species: *Chileolobius notatus* Pakaluk & Ślipiński, 1990.

cekalovici Pakaluk & Ślipiński, 1990: 710. Chile.

chilensis Pakaluk & Ślipiński, 1990: 711. Chile.

convexus Pakaluk & Ślipiński, 1990: 712. Brasil.

notatus Pakaluk & Ślipiński, 1990: 714. Chile.

sinimbu Pakaluk & Ślipiński, 1990: 714. Brasil.

Eidoreus Sharp, 1885

Eidoreus Sharp, 1885: 146.

Type species: *Eidoreus minutus* Sharp, 1885.

Eupsilobius Casey, 1895: 454.

Type species: *Eupsilobius politus* Casey, 1895.

Pseudalexia Kolbe, 1910: 34.

Type species: *Pseudalexia sechellarum* Kolbe, 1910.

Euspilobius Sasaji, 1986: 230. Misspelling.

minutus Sharp, 1885: 146. Seychelles, Samoa, United States (HI).

Pseudalexia sechellarum Kolbe, 1910: 34.

japonicus Sasaji, 1991: 18.

politus (Casey), 1895: 454. United States (FL).

Eupsilobius politus Casey, 1895: 454.

Evolocera Sharp, 1902

Evolocera Sharp, 1902: 632.

Type species: *Evolocera championi* Sharp, 1902.

Adamia Tomaszewska, 2000b: 465.

Type species: *Adamia mexicana* Tomaszewska, 2000b.

championi Sharp, 1902: 632. Costa Rica, Guatemala, Mexico.

Adamia mexicana Tomaszewska, 2000b: 466.

Ibicarella Pakaluk & Ślipiński, 1990

Ibicarella Pakaluk & Ślipiński, 1990: 717.

Type species: *Ibicarella plaumanni* Pakaluk & Ślipiński, 1990.

plaumanni Pakaluk & Ślipiński, 1990: 718. Brasil.

rotundata Pakaluk & Ślipiński, 1990: 719. Brasil.

***Microxenus* Wollaston, 1861**

Microxenus Wollaston, 1861: 139.

Type species: *Microxenus laticollis* Wollaston, 1861.

laticollis Wollaston, 1861: 140. South Africa.

LEIESTINAE Thomson, 1863

Leiestina Thomson, 1863: 306.

Leiestini Seidlitz, 1872–75: 38.

Leiestites Chapuis, 1876: 137.

Liesthini Ganglbauer, 1899b: 925.

Rhanes LeConte & Horn, 1883: 120.

Phymaphorina Jakobson, 1905–1916 [1915]: 961.

***Leiestes* Chevrolat, 1836**

Leiestes Chevrolat, 1836: 440.

Type species: *Cryptophagus seminiger* Gyllenhall, 1808.

Liesthes Ganglbauer, 1899b: 925.

fines (Sasaji), 1995: 24. Japan.

Liesthes fines Sasaji, 1995: 24.

menetriesi (Falderman), 1837: 396. Armenia, Azerbaijan, Georgia, Russia.

Triplax menetriesi Falderman, 1837: 396.

seminiger (Gyllenhall), 1808: 178. Austria, Belgium, Bosnia Herzegovina, Belarus, Croatia, Czech Republic, Estonia, Germany, Hungary, Finland, France, Iran, Italy, Japan, Latvia, Lithuania, Luxembourg, Netherlands, Norway, Russia (NET), Poland, Romania, Serbia & Montenegro, Slovakia, Slovenia, Sweden, Switzerland.

Cryptophagus seminiger Gyllenhall, 1808: 178.

***Panaleies* Tomaszewska, 2000c**

Panaleies Tomaszewska, 2000c: 80.

Type species: *Panamomus decoratus* Gorham, 1887.

decoratus (Gorham), 1887: 648. Japan.

Panamomus decoratus Gorham, 1887: 648.

Leiestes decoratus: Strohecker, 1953a: 36.

***Panamomus* Gorham, 1873b**

Panamomus Gorham, 1873b: 207.

Type species: *Panamomus lewisi* Gorham, 1873b.

brevicornis Gorham, 1887: 649. Japan.

lewisi Gorham, 1873b: 207. Japan.

sawadai Nakane, 1983: 145. Japan.

yoshidai Kiuchi, 1972: 160. Japan.

***Phymaphora* Newman, 1838**

Phymaphora Newman, 1838: 389.

Type species: *Phymaphora pulchella* Newman, 1838.

californica Horn, 1880: 142. United States (CA, NV, OR, WA).

pulchella Newman, 1838: 389. Canada (MB, NB, NS, ON, PE), United States (AL, AR, DC, DE, GA, IN, KY, LA, MD, MO, NJ, NY, OH, PA, WI, WV, VA, VT).

Lycoperdina puncticollis Ziegler, 1845: 271.

Lycoperdina crassicornis Melsheimer, 1847: 176.

Endomychus crassicornis: Melsheimer, 1806: 27.

***Rhanidea* Strohecker, 1953a**

Rhanidea Strohecker, 1953a: 35. Replacement name.

Rhanis LeConte, 1853: 360.

Type species: *Lycoperdina unicolor* Ziegler, 1845.

Rhanis Dejean, 1836: 440. [*nomen nudum*]

unicolor (Ziegler), 1845: 266. Canada (NB, ON), United States (AL, AR, DC, FL, GA, IL, IN, LA, MD, MI, MO, NC, NJ, NY, OH, PA, TN, TX, WI, WV, VA).

Lycoperdina unicolor Ziegler, 1845: 266.

Lycoperdina apicalis Melsheimer, 1847: 177.

Rhanis unicolor: LeConte, 1853: 360.

Phymaphora haemorrhoidalis Guérin–Méneville, 1857c: 275.

***Stethorhanis* Blaisdell, 1931**

Stethorhanis Blaisdell, 1931: 380.

Type species: *Stethorhanis vandykei* Blaisdell, 1931.

borealis Blaisdell, 1934: 325. Canada (BC).

vandykei Blaisdell, 1931: 381. United States (CA).

LYCOPERDININAE Redtenbacher, 1844

Lycoperdinae Redtenbacher, 1844: 118.

Eumorphidae Gistel, 1856: 382.

Eumorphini Gerstaecker, 1857: 214.

Dapsini Gerstaecker, 1858: 170.

Corynomalidae Gorham, 1873a: 14.

Amphicini Csiki, 1910: 25.

Beccariini Arrow, 1925: 278.

Amphisternini Strohecker, 1964: 320.

***Achuarmychus* Tomaszewska & Leschen, 2004**

Achuarmychus Tomaszewska & Leschen, 2004: 207.

Type species: *Achuarmychus carltoni* Tomaszewska & Leschen, 2004.

carltoni Tomaszewska & Leschen, 2004: 214. Ecuador.

***Acinaces* Gerstaecker, 1858**

Acinaces Gerstaecker, 1858: 178.

Types species: *Acinaces lebasii* Gerstaecker, 1858.

collaris Gerstaecker, 1858: 183. Argentina, Bolivia, Brasil, Uruguay.

Acinaces collaris var. *postfaciatus* Pic, 1939: 20.

gerstaeckeri Tomaszewska, 2003b: 515. Colombia.

humeralis Tomaszewska, 2007a: 250. Peru.

laceratus Gerstaecker, 1858: 182. Argentina, Bolivia, Brasil, Paraguay, Peru, Venezuela.

Acinaces lacertosus ab *junctus* Pic, 1938a: 16.

lebasii lebasii Gerstaecker, 1858: 180. Brasil, Colombia, Ecuador, Honduras, Panama, Peru, Venezuela.

Acinaces lebasii Gerstaecker, 1858: 182.

Acinaces curtus Pic, 1938a: 16.

nataliae Tomaszewska, 2007a: 250. Peru.

nigricollis Gerstaecker, 1858: 184. Brasil, Colombia, French Guiana.

ovatus Tomaszewska, 2003b: 523. Brasil, Paraguay, Venezuela.

pakaluki Tomaszewska, 2003b: 525. Bolivia.

stroheckeri Tomaszewska 2003b: 521. Bolivia, Brasil.

Acinaces lebasii stroheckeri Tomaszewska, 2003b: 521.

unicolor Tomaszewska, 2003b: 527. Brasil, Suriname.

***Amphisternus* Germar, 1843**

Amphisternus Germar, 1843: 85.

Type species: *Amphisternus tuberculatus* Germar, 1843.

caudatus Strohecker, 1964: 342. Borneo.

corallifer Gerstaecker, 1857: 216. Cambodia, China, Laos, Myanmar, Vietnam.

Amphisternus laotianus Achard, 1926: 141.

eruptus Gorham, 1901: 196. Myanmar, Sumatra.

grandjeani Pic, 1930b: 6. Indonesia, Malaysia.

lugubris Strohecker, 1968c: 114. Borneo.

malaccanus Pic, 1930b: 5. Malaysia.

mucronatus Gerstaecker, 1857: 217. Borneo.

Amphisternus cultratus Gorham, 1901: 197.

nanus Strohecker, 1964: 340. Sumatra.

opacus Strohecker, 1957a: 281. Borneo.

rufituberus Wang & Ren, 2007: 460. China.

sordidus Arrow, 1928: 342. Vietnam.

tuberculatus Germar, 1843: 85. Java, Malaysia, Myanmar, Sumatra, Thailand.

verrucosus Gorham, 1897: 456. Java.

vomeratus Gorham, 1901: 197. Malaysia, Sumatra.

***Amphistethus* Strohecker, 1964**

Amphistethus Strohecker, 1964: 337.

Type species: *Amphistethus superbus* Strohecker, 1964.

astarte (Strohecker), 1951a: 159. Taiwan.

Amphisternus astarte 1951a: 159.

phyllocerus (Arrow), 1920a: 15. India.

Amphisternus phyllocerus Arrow, 1920a: 15.

pustulifer (Gorham), 1895: 291. Cambodia, Laos, Myanmar, Thailand, Vietnam.

Amphisternus pustulifer Gorham, 1895: 291.

stroheckeri Tomaszewska, 2001b: 143. Laos.

superbus Strohecker, 1964: 338. Vietnam.

***Ancylopus* Costa, 1850**

Ancylopus Costa, 1850: 13.

Type species: *Endomychus melanocephalus* Olivier, 1808.

bisignatus Gerstaecker, 1858: 192. Cote d'Ivoire, D.R. Congo, Ghana, Nigeria, Senegal.

ceylonicus Strohecker, 1971c: 258. India, Sri Lanka.

conjunctus Strohecker, 1974b: 534. D.R. Congo.

ferrugineus Weise, 1903: 202. South Africa, Tanzania, Zimbabwe.

glaberrimus Strohecker, 1972a: 708. Papua–New Guinea.

leleupi Strohecker, 1962b: 76. D.R. Congo.

madecassus Strohecker, 1955c: 154. Madagascar.

melanocephalus (Olivier), 1808: 1073. Bulgaria, Hungary, Italy, Spain.

Endomychus melanocephalus Olivier, 1808: 1073.

meridionalis Strohecker, 1962b: 76. Congo, D.R. Congo, Gabon, Rwanda.

natalensis Gerstaecker, 1858: 78. Burundi, Congo, Rwanda, South Africa.

neglectus Dajoz, 1972c: 1047. Borneo.

phungi borealior Strohecker, 1972a: 708. China.

phungi phungi Pic, 1926: 10. China, Japan, Tibet, Vietnam.

pictus asiaticus Strohecker, 1972a: 706. China, India, Japan, Taiwan, Vietnam.

pictus indianus Strohecker, 1972a: 706. Afghanistan, India, Nepal.

pictus papuanus Strohecker, 1972a: 705. Malaysia, Papua–New Guinea.

pictus philippinicus Strohecker, 1972a: 705. Philippines (MDO).

pictus pictus (Wiedemann), 1823: 78. Borneo, Celebes, Java.

Eumorphus pictus Wiedemann, 1823: 78.

pictus plicatus Pic, 1930c: 10. Sumatra.

pulcher Strohecker, 1962b: 77. D.R. Congo.

quadrimaculatus Pic, 1946a: 80. Kenya.

rufipes Achard, 1926: 141. Cameroon, Congo, D.R. Congo, Gabon, Ghana.

villiersi Dajoz, 1972c: 1046. India, Japan.

***Aphorista* Gorham, 1873a**

Aphorista Gorham, 1873a: 45.

Type species: *Epipocus laetus* LeConte, 1853.

laeta (LeConte), 1853: 358. Canada (BC), United States (CA, ID, OR, WA, WY).

Epipocus laetus LeConte, 1853: 358.

Mycetina laeta: Gerstaecker, 1858: 239.

morosa (LeConte), 1859: 82. United States (AZ, CA, CO, NM, OR, UT).

Mycetina morosa LeConte, 1859: 82.

Aphorista humeralis Gorham, 1873a: 45.

Mycetina pallida Horn, 1870: 96.

vittata (Fabricius), 1787: 44. Canada (ON), United States (AL, AR, CT, DC, FL, GA, IL, IN, LA, MA, MD, MI, MO, NC, NJ, NY, OH, PA, RI, TN, TX, WI, WY, VA).

Tritoma vittata Fabricius, 1787: 44.

Endomychus lineatus Olivier, 1808: 1072.

Eumorphus distinctus Say, 1825: 303.

Aphorista ovipennis Casey, 1916: 144.

***Archipines* Strohecker, 1953a**

Archipines Strohecker, 1953a: 57. Replacement name for *Phalantha* Gerstaecker, 1858.

Phalantha Gerstaecker, 1858: 202.

Type species: *Phalantha exsanguis* Gerstaecker, 1858.

apicicornis apicicornis (Pic), 1930a: 66. Brasil, Peru.

Phalantha apicicornis Pic, 1930a: 66.

Archipines apicicornis: Strohecker, 1953a: 58.

apicicornis fairmairei Tomaszewska, 2002a: 371. Peru.

championi (Gorham), 1887–99: 119. Colombia, Costa Rica, Panama.

Phalantha championi Gorham, 1887–99: 119.

Phalantha multinotata Pic, 1929: 16.

Archipines multinotata: Strohecker, 1953a: 58.

elongata (Pic), 1928b: 1. Argentina, Brasil, Paraguay.

Phalantha elongata Pic, 1928b: 1.

Phalantha elongata var. *interrupta* Pic, 1928b: 1.

exsanguis exsanguis (Gerstaecker), 1858: 204. Colombia, Panama, Venezuela.

Phalantha exsanguis Gerstaecker, 1858: 204.

Archipines exsanguis: Strohecker, 1953a: 58.

Phalantha quadrimaculata Pic, 1928b: 1.

Archipines quadrimaculata: Strohecker, 1953a: 58.

exsanguis sanestebani Tomaszewska, 2002a: 374. Venezuela.

flavida (Pic), 1928b: 1. Brasil, Colombia, French Guiana, Guyana, Suriname, Venezuela.

Phalantha flavida Pic, 1928b: 1.

Phalantha flavida var. *lunulata* Pic, 1930a: 66.

Archipines grandis Strohecker, 1957a: 273.

intricata (Gorham), 1887–99: 119. Belize, Colombia, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama.

Phalantha intricata Gorham, 1887–99: 119.

macromaculata Tomaszewska, 2002a: 377. Peru.

macrospilota Strohecker, 1957a: 273. Brasil, Peru.

oberthuri Tomaszewska, 2002a: 378. Brasil.

peruviensis Tomaszewska, 2002a: 379. Peru.

pictipennis (Gorham), 1875b: 313. Brasil, Guyana.

Phalantha pictipennis Gorham, 1875b: 313.

unicolor Tomaszewska, 2002a: 382. Brasil.

variegata (Gorham), 1873a: 43. Brasil.

Phalantha variegata Gorham, 1873a: 43.

***Avencymon* Strohecker, 1971b**

Avencymon Strohecker, 1971b: 38.

Type species: *Ancylopus concolor* Strohecker, 1951a.

bicolor Tomaszewska, 2003c: 709. Indonesia.

ruficephalus (Ohta), 1931: 221. China, Indonesia, Philippines, Taiwan.

Encymon ruficephalus Ohta, 1931: 221.

Ancylopus concolor Strohecker, 1951a: 159.

Avencymon concolor: Strohecker, 1971b: 38.

***Beccariola* Arrow, 1943**

Beccariola Arrow, 1943: 129. Replacement name for *Beccaria* Gorham, 1885.

Beccaria Gorham, 1885: 521.

Type species: *Beccaria papuensis* Gorham, 1885.

bakeri (Heller), 1923: 7. Philippines (LZN, MDO).

Beccaria bakeri Heller, 1923: 7.

brevicornis (Arrow), 1920b: 333. Laos, Thailand, Vietnam.

Beccaria brevicornis Arrow, 1920b: 333.

cardoni (Gorham), 1897: 464. India, Nepal.

Beccaria cardoni Gorham, 1897: 464.

celebensis Tomaszewska, 2003e: 375. Indonesia.

coccinella (Arrow), 1920a: 74. Borneo, Malaysia, Myanmar, Thailand.

Beccaria coccinella Arrow, 1920a: 74.

confusa Strohecker, 1970: 54. Papua–New Guinea.

cruciata (Arrow), 1923: 488. Philippines (MDO).

Beccaria cruciata Arrow, 1923: 488.

duodecimpunctata (Arrow), 1923: 487. Borneo, Malaysia.

Beccaria duodecimpunctata Arrow, 1923: 487.

elongata Tomaszewska, 2003e: 372. Indonesia.

falcifera Strohecker, 1957c: 65. Java.

fulgurata (Chûjô), 1938: 399. Taiwan.

Beccaria fulgurata Chûjô, 1938: 399.

laeta (Arrow), 1920a: 75. Borneo, Malaysia.

Beccaria laeta Arrow, 1920a: 75.

longicornis (Arrow), 1920b: 333. Laos, Thailand.

Beccaria longicornis Arrow, 1920b: 333.

macra Strohecker, 1953b: 186. Madagascar.

macrospilota Strohecker, 1977a: 838. Java, Malaysia.

major Strohecker, 1970: 53. Papua–New Guinea.

nigricollis (Pic), 1932: 26. Indonesia.

Beccaria nigricollis Pic, 1932: 26.

octomaculata (Pic), 1932: 26. Indonesia, Sumatra.

Beccaria octomaculata Pic, 1932: 26.

orca (Heller), 1898: 41. Celebes, Indonesia.

Beccaria orca Heller, 1898: 41.

ovata (Arrow), 1923: 489. Philippines (MDO).

Beccaria ovata Arrow, 1923: 489.

overbecki (Gunther [in Heller & Gunther]), 1936: 72. India, Java.

Beccaria overbecki Gunther (in Heller & Gunther), 1936: 72.

pallida (Arrow), 1923: 488. India.

Beccaria pallida Arrow, 1923: 488.

papuensis (Gorham), 1885: 522. Papua–New Guinea.

Beccaria papuensis Gorham, 1885: 522.

petiginosa Strohecker, 1970: 53. Papua–New Guinea, Solomon Islands.

philippinica (Arrow), 1920a: 75. Philippines (MDO, SMR).

Beccaria philippinica Arrow, 1920a: 75.

Beccaria septemguttata Strohecker, 1943: 381.

Beccaria denticornis Strohecker, 1943: 382.

selene Strohecker, 1970: 53. Papua–New Guinea.

septemmaculata (Pic), 1932: 26. Malaysia, Indonesia.

Beccaria septemmaculata Pic, 1932: 26.

sexmaculata (Arrow), 1920a: 73. Borneo, Malaysia, Myanmar, Thailand.

Beccaria sexmaculata Arrow, 1920a: 73.

sikkimensis Tomaszewska, 2002c: 374. India.

subdita Strohecker, 1970: 53. Indonesia.

suturalis (Heller), 1923: 6. Philippines (MDO).

Beccaria suturalis Heller, 1923: 6.

wallacei (Gorham), 1897: 463. Indonesia, Papua–New Guinea, Sumatra.

Beccaria wallacei Gorham, 1897: 463.

***Brachytrycherus* Arrow, 1920a**

Brachytrycherus Arrow, 1920a: 12.

Type species: *Brachytrycherus perotteti* Arrow, 1920a.

concolor Arrow, 1937: 109. Borneo.

convexus Strohecker, 1964: 321. India.

femoralis (Arrow), 1928: 347. Laos, Vietnam.

Engonius femoralis Arrow, 1928: 347.

gemmatus (Arrow), 1928: 344. Laos, Myanmar, Thailand.

Engonius gemmatus Arrow, 1928: 344.

Engonius opimus Gorham, 1896: 293.

madurensis Arrow, 1920a: 14. India, Taiwan.

perotteti Arrow, 1920a: 13. India.

***Cacodaemon* Thomson, 1857**

Cacodaemon Thomson, 1857: 153.

Type species: *Eumorphus satanas* Thomson, 1856.

aculeatus (Gerstaecker), 1857: 217. Borneo.

Amphisternus aculeatus Gerstaecker, 1857: 217.

Cacodaemon lucifer Thomson, 1857: 156.

acuminatus (Achard), 1926: 140. Sumatra.

Amphisternus acuminatus Achard, 1926: 140.

armatus (Gorham), 1892: 86. Borneo.

Amphisternus armatus Gorham, 1892: 86.

Amphisternus metallicus Pic, 1930b: 5.

arrowi Strohecker, 1964: 356. Borneo.

atramentus Strohecker, 1964: 353. Sumatra.

auriculatus (Gerstaecker), 1857: 217. Borneo.

Amphisternus auriculatus Gerstaecker, 1857: 217.

bakeri (Strohecker), 1957a: 281. Borneo.

Amphisternus bakeri Strohecker, 1957a: 281.

beliar Strohecker, 1982a: 184. Borneo.

bellicosus (Gerstaecker), 1857: 218. Borneo, China, Malaysia, Sumatra.

Amphisternus bellicosus Gerstaecker, 1857: 218.

Amphisternus papulatus Gorham, 1901: 195.

borneensis (Frivaldszky), 1883: 126. Borneo.

Amphisternus hystricosus var. *borneensis* Frivaldszky, 1883: 126.

freudei (Strohecker), 1957a: 283. Borneo, Sumatra.

Amphisternus freudei Strohecker, 1957a: 283.

gerstaeckeri (Strohecker), 1959c: 180. Borneo.

Amphisternus gerstaeckeri Strohecker, 1959c: 180.

gracilis Strohecker, 1964: 354. Borneo.

hystricosus (Gerstaecker), 1857: 218. Borneo, Malaysia, Sumatra.

Amphisternus hystricosus Gerstaecker, 1857: 218.

inaequalis (Germar), 1843: 85. Java.

Amphisternus inaequalis Germar, 1843: 85.

Eumorphus hamatus Guérin–Méneville, 1844: 316.

Amphisternus hamatus: Strohecker, 1953a: 110.

kaszabi (Strohecker), 1957a: 281. Borneo, Sumatra.

Amphisternus kaszabi Strohecker, 1957a: 281.

laotinus laotinus (Arrow), 1920: 322. Laos.

Amphisternus bellicosus var. *laotinus* Arrow, 1920: 322.

Amphisternus laotinus Achard, 1926: 141.

laotinus yunnanensis (Kryzhanovskij), 1960: 880. China.

Amphisternus laotinus yunnanensis Kryzhanovskij, 1960: 880.

mastophorus (Strohecker), 1957a: 282. Borneo.

Amphisternus mastophorus Strohecker, 1957a: 282.

nigrellus (Strohecker), 1957a: 282. Borneo.

Amphisternus nigrellus Strohecker, 1957a: 282.

proavus Strohecker, 1964: 346. Vietnam.

satanas (Thomson), 1856: 476. Borneo.

Eumorphus satanas Thomson, 1856: 476.

Amphisternus satanas: Strohecker, 1953a: 110.

sexcristatus (Frivaldszky), 1883: 125. Borneo.

Amphisternus sexcristatus Frivaldszky, 1883: 125.

spinicollis (Gerstaecker), 1857: 218. Borneo, Malaysia, Sumatra.

Amphisternus spinicollis Gerstaecker, 1857: 218.

Cacodaemon cerberus Thomson, 1857: 155.

spinosus (Gorham), 1901: 199. Sumatra.

Amphisternus spinosus Gorham, 1901: 199.

tuberifer (Frivaldszky), 1883: 123. Borneo.

Amphisternus tuberifer Frivaldszky, 1883: 123.

***Callimodapsa* Strohecker, 1974b**

Callimodapsa Strohecker, 1974b: 535.

Type species: *Endomychus bivittatus* Percheron, 1837.

afra (Strohecker), 1962a: 42. Congo, Cote d'Ivoire, D.R. Congo.

Indalmus afra Strohecker, 1962a: 42.

Indalmus afer Strohecker, 1968a: 250.

bivittata (Percheron), 1837: 535. Senegal.

Endomychus bivittatus Percheron, 1837: 535.

crassa (Strohecker), 1959c: 179. Tanzania.

Indalmus crassus Strohecker, 1959c: 179.

hova (Arrow), 1920a: 22. Cote d'Ivoire, D.R. Congo, Ghana, Madagascar.

Indalmus hova Arrow, 1920a: 22.

Indalmus bivittatus Fairmaire, 1897: 203.

Indalmus vittiger Strohecker, 1954: 144.

lugubris (Strohecker), 1959c: 179. Togo.

Indalmus lugubris Strohecker, 1959c: 179.

major (Strohecker), 1954: 145. D.R. Congo.

Indalmus major Strohecker, 1954: 145.

nigrescens (Strohecker), 1959c: 180. Cameroon, D.R. Congo.

Indalmus nigrescens Strohecker, 1959c: 180.

nigrofusca (Gorham), 1900: 93. Congo, South Africa, Zimbabwe.

Ancylopus nigrofuscus Gorham, 1900: 93.

Indalmus nigrofuscus: Strohecker, 1954: 144.

obscura (Strohecker), 1954: 144. Congo, D.R. Congo.

Indalmus obscurus Strohecker, 1954: 144.

percheroni (Strohecker), 1954: 145. D.R. Congo.

Indalmus percheroni Strohecker, 1954: 145

pici (Villiers), 1954a: 520. D.R. Congo.

Indalmus pici Villiers, 1954a: 520.

pusilla (Strohecker), 1954: 145. D.R. Congo.

Indalmus pusillus Strohecker, 1954: 145.

rufocincta (Strohecker), 1954: 146. D.R. Congo.

Indalmus rufocinctus Strohecker, 1954: 146.

saegeri (Strohecker), 1962a: 42. Cote d'Ivoire, D.R. Congo.

Indalmus saegeri Strohecker, 1962: 42a.

unicolor (Gerstaecker), 1858: 194. South Africa.

Ancylopus unicolor Gerstaecker, 1858: 194.

Ancylopus fuscipennis Gahan, 1892: 210.

voltana Strohecker, 1974b: 538. Burkina Faso.

***Chetryrus* Villiers, 1953b**

Chetryrus Villiers, 1953b: 1465.

Type species: *Trycherus raffrayi* Gorham, 1885.

diversifasciatus (Pic), 1936b: 11. Congo, D.R. Congo, Equatorial Guinea, Ghana.

Trypherus diversifasciatus Pic, 1936b: 11.

Trycherus lateralis Pic, 1921: 1.

Chetryrus diversifasciatus Strohecker, 1962b: 73.

Trycherus rufocinctus Pic, 1930b: 6.

Trycherus rufocinctus var. *reductus* Pic, 1930b: 9.

Trycherus bifasciatus Villiers, 1953b: 1480.

Trycherus laticlavatus Strohecker, 1954: 149.

L–notatus Strohecker, 1959c: 178. Tanzania.

longus Strohecker, 1968a: 253. Cote d'Ivoire.

notaticollis (Pic), 1930b: 7. D.R. Congo, Tanzania.

Trycherus notaticollis Pic, 1930b: 7.

raffrayi (Gorham), 1885: 520. D.R. Congo, Tanzania.

Trycherus raffrayi Gorham, 1885: 520.

stigmaticus Strohecker, 1955a: 174. Congo, Rwanda.

tricolor (Gerstaecker), 1857: 224. Equatorial Guinea, Guinea, Nigeria.

Trycherus tricolor Gerstaecker, 1857: 224.

wittei (Strohecker), 1952: 8. D.R. Congo.

Trycherus wittei Strohecker, 1952: 8.

***Corynomalus* Chevrolat, 1836**

Corynomalus Chevrolat, 1836: 439.

Type species: *Corynomalus tarsatus* Erichson, 1847.

Amphix Laporte, 1840: 522.

apicalis Gerstaecker, 1857: 236. Brasil.

archetypus (Strohecker), 1957a: 276. Costa Rica.

Amphix archetypus Strohecker, 1957a: 276.

auratus auratus Bates, 1861: 166. Brasil, Colombia, Peru.

Corynomalus auratus Bates, 1861: 166.

auratus violaceus (Strohecker), 1980c: 32. Bolivia, Peru.

Amphix auratus violaceus Strohecker, 1980c: 32.

aurichalceus aurichalceus Gerstaecker, 1857: 236. Brasil, Colombia, Peru.

Corynomalus robustus Bates, 1861: 164.

aurichalceus punctatus Csiki, 1902c: 583. Peru.

Corynomalus punctatus Csiki, 1902c: 583.

aurichalceus speciosus Gerstaecker, 1857: 236. Brasil, Colombia, Ecuador, Guyana, Peru.

Corynomalus speciosus Gerstaecker, 1857: 236.

auronitens Gorham, 1887–99: 116. Costa Rica, Nicaragua.

Amphix auronitens: Blackwelder, 1945: 437.

bahiensis Csiki, 1902c: 585. Brasil.

Amphix bahiensis: Blackwelder, 1945: 437.

batesi (Strohecker), 1980c: 27. Brasil, Colombia, Ecuador, Peru.

Amphix batesi Strohecker, 1980c: 27.

chrysodetus (Strohecker), 1980c: 27. Brasil.

Amphix chrysodetus Strohecker, 1980c: 27.

circumcinctus Bates, 1861: 163. Brasil, French Guiana, Venezuela.

Amphix circumcinctus: Blackwelder, 1945: 437.

Amphix klagesi Strohecker, 1957a: 277.

clavatus Csiki, 1902c: 586. Bolivia, Peru.

Corynomalus peruvianus Csiki, 1902c: 585.

Amphix peruviana: Blackwelder, 1945: 437.

Amphix clavatus: Strohecker, 1953a: 86.

colon Gorham, 1874a: 440. French Guiana.

Amphix colon cayennensis Blackwelder, 1945: 437.

coriaceus Gorham, 1874a: 441. Brasil, French Guiana, Guyana.

Amphix coriacea: Blackwelder, 1945: 437.

csikii csikii (Strohecker), 1945: 3. Peru.

Amphix csikii csikii Strohecker, 1945: 3.

csikii rufipes (Strohecker), 1980c: 27. Ecuador.

Amphix csikii rufipes Strohecker, 1980c: 27.

dentatus (Fabricius), 1801: 7. Belize, Bolivia, Brasil, Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama.

Erotylus dentatus Fabricius, 1801: 7.

Amphix dentatus var. *multimaculatus* Pic, 1931: 7.

discoideus (Fabricius), 1801: 10. Argentina, Brasil, Colombia, Ecuador, French Guiana, Peru.

Aegithus discoideus Fabricius, 1801: 10.

Amphyx aeneipennis Guérin–Méneville, 1857c: 263.

Amphix prolongatus Pic, 1931: 8.

Corynomalus aeneipennis: Blackwelder, 1945: 437.

Amphix discoideus ty. *politus* Strohecker, 1957a: 276.

diversipes diversipes (Pic), 1931: 7. Brasil.

Amphix diversipes diversipes Pic, 1931: 7.

diversipes pallipes (Strohecker), 1980c: 34. Ecuador.

Amphix diversipes pallipes Strohecker, 1980c: 34.

elegans Csiki, 1902c: 582. Colombia, Ecuador, Peru, Venezuela.

erotyloides (Strohecker), 1980c: 26. Colombia, Panama.

Amphix erotyloides Strohecker, 1980c: 26.

felix Gorham, 1875a: 14. Colombia, Ecuador, Peru.

femoralis Gerstaecker, 1857: 235. Colombia, Panama.

Amphix femoralis: Blackwelder, 1945: 437.

gerstaeckeri Bates, 1861: 166. Brasil.

grandjeani (Pic), 1931: 8. Venezuela.

Amphix grandjeani Pic, 1931: 8.

humeralis Bates, 1861: 165. Brasil, Colombia, Peru.

inhumeralis inhumeralis (Pic), 1931: 8. Brasil.

Amphix inhumeralis Pic, 1931: 8.

inhumeralis reductus (Pic), 1931: 8. Peru.

Amphix punctatus reductus Pic, 1931: 8.

laetus Bates, 1861: 165. Brasil, Colombia, Peru.

laevigatus Gerstaecker, 1857: 236. Brasil, Colombia, Costa Rica, Nicaragua, Panama.

Corynomalus castaneicolor Gorham, 1887–99: 117.

lividus Bates, 1861: 167. Brasil, Paraguay.

malkini (Strohecker), 1980c: 31. Ecuador.

Amphix malkini Strohecker, 1980c: 31.

marcapatae Csiki, 1902c: 583. Peru.

Amphix marcapatae: Blackwelder, 1945: 437.

marginatus (Fabricius), 1798: 101. Brasil, Colombia, French Guiana, Guyana.

Erotylus marginatus Fabricius, 1798: 101.

Eumorphus limbatus Olivier, 1808: 1066.

Amphix binotatus Laporte, 1840: 522.

Corynomalus ferrugineus Gerstaecker, 1857: 236.

Amphix semiopacus Pic, 1931: 6.

Amphix marginata: Blackwelder, 1945: 437.

Amphix marginata var. *binotata*: Blackwelder, 1945: 437.

Amphix marginata var. *ferruginea*: Blackwelder, 1945: 437.

maximus Bates, 1861: 161. Bolivia, Brasil, Colombia, French Guiana, Peru.

Corynomalus rugosus Bates, 1861: 162.

Amphix foveolatus Pic, 1931: 6.

Amphix obscurus Pic, 1931: 7.

Amphix maxima: Blackwelder, 1945: 437.

mimus (Strohecker), 1980c: 29. Peru.

Amphix mimus Strohecker, 1980c: 29.

nigripennis Bates, 1861: 169. Brasil, Colombia, Ecuador, Peru.

Corynomalus angulicollis Bates, 1861: 168.

Amphix marginata var. *angulicollis*: Blackwelder, 1945: 437.

Amphix nigripennis: Blackwelder, 1945: 437.

nitidus (Strohecker), 1980c: 22. Peru.

Amphix nitidus Strohecker, 1980c: 22.

obsti Csiki, 1902c: 584. Ecuador, Peru.

paroecus Csiki, 1902c: 586. Peru.

perforatus Gerstaecker, 1857: 238. Belize, Brasil, Colombia, Costa Rica, El Salvador, French Guiana, Guatemala, Honduras, Mexico, Nicaragua, Panama, Peru, Venezuela.

Corynomalus dentatus Gorham, 1887–99: 117.

Corynomalus dentatus ab. *mirus* Csiki, 1902c: 592.

Amphix perforatus: Blackwelder, 1945: 437.

quadrimaculatus Erichson, 1848: 579. Brasil, Colombia, Ecuador, French Guiana, Guyana, Peru.

Corynomalus quadriplagiatus Bates, 1861: 167.

Amphix quadrimaculata: Blackwelder, 1945: 437.

Amphix quadriplagiata: Blackwelder, 1945: 437.

reticulatus (Csiki), 1902c: 591. Colombia, Panama.

Corynomalus cinctus ab. *reticulatus* Csiki, 1902c: 591.

ruficornis cruciatus (Strohecker), 1980c: 29. Peru.

Amphix ruficornis cruciatus Strohecker, 1980c: 29.

ruficornis ruficornis (Strohecker), 1959c: 177. Brasil, Colombia, Ecuador, Peru.

Amphix ruficornis ruficornis Strohecker, 1959c: 177.

rufipennis Gerstaecker, 1857: 235. Brasil, Colombia, Costa Rica, Ecuador, Nicaragua, Panama.

Amphix rufipennis: Blackwelder, 1945: 437.

separandus Kirsch, 1865: 103. Colombia, Peru.

Corynomalus maculicollis Gorham, 1875a: 14.

Amphix separanda: Blackwelder, 1945: 437.

singularis (Pic), 1931: 6. Colombia, Ecuador.

Amphix singularis Pic, 1931: 6.

sinuatipes perpulcher (Strohecker), 1980c: 32. Boliva, Brasil, Peru.

Amphix sinuatipes perpulcher Strohecker, 1980c: 32.

sinuatipes sinuatipes (Strohecker), 1945: 2. Colombia.

Amphix sinuatipes Strohecker, 1945: 2.

splendidus (Strohecker), 1980c: 17. Brasil.

Amphix splendidus Strohecker, 1980c: 17.

subcordatus Gerstaecker, 1857: 237. Brasil, Paraguay.

Amphyx viridipennis Guérin–Méneville, 1857c: 264.

tarsatus Erichson, 1847: 181. Bolivia, Peru.

Corynomalus taedifer Gorham, 1875c: 181.

vestitus vestitus (Voet), 1798: 105. Brasil, Colombia, Ecuador, Peru

Chrysomela vestita Voet, 1798: 105.

Corynomalus interruptus Gerstaecker, 1857: 237.

Amphix dejeani Guérin–Méneville, 1857c: 264.

vestitus cinctus (Fabricius), 1801: 10. Bolivia, Colombia, Costa Rica, French Guiana, Guatemala, Panama, Peru, Trinidad and Tobago, Venezuela.

Aegithus cinctus Fabricius, 1801: 10.

Eumorphus cruciger Latreille, 1811: 355.

Corynomalus saturatus Gorham, 1887–99: 117.

Amphix boliviensis Pic, 1931: 8.

Amphix vestitus cinctus: Strohecker, 1953a: 89.

vexillarius Gorham, 1875a: 13. Ecuador, Peru.

Cymbachus Gerstaecker, 1857

Cymbachus Gerstaecker, 1857: 233.

Type species: *Cymbachus pulchellus* Gerstaecker, 1857.

elegans Arrow, 1920b: 329. Cambodia, Laos, Thailand, Vietnam.

formosus Gorham, 1897: 460. Myanmar.

koreanus Chûjô, Chûjô & Lee, 1993: 95. South Korea.

pulchellus Gerstaecker, 1857: 234. Java.

spilotus Arrow, 1925: 281. India.

Cymones Gorham, 1886

Cymones Gorham, 1886: 157.

Type species: *Cymones cowani* Gorham, 1886.

atroclavatus (Fairmaire), 1883: 365. Madagascar.

Dioedes atroclavatus Fairmaire, 1883: 365.

Encymon armipes Fairmaire, 1899: 469.

Cymones cowani Gorham, 1886: 158.

Cymones atripennis Pic, 1925: 1.

extensus Strohecker, 1959b: 77. Madagascar.

haplosceloides Strohecker, 1953b: 192. Madagascar.

helopioides Gorham, 1886: 158. Madagascar.

humerosus Strohecker, 1953b: 190. Madagascar.

perrieri (Fairmaire), 1902: 327. Madagascar.

Haploscelis perrieri Fairmaire, 1902: 327.

rufus (Fairmaire), 1905: 116. Madagascar.

Encymon rufus Fairmaire, 1905: 116.

Cymones bicoloripes Pic, 1953: 274.

scutatus (Fairmaire), 1902: 325. Madagascar.

Encymon scutatus Fairmaire, 1902: 325.

tenuipes Strohecker, 1953b: 189. Madagascar.

***Dapsa* Latreille, 1829**

Dapsa Latreille, 1829: 159.

Type species: *Endomychus denticollis* Germar & Kaulfuss, 1816.

Phylira Mulsant, 1846: 23.

Type species: *Dapsa trimaculata* Motschulsky, 1835.

adami Tomaszewska, 1997b: 218. India, Nepal.

barbara Lucas, 1849: 552. Algeria.

Dapsa subpunctata Marseul, 1868b: 107.

bertiana Audisio & De Biase, 1996: 109. Algeria.

birmanica Audisio & De Biase, 1996: 116. Myanmar.

caucasica Motschulsky, 1845: 111. Caucasus.

celata Arrow, 1925: 337. India, Nepal.

curta Franz, 1996: 131. Canary Islands.

curvipes Audisio & De Biase, 1996: 104. Algeria.

denticollis (Germar & Kaulfuss), 1816: 8. Austria, Bulgaria, Croatia, Czech Republic, Germany, Hungary, Italy, Poland, Romania, Serbia & Montenegro, Slovakia, Slovenia, Ukraine.

Endomychus denticollis Germar & Kaulfuss, 1816: 8.

Dapsa denticollis var. *nigricollis* Gerstaecker, 1858: 198.

Dapsa denticollis var. *unimaculata* Trella, 1930: 36.

Dapsa denticollis var. *binotata* Trella, 1923: 115.

Dapsa rufa Porta, 1929: 241.

edentata Wollaston, 1864: 432. Canary Islands.

erythraea Pic, 1953b: 96. Eritrea.

Dapsa (*Phylira*) *erythraea* Pic, 1953b: 96.

fodori (Csiki), 1907: 578. Hungary, Slovakia.

Phylira fodori Csiki, 1907: 578.

gemina Audisio & De Biase, 1996: 108. Algeria.

graeca Pic, 1902b: 71. Greece.

grancanariensis Palm, 1974: 32. Canary Islands.

hierrensis Franz, 1996: 130. Canary Islands.

horvathi (Csiki), 1901b: 106. Kazakhstan, Russia (SIB).

Phylira horvathi Csiki, 1901b: 106.

Dapsa roddiana Semenov, 1904: 289.

indica Tomaszewska, 1997b: 218. India.

inornata Gorham, 1873a: 43. Lebanon, Palestine, Syria.

Dapsa syriaca Pic, 1902b: 71.

kabylica Audisio & De Biase, 1996: 105. Algeria.

lederi Reitter, 1880a: 97. Caucasus, Georgia.

limbata Motschulsky, 1835: 323. Armenia, Caucasus, Georgia, Turkey.

Dapsa nigripennis Reitter, 1879: 89.

mizoramica Tomaszewska & Pal, 2003: 54. India.

motschulskyi Nikitsky & Semenov, 2001: 61. Mongolia, Russia (FET).

nikolajevi Nikitsky & Semenov, 2001: 65. Uzbekistan.

obscurissima Pic, 1902a: 10. Algeria, Italy, Tunisia.

Dapsa tyrrhena Audisio, De Biase & Zampetti, 1983: 87.

opuntiae Reitter, 1884b: 117. Albania, Croatia, Greece, Italy, Serbia & Montenegro.

Dapsa opuntiae var. *sahlbergi* Reitter, 1900: 219.

Dapsa intermedia Sahlberg, 1913: 13.

oxiana Iablokoff–Khnzorian, 1964: 167. Tajikistan.

palaestinensis Audisio & De Biase, 1996: 82. Israel.

pallescens Marseul, 1868a: 109. Algeria, Morocco.

palmaensis Franz, 1978: 91. Canary Islands.

pardoi Peyerimhoff, 1949: 274. Morocco.

sculpturata Gorham, 1896: 299. Myanmar.

sellata Marseul, 1868a: 108. Algeria.

spinicollis Fairmaire, 1868: 501. Algeria, Morocco, Spain.

Dapsa acuticollis Reitter, 1882: 231.

trimaculata Motschulsky, 1835: 322. Azerbaijan, Albania, Bosnia Herzegovina, Bulgaria, Croatia, France, Georgia, Greece, Italy, Macedonia, Romania, Serbia & Montenegro, Slovenia, Spain, Russia (SET), Turkey, Ukraine.

Ancylopus testacea Costa, 1882: 36.

trogositoides Gorham, 1896: 300. India, Myanmar.

ussuriensis Nikitsky, Semenov & Audisio, 2001: 67. Russia (FET).

***Daulis* Erichson, 1842**

Daulis Erichson, 1842: 241.

Type species: *Daulis cimicoides* Erichson, 1842.

cimicoides Erichson, 1842: 242. Tasmania.

monteithi Tomaszewska, 2004a: 555. Australia (NSW, QLD).

***Daulotypus* Lea, 1922**

Daulotypus Lea, 1922: 301.

Type species: *Daulotypus picticornis* Lea, 1922.

gibbosipennis Wilson, 1926: 39. Australia.

minor Lea, 1925: 429. Australia (NSW).

picticornis Lea, 1922: 301. Australia.

umbratilis Oke, 1932: 161. Australia.

***Dryadites* Frivaldszky, 1883**

Dryadites Frivaldszky, 1883: 128.

Type species: *Dryadites borneensis* Frivaldszky, 1883.

borneensis Frivaldszky, 1883: 130. Borneo, Sumatra.

Mycetina erubescens Gorham, 1901: 204.

concolor (Arrow), 1937: 109. Borneo.

Brachytrycherus concolor Arrow, 1937: 109.

grandis (Pic), 1930c: 10. Java.

Mycetina grandis Pic, 1930c: 10.

latipennis Arrow, 1920a: 24. Borneo.

purpureus Arrow, 1920a: 25. Borneo.

rudepunctatus (Gorham), 1897: 457. India, Myanmar.

Amphisternus rudepunctatus Gorham, 1897: 457.

Brachytrycherus rudepunctatus: Arrow, 1925: 293.

violaceus Tomaszewska, 2003d: 466. Borneo.

vitalisi Arrow, 1920b: 330. Laos.

***Encymon* Gerstaecker, 1857**

Encymon Gerstaecker, 1857: 232.

Type species: *Encymon violaceus* Gerstaecker, 1857.

Cranterophorus Blackburn, 1895: 232.

Type species: *Mycella clavicornis* Blackburn, 1890

(=*Eumorphus immaculatus* Montruzier, 1855).

ater Pic, 1927b: 1. Laos, Vietnam.

bipustulatus Gorham, 1873a: 38. Indonesia, Papua–New Guinea, Sumatra.

Encymon bipustulatus var. *nigripes* Csiki, 1902a: 30.

Encymon erimae Csiki, 1900a: 123.

buruanus Arrow, 1926b: 125. Indonesia.

cinctipes Gorham, 1897: 459. India, Laos, Myanmar.

cyanipennis Chûjô, 1938: 396. Philippines (LZN, MDO), Taiwan.

Encymon valgus Strohecker, 1951a: 161.

eumera Strohecker, 1972d: 200. Vietnam.

ferialis ferialis Gorham, 1875b: 312. Borneo.

ferialis sumatranus Csiki, 1902a: 35. Java, Sumatra.

gorhami Csiki, 1901a: 19. Papua–New Guinea.

Encymon immaculatus Gorham, 1885: 518.

Encymon gorhami femoratus Csiki, 1902a: 37.

Encymon globosus Arrow, 1943: 130.

immaculatus (Montruzier), 1855: 74. Australia (NSW, QLD), Celebes, Indonesia, Java, Malaysia, Papua–New Guinea, Sumatra.

Eumorphus immaculatus Montruzier, 1855: 74.

Haplomorphus immaculatus: Guérin–Méneville, 1858: 25.

Encymon gerstaeckeri Dohrn, 1863: 135.

Encymon ruficollis Gemminger & Harold, 1876: 3725.

Encymon angulatus Gorham, 1873a: 39.

Mycella clavicornis Blackburn, 1890: 366.

Encymon australasiae Csiki, 1902a: 34.

Encymon limbatus Pic, 1931: 5.

Encymon immaculatus rufofemoratus Csiki, 1902a: 33.

nigricollis Csiki, 1902a: 37. Papua–New Guinea.

Encymon gorhami nigricollis Csiki, 1902a: 37.

papuanus Csiki, 1902a: 34. Papua–New Guinea.

pedanus Strohecker, 1971b: 37. Myanmar.

regalis atripes Csiki, 1902a: 29. Borneo, Java, Sumatra, Vietnam.

Engonius bicoloripes Pic, 1927a: 11.

regalis regalis Gorham, 1874a: 440. Philippines (MDO).

Engonius regalis Gorham, 1874a: 440.

Engonius theresae Pic, 1946b: 6.

resinatus Gorham, 1873a: 40. Borneo, Celebes, Indonesia, Malaysia, Philippines, Sumatra.

Encymon malaccanus Pic, 1931: 5.

Encymon neugebaueri Mader, 1936b: 63.

ruficollis Gorham, 1885: 519. Indonesia, Papua–New Guinea, Solomon Islands.

Encymon intermedius Arrow, 1943: 132.

Encymon latipennis Arrow, 1943: 131.

Encymon maderi Strohecker, 1953a: 77.

schwarzbaueri Mader, 1936b: 62. Papua–New Guinea, Solomon Islands.

scintillans aspilotus Strohecker, 1971b: 31. Solomon Islands.

scintillans scintillans Strohecker, 1951b: 1. Solomon Islands.

Encymon scintillans Strohecker, 1951b: 1.

truncaticollis atriceps Strohecker, 1958a: 36. Philippines (MDO).

truncaticollis truncaticollis Strohecker, 1951a: 161. Philippines (LZN).

Encymon truncaticollis Strohecker, 1951a: 161.

violaceus Gerstaecker, 1857: 233. Borneo, Java, Malaysia, Myanmar, Sumatra, Thailand.

Encymon violaceus cupreatus Mader, 1936b: 63.

***Eumorphus* Weber, 1801**

Eumorphus Weber, 1801: 31.

Type species: *Erotylus quadriguttatus* Illiger, 1800.

Eumorphoides Guérin–Méneville, 1858: 12.

Type species: *Eumorphus tetraspilotus* Hope, 1832.

Enaisimus Guérin–Méneville, 1858: 16.

Type species: *Eumorphus quadrinotatus* Gerstaecker, 1857.

Haplomorphus Guérin–Méneville, 1858: 18.

Type species: *Eumorphus bipunctatus* Perty, 1831.

Heterandrus Guérin–Méneville, 1858: 26.

Type species: *Eumorphus confusus* Guérin–Méneville, 1857c.

alboguttatus Gerstaecker, 1857: 228. Java.

Eumorphus quadrimaculatus Guérin–Méneville, 1857c: 249.

Haplomorphus quadrimaculatus: Guérin–Méneville, 1858: 18.

assamensis assamensis Gerstaecker, 1857: 229. China, India.

Eumorphus assamensis Gerstaecker, 1857: 229.

assamensis subguttatus Gerstaecker, 1857: 229. Cambodia, Laos, Malaysia, Myanmar, Singapore, Sumatra, Thailand, Vietnam.

Eumorphus subguttatus Gerstaecker, 1857: 229.

Eumorphus assamensis sinuatipes Pic, 1927b: 2.

assamensis subsinuatus Pic, 1927b: 2. Philippines (LZN, MDO),

Eumorphus subsinuatus Pic, 1927b: 2.

austerus austerus Gerstaecker, 1857: 227. Cambodia, China, India, Laos, Myanmar, Thailand, Vietnam.

Eumorphus depressus Arrow, 1925: 302.

austerus indianus Strohecker, 1968b: 88. China.

Eumorphus austerus Arrow, 1925: 300.

bicoloripedoides (Mader), 1955: 68. China, India, Laos, Vietnam.

Engonius bicoloripedoides Mader, 1955: 68.

bipunctatus bipunctatus Perty, 1831: 42. Java.

Eumorphus bipunctatus Perty, 1831: 42.

Haplomorphus quadrinotatus Guérin–Méneville, 1858: 18.

bipunctatus crucifer Strohecker, 1968b: 104. Borneo.

bipunctatus mirus Strohecker, 1968b: 104. Sumatra.

bulbosus arrowi Strohecker, 1968b: 103. Celebes, Indonesia.

Eumorphus arrowi Strohecker, 1939: 118.

bulbosus bulbosus Schaufuss, 1887: 142. Celebes, Indonesia.

Eumorphus bulbosus Schaufuss, 1887: 142.

Engonius celebensis Pic, 1946b: 6.

carinatus Gerstaecker, 1857: 229. Java.

coloratus coloratus Gerstaecker, 1857: 230. Java.

Eumorphus coloratus Gerstaecker, 1857: 230.

Eumorphus quadriverrucosus Guérin–Méneville, 1857c: 249.

Enaisimus quadriverrucosus: Guérin–Méneville, 1858: 18.

coloratus vitalisi Arrow, 1920b: 327. Laos, Malaysia, Myanmar, Sumatra, Thailand, Vietnam.

columbinus Gerstaecker, 1857: 227. Java.

constrictus Arrow, 1926a: 249. Sumatra.

costatus Gorham, 1873a: 34. Borneo, Celebes.

cryptus Strohecker, 1968b: 111. Borneo.

csikii Strohecker, 1957a: 280. Sumatra.

cyanescens cyanescens Gerstaecker, 1857: 226. Philippines (MDO).

Eumorphus cyanescens Gerstaecker, 1857: 226.

cyanescens thomsoni (Guérin–Méneville), 1858: 16. Philippines (LZN).

Enaisimus thomsoni Guérin–Méneville, 1858: 16.

Eumorphus expatriatus Gorham, 1873a: 35.

dehaani Guérin–Méneville, 1858: 15. Borneo, Java, Sumatra.

dilatatus Perty, 1831: 42. Borneo, Java, Malaysia, Thailand.

Eumorphus dilatatus turritus Strohecker, 1968b: 84.

drescheri Strohecker, 1957c: 69. Java.

eburatus eburatus Gerstaecker, 1857: 226. Java.

Eumorphus eburatus Gerstaecker, 1857: 226.

Haplomorphus circumcinctus Guérin–Méneville, 1857c: 247.

eburatus guerini Gorham, 1873a: 33. Borneo, Malaysia.

Eumorphus guerini Gorham, 1873a: 33.

elegans Strohecker, 1968b: 95. Philippines (MDO).

eurynotus Strohecker, 1968b: 95. Philippines (MDO).

felix Arrow, 1920a: 17. Borneo.

fraternus Arrow, 1920a: 20. Malaysia, Myanmar, Thailand.

fryanus festivus Arrow, 1920a: 19. Borneo.

Eumorphus festivus Arrow, 1920a: 19.

fryanus fryanus Gorham, 1875a: 13. Borneo, Malaysia, Myanmar, Sumatra.

Eumorphus fryanus Gorham, 1875a: 13.

fryanus quadripustulatus Frivaldszky, 1883: 20. Borneo.

Eumorphus quadripustulatus Frivaldzsky, 1883: 20.

helaeus Arrow, 1920a: 20. Malaysia, Sumatra.

hilaris Arrow, 1928: 348. Vietnam.

inflatus Arrow, 1920b: 328. Laos.

insignis Gorham, 1901: 200. Sumatra.

leptocerus Strohecker, 1968b: 89. Malaysia.

longespinosus Pic, 1930b: 7. Vietnam.

lucidus Gorham, 1892: 87. Borneo.

macrospilotus Arrow, 1920a: 18. Borneo, Sumatra.

marginatus Fabricius, 1801: 12. Borneo, Java, Myanmar, Papua–New Guinea, Philippines (BGO, LZN), Sumatra, Taiwan.

micans Strohecker, 1968b: 93. Borneo.

minor Gerstaecker, 1858: 103. Borneo, Malaysia, Myanmar, Sumatra, Thailand.

Eumorphus tetraspilotus minor Gerstaecker, 1858: 103.

Eumorphus opacicollis Arrow, 1925: 301.

murrayi carinensis Strohecker, 1968b: 101. Myanmar.

murrayi murrayi Gorham, 1874a: 437. India, Myanmar.

Eumorphus murrayi Gorham, 1874a: 437.

Eumorphus sanguinipes Arrow, 1920a: 17.

ocellatus Arrow, 1920b: 327. China, Laos, Vietnam.

oculatus Gerstaecker, 1857: 227. Java.

Eumorphus laetus Guérin–Méneville, 1857c: 246.

panfilovi Kryzhangovskij, 1960: 877. China.

parvus Strohecker, 1968b: 109. Malaysia.

politus Gerstaecker, 1857: 226. Borneo, Myanmar, Sumatra, Thailand.

Eumorphus opalinus Gorham, 1901: 201.

productus Arrow, 1920a: 17. Philippines.

purpureus Strohecker, 1968b: 89. Philippines (PWN).

Eumorphus tetraspilotus Strohecker, 1943: 381.

quadriguttatus andamanensis Gorham, 1875c: 180. India.

quadriguttatus convexicollis Gerstaecker, 1857: 228. Philippines.

Eumorphus convexicollis Gerstaecker, 1857: 228.

Eumorphus confusus Guérin–Méneville, 1857c: 254.

Heterandrus confusus: Guérin–Méneville, 1858: 26.

quadriguttatus pulchripes Gerstaecker, 1857: 228. China, India, Japan, Nepal, Sri Lanka, Taiwan.

Eumorphus pulchripes Gerstaecker, 1857: 228.

Engonius baibaranus Ohta, 1931: 219.

Engonius taitoensis Ohta, 1931: 219.

Eumorphus quadriguttatus formosanus Pic, 1930b: 8.

quadriguttatus quadriguttatus (Illiger), 1800: 124. Borneo, Cambodia, Indonesia, Java, Laos, Malaysia, Myanmar, Papua–New Guinea, Sumatra, Thailand, Vietnam.

Erotylus quadriguttatus Illiger, 1800: 124.

Eumorphus sumatrae Weber, 1801: 59.

Eumorphus immarginatus Fabricius, 1801: 11.

Pedanus laevis Gorham, 1874a: 439.

quadrinotatus Gerstaecker, 1857: 226. Java.

Enaisimus quadrinotatus: Guérin–Méneville, 1858: 16.

sanguinipes (Guérin–Méneville), 1858: 20. India, Laos, Myanmar.

Haplomorphus sanguinipes Guérin–Méneville, 1858: 20.

Eumorphus murrayi Gorham, 1896: 294.

simplex erythromerus Kryzhanovskij, 1960: 880. China, India, Myanmar, Thailand.

Eumorphus rejectus Strohecker, 1939: 118.

simplex simplex Arrow, 1920b: 324. China, Laos.

Eumorphus simplex Arrow, 1920b: 324.

staudingeri Mader, 1936b: 61. Philippines (MDO).

sybarita consobrinus Gerstaecker, 1857: 229. Java, Sumatra.

Eumorphus consobrinus Gerstaecker, 1857: 229.

Haplomorphus quadrimaculatus Guérin–Méneville, 1857c: 250.

Haplomorphus spencei Guérin–Méneville, 1858: 20.

sybarita sybarita Gerstaecker, 1857: 229. Borneo, China, Malaysia, Myanmar, Singapore, Sumatra.

Eumorphus popovi Kryzhanovskij, 1960: 876.

tetraspilotus Hope, 1832: 786. Borneo, Java, Malaysia, Myanmar, Philippines (PWN), Sumatra, Thailand.

Eumorphoides tetraspilotus: Guérin–Méneville, 1858: 12.

thomsoni (Guérin–Méneville), 1858: 16. Philippines (LZN).

Enaisimus thomsoni Guérin–Méneville, 1858: 16.

Eumorphus expatriatus Gorham, 1873a: 35.

Eumorphus cyanescens (in part) Csiki, 1910: 21.

trabeatus Arrow, 1925: 303. Myanmar.

tumescens Gorham, 1892: 86. Borneo.

turritus Gerstaecker, 1857: 225. Borneo, Singapore.

wegneri Strohecker, 1956b: 245. Celebes.

westwoodi cruciatus Arrow, 1926a: 249. Borneo, Sumatra.

westwoodi westwoodi (Guérin–Méneville), 1858: 19. Borneo, India, Malaysia, Myanmar, Sumatra.

Haplomorphus westwoodi Guérin–Méneville, 1858: 19.

Engonius brevipennis Pic, 1946b: 7.

***Gerstaeckerus* Tomaszewska, 2005**

Gerstaeckerus Tomaszewska, 2005: 42. Replacement name.

Engonius Gerstaecker, 1857: 220.

Type species: *Engonius sexguttatus* Gerstaecker, 1857.

brookei (Gorham), 1885: 521. Borneo.

Engonius brookei Gorham, 1885: 521.

chensicieni (Kryzhanovskij), 1960: 874. China.

Engonius chensicieni Kryzhanovskij, 1960: 874.

dalatensis (Pic), 1928c: 6. India, Vietnam.

Engonius dalatensis Pic, 1928c: 6.

gibbosus (Gorham), 1885: 517. Borneo, Malaysia, Myanmar, Singapore, Sumatra, Thailand.

Amphisternus gibbosus Gorham, 1885: 517.

Engonius gibbosus: Strohecker, 1971a: 21.

Engonius tetrasphaera Arrow, 1920a: 15.

gratus (Gorham), 1891: 399. Cambodia, China, India, Laos, Myanmar, Thailand, Vietnam.

Engonius gratus Gorham, 1891: 399.

Engonius effractus Achard, 1922: 28.

herklotsii (Guérin–Méneville), 1857c: 259. Java.

Eumorphus herklotsii Guérin–Méneville, 1857c: 259.

Engonius herklotsii: Gerstaecker, 1858: 78.

humeralis (Arrow), 1928: 345. India, Vietnam.

Engonius humeralis Arrow, 1928: 345.

junctus (Pic), 1930b: 8. Singapore.

Engonius junctus Pic, 1930b: 8.

kamengenensis (Vazirani & Saha), 1972: 77. India.

Engonius kamengenensis Vazirani & Saha, 1972: 77.

klugii (Gerstaecker), 1857: 221. Borneo, Malaysia, Myanmar, Sumatra, Thailand.

Engonius klugii Gerstaecker, 1857: 221.

latenotatus (Pic), 1940b: 11. Vietnam.

Engonius latenotatus Pic, 1940b: 11.

luteofasciatus (Pic), 1940b: 11. Vietnam.

Engonius luteofasciatus Pic, 1940b: 11.

obliquus (Strohecker), 1957a: 279. Sumatra.

Engonius obliquus Strohecker, 1957a: 279.

perspicillaris (Gerstaecker), 1857: 221. Java, Papua–New Guinea.

Engonius perspicillaris Gerstaecker, 1857: 221.

Rhachidophorus chevrolati Guérin–Méneville, 1858: 62.

Engonius semilunatus Pic, 1946b: 6.

rubropictus (Gerstaecker), 1857: 221. Borneo, Java, Malaysia, Sumatra.

Engonius rubropictus Gerstaecker, 1857: 221.

Engonius rubropictus subannularis Pic, 1930b: 8.

sanguinolentus (Gorham), 1875b: 311. Philippines (MDO).

Amphisternus sanguinolentus Gorham, 1875b: 311.

Engonius sanguinolentus: Strohecker, 1953a: 101.

Amphisternus sexplagiatus Heller, 1923: 6.

sexguttatus (Gerstaecker), 1857: 221. Borneo, Malaysia.

Engonius sexguttatus Gerstaecker, 1857: 221.

Heterandrus mniszechi Guérin–Méneville, 1858: 28.

sikkimensis (Strohecker), 1971a: 18. India.

Engonius sikkimensis Strohecker, 1971a: 18.

similis humeralis (Arrow), 1928: 345. Vietnam.

Engonius humeralis Arrow, 1928: 345.

similis similis (Arrow), 1920b: 322. Laos, Thailand, Vietnam.

Engonius similis Arrow, 1920b: 322.

trisignatus (Pic), 1946b: 6. Borneo, Singapore, Thailand.

Engonius trisignatus Pic, 1946b: 6.

Engonius spurius Strohecker, 1971a: 18.

***Haploscelis* Blanchard, 1845**

Haploscelis Blanchard, 1845: 312.

Type species: *Eumorphus atratus* Klug, 1833.

Dioedes Gerstaecker, 1857: 231.

Type species: *Dioedes columbinus* Gerstaecker, 1857.

Hybopterus Fairmaire, 1883: 365.

Type species: *Hybopterus plagiicollis* Fairmaire, 1883.

abdominalis Waterhouse, 1877: 13. Madagascar.

angulatus Strohecker, 1953b: 195. Madagascar.

atratus (Klug), 1833: 126. Madagascar.

Eumorphus atratus Klug, 1833: 126.

Dioedes costipennis Fairmaire, 1884: 242.

Haploscelis madecassus Csiki, 1900c: 401. Madagascar.

Haploscelis nitidus Csiki, 1900c: 400. Madagascar.

attenuatus Strohecker, 1953b: 196. Madagascar.

coerulescens Fairmaire, 1902: 326. Madagascar.

Haploscelis descarpentriesi Strohecker, 1953b: 194.

columbinus (Gerstaecker), 1857: 232. Madagascar.

Dioedes columbinus Gerstaecker, 1857: 232.

Haploscelis metallescens Fairmaire, 1902: 325.

Haploscelis purpureotinctus Pic, 1925: 2.

Haploscelis viridescens Pic, 1925: 1. Madagascar.

compactus Fairmaire, 1898: 259. Madagascar.

consobrinus Strohecker, 1972b: 126. Madagascar.

convexus Strohecker, 1953b: 196. Madagascar.

curtulus Fairmaire, 1898: 259. Madagascar.

Haploscelis cyanipennis Fairmaire, 1902: 326.

Haploscelis nossibeanus Csiki, 1900c: 400.

deflorator Strohecker, 1955c: 158. Madagascar.

dejectus Strohecker, 1972b: 126. Madagascar.

delkeskampi Strohecker, 1959b: 78. Madagascar.

elegans Strohecker, 1972b: 126. Madagascar.

fairmairei Strohecker, 1953b: 198. Madagascar.

gibbosus Strohecker, 1959b: 79. Madagascar.

klugi Strohecker, 1955c: 157. Madagascar.

obesus Strohecker, 1955c: 157. Madagascar.

oblongulus (Fairmaire), 1883: 365. Madagascar.

Dioedes oblongulus Fairmaire, 1883: 365.

pauliani Strohecker, 1953b: 200. Madagascar.

pici Strohecker, 1955c: 155. Madagascar.

plagiicollis (Fairmaire), 1883: 365. Madagascar.

Hybopterus plagiicollis Fairmaire, 1883: 365.

Cymones sharpi Gorham, 1886: 157.

Hybopterus sharpi: Csiki, 1910: 31.

quadricollis Fairmaire, 1898: 259. Madagascar.

sulciclavus Strohecker, 1959b: 78. Madagascar.

vadoni Strohecker, 1955c: 157. Madagascar.

ventralis Strohecker, 1972b: 128. Madagascar.

Hylaia Chevrolat, 1836

Hylaia Chevrolat, 1836: 440.

Type species: *Lycoperdina rubricollis* Germar, 1844.

Hylaia Guérin–Méneville, 1857c: 273. Homonym.

Ceramis Gerstaecker, 1858: 220. Unnecessary replacement name.

Hyleia Klebs, 1910: 239. Misspelling.

cardiophora Wurst, 1997: 108. Azerbaijan.

dalmatina Kaufmann, 1883: 10. Bosnia Herzegovina, Croatia, Serbia & Montenegro.

dryadella Wurst, 1997: 98. Greece.

elongata Apfelbeck, 1912: 657. Albania, Serbia & Montenegro.

Hylaia elongata albanica Apfelbeck, 1912: 657.

podagrica Guérin–Méneville, 1857c: 274. Georgia, Iran, Turkey.

reissi Csiki, 1911: 74. Bulgaria.

Hylaia rambouseki Obenberger, 1917: 29.

Hylaia rambouseki var. *peristorica* Roubal, 1932: 177.

rubricollis (Germar), 1844: pl. 18. Croatia, Moldavia, Romania.

Lycoperdina rubricollis Germar, 1844: pl. 18.

Ceramis rubricollis: Gerstaecker, 1858: 222.

***Indalmus* Gerstaecker, 1858**

Indalmus Gerstaecker, 1858: 185.

Type species: *Eumorphus kirbyanus* Latreille, 1807.

Mycella Chapuis, 1876: 104.

Type species: *Mycella lineella* Chapuis, 1876.

angusticollis Gerstaecker, 1858: 187. Myanmar, Sumatra, Thailand, Vietnam.

Indalmus latus Arrow, 1925: 325.

bivittatus (Percheron), 1837: 2. Madagascar, Senegal.

Endomychus bivittatus Percheron, 1837: 2.

Ancylopus bivittatus: Gerstaecker, 1858: 193.

Ancylopus unicolor Gerstaecker, 1858: 194.

Ancylopus fuscipennis Gahan, 1892: 210.

Ancylopus nigrofuscus Gorham, 1900: 93.

Ancylopus lineatus Pic, 1921: 1.

brevis Strohecker, 1959c: 180. Borneo, Indonesia.

clavipes Arrow, 1920a: 22. India.

coomani coomani (Pic), 1925: 3. Vietnam.

Engonius coomani Pic, 1925: 3.

coomani sinensis Strohecker, 1979f: 289. China.

decipiens Strohecker, 1957a: 274. Cameroon, Congo, Cote d'Ivoire, D.R. Congo, Ghana, Togo.

distinctus Arrow, 1923: 485. China, India, Myanmar.

ephippiatus Gerstaecker, 1858: 410. Congo, Mozambique, South Africa, Zimbabwe.

formosanus (Csiki), 1937: 7. Taiwan.

Phaeomychus formosanus Csiki, 1937: 7.

Indalmus formosanus: Strohecker, 1945: 1.

Mycetina formosana: Strohecker, 1953a: 94.

grandis (Pic), 1921: 1. Cameroon, Cote d'Ivoire, D.R. Congo, Uganda.

Ancylopus grandis Pic, 1921: 1.

grandjeani (Pic), 1930c: 8. Indonesia, Java.

Engonius grandjeani Pic, 1930c: 8.

graphicus (Gorham), 1873a: 41. Cameroon, Congo, D.R. Congo, Gabon, Gambia.

Ancylopus graphicus Gorham, 1873a: 41.

Indalmus perfidus Strohecker, 1957a: 275.

Indalmus strigatus Strohecker, 1954: 146.

hanchunglinensis Li, 1992: 134. China.

hirsutus Strohecker, 1944: 139. Celebes, Java.

ignotus Stohecker, 1975a: 126. D.R. Congo.

indicus (Gorham), 1875b: 312. India.

Ancylopus indicus Gorham, 1875b: 312.

inermipes Strohecker, 1958a: 37. Philippines (MDO).

ingratus Strohecker, 1952: 6. Congo, D.R. Congo, Mozambique, Zimbabwe.

insularum Gorham, 1873a: 40. Indonesia.

kamengensis (Vazirani & Saha), 1972: 77. India.

Engonius kamengensis Vazirani & Saha, 1972: 77.

kirbyanus (Latreille), 1807: 72. Cambodia, China, India, Laos, Myanmar, Nepal, Taiwan, Thailand, Vietnam.

Eumorphus kirbyanus Latreille, 1807: 72.

Ancylopus atricornis Pic, 1921: 2.

Indalmus latefasciatus Pic, 1929: 15.

Ancylopus nigrothoracica Pal, 2003: 113.

lachrymosus Arrow, 1925: 327. Sri Lanka.

lineellus (Chapuis), 1876: 105. Australia (QLD), Papua–New Guinea.

Mycella lineela Chapuis, 1876: 105.

liuchungloi Kryzhanovskij, 1960: 871. China, Laos, Myanmar, Vietnam.

luzonicus Gorham, 1897: 462. Philippines (LZN).

malayanus malayanus Arrow, 1926a: 249. Borneo, Malaysia, Sumatra.

Indalmus malayanus Arrow, 1926a: 249.

malayanus vulcanus Strohecker, 1979f: 287. Java.

Indalmus vulcanus Strohecker, 1979f: 287.

nanus (Arrow), 1920b: 326. Cambodia, Laos, Vietnam.

Eumorphus nanus Arrow, 1920b: 326.

Engonius minutus Pic, 1927a: 11.

oblongulus Fairmaire, 1894a: 678. Cameroon, Congo, Tanzania.

Indalmus gorhami Strohecker, 1939: 119.

pubescens (Arrow), 1925: 311. Cambodia, China, Laos, Myanmar, Vietnam.

Engonius pubescens Arrow, 1925: 311.

quadripunctatus (Ohta), 1931: 222. Japan, Taiwan.

Encymon ruficephalus quadripunctatus Ohta, 1931: 222.

undulatus (Pic), 1930c: 8. Indonesia, Java.

Engonius undulatus Pic, 1930c: 8.

Indalmus stellatus Strohecker, 1957c: 69.

unicolor (Gerstaecker), 1858: 194. Burundi, Congo, Rwanda, South Africa, Tanzania, Zimbabwe.

Anyclopus unicolor Gerstaecker, 1858: 194.

Ancylopus fuscipennis Gahan, 1892: 210.

Lycoperdina Latreille, 1807

Lycoperdina Latreille, 1807: 73.

Type species: *Galleruca bovistae* Fabricius, 1792.

Golgia Mulsant, 1846: 20.

Type species: *Silpha succincta* Linnaeus, 1767.

Lycoperdinodes Arrow, 1923: 485. Replacement name.

Lycoperdinella Arrow, 1920a: 23. Homonym.

Type species: *Lycoperdinella morosa* Arrow, 1920a.

Falsoylaia Pic, 1945: 10.

Type species: *Falsoylaia obscuresuturalis* Pic, 1945.

angusta Arrow, 1948: 48. South Africa.

apicata Fairmaire, 1898: 436. Madagascar.

banatica Ganglbauer, 1899b: 935. Romania.

bovistae (Fabricius), 1792: 20. Belgium, Czech Republic, Denmark, France, Germany, Great Britain, Hungary, Italy, Netherlands, Poland, Slovakia, Sweden, Switzerland.

Galleruca bovistae Fabricius, 1792: 20.

Endomychus bovistae: Fabricius, 1801: 505.

Lycoperdina immaculata Latreille, 1807: 73.

Lycoperdina bovistae var. *rufescens* Pic, 1943: 9.

Lycoperdina bovistae var. *leprieuri* Pic, 1943: 9.

canariensis Gillerfors, 1991: 24. Canary Islands.

castaneipennis Gorham, 1874c: 151. Japan.

clavata Arrow, 1948: 47. D.R. Congo, Uganda.

crassicornis Reitter, 1880a: 97. Romania.

dux Gorham, 1873b: 205. Japan, Taiwan.

ferruginea LeConte, 1824: 172. Canada (BC, NS, ON), United States (AR, CT, DC, GA, IA, IL, IN, KS, LA, MA, MD, MI, MO, NC, NJ, NM, NY, OH, PA, RI, TN, WI, VA).

Eumorphus angulatus Say, 1825: 303.

Lycoperdina glabrata Guérin–Méneville, 1857c: 271.

gomerae Franz, 1978: 87. Canary Islands.

horrida Strohecker, 1957a: 276. Kenya, Uganda.

humeralis Wollaston, 1864: 432. Canary Islands.

kivuensis Strohecker, 1957b: 148. D.R. Congo.

koltzei Reitter, 1887a: 508. Mongolia, North Korea, Russia (SIB), South Korea.

mandarinea Gerstaecker, 1858: 212. Cambodia, China, Japan, Laos, Mongolia, Russia (FET), Taiwan, Vietnam.

maritima Reitter, 1884a: 61. France (Maritime Alps), Italy.

morosa (Arrow), 1920a: 23. Congo, Cote d'Ivoire, D.R. Congo, Ghana, Madagascar, Zimbabwe.

Lycoperdinella morosa Arrow, 1920a: 23.

Lycoperdinodes morosa: Arrow, 1923: 485.

Falsoylaia obscuresuturalis Pic, 1945: 11.

mus Arrow, 1948: 48. South Africa.

pallida Gebler, 1841: 623. Russia (SIB).

penicillata Marseul, 1868a: 96. Algeria, Morocco, Spain.

perrieri Fairmaire, 1898: 436. Madagascar.

pulvinata Reitter, 1884a: 59. Croatia, Greece, Macedonia, Serbia & Montenegro.

Lycoperdina pulvinata var. *obliqua* Reitter, 1884a: 59.

rifensis Franz, 1978: 88. Canary Islands, Morocco.

sanchezi Oromi & Garcia, 1987: 87. Canary Islands.

sericea Gerstaecker, 1858: 411. South Africa.

succincta (Linnaeus), 1767: 573. Austria, Czech Republic, Denmark, Estonia, Finland, Germany, Great Britain, Hungary, Italy, Latvia, Lithuania, Netherlands, Norway, Poland, Romania, Russia (SIB), Slovakia, Spain, Sweden, Switzerland.

Silpha succincta Linnaeus, 1767: 573.

Galleruca quadripustulata Fabricius, 1792: 33.

Lycoperdina (*Golgia*) *succincta*: Mulsant, 1846: 17.

Lycoperdina succincta ab. *disca* Gerstaecker, 1858: 213.

Endomychus succincta ab. *fasciata* Fabricius, 1801: 505.

Lycoperdina succincta ab. *humeralis* Schilsky, 1888: 184.

Lycoperdina succincta ab. *jakolevi* Semenov, 1904: 290.

validicornis Gerstaecker, 1858: 217. France, Italy.

Lycoperdina validicornis var. *subpubescens* Reitter, 1884a: 60.

***Malindus* Villiers, 1953a**

Malindus Villiers, 1953a: 181.

Type species: *Malindus excavatus* Villiers, 1953a.

excavatus Villiers, 1953a: 182. Cameroon.

***Microtrycherus* Pic, 1937a**

Microtrycherus Pic, 1937a: 488.

Type species: *Microtrycherus luteosignatus* Pic, 1937a.

luteosignatus Pic, 1937a: 488. Angola.

Trycherus luteosignatus: Strohecker, 1953a: 98.

rugicollis (Strohecker), 1953d: 93. D.R. Congo.

Trycherus rugicollis Strohecker, 1953d: 93.

seydeli Strohecker, 1962b: 71.

vittatus (Strohecker), 1944: 139. Nigeria.

Trycherus vittatus Strohecker, 1944: 139.

Trycherus maculatus Strohecker, 1939: 120.

***Mycetina* Mulsant, 1846**

Mycetina Mulsant, 1846: 15.

Type species: *Chrysomela cruciata* Schaller, 1783.

Phaeomychus Gorham, 1887: 649.

Type species: *Endomychus rufipennis* Motschulsky, 1861.

Mycetinina Pic, 1929: 35.

Type species: *Pseudindalmus testaceitarsis* Pic, 1926.

aequatorialis Arrow, 1948: 49. D.R. Congo, Uganda.

africana Gorham, 1874a: 442. Cameroon, Congo, D.R. Congo, Ghana.

amabilis Gorham, 1873b: 206. Japan.

Mycetina amabilis f. *humeropicta* Nakane, 1958: 35.

Mycetina amabilis f. *takahashii* Nakane, 1958: 35.

ancoriger Gorham, 1873b: 206. Japan.

apicalis (Motschulsky), 1835: 321. Azerbaijan, Armenia, Georgia, Iran.

Endomychus apicalis Motschulsky, 1835: 321.

Mycetina cruciata var. *b*. Gerstaecker, 1858: 229.

aptera Strohecker, 1957a: 277. Tanzania.

arrowi Villiers, 1949: 208. Cote d'Ivoire.

atricollis Pic, 1922b: 9. Vietnam.

atrimembris (Pic), 1922b: 10. India.

Endomychus atrimembris Pic, 1922b: 10.

bakeri Strohecker, 1979g: 69. Borneo.

bistripunctata Mader, 1938: 43. China.

brevicollis Gorham, 1901: 205. Borneo.

brevipes (Arrow), 1920b: 323. Cambodia, Laos, Vietnam.

Engonius brevipes Arrow, 1920b: 323.

brevis (Arrow), 1928: 351. Vietnam.

Phaeomychus brevis Arrow, 1928: 351.

castanea Gerstaecker, 1858: 233. Sri Lanka.

Mycetina candens Gorham, 1874a: 441.

ceramica Strohecker, 1975c: 626. India.

cinctipennis Arrow, 1920a: 32. Malaysia, Myanmar, Sumatra, Thailand.

compacta Fairmaire, 1891: 219. China.

corallina Arrow, 1920a: 26. Borneo, Malaysia.

cruciata (Schaller), 1783: 273. Austria, Belgium, Bosnia Herzegovina, Bulgaria, Belarus, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Germany, Hungary, Italy, Latvia, Liechtenstein, Lithuania, Luxembourg, Moldavia, Netherlands, Norway, Poland, Romania, Serbia & Montenegro, Slovakia, Slovenia, Spain, Sweden, Switzerland, Ukraine.

Chrysomela cruciata Schaller, 1783: 273.

Galleruca cruciata: Fabricius, 1793: 20.

Endomychus cruciatus: Fabricius, 1798: 100.

Opatrum lithophila Herbst, 1783: 37.

Eumorphus calabra Costa, 1839: 158.

Lycoperdina binotata Costa, 1850: 10.

Mycetina cruciata var. *interrupta* Gredler, 1870: 17.

Mycetina cruciata var. *balanica* Csiki, 1900c: 401.

Mycetina cruciata var. *fussi* Csiki, 1900d: 150.

cyanescens Strohecker, 1943: 382. China.

cyanipennis Arrow, 1920a: 30. Malaysia.

doriae Gorham, 1885: 524. Borneo.

emmerichi Mader, 1938: 43. China.

evansi Arrow, 1948: 50. D.R. Congo, Zimbabwe.

felix Arrow, 1920a: 30. Java.

fulva Chûjô, 1938: 394. Taiwan.

gabonica Pic, 1922b: 10. Gabon.

gedyei Arrow, 1936: 377. Kenya.

globosa Arrow, 1920a: 28. Borneo.

heteropunctata Heller, 1898: 39. Celebes.

hornii Crotch, 1873: 360. United States (CA).

humerosignata Nakane, 1968: 135. Taiwan.

idahoensis Fall, 1907: 174. Canada (BC), United States (CA, ID, MT, OR, WA).

inapicalis Pic, 1904: 90. Syria.

kamikochiana Nakane, 1982: 50. Japan.

karin Sasaji, 1995: 26. Japan.

klapperichi Mader, 1955: 68. China.

laticollis laticollis Gorham, 1887: 644. Japan.

laticollis satsumana Nakane, 1984: 146. Japan.

longicornis Strohecker, 1979g: 70. Vietnam.

lurida Arrow, 1920a: 27. Borneo.

luzonica Arrow, 1920: 29. Philippines (LZN).

maderi Strohecker, 1982b: 310. China.

marginalis (Gebler), 1830: 227. Russia (FET, SIB).

Lycoperdina marginalis Gebler, 1830: 227.

Mycetina obliquesignata Gorham, 1873a: 44.

Engonius konumaensis Ohta, 1931: 220.

Phaeomychus konumaensis: Chûjô, 1938: 394.

minima Pic, 1927b: 1. Vietnam.

minor Strohecker, 1951a: 160. Celebes.

montivaga Csiki, 1900c: 401. India.

nebulosa Arrow, 1920a: 33. Myanmar, Thailand.

pallida Arrow, 1920a: 32. Myanmar.

perpulchra (Newman), 1838: 390. Canada (NB, NS, ON), United States (AL, AR, CT, DC, GA, IN, LA, MD, ME, NC, NH, NJ, NY, OH, PA, RI, TN, WI, WV, VA).

Endomychus perpulchra Newman, 1838: 390.

Lycoperdina quadriguttata Melsheimer, 1847: 176.

picturata Strohecker, 1957b: 149. Kenya.

plumicornis Strohecker, 1967: 247. Congo.

pulchella Arrow, 1920a: 29. Malaysia, Myanmar, Thailand.

pusilla Arrow, 1920a: 31. Myanmar.

rhodoptera Strohecker, 1979g: 69. Borneo.

rubescens Strohecker, 1952: 4.

rufipennis koyana Nakane, 1958a: 33. Japan.

rufipennis rufipennis (Motschulsky), 1861: 18. Japan, Russia (FET), Taiwan.

Endomychus rufipennis Motschulsky, 1861: 18.

Phaeomychus rufipennis: Gorham, 1887: 649.

sasajii Strohecker, 1982b: 308. Taiwan.

similis (Chûjô), 1938: 395. Taiwan.

Phaeomychus similis Chûjô, 1938: 395.

soror Arrow, 1920a: 28. Malaysia, Myanmar, Sumatra, Thailand.

stackelbergi Kryzhanovskij, 1977: 39. Russia (FET).

superba Mader, 1941b: 932. China.

testaceitarsus (Pic), 1926: 10. Vietnam.

Pseudindalmus testaceitarsus Pic, 1926: 10.

Mycetina (*Mycetinina*) *testaceitarsus*: Pic, 1929: 35.

tetrasticta Arrow, 1920a: 20. India.

tonkinea Pic, 1931: 5. Vietnam.

trimaculata Gorham, 1885: 524. Java.

turneri Arrow, 1936: 376. Congo, South Africa.

variicornis (Arrow), 1925: 317. India.

Engonius variicornis Arrow, 1925: 317.

***Ohtaius* Chûjô, 1938**

Ohtaius Chûjô, 1938: 398.

Type species: *Brachytrycherus mushanus* Ohta, 1931.

annularis (Gerstaecker), 1857: 221. India, Sri Lanka.

Engonius annularis Gerstaecker, 1857: 221.

laticollis (Achard), 1922: 28. China.

Engonius laticollis Achard, 1922: 28.

lunulatus (Gerstaecker), 1857: 222. Sri Lanka.

Engonius lunulatus Gerstaecker, 1857: 222.

mushanus (Ohta), 1931: 216. China, Taiwan.

Brachytrycherus mushanus Ohta, 1931: 216.

Engonius mushanus: Strohecker, 1953a: 101.

opacicollis (Arrow), 1920b: 323. Laos.

Engonius opacicollis Arrow, 1920b: 323.

signatus Strohecker, 1964: 327. India, Thailand.

signifer (Gorham), 1875b: 311. India, Myanmar, Nepal.

Engonius signifer Gorham, 1875b: 311.

vicinus (Arrow), 1925: 313. India.

Engonius vicinus Arrow, 1925: 313.

***Parindalmus* Achard, 1922**

Parindalmus Achard, 1922: 29.

Type species: *Parindalmus tonkineus* Achard, 1922.

Pedanus Gerstaecker, 1857: 230.

Type species: *Pedanus quadrilunatus* Gerstaecker, 1857.

quadrilunatus (Gerstaecker), 1857: 230. Borneo, Malaysia, Myanmar, Sumatra, Taiwan.

Pedanus quadrilunatus Gerstaecker, 1857: 230.

Pedanus affinis Gerstaecker, 1857: 231.

Pedanus gerstaeckeri Gorham, 1873a: 37.

Engonius bimaculatus Pic, 1925: 3.

schneideri (Schoenherr), 1808: 329. India, Pakistan, Sri Lanka.

Eumorphus schneideri Schoenherr, 1808: 329.

Pedanus schneideri: Gerstaecker, 1858: 132.

sinensis Strohecker, 1971a: 25. China.

tonkineus Achard, 1922: 29. China, Laos, Thailand, Vietnam.

Parindalmus tonkineus var. *semirufescens* Pic, 1927b: 1.

Parindalmus westermanni Kryzhanovskij, 1960: 893.

vestitus (Arrow), 1925: 322. India.

Pedanus vestitus Arrow, 1925: 322.

westermanni (Gerstaecker), 1857: 231. China, India, Java, Malaysia, Myanmar, Thailand.

Pedanus westermanni Gerstaecker, 1857: 231.

Haplomorphus westermanni: Guérin–Méneville, 1858: 24.

Platindalmus **Strohecker, 1979f**

Platindalmus Strohecker, 1979f: 290.

Type species: *Eumorphus calcaratus* Arrow, 1920b.

calcaratus australis Strohecker, 1979f: 291. Laos.

calcaratus calcaratus (Arrow), 1920b: 325. Cambodia, Laos, Vietnam.

Eumorphus calcaratus Arrow, 1920b: 325.

***Pseudindalmus* Arrow, 1920b**

Pseudindalmus Arrow, 1920b: 330.

Type species: *Pseudindalmus tonkinensi*s Arrow, 1920b.

Falsodanae Pic, 1940b: 11.

Type species: *Falsodanae rufonotata* Pic, 1940b.

andamanicus Arrow, 1920a: 33. India.

biguttatus Strohecker, 1939: 120. Indonesia.

borneensis Arrow, 1920a: 34. Borneo.

burckhardti Tomaszewska, 2001a: 135. Malaysia.

depressus (Gerstaecker), 1858: 235. Borneo, Malaysia, Singapore.

Mycetina depressa Gerstaecker, 1858: 235.

Mycetina malayensis Arrow, 1923: 486.

javanicus Strohecker, 1977b: 373. Java.

longicornis Tomaszewska, 2001a: 136. Taiwan.

malaccanus (Pic), 1930b: 9. Malaysia, Singapore.

Mycetina malaccana Pic, 1930b: 9.

quadrimaculatus (Pic), 1930b: 9. Singapore.

Mycetina quadrimaculata Pic, 1930b: 9.

rufonotatus (Pic), 1940b: 11. Cambodia, Laos, Vietnam.

Falsodanae rufonotata Pic, 1940b: 11.

similis Tomaszewska, 2001a: 137. Thailand.

sumatrensis Tomaszewska, 2001a: 135. Sumatra.

tonkinensis Arrow, 1920b: 331. Laos, Vietnam.

Sinocymbachus **Strohecker & Chûjô, 1970**

Sinocymbachus Strohecker & Chûjô, 1970: 511.

Type species: *Engonius excisipes* Strohecker, 1943.

angustefasciatus (Pic), 1940b: 11. China.

Engonius angustefasciatus Pic, 1940b: 11.

bimaculatus (Pic), 1927a: 11. Vietnam.

Amphisternus bimaculatus Pic, 1927a: 11.

Cymbachus bimaculatus: Strohecker, 1953a: 90.

decorus Strohecker & Chûjô, 1970: 516. China.

excisipes (Strohecker), 1943: 383. China.

Engonius excisipes Strohecker, 1943: 383.

Cymbachus excisipes: Strohecker, 1953a: 90.

humerosus (Mader), 1938: 40. China, Taiwan.

Cymbachus humerosus Mader, 1938: 40.

Amphisternus quadrinotatus Chûjô, 1938: 396.

luteomaculatus (Pic), 1921: 1. China.

Engonius luteomaculatus Pic, 1921: 1.

Cymbachus luteomaculatus: Strohecker, 1953a: 91.

parvimaculatus (Mader), 1938: 40. China.

Cymbachus parvimaculatus Mader, 1938: 40.

politus Strohecker & Chûjô, 1970: 515. Taiwan.

quadrimaculatus (Pic), 1927a: 11. China, Vietnam.

Amphisternus quadrimaculatus Pic, 1927a: 11.

Cymbachus quadrimaculatus: Strohecker, 1953a: 91.

quadriundulatus (Chûjô), 1938: 397. Taiwan.

Amphisternus quadriundulatus Chûjô, 1938: 397.

***Spathomeles* Gerstaecker, 1857**

Spathomeles Gerstaecker, 1857: 218.

Type species: *Spathomeles anaglyptus* Gerstaecker, 1857.

Rhachidophorus Guérin–Méneville, 1857b: 581.

Type species: *Cacodaemon hopei* Thomson, 1857

(=*Eumorphus hopei* Guérin–Méneville, 1857c).

anaglyptus Gerstaecker, 1857: 219. Borneo, Java, Malaysia, Myanmar, Sumatra, Thailand.

Cacodaemon hopei Thomson, 1857: 154.

Eumorphus hopei: Guérin–Méneville, 1857c: 255.

Rhachidophorus hopei: Guérin–Méneville, 1858: 29.

Rhachidophorus hopei var. *insuspectus* Gorham, 1873a: 31.

Spathomeles anaglyptus insuspectus Strohecker, 1982a: 180.

anceps (Gorham), 1895: 328. India.

Amphisternus anceps Gorham, 1895: 328.

bonthainicus Heller, 1898: 39. Celebes.

darwinista darwinista Dohrn, 1873: 322. Philippines (LZN).

darwinista pyramidalis Gorham, 1873a: 31. Philippines.

Spathomeles pyramidalis Gorham, 1873a: 31.

decoratus Gerstaecker, 1857: 219. India, Java, Laos, Myanmar.

Cacodaemon hamatus Thomson, 1857: 154.

Rhachidophorus latreillei Guérin–Méneville, 1858: 61.

Spathomeles decoratus var. *ornatus* Gorham, 1886: 155.

dohrnii Gerstaecker, 1857: 219. Java, Sumatra.

Eumorphus quadrisignatus Guérin–Méneville, 1857c: 257.

Rhachidophorus quadrisignatus: Guérin–Méneville, 1858: 61.

elegans Gorham, 1873a: 32. Borneo, Malaysia, Sumatra.

frivaldszkyi Strohecker, 1957a: 280. Borneo.

lazarus Strohecker, 1968c: 114. Borneo, Sumatra.

moloch Strohecker, 1958a: 41. Philippines (MDO).

politus Strohecker, 1964: 332. Celebes.

retiarius Strohecker, 1949a: 438. Borneo.

rizali Strohecker, 1964: 336. Philippines (MDO).

turritus Gerstaecker, 1857: 220. Borneo, Malaysia.

Spathomeles turritus var. *dispar* Frivaldszky, 1883: 126.

wegneri Strohecker, 1958c: 243. Borneo.

***Stictomela* Gorham, 1886**

Stictomela Gorham, 1886: 155.

Type species: *Stictomela chrysomeloides* Gorham, 1886.

besucheti Strohecker, 1975c: 625. India.

chrysomeloides Gorham, 1886: 156. Sri Lanka.

inflata (Gorham), 1886: 154. Sri Lanka.

Spathomeles inflatus Gorham, 1886: 154.

opulenta Gorham, 1886: 156. Sri Lanka.

Stroheckeria Tomaszewska, 2006

Stroheckeria Tomaszewska, 2006: 466.

Type species: *Stroheckeria quadrimaculata* Tomaszewska, 2006.

quadrimaculata Tomaszewska, 2006: 469. Vietnam.

Trycherus Gerstaecker, 1857

Trycherus Gerstaecker, 1857: 222.

Type species: *Trycherus bifasciatus* Gerstaecker, 1857.

Olena Blanchard, 1851: 522.

Olenus Thomson, 1857: 157.

Type species: *Trycherus senegalensis* Gerstaecker, 1857.

Balius Guérin–Méneville, 1857: 261. Replacement name.

Trypherus Pic, 1936b: 11. Misspelling.

aberrans Strohecker, 1967: 248. Congo.

angolensis Gorham, 1897: 458. Angola, Congo.

Trycherus angolensis var. *apicalis* Pic, 1930c: 9.

appendiculatus Gerstaecker, 1857: 223. Congo, Cote d'Ivoire, Equatorial Guinea.

Trycherus appendiculatus var. *inapicalis* Pic, 1930c: 9.

Trycherus appendiculatus var. *nigrithorax* Pic, 1930c: 10.

Trycherus appendiculatus triplex Strohecker, 1953c: 81.

ardoini Villiers, 1959: 602. Guinea, Uganda.

arrowi Villiers, 1953b: 1491. Cote d'Ivoire, D.R. Congo, Sierra Leone.

attenuatus Arrow, 1920a: 9. Angola, Uganda.

avus Strohecker, 1957a: 279. Tanzania.

bancoensis Villiers, 1953b: 1496. Cote d’Ivoire.

basilewskyi Strohecker, 1953c: 81. Congo.

bifasciatus Gerstaecker, 1857: 223. Congo, Cote d’Ivoire, Equatorial Guinea.

Trycherus gerstaeckeri Villiers, 1953b: 1482.

bipunctatus Villiers, 1953b: 1499. D.R. Congo.

bomansi Strohecker, 1953d: 92. D.R. Congo.

brinae Villiers, 1953b: 1502. D.R. Congo.

cantaloubei Villiers, 1959: 605. Cameroon.

centurio Strohecker, 1957a: 278. Cameroon.

chopardi Villiers, 1953b: 1478. Congo, Cote d'Ivoire, D.R. Congo, Gabon.

conradti Villiers, 1953b: 1497. Cameroon.

convexus Villiers, 1953b: 1488. Central African Republic.

decellei Strohecker, 1968a: 251. Cote d'Ivoire.

descarpentriesi Strohecker, 1974b: 533. Cameroon.

donckieri Pic, 1930c: 6. Congo.

dubius Strohecker, 1953c: 84. Congo.

elegans Csiki, 1900c: 400. Cameroon, Cote d’Ivoire.

Trycherus longanimis Fairmaire, 1902: 327.

Trycherus appendiculatus Villiers, 1953b: 1477.

elongatus Pic, 1936b: 11. Cameroon.

endroedium Strohecker, 1972c: 197. Ghana.

erotyloides Gerstaecker, 1857: 223. Congo, Equatorial Guinea, Ghana.

fenestratus Pic, 1930c: 9. Congo, Gabon, Somalia.

Trycherus ciliatipes Strohecker, 1953c: 84.

flavipes Arrow, 1920a: 10. Nigeria.

frater Arrow, 1920a: 8. Cameroon, Uganda.

fryanus Gorham, 1875a: 12. Angola, Congo, D.R. Congo, Rwanda, Somalia, Tanzania, Zimbabwe.

Trycherus recticollis Harold, 1879: 220.

Trycherus monardi Pic, 1937a: 487.

ghanensis Strohecker, 1972c: 195. Ghana.

gigas Villiers, 1953b: 1473. D.R. Congo.

gracilipes Strohecker, 1955a: 173. Burundi, Rwanda.

hiekei Strohecker, 1979b: 111. Cameroon.

hydroporoides Gorham, 1873a: 33. Congo, Cote d'Ivoire, Senegal.

imperator Strohecker, 1953d: 92. Congo.

josephus Duvivier, 1891: 382. Congo.

kenyanus Strohecker, 1959c: 178. Kenya.

kiloensis Strohecker, 1962b: 58. D.R. Congo.

kinduensis Villiers, 1953b: 1501. D.R. Congo.

lamottei Villiers, 1953b: 1468. Guinea.

latens Strohecker, 1962b: 63. D.R. Congo.

latipes Strohecker, 1954: 148. D.R. Congo.

latus Arrow, 1920a: 9. Uganda.

lobiventris Strohecker, 1953c: 84. Congo.

longanimis (Thomson), 1858: 238. Congo, D.R. Congo, Gabon, Rwanda, Senegal.

Balius longanimis Thomson, 1858: 238.

lootensi Strohecker, 1962b: 61. D.R. Congo.

maculatus Pic, 1921: 1. Congo, Nigeria.

m–flavus Arrow, 1920a: 7. Uganda.

minor Strohecker, 1962b: 59. D.R. Congo.

minutus (Guérin–Méneville), 1857c: 262. Java.

Balius minutus Guérin–Méneville, 1857c: 262.

mocquerysi Villiers, 1953b: 1481. Congo.

mongonensis Strohecker, 1954: 148. Equatorial Guinea.

niger Strohecker, 1954: 148. Cote d'Ivoire, Equatorial Guinea.

nigromaculatus Pic, 1937b: 16. Congo.

Trycherus burgeoni Villiers, 1953b: 1484.

nitidus Arrow, 1920a: 11. Angola, Uganda.

oberthuri Villiers, 1953b: 1483. Cameroon, Cote d’Ivoire.

occultus Strohecker, 1962b: 61. Cameroon, Cote d’Ivoire, D.R. Congo, Sudan.

ornatus Villiers, 1953b: 1489. D.R. Congo.

ovatus Arrow, 1920a: 8. Congo, Sudan, Uganda.

rex Arrow, 1920a: 6. Uganda.

royi Villiers, 1953b: 1468. Guinea.

satrapes Strohecker, 1962b: 64. D.R. Congo, Sudan, Uganda.

Trycherus rex Strohecker, 1953d: 94.

semiobliteratus Pic, 1939: 20. Gabon.

senegalensis Gerstaecker, 1857: 223. Cameroon, Congo, Cote d'Ivoire, D.R. Congo, Equatorial Guinea, Gabon, Ghana, Senegal.

Trycherus spinipes Arrow, 1920a: 12.

sexpunctatus Villiers, 1953b: 1503. Guinea.

stanleyi Strohecker, 1953d: 93. Congo.

straeleni Strohecker, 1952: 9. D.R. Congo.

stroheckeri Villiers, 1953b: 1483. Congo, Cameroon.

unifasciatus Pic, 1930b: 7. Congo.

villiersi Strohecker, 1954: 146. D.R. Congo.

virilis Strohecker, 1953c: 82. Congo.

MEROPHYSIINAE Seidlitz, 1872-75

Merophysiinae Seidlitz, 1872–75: 39.

Merophysiini Reitter, 1875: 300.

Merophysiaires Belon, 1879: 184.

Holoparamecini Reitter, 1887b: 8.

Merophysina Fowler, 1889: 276.

Holoparamecinae Ganglbauer, 1899a: 772.

Merophysiinae Sharp, 1902: 626.

Merophysiina Jakobson, 1905–1916 [1915]: 921.

Holoparamecina Jakobson, 1905–1916 [1915]: 921.

Cholovocera Motschulsky, 1838

Cholovocera Motschulsky, 1838: 177.

Type species: *Cholovocera formicaria* Motschulsky, 1838.

Coluocera Gemminger & Harold, 1868: 905. Unjustified emendation.

Colovocera Belon, 1879: 185. Misspelling.

Choluocera Kraatz, 1858: 140. Unnecessary replacement name.

afghana Johnson, 1977: 123. Afghanistan.

attae (Kraatz), 1858: 140. Algeria, France, Greece, Hungary, Italy, Montenegro, Morocco, Serbia, Tunisia.

Choluocera attae Kraatz, 1858: 140.

beloni (Wasmann), 1899: 160. India, Sri Lanka.

Coluocera beloni Wasmann, 1899: 160.

Displotera (*Mussardia*) *grandis* Dajoz, 1975: 201.

brevicornis Johnson, 1977: 124. Afghanistan.

fleischeri Reitter, 1902: 5. Italy, Malta, Montenegro, Serbia.

formicaria Motschulsky, 1838: 179. Albania, Algeria, France, Greece, Italy, Malta, Morocco, Spain, Switzerland, Tunisia, Turkey.

Coluocera gallica Schaufuss, 1876: 398.

Merophysia subterranea Motschulsky, 1845: 111.

major Reitter, 1887b: 10. Turkey.

punctata Märkel, 1845: 255. Algeria, France, Italy, Spain, Switzerland, Tunisia.

Cholovocera formiceticola Rosenhauer, 1856: 355.

sardoa Reitter, 1911a: 70. Italy (Sardinia).

***Cholovocerida* Belon, 1884**

Cholovocerida Belon, 1884: 163.

Type species: *Cholovocerida unicurva* Belon, 1884.

Displotera Reitter, 1887b: 10. [new synonym]

Type species: *Displotera simoni* Reitter, 1887.

Lioclemmus Jeannel, 1934: 172.

Type species: *Lioclemmus petiti* Jeannel, 1934.

ecitonis (Wasmann), 1890: 302. Brasil. [new combination]

Coluocera ecitonis Wasmann, 1890: 302.

maderae (Wollaston), 1854: 180. Antilles, Brasil, Ecuador (Galapagos I.), Ghana, Hispaniola, Madagascar, Madeira, Myanmar, Trinidad, United States (HI). [new combination]

Cholovocera maderae Wollaston, 1854: 180.

Lioclemmus petiti Jeannel, 1934: 173.

Displotera simoni Reitter, 1887b: 10.

Colovocera oculata Belon, 1891: 878.

unicurva Belon, 1884: 164. Chile.

***Hexasternum* Rücker, 1983**

Hexasternum Rücker, 1983: 679.

Type species: *Hexasternum orbiculare* Rücker, 1983.

orbiculare Rücker, 1983: 680. Kenya.

***Holoparamecus* Curtis, 1833**

Holoparamecus Curtis, 1833: 186.

Type species: *Holoparamecus depressus* Curtis, 1833.

Calyptobium Aubé, 1843: 242.

Type species: *Calyptobium caularum* Aubé, 1843.

Tomyrium Reitter, 1881a: 49.

Type species: *Holoparamecus bertouti* Aubé, 1861.

Microparamecus Dajoz, 1967: 589.

Type species: *Microparamecus castrii* Dajoz, 1967.

Neoparamecus Dajoz, 1974: 1074.

Type species: *Neoparamecus peruvianus* Dajoz, 1974.

Amphibolonarzon Villa & Villa, 1833: 26.

Calyptobides Strand, 1933: 123.

Tocalium Motschulsky, 1867: 97.

Type species: *Tocalium orientale* Motschulsky, 1867.

Blumenus Belon, 1887: 219.

Holoparmecus Klebs, 1910: 240. Misspelling.

aeger SenGupta & Pal, 1983: 143. India.

aelleni Rücker, 1988: 1027. Antilles.

africanus Dajoz, 1970d: 438. Congo.

amabilis Sasaji, 1991: 22. Japan.

angulatus (Rücker), 1982: 75. Sri Lanka.

Tomyrium angulatus Rücker, 1982: 75.

atomus Ragusa, 1888: 37. Italy.

attenuatus (Motschulsky), 1867: 101. India, Sri Lanka.

Calyptobium attenuatum Motschulsky, 1867: 101.

Calyptobium clavipes Motschulsky, 1867: 102.

Holoparamecus (Calyptobium) ceylonicus Dajoz, 1975: 201.

barretoi Bruch, 1938: 162. Argentina.

beloni Reitter, 1884a: 63. Bosnia and Herzegovina, Greece, Italy, Serbia & Montenegro.

bertouti (Aubé), 1861: 198. Arab Emirates, France, Italy (Sardinia, Sicily), Malta, Tunisia, Yemen.

Tomyrium bertouti Aubé, 1861: 198.

Tomyrium similis Belon, 1885b: 39.

bipartitus Wollaston, 1867: 73. Cape Verde Islands.

brasiliensis Motschulsky, 1867: 99. Brasil.

brosciformis Sharp, 1902: 627. Guatemala.

castaneus Broun, 1893: 1448. New Zealand.

castrii Dajoz, 1967: 591. Chile.

Holoparamecus (*Microparamecus*) *castrii* Dajoz, 1967: 591.

caularum (Aubé), 1843: 244. Algeria, Austria, Azores, Bosnia Herzegovina, Belgium, Bulgaria, Cameroon, Canada, Canary Islands, China, Congo, Czech Republic, Denmark, Egypt, Finland, France, Germany, Great Britain, Greece, Hungary, Italy, Malta, Mexico, Morocco, Netherlands, Poland, Reunion, Russia (CET), Serbia & Montenegro, Slovakia, Spain, Sweden, Switzerland, Syria, Tunisia, Ukraine, United States (CA, FL, HI, MI). Cosmopolitan.

Calyptobium caularum Aubé, 1843: 244.

Calyptobium panckoucki Guérin–Méneville, 1844: 34.

Calyptobium obtusicorne Motschulsky, 1867: 101.

Calyptobium tuberculum Motschulsky, 1867: 102.

Calyptobium beauchenei Croissandeau, 1891: 154.

constrictus (Sharp), 1902: 628. Guatemala, Mexico.

Calyptobium constrictus Sharp, 1902: 628.

contractus Wollaston, 1874: 203. Japan.

convexus Rücker, 1982: 76. Thailand.

Holoparamecus (*Holoparamecus*) *convexus* Rücker, 1982: 76.

cordicollis SenGupta & Pal, 1983: 149. India.

Holoparamecus (Calyptobium) cordicollis SenGupta & Pal, 1983: 149.

depressus Curtis, 1833: 186. Australia, Belgium, Brasil, Cameroon, Canada, China, Denmark, France, Great Britain, Greece, Hispaniola, Italy, Japan, Madagascar, Madeira, Martinique, Mauritius, Mexico, Myanmar, Netherlands, New Caledonia, Reunion, Senegal, Serbia & Montenegro, Switzerland, United States (CA, GA, NY), Vietnam. Cosmopolitan.

Holoparamecus integer Rey, 1889: 54.

Calyptobium kunzei Aubé, 1843: 245.

dispar Belon, 1885a: 242. Brasil, Venezuela.

ellipticus Wollaston, 1874: 201. China, Japan.

erebus Rücker, 1985: 168. Indonesia.

externus (Motschulsky), 1867: 97. India.

Tocalium externum Motschulsky, 1867: 97.

floridanus Fall, 1899: 109. Canada, Mexico, United States (FL).

franzi Rücker, 1985: 166. Galapagos I.

gabrielae Rücker, 2003: 10. Mexico.

garambae Dajoz, 1970c: 7. D.R. Congo.

Holoparamecus (*Calyptobium*) *garambae* Dajoz, 1970c: 7.

gracilis Rücker, 1983: 684. Senegal.

horni Wasmann, 1902: 156. Sri Lanka.

imporcitis SenGupta & Pal, 1983: 141. India.

impressus Rücker, 1979: 195. Vietnam.

insularis Dajoz, 1972b: 1053. Mauritius.

Holoparamecus (*Calyptobium*) *insularis* Dajoz, 1972b: 1053.

integer Rücker, 1985: 167. Bolivia.

johnsoni Rücker, 1981: 54. Brasil.

Holoparamecus (*Blumenus*) *johnsoni* Rücker, 1981: 54.

lanatus Rücker, 1985: 169. Indonesia.

lederi Reitter, 1877a: 295. Caucasus.

Holoparamecus (*Calyptobium*) *lederi* Reitter, 1877a: 295.

lyratus Reitter, 1891: 22. Uzbekistan.

microps Belon, 1895: 79. Morocco, Tunisia.

Holoparamecus nigriceps Belon, 1897: 122.

niger (Aubé), 1843: 246. Algeria, Canary Islands, Egypt, France, Greece, Italy, Libya, Madeira, Malta, Morocco, Spain, Switzerland, Tunisia.

Calyptobium nigrum Aubé, 1843: 246.

Holoparamecus argodi Croissandeau, 1891: 153.

Holoparamecus lowei Wollaston, 1879: 233.

Holoparamecus occultus Leder, 1872: 139.

obtusum Reitter, 1884a: 63. Syria.

orientalis (Motschulsky), 1867: 97. India.

Tocalium orientale Motschulsky, 1867: 97.

pacificus (LeConte), 1863: 72. Canada, Mexico, United States (CA)

Calyptobium pacificus LeConte, 1863: 72.

peruvianus Dajoz, 1974: 1074. Peru.

piliger Rücker, 1993: 95. Thailand.

pumilus (Sharp), 1902: 627. Mexico.

Blumenus pumilus Sharp, 1902: 627.

punctulatus Reitter, 1908b: 244. Italy.

raffrayi Belon, 1898: 440. South Africa (Cape Town).

Holoparamecus (*Calyptobium*) *raffrayi* Belon, 1898: 440.

ragusae Reitter, 1875: 309. Belgium, Canada, Chile, Czech Republic, France, Hungary, Italy, Japan, Mexico, Netherlands, Switzerland, United States (IN, MO, PA).

sanguineus SenGupta & Pal, 1983: 146. India.

Holoparamecus (Calyptobium) sanguineus SenGupta & Pal, 1983: 146.

saulcyi Baudi di Selve, 1870: 60. Cyprus.

signatus Wollaston, 1874: 202. China, Japan.

Holoparamecus capitatus Wollaston, 1874: 202.

singularis (Beck), 1817: 14. Algeria, Azores, Belgium, Canada, Canary Islands, China, Cyprus, Egypt, France, Great Britain, Greece, India, Israel, Italy, Lebanon, Libya, Madeira, Mexico, Morocco, Netherlands, South Korea, Spain, Switzerland, Tunisia, Turkey, United States (CA, NY). Cosmopolitan.

Silvanus singularis Beck, 1817: 14.

Holoparamecus azoricus Mequignon, 1942: 10.

Holoparamecus longipennis Motschulsky, 1867: 100.

Holoparamecus populi Motschulsky, 1867: 99.

Holoparamecus obtusus Reitter, 1884a: 63.

Calyptobium villae Aubé, 1843: 243.

spinosus Dajoz, 1967: 589. Chile.

Holoparamecus (*Microparamecus*) *spinosus* Dajoz, 1967: 589.

tenuis Reitter, 1880b: 178. New Zealand.

Holoparamecus lucidus Broun, 1880: 232.

testaceus (Broun), 1893: 1448. New Zealand.

Calyptobium testaceus Broun, 1893: 1448.

truquii Baudi di Selve, 1861: 182. Cyprus, Lebanon.

velutinus SenGupta & Pal, 1983: 147. India.

Holoparamecus (Calyptobium) velutinus SenGupta & Pal, 1983: 147.

villiger (Belon), 1887: 219. Brasil.

Blumenus villiger Belon, 1887: 219.

Lathrapion **Rücker, 1983**

Lathrapion Rücker, 1983: 681.

Type species: *Lathrapion convexus* Rücker, 1983.

convexus Rücker, 1983: 681. Kenya.

***Lixella* Peyerimhoff, 1913**

Lixella Peyerimhoff, 1913: 516.

Type species: *Lixella crassipes* Peyerimhoff, 1912.

crassipes Peyerimhoff, 1913: 516. North Africa.

***Lycoperdinella* Champion, 1913**

Lycoperdinella Champion, 1913: 114.

Type species: *Lycoperdinella subcaeca* Champion, 1913.

subcaeca Champion, 1913: 115. Costa Rica, Guatemala.

***Merophysia* Lucas, 1852**

Merophysia Lucas, 1852: 29.

Type species: *Merophysia formicaria* Lucas, 1852.

Merophysiops Semenov, 1899: 15.

Type species: *Merophysia bicarinata* Reitter, 1897.

andreinii Gridelli, 1930: 142. Libya.

baudueri Reitter, 1877b: 6. Algeria, Morocco, Spain, Tunisia.

Merophysia acuminata Fairmaire, 1879: 168.

beloni Peyerimhoff, 1929: 213. Algeria.

bicarinata Reitter, 1897: 212. Uzbekistan.

biplicata Reitter, 1884c: 253. Greece, Israel, Syria.

Merophysia saulcyi Belon, 1879: 200.

bisinuata Reitter, 1908a: 213. Israel, Jordan, Turkey.

bistriata Reitter, 1889b: 255. Greece.

carinulata Rosenhauer, 1856: 354. Algeria, Great Britain?, Israel, Jordan, Spain, Syria.

carmelitana Saulcy, 1864: 423. Algeria, Cyprus, Greece, Israel, Lebanon, Morocco, Syria, Tunisia.

Merophysia minor Baudi di Selve, 1870: 59.

cretica Kiesenwetter, 1872: 163. Cyprus, Greece (Crete), Pakistan, Turkey.

cyrenaica Gridelli, 1930: 139. Libya.

formicaria Lucas, 1852: 29. Algeria, Cyprus, France, Greece, Italy, Malta, Morocco, Portugal, Spain, Switzerland, Tunisia, Turkey.

Merophysia ragusae Belon, 1895: 78.

Merophysia lusitanica Reitter, 1913: 654.

foveolata Baudi di Selve, 1870: 59. Cyprus, Israel, Jordan, Syria.

lata Kiesenwetter, 1872: 164. Greece, Malta, Turkey.

letourneuxi Pic, 1914: 49. France (Corsica), Egypt, Israel, Lebanon, Syria.

longicornis Reitter, 1887b: 12. Algeria, Cyprus, Egypt, Israel, Jordan, Morocco, Syria, Tunisia.

madoni Belon, 1885a: 241. Cyprus, Italy (Sardinia).

nana Reitter, 1887b: 12. Israel, Syria.

oblonga Kiesenwetter, 1872: 164. Greece, Italy, Malta, Turkey.

Merophysia oblonga var. *escherichi* Wasmann, 1896: 239.

orientalis Saulcy, 1864: 422. Algeria, Greece, Israel, Jordan, Lebanon, Syria, Turkey, Ukraine.

Merophysia ovalipennis Coye, 1870: 376.

procera Reitter, 1875: 304. Israel, Jordan.

sekerae Reitter, 1908b: 244. Italy.

sicula Kiesenwetter, 1872: 166. France, Greece, Italy, Tunisia.

silvestrii Gridelli, 1927: 237. Libya.

striatella Reitter, 1890: 388. Greece, Italy, Ukraine (Krym).

uniplicata Reitter, 1884c: 253. Morocco.

Pseudevolocera Champion, 1913

Pseudevolocera Champion, 1913: 113.

Type species: *Pseudevolocera atomarioides* Champion, 1913.

atomarioides Champion, 1913: 114. Costa Rica, Guatemala.

Pseudoparamecus Brèthes, 1922

Pseudoparamecus Brèthes, 1922: 31.

Type species: *Pseudoparamecus extraneus* Brèthes, 1922.

extraneus Brèthes, 1922: 32. Argentina.

Pythlarhinus Dajoz, 1970c

Pythlarhinus Dajoz, 1970c: 9.

Type species: *Pythlarhinus verschureni* Dajoz, 1970c.

verschureni Dajoz, 1970c: 10. Cameroon, D.R. Congo.

Reitteria Leder, 1872

Reitteria Leder, 1872: 137.

Type species: *Reitteria lucifuga* Leder, 1872.

Cereaxina Jeannel, 1934: 169.

Type species: *Cereaxina troglodytes* Jeannel, 1934.

balcanica Karaman, 1936: 131. Macedonia.

escherichi Wasmann, 1896: 238. Cyprus, Italy, Turkey.

Cereaxina troglodytes Jeannel, 1934: 172.

lucifuga Leder, 1872: 138. Algeria.

Reitteria pallida Pic, 1940a: 5.

MYCETAEINAE Jacquelin du Val, 1857

Mycetaeinae Jacquelin du Val, 1857: 102.

Mycetaeidae Dajoz, 1972a: 210.

Agaricophilus **Motschulsky, 1838**

Agaricophilus Motschulsky, 1838: 175.

Type species: *Agaricophilus reflexus* Motschulsky, 1838.

Hygrotophila Kolenati, 1846: 56.

dieneri Reitter, 1911b: 294. Slovakia.

reflexus Motschulsky, 1838: 177. Russia (SET).

Hygrotophila glabratus Kolenati, 1846: 56.

Agaricophilus subaeneus Reitter, 1876: 294.

Mycetaea **Stephens, 1829**

Mycetaea Stephens, 1829: 87.

Type species: *Mycetaea fumata* Stephens, 1829

(=*Dermestes subterraneus* Fabricius, 1801).

Silpha Marsham, 1802: 124.

Type species: *Silpha hirta* Marsham, 1802.

ciliata Arrow, 1948: 54. South Africa.

ovulum Wollaston, 1861: 139. South Africa.

pilosella Blackburn, 1891: 122. Australia?.

subterranea (Fabricius), 1801: 318. Austria, Azerbaijan, Belgium, Belarus, Canada (BC, NS, ON, PE, QB), Croatia, Czech Republic, Denmark, Estonia, Finland, France, Germany, Great Britain, Hungary, Iceland, Ireland, Italy, Latvia, Lithuania, Luxembourg, Netherlands, Norway, Poland, Romania, Russia (CET, NET), Slovakia, Slovenia, Sweden, Spain, Switzerland, Tasmania, United States (CA, CT, DC, MA, MD, MI, NC, NY, OR, PA, WI). Cosmopolitan.

Dermestes subterraneus Fabricius, 1801: 318.

Silpha hirta Marsham, 1802: 124.

Cryptophagus villosus Beck, 1817: 12.

Mycetaea fumata Stephens, 1829: 81.

Idiophyes dubia Lea, 1921a: 367.

tafilaletica Smirnoff, 1957: 55. Morocco. [*nomen nudum*]

PLEGANOPHORINAE Jacquelin du Val, 1858

Pleganophorides Jacques du Val, 1858: 186.

Endomychidae adsciti Gerstaecker, 1858: 377.

Paussoideidae Gorham, 1873a: 29.

Trochoideites Chapuis, 1876: 146.

Pleganophorini Reitter, 1881c: 926.

Trochoideinae Ganglbauer, 1899b: 926.

***Dadocerus* Arrow, 1920a**

Dadocerus Arrow, 1920a: 76.

Type species: *Dadocerus nitidus* Arrow, 1920a.

nitidus Arrow, 1920a: 76. Borneo.

***Pleganophorus* Hampe, 1855**

Pleganophorus Hampe, 1855: 97.

Type species: *Pleganophorus bispinosus* Hampe, 1855.

bispinosus bispinosus Hampe, 1855: 98. Bulgaria, Croatia, Czech Republic, Greece, Hungary, Romania, Slovakia.

bispinosus slovenicus Olexa, 1954: 48. Slovakia.

***Trochoideus* Westwood, 1833**

Trochoideus Westwood, 1833: 673.

Type species: *Paussus cruciatus* Dalman, 1825.

Trochoides Chapuis, 1876: 147. Unnecessary replacement name.

Pseudopaussus Schulze, 1916: 292.

Type species: *Pseudopaussus monstrosus* Schulze, 1916.

americanus Buquet, 1840: 174. Bolivia, Colombia, Costa Rica, Panama, Venezuela.

bicolor Csiki, 1909: 342. Sumatra.

boliviensis Strohecker, 1978a: 350. Bolivia, Peru.

coeloantennatus Strohecker, 1943: 391. Argentina.

dalmani Westwood, 1838: 86. Madagascar.

Trochoideus dalmani junctus Pic, 1950: 11.

Trochoideus oberthuri Wasmann, 1897: 271.

desjardinsi Guérin–Méneville, 1838: 22. Borneo, Fiji Islands, India, Indonesia, Japan, Java, Kenya, Madagascar, Malaysia, Mauritius, Micronesia, Myanmar, Papua–New Guinea, Philippines, Samoa, Seychelles, Sri Lanka, Taiwán, Tanzania, Uganda, United Status (FL). Cosmopolitan.

Trochoideus amphora Cantor, 1846: 282.

Trochoideus termitophilus Roepke, 1919: 34.

Trochoideus rouyeri Pic, 1922a: 8.

Trochoideus particularis Pic, 1922a: 8.

Pseudopaussus monstrosus Schulze, 1916: 292.

fea Gorham, 1896: 301. Myanmar.

globulicornis Joly & Bordon, 1996: 9. Venezuela.

goudoti Guérin–Méneville, 1857a: 191. Colombia, Costa Rica, Panama.

masoni Strohecker, 1978a: 353. Colombia.

mexicanus Strohecker, 1978a: 351. Mexico.

microphthalmus Wasmann, 1922: 37. Java.

minutus Csiki, 1909: 342. Malaysia.

mirabilis Strohecker, 1958a: 22. Philippines (MDO).

peruvianus Kirsch, 1876: 116. Peru.

sansibaricus Kolbe, 1897: 118. Tanzania.

tonkineus Strohecker, 1980a: 92. Vietnam.

venezuelensis Joly & Bordon, 1996: 6–7. Venezuela.

wasmanni Strohecker, 1959b: 85. Madagascar.

STENOTARSINAE Chapuis, 1876

Stenotarsites Chapuis, 1876: 125.

Dapsini (in part) Gerstaecker, 1858: 170.

Paleomorphidae Gorham, 1873a: 24.

Stenotarsini Csiki, 1901a: 37.

***Africanasaula* Pic, 1946c**

Africanasaula Pic, 1946c: 123.

Type species: *Africanasaula impressipennis* Pic, 1946c.

impressipennis Pic, 1946c: 123. Cote d'Ivoire, South Africa.

Saula (*Africanasaula*) *impressipennis* Pic, 1946c: 123.

serraticollis (Strohecker), 1944: 144. Cameroon, Congo, Cote d'Ivoire.

Saula serraticollis Strohecker, 1944: 144.

***Chondria* Gorham, 1887**

Chondria Gorham, 1887: 651.

Type species: *Chondria lutea* Gorham, 1887.

agilis Arrow, 1943: 134. Japan, Papua–New Guinea.

angusticollis Strohecker, 1958a: 26. Philippines (MDO).

apicalis Arrow, 1923: 492. Philippines (LZN).

araneola Arrow, 1925: 366. India.

armipes Strohecker, 1978b: 158. Papua–New Guinea.

auritarsis Strohecker, 1978b: 162. Papua–New Guinea.

brevior Strohecker, 1978b: 157. Papua–New Guinea.

buruana Arrow, 1926b: 126. Indonesia.

cardiaca Strohecker, 1955b: 331. Borneo.

chrysoptera Strohecker, 1958a: 25. Philippines (MDO).

crenata Strohecker, 1979g: 73. Borneo.

elegans Strohecker, 1979g: 73. Borneo.

elliptica Strohecker, 1957c: 65. Java.

formosana Sasaji, 1970: 9. Taiwan.

furva Strohecker, 1978b: 160. Papua–New Guinea.

globulosa Arrow, 1920a: 61. Borneo.

humeralis Strohecker, 1958a: 25. Philippines (MDO).

indica Arrow, 1920a: 59. India.

longicornis Arrow, 1943: 134. Philippines (MDO).

longipes Arrow, 1943: 134. Japan, Papua–New Guinea.

lutea Gorham, 1887: 651. Japan.

mimica Strohecker, 1958a: 25. Philippines (MDO).

minima Strohecker, 1971c: 257. Sri Lanka.

montislinae Strohecker, 1978b: 160. Papua–New Guinea.

nigra Strohecker, 1978b: 158. Papua–New Guinea.

nigricollis Strohecker, 1979g: 73. Vietnam.

nigropectus Strohecker, 1978b: 161. Papua–New Guinea.

nigropunctata Nakane, 1951: 113. Japan, Taiwan.

nitida Arrow, 1920a: 61. Borneo.

ovalis Arrow, 1920a: 60. Malaysia.

pachyceras Strohecker, 1978b: 162. Papua–New Guinea.

parallela Strohecker, 1958a: 27. Philippines (MDO).

plagiata Strohecker, 1958a: 24. Philippines (MDO).

rhipiphora Strohecker, 1978b: 161. Japan, Papua–New Guinea.

rhodura Strohecker, 1978b: 161. Papua–New Guinea.

seriesetosa Arrow, 1920a: 58. Borneo.

stigmatica Strohecker, 1966: 360. Philippines.

triplex Arrow, 1920a: 60. Java.

truncata Strohecker, 1978b: 157. Papua–New Guinea.

xanthomata Strohecker, 1978b: 160. Papua–New Guinea.

***Danae* Reiche, 1847**

Danae Reiche, 1847: 408.

Type species: *Danae rufula* Reiche, 1847.

Oediarthrus Gerstaecker, 1858: 344.

Type species: *Oediarthrus natalensis* Gerstaecker, 1858.

Rhabduchus Gorham, 1873c: 257.

Type species: *Rhabduchus denticornis* Gorham, 1873c.

Coniopoda Gorham, 1873b: 205.

Type species: *Coniopoda orientalis* Gorham, 1873b.

Pseudodanae Pic, 1945: 15.

Type species: *Danae* (*Pseudodanae*) *diversicornis* Pic, 1945.

abdominalis Weise, 1903: 201. Kenya, Tanzania, Uganda.

aetha Strohecker, 1962a: 48. Congo, D.R. Congo, Ghana.

algoensis (Gorham), 1905: 280. South Africa.

Oediarthrus algoensis Gorham, 1905: 201.

androgyna Strohecker, 1974b: 538. D.R. Congo, Mozambique, South Africa, Tanzania, Zambia.

Danae ruficornis Strohecker, 1952: 19.

antennata Strohecker, 1962b: 79. D.R. Congo

armata Arrow, 1920a: 36. Congo, D.R. Congo, Ghana, Malawi, Nigeria.

arrowi Strohecker, 1952: 15. D.R. Congo.

ascipes Strohecker, 1957b: 149. Congo.

atrimembris Pic, 1946a: 80. Kenya.

atronotata Pic, 1922a: 9. Cambodia.

attenuatus Strohecker, 1962b: 79. D.R. Congo.

augusticlava Strohecker, 1953c: 88. Congo.

babaulti Pic, 1922c: 238. Kenya, Tanzania, Uganda.

borneensis Strohecker, 1979g: 74. Borneo.

brevicollis Strohecker, 1959c: 184. D.R. Congo, Tanzania.

bulbifera Weise, 1903: 201. Rwanda, Tanzania.

calcarata Arrow, 1936: 375. South Africa.

capnicera Strohecker, 1953c: 90. Congo, D.R. Congo.

caprella Strohecker, 1949b: 6. D.R. Congo.

castanea Sasaji, 1978: 23. Japan.

cavicollis Arrow, 1920a: 40. D.R. Congo, South Africa, Zimbabwe.

chappuisi Pic, 1946a: 81. Kenya.

chinensis Strohecker, 1951a: 162.

ciliatipes Arrow, 1920a: 41. Myanmar.

clauda Arrow, 1925: 390. India.

compressa Strohecker, 1960: 266. D.R. Congo, Ghana, Uganda

compsa Strohecker, 1962a: 50. D.R. Congo.

cordicornis Strohecker, 1959c: 184. D.R. Congo, Tanzania.

curvicrus Strohecker, 1953c: 86. Congo, D.R. Congo.

curvipes Arrow, 1920a: 39. Congo, D.R. Congo, Malawi.

cylindrica Strohecker, 1952: 14. D.R. Congo.

damnifica Strohecker, 1952: 17. D.R. Congo.

denticornis (Gorham), 1873c: 257. Japan.

Rhabduchus denticornis Gorham, 1873c: 257.

dentipes Arrow, 1920a: 38. Zimbabwe.

difficilis Strohecker, 1952: 17. D.R. Congo.

diversicornis Pic, 1945: 15. Kenya, Tanzania, Uganda.

Pseudodanae diversicornis Pic, 1945: 15.

elgonensis Pic, 1946a: 81. Kenya.

elliptica Strohecker, 1957a: 271. Ethiopia.

exhauriens Strohecker, 1955a: 172. Rwanda.

femoralis Arrow, 1920a: 38. Malawi.

foveata Strohecker, 1953c: 88. Congo.

foveicornis Strohecker, 1957a: 271. Kenya, Tanzania, Uganda.

gazella Strohecker, 1973: 132. Congo, D.R. Congo.

gestroi Strohecker, 1967: 244. Congo.

globifera Strohecker, 1953c: 88. Congo.

goffarti Pic, 1945: 11. Burundi, D.R. Congo, Rwanda.

gracilis Strohecker, 1952: 13. D.R. Congo.

gracillima Strohecker, 1968a: 254. Cote d'Ivoire.

heliobleta Strohecker, 1953c: 90. Congo.

hirsutipes Strohecker, 1979g: 74. Borneo.

incerta Strohecker, 1962a: 46. D.R. Congo, Ghana.

incisa Strohecker, 1962b: 80. D.R. Congo.

indefinita Strohecker, 1957b: 150. Congo.

jeanneli Pic, 1946a: 81. Kenya.

jucunda Arrow, 1936: 374. Ethiopia.

latipes Strohecker, 1954: 150. D.R. Congo.

leona Strohecker, 1962a: 51. D.R. Congo.

longa Strohecker, 1957a: 272. Kenya.

longicornis Arrow, 1920a: 40. South Africa.

longipennis Strohecker, 1953c: 90. Congo.

macra Strohecker, 1952: 11. D.R. Congo.

masculina Strohecker, 1957a: 272. D.R. Congo, Uganda.

microdera Arrow, 1936: 374. Sudan.

natalensis (Gerstaecker), 1858: 346. South Africa, Zimbabwe.

Oediarthrus natalensis Gerstaecker, 1858: 346.

nigrosignata Strohecker, 1944: 143. Java.

nimbensis Villiers, 1954b: 167. D.R. Congo.

orientalis (Gorham), 1873b: 205. Japan.

Coniopoda orientalis Gorham, 1873b: 205.

ornata Arrow, 1925: 392. India.

ovata Arrow, 1948: 53. D.R. Congo, Ghana, Zimbabwe.

parallela Strohecker, 1959c: 183. D.R. Congo, Kenya, Tanzania.

parvicornis Strohecker, 1952: 16. D.R. Congo.

parvidens Strohecker, 1953c: 86. Congo, Rwanda.

pulchella Gestro, 1895: 474. Kenya, Tanzania, Uganda.

pusilla Strohecker, 1957a: 271. Kenya.

pygmaea Strohecker, 1957b: 150. Congo.

recta Strohecker, 1973: 132. Congo, D.R. Congo.

ruficornis Pic, 1945: 11. Congo, Kenya, Zimbabwe.

rufipes Pic, 1946a: 81. Kenya.

rufula Reiche, 1847: 408. Ethiopia.

seminicornis Strohecker, 1952: 18. D.R. Congo.

senegalensis (Gerstaecker), 1858: 346. Benin, D.R. Congo, Malawi, Senegal.

Oediarthrus senegalensis Gerstaecker, 1858: 346.

Danae rufescens Pic, 1921: 2.

Danae nigricornis Arrow, 1948: 52.

Danae laticollis Strohecker, 1952: 12.

sericea Arrow, 1925: 391. India.

shibatai Nakane, 1958: 35. Japan.

sibutensis Pic, 1921: 2. Central African Republic.

similis Weise 1903: 202. South Africa.

simplex Strohecker, 1962b: 79. D.R. Congo.

subcurvipes Pic, 1946a: 81. Kenya.

taiwana Chûjô, 1938: 399. Taiwan.

testacea (Ziegler), 1845: 272. Canada (NS, ON), United States (AL, CT, DC, FL, GA, IN, LA, MA, MI, MS, NC, NJ, NY, PA, TN, WI, WV, VA).

Lycoperdina testacea Ziegler, 1845: 272.

Lycoperdina lutea Melsheimer, 1847: 176.

Lycoperdina pilosa Melsheimer, 1847: 176.

Mycetina testacea: LeConte, 1853: 359.

Epipocus ferrugineus Guérin–Méneville, 1857: 267.

Stenotarsus testacea: Blatchley, 1910: 539.

tibialis Arrow, 1920a: 37. Kenya, Malawi.

Danae tibialis basipes Pic, 1946a: 81.

tournieri Villiers, 1954b: 168. D.R. Congo.

trigona Strohecker, 1962a: 50. D.R. Congo.

turneri Arrow, 1948: 54. South Africa.

uelensis Strohecker, 1974b: 538. D.R. Congo.

valga Strohecker, 1952: 12. D.R. Congo.

venustula Gestro, 1895: 475. Tanzania.

weisei Strohecker, 1954: 151. D.R. Congo.

***Ectomychus* Gorham, 1887**

Ectomychus Gorham, 1887: 646.

Type species: *Ectomychus basalis* Gorham, 1887.

africanus Strohecker, 1944: 142. Cameroon.

atriventris Strohecker, 1975b: 220. D.R. Congo.

basalis Gorham, 1887: 646. Japan, Russia (FET).

callipygus Strohecker, 1975b: 223. D.R. Congo.

cinctus Strohecker, 1975b: 223. D.R. Congo.

deformis Strohecker, 1952: 19. D.R. Congo.

elongatus Strohecker, 1975b: 222. D.R. Congo.

ferreus Strohecker, 1975b: 221. D.R. Congo.

flavipes Arrow, 1925: 368. India.

luluensis (Arrow), 1948: 51. Congo, D.R. Congo.

Stenotarsus luluensis Arrow, 1948: 51.

monticola Arrow, 1920a: 62. India.

musculus (Gorham), 1887: 645. Japan.

Stenotarsus musculus Gorham, 1887: 645.

nakanei Chûjô, 1941: 81. Japan.

nepalensis Strohecker, 1982b: 310. Nepal.

nigriclavis (Gorham), 1873b: 206. Japan.

Stenotarsus nigriclavis Gorham, 1873b: 206.

nigripes Arrow, 1925: 369. India.

nigrofasciatus Sasaji, 1988: 19. Japan.

nimbiferus Strohecker, 1975b: 222. D.R. Congo.

ovatus Arrow, 1928: 369. Cambodia, India, Laos, Myanmar, Vietnam.

pauli (Weise), 1903: 203. Kenya, Tanzania, Uganda.

Stenotarsus pauli Weise, 1903: 203.

sakaii Chûjô & Kiuchi, 1974: 4. Japan.

sulcatus Strohecker, 1954: 152. D.R. Congo.

tappanus Ohta, 1931: 230. Taiwan.

werneri Strohecker, 1958a: 23. Philippines (MDO).

yukihikoi Sasaji, 1995: 28. Japan.

Paniegena **Heller, 1916**

Paniegena Heller, 1916: 282.

Type species: *Paniegena suturalis* Heller, 1916.

atricollis Strohecker, 1979d: 223. New Caledonia.

baloghi Strohecker, 1979d: 223. New Caledonia.

suturalis Heller, 1916: 282. New Caledonia.

Perrisina **Strand, 1921**

Perrisina Strand, 1921: 106. Replacement name.

Perrisia Marseul, 1868a: 113.

Type species: *Lycoperdina brevis* Perris, 1864.

brevis (Perris), 1864: 303. Algeria.

Lycoperdina brevis Perris, 1864: 303.

Perrisia theresae Pic, 1944: 1.

Saula **Gerstaecker, 1858**

Saula Gerstaecker, 1858: 223.

Type species: *Saula nigripes* Gerstaecker, 1858.

Aediarthromorpha Pic, 1922c: 239.

Type species: *Danae* (*Aediarthromorpha*) *simplicicollis* Pic, 1922.

atricornis Pic, 1922b: 8. Vietnam.

biroi Csiki, 1899: 478. Malaysia.

chujoi Sasaji, 1970: 7. Taiwan.

clavipes Arrow, 1923: 497. Philippines (LZN).

crassicornis Arrow, 1923: 499. Philippines (MDO).

curvipes Arrow, 1923: 496. Philippines (PWN).

dentipes Strohecker, 1951a: 164. Philippines (LZN).

excisipes Arrow, 1923: 497. Malaysia.

ferruginea Gerstaecker, 1858: 225. India, Sri Lanka, Sumatra.

Saula occidentalis Arrow, 1923: 493.

filicornis Arrow, 1923: 495. Philippines (LZN, MDO).

Saula elongata Heller, 1923: 7.

fuscicornis Fairmaire, 1889: 378. Cambodia, Laos, Vietnam.

Saula fuscicornis var. *diversipes* Pic, 1922b: 9.

japonica Gorham, 1874: 224. Japan, Taiwan.

lobatipes Strohecker, 1943: 384. Philippines (LZN, NGS).

Saula luzonica Strohecker, 1951a: 165.

longiclava Strohecker, 1951a: 165. Philippines (SRO)

longior Strohecker, 1951a: 164. India.

malleicornis Arrow, 1923: 500. Philippines (MDO).

nigripes Gerstaecker, 1858: 224. Sri Lanka, Taiwan.

oculata Arrow, 1923: 494. Borneo, Sumatra.

pallida Pic, 1929: 16. Vietnam.

polita Strohecker, 1957a: 272. Sumatra.

posticalis Arrow, 1923: 499. Vietnam.

simplicicollis (Pic), 1922c: 238. Kenya, Tanzania, Uganda.

Danae (*Aediarthromorpha*) *simplicicollis* Pic, 1922c: 238.

taiwana Chûjô, 1938: 399. Taiwan.

testaceipes Pic, 1922b: 9. Vietnam.

tibialis Arrow, 1923: 494. Borneo.

variipes Arrow, 1923: 498. Borneo, Celebes, Indonesia, Malaysia, Myanmar, Thailand.

***Stenotarsus* Perty, 1832**

Stenotarsus Perty, 1832: 112.

Type species: *Stenotarsus brevicollis* Perty, 1832.

Quirinus Thomson, 1857: 157.

Type species: *Quirinus sulcithorax* Thomson, 1857.

Systaechea Gorham, 1887–99: 132.

Type species: *Systaecha cyanoptera* Gorham, 1887–99.

Stenotarsoides Csiki, 1900c: 401.

Type species: *Stenotarsoides quadrimaculatus* Csiki, 1900c.

abdominalis Strohecker, 1978b: 150. Papua–New Guinea.

aberrans Strohecker, 1957c: 67. Java.

acrophilus Strohecker, 1974d: 306. Madagascar.

adumbratus Gorham, 1873a: 63. Colombia, Costa Rica, Panama.

affinis (Arrow), 1943: 135. Papua–New Guinea.

Chondria affinis Arrow, 1943: 135.

agnus Strohecker, 1957a: 260. Brasil.

agusanus Strohecker, 1978b: 72. Philippines (MDO).

albertisii Gorham, 1885: 527. Japan, Papua–New Guinea.

alternatus Lea, 1921a: 366. Australia (NSW).

angulipennis Franz, 1974: 44. New Caledonia.

angustulus Gerstaecker, 1858: 327. Brasil.

anisotomoides Gerstaecker, 1858: 328. Colombia.

anomalus Strohecker, 1975c: 626. India.

antennatus Fairmaire, 1905: 117. Madagascar.

aokii Chûjô, 1942: 79. Taiwan.

apterus Strohecker, 1974d: 306. Madagascar.

arcuatus Strohecker, 1955c: 165. Madagascar.

ardens Gerstaecker, 1858: 305. Brasil.

argentinus Pic, 1922a: 9. Argentina.

arithmeticus Blackburn, 1895: 233. Australia.

arrowi (Mader), 1934: 40. Borneo.

Stenotarsoides arrowi Mader, 1934: 40.

Stenotarsus musculus Arrow, 1920a: 54.

atratus Strohecker, 1978b: 156. Papua–New Guinea.

atricollis Pic, 1936a: 9. Bolivia, Brasil.

atripennis Strohecker, 1943: 386. Philippines (NGS).

atripes Strohecker, 1978b: 155. Papua–New Guinea.

atriventris Strohecker, 1975c: 626. India.

attenuatus Achard, 1926: 142. Peru.

aureolus Gerstaecker, 1858: 314. Brasil, Paraguay.

auricomus Gorham, 1873a: 63. Venezuela.

basalis Arrow, 1920a: 56. Borneo.

beccarii Strohecker, 1957a: 262. Sumatra.

bicolor Gerstaecker, 1858: 343. Cambodia, India, Laos, Myanmar, Vietnam.

Stenotarsus indianus Gorham, 1874a: 446.

Stenotarsoides alfierii Pic, 1922b: 9.

Stenotarsoides medianus Pic, 1922b: 9.

bicoloriceps Pic, 1924a: 87. Brasil.

bimaculatus (Pic), 1930a: 66. Borneo.

Stenotarsoides bimaculatus Pic, 1930a: 66.

Stenotarsus ursinus Arrow, 1920a: 49.

bimaculipennis Lea, 1922: 299. Australia (QLD).

birmanicus Gorham, 1896: 297. Myanmar.

biroi Csiki, 1900: 124. Papua–New Guinea.

bivulnerus Strohecker, 1978b: 156. Papua–New Guinea.

blackburni Strohecker, 1944: 146. Australia (NSW)

blatchleyi Walton, 1928: 216. United States (AL, AR, FL, GA, LA, TX, VA).

brevicollis Perty, 1832: 112. Brasil.

brevis Gorham, 1885: 526. Sumatra.

brunneus Gorham, 1873a: 64. Colombia.

buchgraberi Mader, 1936b: 65. Cameroon.

callistus Strohecker, 1978b: 153. Papua–New Guinea.

caracasensis Pic, 1936a: 9. Venezuela.

cardisoma Strohecker, 1959c: 182. Peru.

castaneus Gerstaecker, 1858: 340. Sri Lanka.

cavicollis Strohecker, 1957c: 67. Java.

cheesmanae Strohecker, 1978b: 147. Borneo, Papua–Guinea.

chiriquinus Arrow, 1920a: 51. Panama.

Stenotarsus globosus Gorham, 1887–99: 136.

chrysoceras Strohecker, 1978b: 156. Papua–New Guinea.

chrysomelinus Gorham, 1887: 644. Japan.

chujoi Strohecker, 1957a: 262. Taiwan.

cinctus Strohecker, 1957c: 66. Java.

cingulatus Strohecker, 1978b: 155. Papua–New Guinea.

circumdatus Gerstaecker, 1858: 323. Mexico.

clarus Strohecker, 1959b: 80. Madagascar.

clavicornis Pic, 1936a: 10. Bolivia.

claviger Gerstaecker, 1858: 331. Brasil.

clemmus Strohecker, 1955c: 162. Madagascar.

coccineus Gerstaecker, 1858: 302. Brasil, Colombia, Peru.

Stenotarsus baeri Pic, 1922b: 9.

commodus Blackburn, 1895: 233. Australia.

compactus Franz, 1974: 43. New Caledonia.

conspicuous Kirsch, 1876: 114. Peru.

convexicollis Strohecker, 1957a: 262. Peru.

convexus Pic, 1921: 2. Madagascar.

cordipennis Strohecker, 1974d: 305. Madagascar.

crassicornis Gerstaecker, 1858: 309. Brasil.

crassiusculus Fairmaire, 1905: 117. Madagascar.

cupreus Strohecker, 1957a: 260. Bolivia.

cuprivestis Gorham, 1887–99: 139. Panama.

cyanopterus (Gorham), 1887–99: 133. Panama.

Systaechea cyanoptera Gorham, 1887–99: 133.

decorus Strohecker, 1960: 267. Tanzania.

delicatulus Strohecker, 1955c: 163. Madagascar.

dentipes Arrow, 1925: 382. Myanmar.

descarpentriesi Strohecker, 1955c: 165. Madagascar.

discipennis Gorham, 1887–99: 136. Costa Rica, Guatemala, Mexico.

discoidalis (Csiki), 1902: 352. Papua–New Guinea.

Stenotarsoides discoidalis Csiki, 1902: 352.

distinguendus Arrow, 1920a: 51. Guatemala.

Stenotarsus sallei Gorham, 1887–99: 140.

ellipticus Strohecker, 1966: 358. Papua–New Guinea.

erotyloides Gerstaecker, 1858: 303. Brasil.

exiguus Gorham, 1887–99: 141. Belize, Guatemala.

fairmairei Strohecker, 1953a: 52. Madagascar.

Stenotarsus bicolor Fairmaire, 1905: 116.

favareli Pic, 1922a: 9. Gabon.

femoralis Arrow, 1920a: 57. Java, Malaysia.

ferruginatus Strohecker, 1958a: 29. Philippines (MDO)

flavago Gorham, 1873a: 53. French Guiana.

flavicornis Gorham, 1873a: 52. Brasil.

flavipennis Franz, 1974: 42. New Caledonia.

flavipes Heller, 1916: 283. New Caledonia.

flavomaculatus Strohecker, 1943: 387. Philippines (NGS).

flavoscapularis Strohecker, 1943: 388. Philippines (MDO).

flavotestaceus (Csiki), 1900c: 402. Papua–New Guinea.

Stenotarsoides flavotestaceus Csiki, 1900c: 402.

floccosus Strohecker, 1957a: 262. Brasil.

foveatus Strohecker, 1959a: 464. Brasil.

fryanus Strohecker, 1978b: 72. Vietnam.

fuscicornis Gorham, 1896: 297. Borneo, Cambodia, Laos, Myanmar, Vietnam.

globosus Guérin–Méneville, 1857: 270. Bolivia, Colombia, Guatemala, Guyana, Honduras, Mexico, Panama, Peru.

Stenotarsus cordatus Gorham, 1887–99: 134.

globulus Arrow, 1920a: 55. Borneo.

gracilis Strohecker, 1959b: 82. Madagascar.

grandis Gorham, 1873a: 52. Bolivia, Colombia, Ecuador.

gravidus Arrow, 1925: 373. India.

guatemalae Arrow, 1920a: 51. Guatemala.

Stenotarsus adumbratus Gorham, 1887–99: 140.

guineensis Gerstaecker, 1858: 335. Central African Republic, Congo, Cote d'Ivoire, Ghana.

Quirinus sulcicollis Thomson, 1858: 236.

Stenotarsus aequatus Gorham, 1873a: 55.

guttatus Strohecker, 1978b: 155. Papua–New Guinea.

haemorrhoidalis Gerstaecker, 1858: 334. Madagascar.

hilaris Arrow, 1925: 384. India.

hispidus (Herbst), 1799: 374. United States (AL, CT, DC, FL, GA, IN, LA, MS, NC, NJ, OH, RI, VA).

Erotylus hispidus Herbst, 1799: 374.

Mycetina hispida: LeConte, 1853: 359.

Ephebus limbatus Guérin–Méneville, 1857: 270.

Lycoperdina vestita Say, 1827: 304.

Stenotarsus solidus Casey, 1916: 144.

honestus Schaufuss, 1887: 145. Celebes.

Stenotarsus honestus var. *maculatus* Schauffuss, 1887: 146.

humerosus Strohecker, 1959b: 81. Madagascar.

ictericus Gerstaecker, 1858: 307. Brasil.

incertus Strohecker, 1978b: 149. Papua–New Guinea.

insolitus Strohecker, 1978b: 163. Solomon Islands.

internexus Gorham, 1887: 645. Japan.

javanicus Strohecker, 1956b: 247. Java.

kokodensis Arrow, 1943: 132. Papua–New Guinea.

kurosai Nakane, 1981: 55. Japan.

lanuginosus Achard, 1926: 142. Argentina.

latemaculatus Pic, 1938b: 77. Argentina.

lateniger Pic, 1924b: 2. Madagascar.

laticollis Strohecker, 1974a: 153. Sri Lanka.

latipes Arrow, 1920a: 52. Guatemala, Mexico.

Stenotarsus angustulus Gorham, 1887–99: 138.

lemniscatus Gorham, 1887–99: 139. Costa Rica, Guatemala, Panama.

leoninus Gorham, 1874a: 444. Philippines (MDO).

lignarius Fairmaire, 1894b: 159. Madagascar.

lituratus Gerstaecker, 1858: 341. Java.

loebli Strohecker, 1983a: 336. India.

lombardeaui Perroud & Montrouzier, 1864: 219. New Caledonia.

longicornis Strohecker, 1959c: 183. Peru.

longulus Gerstaecker, 1858: 330. Argentina, Brasil, Paraguay.

longus Strohecker, 1978b: 157. Papua–New Guinea.

maculicollis Gerstaecker, 1858: 333. Brasil.

maculosus Fairmaire, 1888: 158. China.

madecassus Pic, 1924b: 2. Madagascar.

madurensis Arrow, 1925: 374. India.

malayensis Arrow, 1920a: 54. Borneo, Malaysia.

malleri Pic, 1936a: 9. Brasil.

marginalis Arrow, 1920a: 50. Guatemala.

Stenotarsus maculicollis Gorham, 1887–99: 141.

microsetosus Strohecker, 1974d: 305. Madagascar.

militaris Gerstaecker, 1858: 325. Mexico.

minimus Pic, 1936a: 9. Brasil.

minor Pic, 1936a: 8. Bolivia.

minutissimus Pic, 1936a: 10. Bolivia.

minutus Gerstaecker, 1858: 332. Brasil.

mollis Gerstaecker, 1858: 316. Brasil.

mombonensis Weise, 1903: 202. Botswana, Malawi.

monrovius Strohecker, 1943: 386. Liberia.

musculus Gorham, 1887: 645. Japan.

mysorensis Strohecker, 1977a: 839. India.

nakanoshimensis Nakane, 1959: 60. Japan.

nanus Strohecker, 1978b: 152. Papua–New Guinea.

nietneri Gerstaecker, 1858: 339. Sri Lanka.

nigerrimus Strohecker, 1978b: 155. Papua–New Guinea.

nigricans Gorham, 1887–99: 135. Guatemala.

nigriclavis Gorham, 1873b: 206. Japan.

nigricollis Gorham, 1873a: 54. French Guiana.

nigricornis Guérin–Méneville, 1857: 269. French Guiana.

nigripes Arrow, 1920a: 55. India.

nigrocyaneus Strohecker, 1978b: 157. Papua–New Guinea.

nigrivestis Shockley, 2007: 480. Dominican Republic.

nilgiricus Arrow, 1925: 377. India.

nobilis Gerstaecker, 1858: 338. Myanmar, Philippines (MDO, PPG).

Stenotarsus plagiatus Gorham, 1896: 296.

Stenotarsus nobilis var. *plagiatus* Gorham, 1885: 525.

Stenotarsus nobilis var. *triplagiatus* Achard, 1926: 142.

Stenotarsus nobilis lucifer Strohecker, 1958a: 29.

nossibeanus Strohecker, 1959b: 80. Madagascar.

notaticollis (Pic), 1922b: 9. Philippines.

Stenotarsoides notaticollis Pic, 1922b: 9.

nudus Strohecker, 1974d: 304. Madagascar.

obesus Strohecker, 1957a: 260. Brasil.

oblongulus Gorham, 1887–99: 138. Guatemala.

obscurus Arrow, 1943: 133. Papua–New Guinea.

obtusus Gerstaecker, 1858: 310. Bolivia, French Guiana, Guatemala, Guyana, Panama.

oodes Strohecker, 1959b: 81. Madagascar.

orbicularis Gerstaecker, 1858: 322. Guatemala.

oshimanus Nakane, 1981: 57. Japan.

ovalis Arrow, 1920a: 50. Guatemala, Panama, Venezuela.

Stenotarsus orbicularis Gorham, 1877–99 [1890]: 134.

Stenotarsus rotundus Arrow, 1920a: 52.

Stenotarsus pilatei Gorham, 1887–99: 135.

ovatulus Gerstaecker, 1858: 308. Brasil.

ovoideus Strohecker, 1955: 163. Madagascar.

ovulum Fairmaire, 1894b: 160. Madagascar.

pallidipennis Lea, 1922: 300. Australia (QLD).

panamanus Gorham, 1887–99: 138. Panama.

pantherinus Gorham, 1875a: 19. Borneo, Malaysia, Sumatra.

papuensis Strohecker, 1983b: 560. Papua–New Guinea.

parallelus Lea, 1921a: 365. Australia (NSW).

pardalis Gerstaecker, 1858: 336. Singapore.

parvicornis Fairmaire, 1905: 117. Madagascar.

peguensis Gorham, 1896: 297. India, Japan, Myanmar, Vietnam.

perforatus Arrow, 1923: 490. Philippines.

persimilis Strohecker, 1959b: 80. Madagascar.

perturbans Strohecker, 1978b: 152. Papua–New Guinea.

philippinarum Gorham, 1874a: 444. Philippines.

picticollis Lea, 1921b: 239. Australia.

pilatei Gorham, 1873a: 53. Belize, Costa Rica, Guatemala, Mexico, Nicaragua.

pisoniae Lea, 1921b: 239. Australia.

planicollis Gerstaecker, 1858: 329. Brasil.

politus Strohecker, 1958b: 108. Micronesia.

porcellus Strohecker, 1957a: 261. Peru.

profectus Strohecker, 1959c: 182. Peru.

pulcher (Csiki), 1900c: 402. Papua–New Guinea.

Stenotarsoides pulcher Csiki, 1900c: 402.

pulcherrimus Strohecker, 1983b: 559. Papua–New Guinea.

pumilio Schaufuss, 1887: 146. Celebes.

punctatostriatus Gorham, 1875a: 20. Congo, Nigeria.

purpuratus Gerstaecker, 1858: 318. Bolivia, Brasil, Colombia, Costa Rica, Ecuador, Panama, Peru.

Stenotarsus macroceras Gorham, 1875a: 18.

Stenotarsus amazonicus Pic, 1936a: 8.

Stenotarsus boliviensis Pic, 1936a: 8.

pusillus Gerstaecker, 1858: 317. Costa Rica, French Guiana.

pygmaeus Strohecker, 1959a: 465. Brasil.

quadrimaculatus (Csiki), 1900c: 401. Australia (NSW).

Stenotarsoides quadrimaculatus Csiki, 1900c: 401.

quadrisignatus Gorham, 1896: 298. India, Myanmar.

quinarius Lea, 1922: 299. Australia (QLD).

quinquemaculatus Pic, 1938c: 123. Vietnam.

quinquenotatus Lea, 1921b: 239. Australia (NSW, QLD).

rubicundus Gerstaecker, 1858: 321. Colombia.

rubiginosus Gerstaecker, 1858: 304. Brasil.

rubripennis Strohecker, 1979g: 71. Laos, Vietnam.

rubrocinctus Gerstaecker, 1858: 324. Mexico.

ruficollis Strohecker, 1978b: 151. Papua–New Guinea.

ruficornis Gerstaecker, 1858: 306. Brasil.

rufipes Strohecker, 1978b: 150. Papua–New Guinea.

rufitarsis Pic, 1938c: 123. Vietnam.

rufiventris Strohecker, 1978b: 153. Papua–New Guinea.

russatus Gorham, 1874a: 446. India, Sri Lanka.

Stenotarsus ceylonicus Motschulsky, 1866: 398.

rutilus Guérin–Méneville, 1857: 267. Colombia.

ryukyuensis Chûjô & Kiuchi, 1974: 5. Japan.

sallaei Gorham, 1873a: 63. Costa Rica, Mexico.

schereri Strohecker, 1974c: 136. India.

scymnoides Gorham, 1875a: 19. Brasil.

secticollis Strohecker, 1974c: 136. India.

semifasciatus Pic, 1936a: 7. Brasil.

seminalis Arrow, 1925: 384. India.

seniculus Gerstaecker, 1858: 315. Brasil.

sericatus Gerstaecker, 1858: 319. Colombia.

sicarius Gorham, 1886: 161. Sri Lanka.

smithi Gorham, 1887–99: 140. Mexico.

striatocollis Fairmaire, 1905: 116. Madagascar.

striatus Strohecker, 1978b: 150. Papua–New Guinea.

subglaber Strohecker, 1974d: 303. Madagascar.

subtilis Arrow, 1920a: 53. Panama.

Stenotarsus gigante Nedved, 1996: 3. [*nomen nudum*] *sudanicus* Strohecker, 1962a: 52. Congo, Sudan.

sulcithorax (Thomson), 1857: 157. Madagascar.

Quirinus sulcithorax Thomson, 1857: 157.

tabidus Gorham, 1874a: 445. Philippines.

tarsalis Gorham, 1887–99: 137. Mexico.

Stenotarsus circumdatus var. *tarsalis* Arrow, 1920a: 50.

tenuicornis Strohecker, 1953c: 90. Congo.

testaceicornis Pic, 1936a: 8. Peru.

thoracicus Gorham, 1887–99: 136. Mexico.

tomentosus Gerstaecker, 1858: 341. Sri Lanka.

transiens Strohecker, 1959c: 183. Peru.

trimaculatus Strohecker, 1956b: 246. Java, Sumatra.

triplagiatus Achard, 1926: 142. Laos, Thailand.

tristis Arrow, 1920a: 57. Borneo.

tympanizans (Arrow), 1943: 135. Papua–New Guinea.

Chondria tympanizans Arrow, 1943: 135.

umbrosus Gerstaecker, 1858: 320. Colombia, Peru.

ursinus Gerstaecker, 1858: 337. Borneo.

usambaricus Weise, 1903: 203. Tanzania.

validicornis Gerstaecker, 1858: 331. Colombia, Costa Rica, French Guiana, Panama.

Stenotarsus claviger Gorham, 1887–99: 141.

vallatus Gerstaecker, 1858: 342. Sri Lanka.

varicornis Kirsch, 1876: 116. Peru.

ventricosus Gerstaecker, 1858: 313. French Guiana.

vulpes Kirsch, 1876: 115. Peru.

yoshionis Chûjô, 1938: 402. Taiwan.

***Tragoscelis* Strohecker, 1953a**

Tragoscelis Strohecker, 1953a: 61. Replacement name.

Heliobletus Gorham, 1873a: 41.

Type species: *Heliobletus servilis* Gorham, 1873a.

acuticollis (Arrow), 1920a: 43. Borneo.

Heliobletus acuticollis Arrow, 1920a: 43.

angustus Strohecker, 1979g: 75. Borneo.

latipes (Arrow), 1920a: 44. Borneo.

Heliobletus latipes Arrow, 1920a: 44.

malayanus Strohecker, 1979g: 75. Malaysia.

philippinensis (Strohecker), 1943: 384. Philippines (MDO).

Heliobletus philippinensis Strohecker, 1943: 384.

punctulatus (Arrow), 1920a: 42. Borneo.

Heliobletus punctulatus Arrow, 1920a: 42.

servilis (Gorham), 1873a: 42. Borneo.

Heliobletus servilis Gorham, 1873a: 42.

tarsalis (Arrow), 1939: 6. Myanmar.

Heliobletus tarsalis Arrow, 1939: 6.

XENOMYCETINAE Strohecker, 1962c

Xenomycetinae Strohecker, 1962c: 801.

Xenomycetes Horn, 1880

Xenomycetes Horn, 1880: 141.

Type species: *Xenomycetes morrisoni* Horn, 1880.

laversi Hatch, 1962: 237. United States (WA).

morrisoni Horn, 1880: 141. United States (CA, NV, WA).

GENERA INCERTAE SEDIS

Atrichonota Arrow, 1925

Atrichonota Arrow, 1925: 386.

Type species: *Atrichonota flavipennis* Arrow, 1925.

flavipennis Arrow, 1925: 387. Myanmar, Taiwan.

Cyclotomima Pic, 1925

Cyclotomima Pic, 1925: 2.

Type species: *Cyclotomima luteonotata* Pic, 1925.

lunulata Pic, 1928a: 133. Vietnam.

luteonotata Pic, 1925: 2. Vietnam.

Opetius Mulsant, 1851

Opetius Mulsant, 1851: 73.

Type species: *Opetius fasciolatus* Mulsant, 1851.

fasciolatus Mulsant, 1851: 73. South America.

Polymus Mulsant, 1846

Polymus Mulsant, 1846: 10.

Type species: *Polymus nigricornis* Mulsant, 1846.

nigricornis Mulsant, 1846: 10. France.

FOSSIL ENDOMYCHIDS

ENDOMYCHIDAE Leach, 1815

Endomychides Leach, 1815: 116.

Fungicolae Latreille, 1825: 406.

Endomychidae Stephens, 1831: 398.

Endomycites Newman, 1834: 420.

Lycoperdinae Redtenbacher, 1844: 117.

Sulcicolles Mulsant, 1846: 1.

Endomychidea Costa, 1850: 1.

Endomycici Gorham, 1873: 1.

Endomychoidea Verhoeff, 1895: 272.

ANAMORPHINAE Strohecker, 1953a

Anamorphini Strohecker, 1953a: 15.

Mychotheninae Sasaji, 1978: 8.

Mychothenidae Sasaji, 1987: 44.

Acritosomatinae Pakaluk & Ślipiński, 1995: 328.

Discolomopsis Shockley, 2006

Discolomopsis Shockley, 2006: 211.

Type species: *Discolomopsis dominicana* Shockley, 2006.

dominicana Shockley, 2006: 212. Dominican amber.

Symbiotes Redtenbacher, 1849

Symbiotes Redtenbacher, 1849: 198.

Type species: *Symbiotes latus* Redtenbacher, 1849.

Microchondrus Wollaston, 1854: 196.

Type species: *Microchondrus domuum* Wollaston, 1854.

Eponomastus Buysson, 1891: 95. Unnecessary replacement name.

sp. Klebs, 1910: 239. Baltic amber.

LEIESTINAE Thomson, 1863

Leiestina Thomson, 1863: 306.

Leiestini Seidlitz, 1872–75: 38.

Leiestites Chapuis, 1876: 137.

Liesthini Ganglbauer, 1899b: 925.

Rhanes LeConte & Horn, 1883: 120.

Phymaphorina Jakobson, 1905–1916 [1915]: 961.

***Leiestes* Chevrolat, 1836**

Leiestes Chevrolat, 1836: 440.

Type species: *Cryptophagus seminiger* Gyllenhall, 1808.

Liesthes Ganglbauer, 1899b: 925. Unnecessary replacement name.

sp. Klebs, 1910: 239. Baltic amber.

***Phymaphoroides* Motschulsky, 1856**

Phymaphoroides Motschulsky, 1856: 27.

Type species: *Phymaphoroides antennatus* Motschulsky, 1856.

antennatus Motschulsky, 1856: 27. Baltic amber.

LYCOPERDININAE Redtenbacher, 1844

Lycoperdinae Redtenbacher, 1844: 118.

Eumorphidae Gistel, 1856: 382.

Eumorphini Gerstaecker, 1857: 214.

Dapsini Gerstaecker, 1858: 170.

Corynomalidae Gorham, 1873a: 14.

Amphicini Csiki, 1910: 25.

Beccariini Arrow, 1925: 278.

Amphisternini Strohecker, 1964: 320.

***Gerstaeckerus* Tomaszewska, 2005**

Gerstaeckerus Tomaszewska, 2005: 42. Replacement name.

Engonius Gerstaecker, 1857: 220.

Type species: *Engonius sexguttatus* Gerstaecker, 1857.

alviolatus (Hong), 1983: 3. Diatomaceous compression.

Miocarabus alviolatus Hong, 1983: 3.

Engonius alviolatus Zhang, 1989: 139.

***Hylaia* Chevrolat, 1836**

Hylaia Chevrolat, 1836: 440.

Type species: *Lycoperdina rubricollis* Germar, 1844.

Hylaia Guérin–Méneville, 1857c: 273. Homonym.

Ceramis Gerstaecker, 1858: 220. Unnecessary replacement name.

Hyleia Klebs, 1910: 239. Misspelling.

sp. (Klebs), 1910: 239. Baltic amber.

Hyleia sp. Klebs, 1910: 239.

***Lycoperdina* Latreille, 1807**

Lycoperdina Latreille, 1807: 73.

Type species: *Galleruca bovistae* Fabricius, 1792.

Golgia Mulsant, 1846: 20.

Type species: *Silpha succincta* Linnaeus, 1767.

Lycoperdinodes Arrow, 1923: 485. Replacement name.

Lycoperdinella Arrow, 1920a: 23. Homonym

Type species: *Lycoperdinella morosa* Arrow, 1920a.

Falsoylaia Pic, 1945: 10.

Type species: *Falsoylaia obscuresuturalis* Pic, 1945.

sp. Berendt, 1845: 56. Baltic amber.

sp. Menge, 1856: 21. Baltic amber.

***Mycetina* Mulsant, 1846**

Mycetina Mulsant, 1846: 15.

Type species: *Chrysomela cruciata* Schaller, 1783.

Phaeomychus Gorham, 1887: 649.

Type species: *Endomychus rufipennis* Motschulsky, 1861.

Mycetinina Pic, 1929: 35.

Type species: *Pseudindalmus testaceitarsis* Pic, 1926.

sp. Helm, 1896: 229. Baltic amber.

***Trycherus* Gerstaecker, 1857**

Trycherus Gerstaecker, 1857: 222.

Type species: *Trycherus bifasciatus* Gerstaecker, 1857.

Olena Blanchard, 1851: 522.

Olenus Thomson, 1857: 157.

Type species: *Trycherus senegalensis* Gerstaecker, 1857.

Balius Guérin–Méneville, 1857: 261. Replacement name.

Trypherus Pic, 1936b: 11. Misspelling.

castaneus (Hope), 1837: 55. Malabar kino.

Eumorphus castaneus Hope, 1837: 55.

MEROPHYSIINAE Seidlitz, 1872-75

Merophysiinae Seidlitz, 1872–75: 39.

Merophysiini Reitter, 1875: 300.

Merophysiaires Belon, 1879: 184.

Holoparamecini Reitter, 1887b: 8.

Merophysina Fowler, 1889: 276.

Holoparamecinae Ganglbauer, 1899a: 772.

Merophysiinae Sharp, 1902: 626.

Merophysiina Jakobson, 1905–1916 [1915]: 921.

Holoparamecina Jakobson, 1905–1916 [1915]: 921.

***Holoparamecus* Curtis, 1833**

Holoparamecus Curtis, 1833: 186.

Type species: *Holoparamecus depressus* Curtis, 1833.

Calyptobium Aubé, 1843: 242.

Type species: *Calyptobium caularum* Aubé, 1843.

Tomyrium Reitter, 1881a: 49.

Type species: *Holoparamecus bertouti* Aubé, 1861.

Microparamecus Dajoz, 1967: 589.

Type species: *Microparamecus castrii* Dajoz, 1967.

Neoparamecus Dajoz, 1974: 1074.

Type species: *Neoparamecus peruvianus* Dajoz, 1974.

Amphibolonarzon Villa & Villa, 1833: 26.

Calyptobides Strand, 1933: 123.

Tocalium Motschulsky, 1867: 97.

Type species: *Tocalium orientale* Motschulsky, 1867.

Blumenus Belon, 1887: 219.

Holoparmecus Klebs, 1910: 240. Misspelling.

sp. (Klebs), 1910: 240. Baltic amber.

Holoparmecus sp. Klebs, 1910: 240.

MYCETAEINAE Jacquelin du Val, 1857

Mycetaeinae Jacquelin du Val, 1857: 102.

Mycetaeidae Dajoz, 1972a: 210.

Mycetaea **Stephens, 1829**

Mycetaea Stephens, 1829: 87.

Type species: *Mycetaea fumata* Stephens, 1829
(=*Dermestes subterraneus* Fabricius, 1801).

Silpha Marsham, 1802: 124.

Type species: *Silpha hirta* Marsham, 1802.

sp. Klebs, 1910: 239. Baltic amber.

PLEGANOPHORINAE Jacquelin du Val, 1858

Pleganophorides Jacques du Val, 1858: 186.

Endomychidae adsciti Gerstaecker, 1858: 377.

Paussoideidae Gorham, 1873a: 29.

Trochoideites Chapuis, 1876: 146.

Pleganophorini Reitter, 1881c: 926.

Trochoideinae Ganglbauer, 1899b: 926.

***Trochoideus* Westwood, 1833**

Trochoideus Westwood, 1833: 673.

Type species: *Paussus cruciatus* Dalman, 1825.

Trochoides Chapuis, 1876: 147. Unnecessary replacement name.

Pseudopaussus Schulze, 1916: 292.

Type species: *Pseudopaussus monstrosus* Schulze, 1916.

cruciatus (Dalman), 1825: 400. Madagascan copal.

Paussus cruciatus Dalman, 1825: 400.

Trochoideus cruciatas semiobliteratus Pic, 1950: 11.

sp. Hieke & Pietrzeniuk, 1984: 310. Baltic amber.

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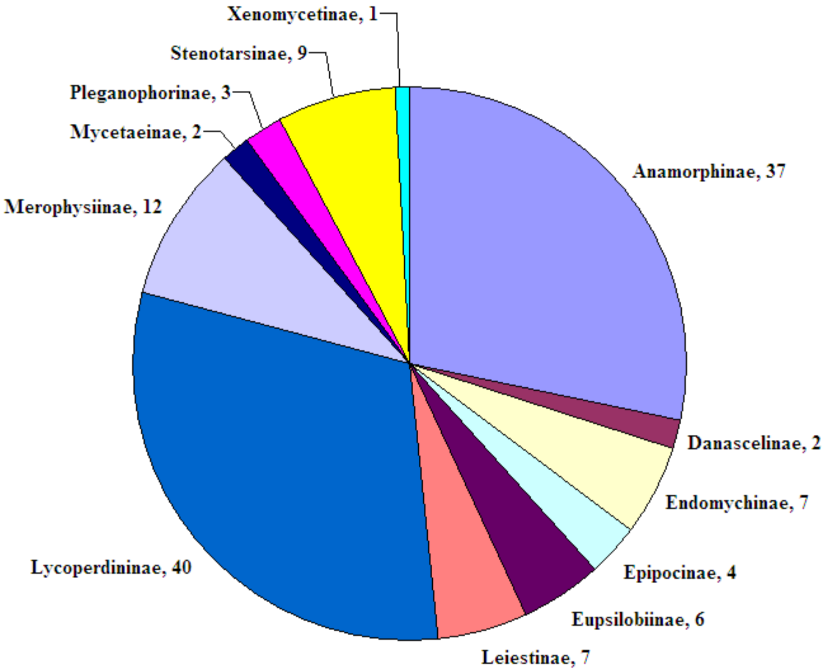

Figure 2.1. Generic diversity of subfamilies of Endomychidae.

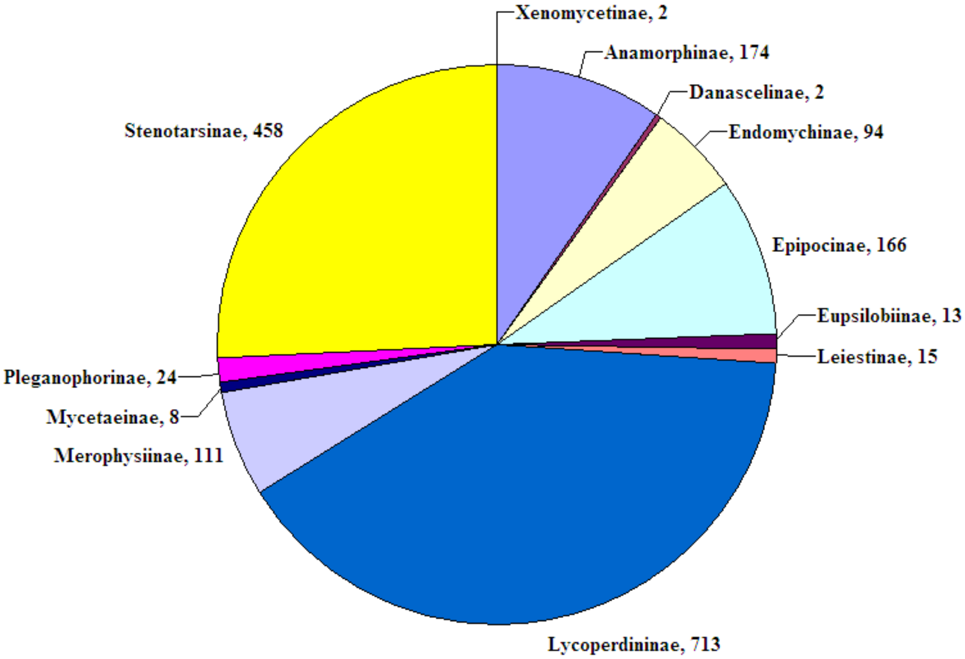

Figure 2.2. Species-level diversity of subfamilies of Endomychidae.

Supplemental Material 2.1. Coden abbreviations for selected regions, provinces and states referenced in the checklist.

Australia

LHI	Lord Howe Island
NSW	New South Wales
QLD	Queensland
VIC	Victoria

Canada

AB	Alberta
BC	British Columbia
MB	Manitoba
NB	New Brunswick
NF	Newfoundland
NS	Nova Scotia
ON	Ontario
PE	Prince Edward Island
QB	Quebec

Philippine Islands

BGO	Baguio
ISB	Isabela
LZN	Luzon
MDO	Mindanao
NGS	Negros
PPG	Pulo Penang
PWN	Palawan
SMR	Samar
SRO	Siargao

Russian Territories

CET	Central European Territory
FET	Far East Territory
NET	Northern European Territory
SET	Southern European Territory
SIB	Siberia

United States

AL	Alabama
AR	Arkansas
AZ	Arizona
CA	California
CO	Colorado
CT	Connecticut
DC	District of Columbia
DE	Delaware
FL	Florida
GA	Georgia
IA	Iowa
HI	Hawaii
ID	Idaho
IL	Illinois
IN	Indiana
KS	Kansas
KY	Kentucky
LA	Louisiana
MA	Massachusetts
MD	Maryland
ME	Maine
MI	Michigan
MO	Missouri
MS	Mississippi
MT	Montana
NC	North Carolina
NH	New Hampshire
NJ	New Jersey
NM	New Mexico
NY	New York
NV	Nevada
OH	Ohio
OK	Oklahoma
OR	Oregon
PA	Pennsylvania
RI	Rhode Island
SC	South Carolina
SD	South Dakota
TN	Tennessee
TX	Texas
UT	Utah
VA	Virginia
WA	Washington
WV	West Virginia
WI	Wisconsin
WY	Wyoming
VT	Vermont

CHAPTER 3

REVIEW OF THE NATURAL HISTORY OF THE HANDSOME FUNGUS BEETLES (COLEOPTERA: CUCUJOIDEA: ENDOMYCHIDAE)[1]

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[1] Shockley, F.W., K.W. Tomaszewska and J.V. McHugh. 2009. *Insecta Mundi* 0072: 1-24. Reprinted here with permission of the Center for Systematic Entomology.

ABSTRACT

The literature pertaining to natural history of Endomychidae (Coleoptera: Cucujoidea) is reviewed. One hundred fungal host records are provided for 32 endomychid species. Twenty-three records of endomychid yeast endosymbionts are compiled. Summaries are also presented for feeding preferences, interactions with natural enemies, non-lethal symbiotic relationships, and pest activity within the family. Unusual endomychid behaviors and habitats are reviewed, with particular attention to gregariousness and defensive strategies within Endomychidae.

Key Words: beetles, ecology, behavior, inquilinism, mimicry, symbiosis, mycophagy.

INTRODUCTION

The beetle family Endomychidae is classified within the Cerylonid Series of the superfamily Cucujoidea (Crowson 1955). The family currently includes approximately 130 genera and 1782 species arranged among 12 subfamilies (Shockley *et al.* 2009). Endomychidae is represented in all major biogeographical regions, but species diversity is greatest in the tropical regions of Africa, Asia and the Americas. Most species are mycophagous, feeding on hyphae, spores and spore-bearing tissue and the supporting tissues of fungal fruitings; however, other feeding strategies and food sources are used by endomychids as well (*e.g.*, phytophagy, predation, necrophagy and myxomycophagy).

While most endomychid publications are comprised of isolated taxonomic descriptions, the limited published natural history information reveals a wide array of interesting behaviors and ecological relationships for this family. Although endomychids make up a significant part of the mycophagous entomofauna in many places and can become pests to humans under certain environmental conditions, relatively little is known about their natural history.

Little effort has been made to consolidate information about the natural history of this group into a single treatment. To complicate matters, notes about natural history and behavior are scattered widely throughout 172 years of scientific literature making them difficult to compile and synthesize. This work represents the first attempt to review the known ecological interactions of Endomychidae and summarizes other interesting aspects of endomychid natural history.

METHODS

The data presented in this review are largely the result of an extensive search of the literature. Some additional data are based on original observations made by the authors. More than 600 taxonomic treatments and 190 general ecological references were gleaned for biological data pertaining to Endomychidae. Two major databases, MYCOL database (Q. Wheeler *in litt.*) and BeetleBellYeast project database (M. Blackwell *in litt.*; database presently accessible at the following URL: http://lsb380.plbio.lsu.edu/beetlebellyfolder/beetlebelly.yeasts), provided additional data for fungal host records and endosymbiotic yeast associations, respectively. Historical references to endomychid taxa have been updated with currently valid names. The names of most non-endomychid taxa have been updated by consulting a variety of references, but some are listed exactly as they occur in the source publications.

Records perceived to be uninformative, ambiguous, doubtful or incidental were ignored. For example, many older records list hosts as simply “fungus” or “bracket fungus” with inadequate information to allow accurate identification at even the highest taxonomic levels. An attempt was made to list only original published records. Subsequent iterations of these records were ignored. Host associations gleaned from the literature and from specimen label data must be viewed with some skepticism since many fungal host identifications were made by entomologists without confirmation by mycologists. This is a serious concern for the present study because many endomychid species feed on fungi that are very difficult or impossible to identify in the field.

RESULTS

Feeding Strategies

Mycophagy

Some estimates suggest as many as 25 beetle families are primarily mycophagous and fully half of the known families may be indirectly mycophagous, (*i.e.*, feeding on vegetative material that has been in some way altered by fungal enzymes) (Lawrence 1989). To date, few efforts have been made to consolidate the published fungal host records for Endomychidae. Even in comprehensive lists of beetle/fungus associations such as Benick (1952) and Leschen (1988), Endomychidae usually make up only a small fraction of the records, a reflection of the rarity of reliable records in the literature. Although the dangers of compiling a "complete" fungal host list have been discussed above, a single source list can be useful to researchers and naturalists (Table 3.1). Such resources encourage more diligent documentation of hosts and promote collaborations between entomologists and mycologists to make new host records more reliable.

Mycophagy generally refers to feeding on the softer hyphae and fruiting bodies of fungi. Most endomychids feed primarily on macro-Basidiomycetes (Hymenomycetes and

Aphyllophorales). Within Endomychidae numerous species exhibit a special form of mycophagy known as sporophagy. In the case of sporophagy, the beetles have shifted from feeding on the hyphae of their fungal hosts to feeding on the spores. This condition may be facultative in taxa that feed on the mature fruiting bodies of basidiomycetes, but it may be obligate in some taxa. Obligate sporophagy has been hypothesized for all species of the subfamily Anamorphinae, at least in the larval stages (Pakaluk 1986, Leschen and Carlton 1993, Tomaszewska 2000), and sporophagy is the most common feeding strategy among taxa that feed on zygomycete molds.

Another specialized form of mycophagy known as lichenophagy has also been recorded within Endomychidae. Lichenophagy is defined as feeding on lichens during at least part of the life cycle. Lichens are the product of the symbiotic relationship between a fungus (the mycobiont) and a photosynthetic alga or cyanobacterium (the photobiont). Strohecker (1953) reported larvae of *Trycherus* Gerstaecker feeding on lichens. The feeding habits of adult *Trycherus* have not yet been recorded in the literature, but they are presumed to be truly mycophagous, as defined above, so it is unclear if this was a rare occurrence or typical for *Trycherus* larvae.

Species of Eupsilobiinae and Merophysiinae, several of which are social insect inquilines, are known to feed on a combination of spores and hyphae of microfungi (Skelley and Leschen 2002). Specifically what these endomychids eat under the conditions within the nests of their social insect hosts is unclear, so the nature of these relationships remains unknown. Endomychids may be feeding directly on the fungal gardens cultivated by their hosts (as nest parasites). Alternatively, they may also be living mutualistically with their hosts and feeding on adventitious and destructive molds growing on these fungal gardens. Of course, the beetles may be feeding entirely on some other fungal substrate found only in these microhabitats.

Phytophagy

While many endomychid species are frequently observed on foliage (Fig. 3.1), phytophagy is rarely proposed as their primary mode of feeding. Endomychids, like many other mycophagous beetles, frequently wander onto and even nibble on any substrate, including plant tissue. Thus, it is not surprising that records of endomychids associated with plants typically lack specific information about a food source. Strohecker (1953) reported *Beccariola* Arrow associated with leaves of coffee plants. Arriaga-Varela *et al.* (2007) recorded *Anidrytus mexicanus* Strohecker from inside a bromeliad and *Catapotia laevissima* Thomson from orchids. Blatchley (1910) collected specimens of *Rhanidea unicolor* (Ziegler) from thoroughwort flowers (Asteraceae). Stuntz (2001) found several endomychid species associated with epiphytes. Thornton (1957) recovered larvae, pupae and adults of a species of *Danae* Reiche from inside the umbels of papyrus sedge (paper reed), *Cyperus papyrus* L. (Cyperaceae). *Eumorphus quadriguttatus* (Illiger) was reported damaging betel pepper plants, *Piper betel* (L.) (Piperaceae) (Mondal *et al.* 2003). For all published accounts of plant feeding, facultative herbivory must be assumed because the endomychid species involved are known to be mycophagous.

Endomychid associations with decaying plant material are difficult to interpret because it is often unclear whether the beetles are feeding on the decaying plant material itself, on the adventitious microfungi growing on that material, or on both. Arriaga-Varela *et al.* (2007) listed records of *Exysma laevigata* Gorham recovered from decaying pineapple and *Archipines intricata* (Gorham), *Epipocus punctatus* LeConte and *Epipocus tibialis* (Chevrolat) on banana debris. *Trochoideus desjardinsi* Guérin–Méneville is commonly collected from rotting coconut husks of the Coconut Palm (Arrow 1925). Many records associate endomychids with specific tree species (*e.g.*, under bark of *Fagus* L.), but these records are generally vague and somewhat misleading. These associations are probably indirect, reflecting an association between the beetles' host fungus and specific tree species rather than between the beetles and the trees directly.

Predation: Entomophagy/Acariphagy

Only two genera of Endomychidae are known to contain predaceous species. The genus *Saula* Gerstaecker, which includes 26 species primarily from the Indomalaysian bioregion, is presumed to be entirely predaceous (Leschen 2000). This generalization, however, is based on published information about only two representative species. *Saula japonica* Gorham is a highly effective predator of arrowhead scale, *Unaspis yanonensis* (Kawana) (Hemiptera: Diaspididae) (Sasaji 1978, Takagi and Ogata 1985, Takagi 1999), but also feeds on cottony cushion scale, *Icerya purchasi* (Maskell) (Hemiptera: Margarodidae) (Leschen 2000), the citrus red mite, *Panonychus citri* (McGregor) (Acari: Tetranychidae) (Sasaji 1978), and the spiraling whitefly, *Aleurodicus dispersus* Russell (Hemiptera: Aleyrodidae) (Wen 1995, Chien *et al.* 2002). Another species, *Saula variipes* Arrow (as *Saura variipes*), was recorded as a predator of coconut bagworm, *Mahasena corbetti* Tams (Lepidoptera: Psychidae) (Mariau 2001).

Smirnoff (1957) recounted observing "*Mycetaea tafilaletica*" feeding on Parlatoria date scale, *Parlatoria blanchardi* (Targioni Tozzetti) (Hemiptera: Diaspididae), at a Saharan oasis in northern Africa. *Mycetaea* Stephens is a small genus including five extant species that feed primarily on molds. Leschen (2000) suggested that the attraction to the molds growing in association with sternorrhynchan exudates may serve as an important step in the transition from mycophagy to predation. While the beetles could have been attracted to the black sooty mold growing on the honeydew produced by the scales, Smirnoff noted that they were feeding directly on the scales. Smirnoff (1958) later reported "*M. tafilaletica*" was successfully cultured on an artificial diet containing sucrose, honey, alfalfa flour, yeast, royal jelly and agar supplemented with dried pulverized prey. Unfortunately, Smirnoff (1957) failed to formally describe this species. A search of the Zoological Record yielded no additional references to this species, so the name remains a *nomen nudum* (Shockley *et al.* 2009). Nonetheless, if Smirnoff's generic determination was correct then this instance of *Mycetaea* preying on scale insects is still noteworthy.

Necrophagy

Watson (2004) recovered *Lycoperdina* Latreille (as "*Opadina* sp.") (*lapsus calami*, C. Carlton pers. comm.) from pitfall traps associated with wildlife carrion in Louisiana. *Lycoperdina ferruginea* LeConte is the only species occurring in North America and is frequently collected from inside puffball mushrooms and from leaf litter (Pakaluk 1984, Price and Young 2007). Interestingly, Kočárek (2003) recorded another species, *L. bovistae* (Fabricius), from pitfall traps associated with rat carrion in the Czech Republic. Although the proximity of two different *Lycoperdina* spp. to carrion independently makes their occurrences noteworthy, the presence of both species was likely incidental.

Aphorista vittata (Fabricius) and *Endomychus biguttatus* Say were found feeding directly on the putrefying flesh of pig carcasses during the advanced decay stage of decomposition (Payne and King 1970). *Mycetaea subterranea* (Fabricius) was collected in association with stored bones (Aitken 1975), so this species may also facultatively feed on carrion during the later, dry stages of decomposition. As with herbivory, necrophagy is assumed to be facultative since all of these endomychid species are known to be primarily mycophagous.

Myxomycophagy

Keller and Snell (2002) listed Endomychidae among beetle families that feed on myxomycetes. Similarly, Blackwell (1984) recorded Endomychidae feeding on myxomycetes representing three genera: *Fuligo* Haller, *Stemonitis* Roth and *Brefeldia* Rostaf. However, neither reference provided a specific list of the endomychid species involved. *Aphorista morosa* LeConte was found in association with a yellow slime mold plasmodium (Lawrence 1991), but no direct evidence suggests that plasmodia are used as a food source by any endomychid species.

Interactions with other organisms

Predators of Endomychids

Erwin and Erwin (1976) reported larvae and adults of *Eurycoleus macularis* Chevrolat (Coleoptera: Carabidae) feeding on larvae, pupae and teneral adults of *Corynomalus* Chevrolat (as *Amphix*) (Fig. 3.2). A species of *Rhymbus* Gerstaecker (=*Bystus* Guérin–Méneville) was listed as a potential prey item of the army ant, *Eciton hamatum* Fabricius (Hymenoptera: Formicidae) (Wheeler 1925); however, the beetles' presence was later questioned as incidental (*i.e.*, they were already on the tree when the ants formed their bivouac) (Mann 1925). Denlinger (1994) noted reduviid nymphs feeding on aggregating adults of *Stenotarsus subtilis* Arrow on Barro Colorado Island in Panama, and unidentified pentatomid nymphs were observed feeding on late–instar larvae of *Corynomalus laevigatus* Gerstaecker in Costa Rica and *C. tarsatus*

Erichson in Bolivia (F. Shockley pers. obs.). Wharton (1946) listed *Ascoschongastia indica* (Hirst) (Acari: Trombiculidae), an egg predator of *Tribolium castaneum* (Herbst), as a potential egg predator of endomychids.

Among vertebrate predators, only two bat species and one frog species have been recorded preying on endomychids, and all three are considered generalist insectivores. In each case, endomychids made up only a small fraction of the diet, and none were identified beyond family–level. Whitaker *et al.* (1999) recovered endomychids in scat of the Indian pygmy bat, *Pipistrellus mimus* Wroughton. Rajemison and Goodman (2007) found a single endomychid in the scat of an endemic Malagasy bat, *Myzopoda schliemanni* Goodman, Rakotondraparany and Kofoky. Johnson and Christiansen (1976) found a single endomychid among the stomach contents of Blanchard's cricket frog, *Acris crepitans blanchardi* (Harper), in Iowa.

Parasitoids attacking Endomychids

Only three parasitoids have been recorded thus far from endomychids, all targeting species of *Endomychus* Panzer. Walker (1836) described *Pteromalus endomychi* (Hymenoptera: Pteromalidae), reared from the larvae of *Endomychus coccineus* (L.). *Endomychobius* Ashmead was erected for the single species *Endomychobius flavipes* (Hymenoptera: Pteromalidae) (Fig. 3.3), reared from the larvae of *Endomychus biguttatus* (Ashmead 1896, Leschen and Allen 1987). *Pteromalus endomychi* Walker was later transferred to *Endomychobius* by Ruschka (1924). In addition, Reinhard (1958) reported larvae of *Endomychus biguttatus* parasitized by *Phyllophilopsis evanida* Reinhard (Diptera: Tachinidae).

Pathogens/Parasites of Endomychids

One of the most widespread pathogen groups infecting insects are bacteria of the genus *Wolbachia* Hertig which infect 16% of all insect species including representatives from all major insect orders (Werren 1997, Kozek and Rao 2007). As many as 70% of insect species are potential hosts (Werren 1997, Kozek and Rao 2007). Werren *et al.* (1995) tested *Stenotarsus subtilis* for the presence of *Wolbachia*, but failed to recover the bacterium. To date, *S. subtilis* is the only endomychid species to be tested for the presence of *Wolbachia*.

The only ectoparasites reported for Endomychidae all belong to Laboulbeniales, a large order of ascomycete fungi containing many species that are obligate ectoparasites of insects. Weir and Hammond (1997) reported that, of 46 endomychid species collected in a 500 ha tract of lowland rain forest in Northern Sulawesi, only three were infected with Laboulbeniales (6.5%). Records of infection of endomychids by Laboulbeniales appear to be relatively rare, and known ectoparasites are restricted currently to species of the genus *Rickia* Cavara.

Thaxter (1916) described eight species of *Rickia* attacking Endomychidae in two different subfamilies (Lycoperdininae and Stenotarsinae): *Rickia gracilis*, *Rickia latior* and *Rickia stenotarsi* from *Stenotarsus guineensis* Gerstaecker in Cameroon; *Rickia danaelis* from *Danae senegalensis* (Gerstaecker) in Cameroon; *Rickia ancylopi* from *Ancylopus bisignatus* Gerstaecker in Cameroon, *Rickia eumorphi* from *Eumorphus cyanescens* Gerstaecker in Mindanao (Philippines), *Rickia saulae* from a species of *Saula* Gerstaecker in Mindanao (Philippines), and *Rickia lycopodinae* on a species of *Lycoperdina* in Madagascar. *Rickia eumorphi* was later found on *Eumorphus cyanescens* (Weir 1998) and has since been found on five additional species of *Eumorphus* Weber in Peninsular Malaysia, Thailand and Borneo: *E. festivus* Arrow, *E. macrospilotus* Arrow, *E. minor* Gerstaecker, *E. turritus* Gerstaecker and *E.*

tetraspilotus Hope (Sugiyama and Mochizuka 1979, Sugiyama and Yamamoto 1982, Sugiyama and Phanichapol 1984). Kaur and Mukerji (1996) reported the first collection of *Rickia ancylopi* on *Ancylopus* Costa in India, and it has since been found in Japan, Peninsular Malaysia, Taiwan and Korea (Sugiyama 1973, Terada 1978, Lee and Lee 1981, Sugiyama and Majewski 1985, Majewski 1988).

Endosymbionts of Endomychids

The only known endosymbionts of endomychids are yeasts located primarily in the gastric caecae (Table 3.2). McHugh *et al.* (1997) speculated that endosymbionts in another mycophagous beetle, *Megalodacne heros* (Say) (Coleoptera: Erotylidae), might serve a function in the digestion of fungal tissue. A recent series of studies (Suh and Blackwell 2004, Suh *et al.* 2004, Suh *et al.* 2005) isolating, culturing and identifying endosymbiotic yeasts occurring in the gut of mycophagous beetles has led to the description of six new species of yeast endosymbionts from endomychids. However, many additional yeast endosymbiont species remain undescribed (Ganter 2006).

Phoresy on Endomychids

Phoresy on endomychids is rare compared to other taxa of similar habits (*i.e.*, erotylids, tenebrionids), perhaps due to differences in grooming or defensive chemistry (addressed elsewhere). Aguiar and Buhrnheim (1998) listed the pseudoscorpion *Paratemnoides minor* (Balzan) (Atemnidae) riding phoretically on endomychids, but the beetles were left undetermined beyond the family-level. Phoretic pseudoscorpions are often found in association with rotting wood where they are predaceous on other small invertebrates.

Most known phoretics of endomychids are mites. Crawford (2005) noted the presence of undetermined phoretic mites on the venter of *Aphorista laeta* LeConte. Mites from two undescribed genera of Rhizoglyphinae are phoretic on *Lycoperdina koltzei* Reitter and *Mycetina marginalis* (Gebler) (Klimov 2000). Wheeler and Blackwell (1984) mentioned another phoretic rhizoglyphine occurring on *Lycoperdina ferruginea*. Mašán (2001) recorded the uropodine mite *Oodinychus ovalis* (Koch) (as *Trichouropoda ovalis*) (Acari: Mesostigmata: Uropodina) associated with *Endomychus coccineus*. Both rhizoglyphines and uropodines are obligate mycetophagous inhabitants of decaying wood and are commonly phoretic on mycophagous beetles (Błoszyk *et al.* 2006).

Endomychids as Inquilines

Endomychidae includes a number of species closely associated with social insects, particularly ants and termites (Table 3.3). Wasmann (1894) listed 11 endomychids associated with ants. Price and Young (2007) noted the close proximity of adults of *Rhanidea unicolor* to a colony of *Lasius* Fabricius ants, although no direct association was inferred. Myrmecophily is the most common form of social insect inquilinism among endomychids; however, termitophilous and melittophilous species are also known. Endomychids have also been recovered from birds' nests. Hicks (1959) generated a checklist of insects found in bird nests, including three species of Endomychidae: *Symbiotes gibberosus* (Lucas), *Holoparamecus caularum* (Aubé), and *Mycetaea subterranea* (Table 3.4).

Habitat, habits and behavior

Habitat Specialization

Two types of habitats are preferred by many endomychid species: 1) the subcortical region of standing or fallen dead trees where they are closely associated with the fruiting bodies of macrofungi, and 2) leaf litter where they feed on the spores and hyphae of microfungi (Lawrence 1991, Price and Young 2007). However, endomychids are commonly found in many other habitats, reflecting the behavioral diversity of the family. Dajoz (1966) listed *Symbiotes gibberosus* and *Mycetaea subterranea* among beetles collected from tree holes, suggesting possible dendrolimnetophily. However, this condition has not been formally proposed for any other endomychid species, and even Dajoz questioned their presence as merely accidental. Price and Young (2007) recently reported *Phymaphora pulchella* Newman from damp tree-hole litter.

No endomychids are known to be obligately xylophagous (*i.e.*, feeding directly and exclusively on wood), so the presence of subcortical and dendrolimnetophilic species is more likely linked to other ecological processes active in stressed, dying or dead trees. Shockley *et al.* (2008) speculated that *Micropsephodes lundgreni* Leschen and Carlton may orient to turpentine (a monoterpene released after tree wounding), verbenone (bark beetle anti–aggregation pheromone) and frontalin (bark beetle aggregation pheromone). Likewise, Skelley and Burgess (1995) reported collecting *Trochoideus desjardinsi* from ethanol/turpentine traps suggesting it may also orient to wounded trees. Price and Young (2007) recovered *Phymaphora pulchella*, *Rhanidea unicolor*, *Endomychus biguttatus*, *Danae testacea* (Ziegler) and *Symbiotes gibberosus* from Lindgren funnels baited with ipsdienol, though none were collected in large numbers and may be incidental.

Collection data for endomychids show a strong bias for habitats close to the ground (*e.g.*, fallen logs, stumps, leaf litter, etc.). To date, no work has focused on endomychid diversity at heights above three meters, but several large–scale ecological studies have recovered endomychids from the canopy. Ulyshen and Hanula (2007) collected substantial numbers of *Micropsephodes lundgreni* from the canopy of a temperate deciduous forest, leading them to propose it may be a canopy specialist. Hammond (1994) reported 7 of 41 endomychid species (~17%) collected from the Sulawesian canopy were exclusive canopy specialists, and canopy specialization by some endomychids is further supported by other surveys of canopy beetles (*e.g.*, Allison *et al.* 1997, Stork 1991). Marques *et al.* (2006) found endomychids to be the dominant fungivores in the Brazilian rainforest canopy at one site.

Cave–dwelling Endomychids

Very few endomychid species exhibit cavernicolous or troglodytic habits. Some species may be associated with bat guano, as with *Holoparamecus gabrielae* Rücker (Rücker 2003), but for most, the natural history remains unknown. Jeannel (1926) recorded *Mycetaea subterranea* (as *M. hirta*) from inside the mouth of a cave in France. This species is known to occur in dark cellars and grain bins where it feeds on mold so it is not unreasonable to speculate similar habits in caves. Jeannel (1934) described a new anamorphine, *Cereaxina troglodytes* (later synonymized under *Reitteria escherichi* Wasmann [Merophysiinae]) from a cave in Asia Minor. Reddell and Veni (1996) collected a species of *Anamorphus* LeConte in a cave in Belize. Hoffman *et al.* (2004) listed a species of *Rhymbus* (=*Bystus*) collected in a cave in the Yucatan Peninsula. Moulds (2004) recorded an unidentified endomychid from Ashford Cave, New South Wales, Australia.

Endomychids as Pests

Chen and Cheng (2000) recorded a species of *Idiophyes* Blackburn as a nuisance pest in homes in China. Chuter (1999) noted that *Endomychus coccineus* facultatively colonized old, decaying particle/chip board. Endomychids are not usually considered pests of cultivated fungi since most species prefer hard bracket or shelf fungi to the more commonly cultivated agarics. *Symbiotes* Redtenbacher, however, includes several species that feed on oyster mushrooms, *Pleurotis ostreatus* Fries, a commonly harvested fungus for human consumption (Cline and Leschen 2005). *Mycetaea subterranea* was documented infesting stored caches of research–grade fungal pathogens (ergot sclerotia) (Singh and Tripathi 1990). In most cases where endomychids are considered pests, the beetles infest stored food products that have spoiled, feeding primarily on molds and secondarily on the product itself.

All recorded stored product pests within Endomychidae belong to four genera—*Holoparamecus* Curtis and *Merophysia* Lucas (Merophysiinae), *Mycetaea* (Mycetaeinae) and *Trochoideus* Westwood (Pleganophorinae) (Table 3.5). Commercial exportation of stored products has resulted in multiple introductions of pest species throughout the world, and many have become established. *Holoparamecus* species are the primary endomychid pests with at least six species known to infest stored products. The three remaining genera each include a single stored product pest species: *Merophysia letourneuxi*, *Mycetaea subterranea* and *Trochoideus desjardinsi*.

Aggregation/Diapause

Endomychids often cluster together in small groups in the field (F. Shockley pers. obs.), but this may be an artifact of the patchiness of their host fungi. Within Endomychidae, only two species have been documented as regularly forming larger non–feeding aggregations, both members of *Stenotarsus* Perty. Roubik and Skelley (2001) noted *Stenotarsus latipes* Arrow sometimes forms aggregations, but Arriaga-Varela *et al.* (2007) argued this species never forms aggregations in Mexico. Denlinger (1996) noted *Stenotarsus* spp. form aggregations, but it was unclear if he was referring to *S. latipes* or other *Stenotarsus* spp. that also aggregate.

Much work has been done on the aggregation behavior and diapause of *Stenotarsus subtilis* (frequently misidentified in the literature as *S. rotundus* Arrow, a junior synonym of the non–aggregating species *S. ovalis* Arrow) (Roubik and Skelley 2001). Adults of *S. subtilis* form large aggregations of up to 70,000 individuals (Denlinger 1994) in association with diapause, which may last up to 10 months per year (Tanaka 1988, Wolda and Denlinger 1984). These beetles do not fly during diapause, but migrate up and down the base of the tree on which they are aggregating based on humidity cues (Denlinger 1986). While other beetles often aggregate for reproduction, aggregations of *S. subtilis* consist of sexually immature virgin females and sexually mature males) (Nedvěd and Windsor 1994a, Roubik and Skelley 2001, Tanaka 1986). Males abstain from mating until triggered by the first wet season rains (Tanaka *et al.* 1987b, Tanaka *et al.* 1987c, Wolda 1992).

On Barro Colorado Island, Panama, where many of these studies were conducted, known aggregations of *S. subtilis* form at the base of two trees, an *Oenocarpus panamanus* Bailey (Arecaceae) and a *Tetragastris panamensis* (Engler) (Burseraceae). Interestingly, the beetles often aggregate on the exact tree used the previous year, despite aggregations consisting exclusively of newly eclosed, naïve univoltine adults (Tanaka *et al.* 1987b). Aggregating beetles do not feed and so must conserve water (Tanaka 2000, Yoder *et al.* 1992), relying upon fat reserves stored during larval instars (Wolda 1989, Nedvěd and Windsor 1994b). Dormant beetles are resistant to suboptimal temperatures due to accumulated glycerol and glucose in the hemolymph (Pullin and Wolda 1993, Nedvěd 2000). A variety of factors can influence the beetles' metabolic rates and the timing of diapause termination such as daylength and humidity (Tanaka *et al.* 1987a, c; 1988b), size of the aggregation (Tanaka *et al.* 1988a) and disturbance (*i.e.*, handling the beetles (Tanaka *et al.* 1987b)).

Defensive Strategies

Endomychids have a variety of physical and chemical defenses that help them ward off or evade potential predators. Endomychids have been suggested as participants in mimicry complexes with beetles from a variety of families including Carabidae (Arrow 1925, Brown 1985), Chrysomelidae, Coccinellidae (Donisthorpe 1901, Crowson 1981), Erotylidae (Marshall 1902) and Tenebrionidae (Brown 1985). Whether the mimicry proposed was Batesian or Müllerian remains unclear. In complexes involving predators, the mimicry may also be aggressive on the part of the predator. Leschen and Carlton (1993) described a special case of crypsis (mimicking inanimate objects) in the larvae of *Bystus decorator* Leschen and Carlton in which the larvae cover themselves with frass and pieces of bark and fungi to blend into their surroundings and shield themselves from predation. Females of *Endomychus biguttatus* often use the tough hyphae of their obligate reproductive host, *Schizophyllum commune* Fries, to camouflage their eggs (Leschen 1994).

In addition to the mimicry described above, a few taxa may exhibit Wasmannian mimicry (a social insect parasite/inquiline mimicking its host). Escherich (1911) described a larva associated with the termite *Eutermes ceylonicus* Holmgren. Arrow (1925) later identified this larva as that of *Trochoideus desjardinsi*, noting that the larva so strongly resembled the host that dorsally it was difficult to differentiate the two. Lawrence and Reichardt (1969) list *Trochoideus* spp. as potential ant mimics based on their highly modified antennae, a common feature of myrmecophiles. The myrmecophile *Cholovocerida maderae* (Wollaston) readily detects and follows the trail pheromone of its host ant, *Paratrechina longicornis* (Latreille). Interestingly, beetles are completely unmolested by workers, suggesting possible chemical mimicry of nest–mate recognition pheromones (Kistner 1982). This endomychid species also has a morphological adaptation in the pronotum that allows each beetle to be lifted by the ants without injury and transported along with the eggs when the host nest is disturbed (Kistner 1982).

Dettner (1987) and Skelley and Leschen (2002) suggested that some endomychids are likely to have chemical defenses, but few defensive chemicals have been identified. The terpenoid stenotarsol was recently isolated from *Stenotarsus subtilis* (Laurent *et al.* 2005), and *sec*-butyl 2–methoxy–3–alkylpyrazine was isolated from *Eumorphus tetraspilotus* (Moore *et al.* 1990). Numerous endomychid species have evolved the ability to reflexively bleed hemolymph in response to agitation, particularly from the femoro–tibial joints (Dettner 1987, Laurent *et al.* 2005, Skelley and Leschen 2002). This behavior has been documented in species of *Endomychus* (Endomychinae), *Lycoperdina* (Lycoperdininae), *Rhanidea* Strohecker (Leiestinae), *Corynomalus* (Lycoperdininae) and *Eumorphus* Weber (Lycoperdininae) (Skelley and Leschen 2002, F. Shockley pers. obs., Z. Simmons pers. comm.). Once secreted, beetles immediately begin to fastidiously clean the appendage from which the hemolymph cocktail was exuded (Z.

Simmons pers. comm.). In some *Eumorphus* spp., beetles can selectively bleed from the leg or legs closest to the stimulus source, suggesting that the compounds may be costly to produce. If beetles are continuously stimulated without a recovery period, the amount of exudate released is reduced with each agitation until the beetles eventually cease to exude droplets altogether (Z. Simmons pers. comm.).

Whether the compounds exuded by endomychids are produced internally or sequestered from external sources (*e.g.*, their fungal hosts) and then chemically altered for exudation remains unclear. In some cases, endomychids may actively seek out alternative defensive compounds not internally produced or externally acquired from their primary hosts. For example, several endomychid species are attracted to the biologically active deterrent compound cantharidin. *Aphorista laeta*, *A. vittata*, *Lycoperdina ferruginea*, *Danae testacea* and *Xenomycetes morrisoni* Horn preferentially orient to pitfall traps baited with cantharidin (Dettner 1987, 1997; Hemp and Dettner 2001; Price and Young 2007, Young 1984a, 1984b, 1989). Since many insect species respond to cantharidin, sensitivity to it or interspecific acquisition of it may be widespread throughout insects. Although a role in chemical defense of endomychids was explicitly implied in the studies referenced above, no specific mechanism was proposed for how endomychids might acquire cantharidin, why they would prefer it to other more readily available compounds, and whether or not they can even sequester it or chemically modify it prior to exudation.

Non–chemical Communication

Endomychids also have several mechanisms for communication via stridulation. In the field, stridulation by females of *Corynomalus* spp. has been observed to “corral” larvae, but more often serves as a distress signal encouraging conspecifics to move away from the area (F.

Shockley pers. obs.). Gorham (1885) was the first to note the presence of a stridulatory apparatus on *Encymon ruficollis* Gorham, attributing it to be a sexually dimorphic feature of males. Gahan (1900) rejected this assertion and discussed the form and function of the stridulatory apparatus in Endomychidae. The stridulatory organ is composed of a file located dorsally on the posteromedial region of the head and a membrane on the anterior margin of the pronotum which move in opposition to produce sound. This feature is a synapomorphy of the subfamily Lycoperdininae.

Arrow (1924) also described a stridulatory alar organ consisting of a set of modified patches on the posterior margin of the dorsal surface of the hind wing and a complimentary file on the inner surface of the medial margins of the elytra. The alar organ is present in many endomychids, albeit sometimes in highly modified or reduced form, and has specifically been observed within Anamorphinae (*Bystus*), Endomychinae (*Endomychus*), Epipocinae (*Epipocus* Germar), Lycoperdininae (*Amphisternus* Germar, *Eumorphus*, *Corynomalus*, *Cymbachus* Gerstaecker), and Stenotarsinae (*Stenotarsus* and *Danae*).

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Table 3.1. Known fungal hosts of Endomychidae.

Endomychid Taxon	Host Fungus[1]		Ref [2]
	Family	Genus/Species	
Anamorphinae			
Bystus sp.	Pleurotaceae	*Pleurotus* sp.	32
	Polyporaceae	*Favolus brasiliensis*	32
	Polyporaceae	*Favolus* sp.	32
	Polyporaceae	*Polyporus* sp.	32
	Polyporaceae	*Poria* sp.	32
	Xylariaceae	*Daldinia* sp.	32
	Xylariaceae	*Hypoxylon* sp.	32
	Xylariaceae	*Xylaria* sp.	32
Symbiotes duryi Blatchley	Pleurotaceae	*Pleurotus ostreatus*	8
Symbiotes impressus Dury	Pleurotaceae	*Pleurotus ostreatus*	8
Symbiotes latus Redtenbacher	Hymenochaetaceae	*Inonotus hispidus*	36
Symbiotes sp.	Pleurotaceae	*Pleurotus ostreatus*	19
Endomychinae			
Endomychus biguttatus	Auriculariaceae	*Auricularia auricula-judae*	23
	Auriculariaceae	*Auricularia mesenterica*	23
	Fomitopsidaceae	*Piptoporus betulinus*	32
	Schizophyllaceae	*Schizophyllum commune*	35
Endomychus coccineus	Auriculariaceae	*Auricularia mesenterica*	11
	Boletaceae	*Boletus suberosus*	12
	Lycoperdaceae	*Bovista* sp.	34
	Polyporaceae	*Panus conchatus*	28
	Polyporaceae	*Polyporus* sp.	36
	Polyporaceae	*Trametes hirsuta*	30
	Polyporaceae	*Trametes versicolor*	28
Epipocinae			
Epipocus longicornis Gerstaecker	Boletaceae	*Boletus edulis*	2
	Sirobasidiaceae	*Sirobasidium sanguineum*	2
Epipocus tibialis	Auriculariaceae	*Auricularia mesenterica*	2
Epipocus unicolor Horn	Boletaceae	*Fistulinella* sp.	2
	Polyporaceae	*Coriolopsis gallica*	10
Leiestinae			
Leiestes seminiger (Gyllenhall)	Fomitopsidaceae	*Piptoporus betulinus*	36
Phymaphora pulchella Newman	Meruliaceae	*Climacodon pulcherrimus*	7, 32
	Fomitopsidaceae	*Piptoporus betulinus*	24, 32
Rhanidea unicolor	Steccherinaceae	*Irpex lacteus*	7, 32
Lycoperdininae			
Aphorista laeta	Ganodermataceae	*Ganoderma applanatum*	4
Aphorista morosa	Gomphaceae	*Gomphus floccosus*	4
	Crepidotaceae	*Crepidotus mollis*	4
	Paxillaceae	*Paxillus* sp.	4
	Pluteaceae	*Pluteus cervinus*	4
	Polyporaceae	*Coriolopsis gallica*	10
Aphorista vittata	Coniophoraceae	*Coniophora arida*	15
	Russulaceae	*Lactarius argillaceifolius*	22
	Russulaceae	*Russula* sp.	22

Table 3.1. cont'd.

Endomychid Taxon	Host Fungus[1] Family	Host Fungus[1] Genus/Species	Ref [2]
Lycoperdininae			
Aphorista vittata	Marasmiaceae	*Armillaria mellea*	22
	Marasmiaceae	*Armillaria tabescens*	22
Eumorphus marginatus Fabricius	Polyporaceae	*Polyporus* sp.	3
Eumorphus sp.	Ganodermataceae	*Ganoderma* sp.	20
Lycoperdina bovistae	Boletaceae	*Boletus* sp.	36
	Geastraceae	*Geastrum fimbriatum*	28
	Geastraceae	*Geastrum rufescens*	28
	Lycoperdaceae	*Langermannia gigantea*	13
	Lycoperdaceae	*Bovista* sp.	14
	Lycoperdaceae	*Handkea excipuliformis*	28
	Lycoperdaceae	*Handkea utriformis*	5, 17
	Lycoperdaceae	*Lycoperdon bovista*	5
	Lycoperdaceae	*Lycoperdon gemmatum*	28
	Lycoperdaceae	*Lycoperdon perlatum*	17
	Lycoperdaceae	*Lycoperdon pyriforme*	5
	Lycoperdaceae	*Lycoperdon verrucosum*	29
	Russulaceae	*Lactarius piperatus*	28
	Russulaceae	*Russula delica*	28
	Marasmiaceae	*Armillaria mellea*	28
	Tricholomataceae	*Clitocybe nebularis*	28
	Tricholomataceae	*Gymnopus fuscipes*	28
	Tricholomataceae	*Lepista flaccida*	27
Lycoperdina ferruginea	Hydnaceae	*Hydnum* sp.	22
	Lycoperdaceae	*Calvatia cyathiformis*	25
	Lycoperdaceae	*Langermannia gigantea*	25
	Lycoperdaceae	*Lycoperdon molle*	25
	Lycoperdaceae	*Lycoperdon perlatum*	25
	Lycoperdaceae	*Lycoperdon pyriforme*	35
	Lycoperdaceae	*Lycoperdon subvelatum*	25
	Lycoperdaceae	*Lycoperdon umbrinum*	25
	Lycoperdaceae	*Lycoperdon* sp.	1
	Pezizaceae	*Peziza* sp.	25
	Pluteaceae	*Pluteus cervinus*	22
Lycoperdina penicillata Marseul	Lycoperdaceae	*Bovista plumbea*	26
	Lycoperdaceae	*Lycoperdon gemmatum*	26
Lycoperdina succincta (L.)	Geasteraceae	*Geastrum triplex*	33
	Lycoperdaceae	*Bovista nigrescens*	16
	Lycoperdaceae	*Lycoperdon gemmatum*	11
Mycetina cruciata (Schaller)	Pleurotaceae	*Pleurotus* sp.	9
	Polyporaceae	*Trametes suaveolens*	21
	Polyporaceae	*Polyporus* sp.	36
Mycetina idahoensis Fall	Polyporaceae	*Polyporus* sp.	36
Mycetina perpulchra (Newman)	Coniophoraceae	*Coniophora arida*	15
	Meripilaceae	*Meripilus giganteus*	22
Mycetaeinae			
Mycetaea subterranea	Coniophoraceae	*Serpula lacrymans*	5, 21
	Polyporaceae	*Polyporus squamosus*	36
	Polyporaceae	*Laetiporus sulphureus*	9
	Polyporaceae	*Polyporus* sp.	6
	Polyporaceae	*Trametes pubescens*	31

Table 3.1. cont'd.

Endomychid Taxon	**Host Fungus[1]**		**Ref [2]**
	Family	**Genus/Species**	
Pleganophorinae			
Trochoideus desjardinsi	Auriculariaceae	*Auricularia* sp.	20
Stenotarsinae			
Stenotarsus circumdatus Gerstaecker	Russulaceae	*Russula* sp.	2
Stenotarsus latipes	Russulaceae	*Russula* sp.	2
	Russulaceae	*Lactarius deliciosus*	2
	Russulaceae	*Lactarius* sp.	2
	Sirobasidiaceae	*Sirobasidium sanguineum*	2
Stenotarsus marginalis Arrow	Russulaceae	*Russula mexicana*	2
	Russulaceae	*Lactarius* sp.	2
Stenotarsus sp.	Polyporaceae	*Favolus tenuiculus*	2
Xenomycetinae			
Xenomycetes laversi Hatch	Paxillaceae	*Paxillus atrotomentosus*	18

[1] Host fungus family and species names verified using the electronic Index Fungorum, http://www.indexfungorum.org/. Accessed 9 April, 2008.

[2] References: 1) Ackerman & Shenefelt 1973; 2) Arriaga *et al.* 2007; 3) Arrow 1925; 4) J.S. Ashe *pers. comm.*; 5) Benick 1952; 6) Bercio 1930-31 ; 7) Burakowski & Ślipiński 2000; 8) Cline & Leschen 2005; 9) Dajoz 1966; 10) Dajoz 1996; 11) Donisthorpe 1935; 12) d'Orbigny 1846; 13) Fowler 1887-1891; 14) Ganglbauer 1899; 15) Hoebeke *et al.* 1987; 16) Horion 1961; 17) Hyman & Parsons 1992; 18) Johnson 1986; 19) Lawrence 1991; 20) Lawrence & Milner 1996; 21) Lentz 1879; 22) Leschen 1988; 23) Leschen & Carlton 1988; 24) Majka 2007; 25) Pakaluk 1984; 26) Peyerimhoff 1915; 27) Rapp 1934; 28) Rehfous 1955; 29) Rouget 1858; 30) Scheerpelz & Höfler 1948; 31) Selonen *et al.* 2005; 32) F.W. Shockley pers. obs./museum specimens; 33) Sunhede 1974; 34) Weiss 1924; 35) Weiss & West 1920; 36) Q.D. Wheeler *in litt.*, MYCOL database.

Table 3.2. Yeast gut endosymbionts of Endomychidae.

Endomychid Taxon	Yeast Isolate	Ref [1]
Anamorphinae		
Bystus piceus (Gorham)	*Candida ambrosiae*	4
	Candida barrocoloradensis	4
	Candida boleticola	4
	Candida homilentoma	4
Epipocinae		
Epipocus tristus tristus Guérin-Méneville	*Candida athensensis*	4
Lycoperdininae		
Corynomalus laevigatus	*Ambrosiozyma monospora*	3
	Candida amphixiae	4
	Candida endomychidarum	3
	Candida sinolaborantium	3
	Candida michaelii	3
Corynomalus vestitus cinctus (Fabricius)	*Candida emberorum*	1
	Candida halonitratophila	4
	Pichia nakazawae	3
	Trichomonoascus petasosporus	4
Lycoperdina ferruginea	*Asterotremella humicola*	4
Stenotarsinae		
Stenotarsus lemniscatus Gorham	*Candida cylindracea*	4
	Candida haemulonii	4
	Candida panamensis	4
	Pseudozyma rugulosa	4
Stenotarsus obtusus Gerstaecker	*Candida panamensis*	4
Stenotarsus validicornis Gerstaecker	*Candida nodaensis*	4
Endomychidae (Undetermined)		
Larva	*Candida athensensis*	4
Larva	*Candida smithsonii*	2

[1] References: 1) Suh *et al.* 2004; 2) Suh & Blackwell 2004; 3) Suh *et al.* 2005; 4) M. Blackwell *in litt.*, BeetleBellYeast Project Database.

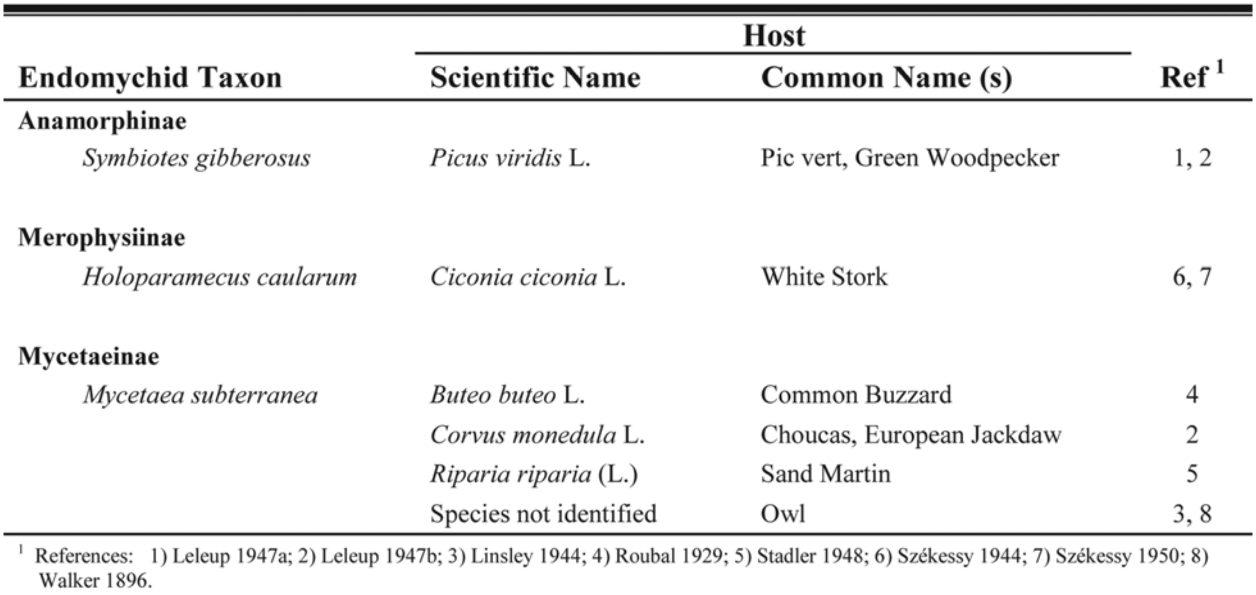
Table 3.3. Published records for endomychid inquilines of social insects.

Endomychid Taxon	Ass.[1]	Specific Host Taxon (if known)	Ref[2]
Anamorphinae			
Rhymbillus hospes Reich.	A	No specific host listed	7, 14
Symbiotes latus	A	*Lasius brunneus*	4, 7, 18
Eupsilobiinae			
Chileolobius convexus	A	*Pachycondyla* sp.	13
Eidoreus minutus Sharp	A	*Pheidole punctulata*	2, 9
Evolocera championi Sharp	A	No specific host listed	16
Evolocera sp.	B	*Ancyloscelis apiformis*, *Melitoma marginella*	19
Microxenus laticollis Woll.	A	No specific host listed	1
Merophysiinae			
Cholovocera attae (Kraatz)	A	*Messor barbara, M. structor*	6
Cholovocera beloni (Wasmann)	A	*Holcomyrmex scabriceps*, *Pheidole sulcaticeps poonensis*, *Ph. wroughtoni*, *Ph. latinoda*, *Paratrechina longicornis*	6, 8
Cholovocera fleischeri Reitter	A	*Atta* sp.	6
Cholovocera formicaria Motschulsky	A	*Aphaenogaster testaceopilosa*, *Messor barbara*, *M. structor, Pheidole pusilla, P. megacephala*	4, 18
Cholovocerida ecitonis (Wasm.)	A	*Eciton praedator, E. omnivorum*	18
Cholovocerida maderae (Woll.)	A	*Paratrechina longicornis*	8, 18
Holoparamecus spp.	A	*Atta mexicana*	12, 15
Merophysia carinulata Rosenhauer	A	*Aphaenogaster testaceopilosa, Pheidole pusilla, Ph. megacephala*	18
Merophysia carmelitana Saulcy	A	*Messor barbara*	6
Merophysia formicaria Lucas	A	*Messor barbara, Aphaenogaster testaceopilosa, Pheidole pusilla, Ph. megacephala*	18
Merophysia oblonga Kiesenwetter	A	*Aphaenogaster testaceopilosa*, *Pheidole pallidula*, *Tetramorium caespitum*	6, 18
Reitteria escherichi	A	*Pheidole pallidula, Camponotus aethiops*	6
Mycetaeinae			
Mycetaea subterranea	B	No specific host listed	5, 11
	A	*Formica rufa, F. protensis, F. exsecta, Lasius niger, L. fuliginosis*	4, 18
Pleganophorinae			
Pleganophorus bispinosus Hampe	A	*Lasius brunneus*	18
Trochoideus desjardinsi	A	*Plagioleps longipes*	7, 10, 18
Trochoideus desjardinsi	C	*Eutermes ceylonicus*, *Termes gilvus*	3
Stenotarsinae			
Stenotarsus secticollis Strohecker	C	No specific host listed (implied only)	17

[1] Associations: A = Myrmecophilous, B = Melittophilous, C = Termitophilous.

[2] References: 1) Arriaga-Varela *et al.* 2007; 2) Arrow 1922; 3) Arrow 1925; 4) Bernard 1968; 5) Ganglbauer 1899; 6) Hetschko 1926; 7) Hölldobler & Wilson 1990; 8) Kistner 1982; 9) Kolbe 1910; 10) Lawrence & Reinhardt 1969; 11) Marseul 1867-68; 12) Navarette-Heredia 2001; 13) Pakaluk & Ślipiński 1990; 14) Reichensperger 1915; 15) Rojas 1989; 16) Sharp 1891; 17) Skelley 1999; 18) Wasmann 1894; 19) Yanega & Leschen 1994.

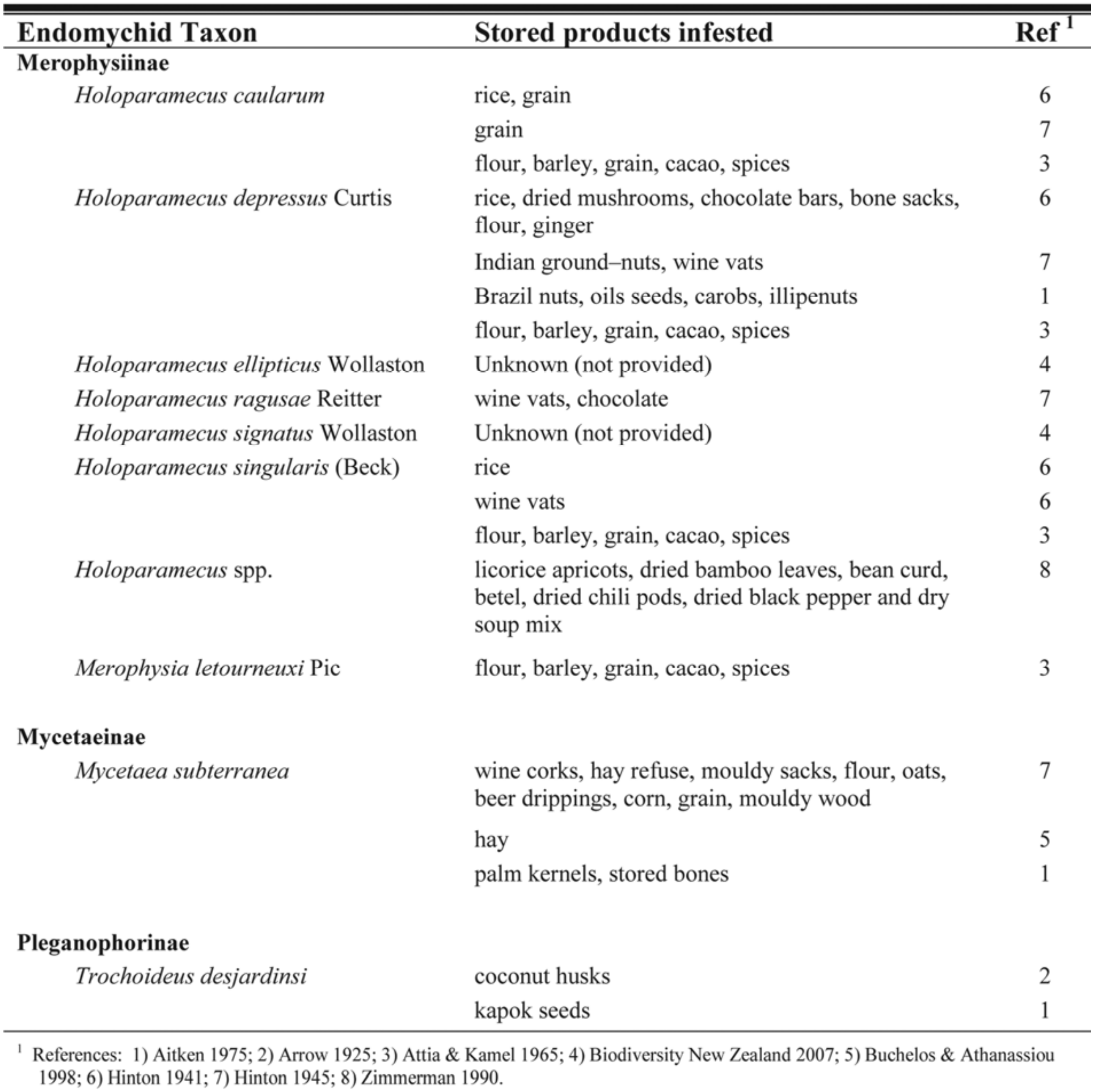
Table 3.4. Published records for endomychids as nest associates of birds. Modified from Hicks (1959).



Endomychid Taxon	Host		Ref [1]
	Scientific Name	Common Name (s)	
Anamorphinae			
Symbiotes gibberosus	*Picus viridis* L.	Pic vert, Green Woodpecker	1, 2
Merophysiinae			
Holoparamecus caularum	*Ciconia ciconia* L.	White Stork	6, 7
Mycetaeinae			
Mycetaea subterranea	*Buteo buteo* L.	Common Buzzard	4
	Corvus monedula L.	Choucas, European Jackdaw	2
	Riparia riparia (L.)	Sand Martin	5
	Species not identified	Owl	3, 8

[1] References: 1) Leleup 1947a; 2) Leleup 1947b; 3) Linsley 1944; 4) Roubal 1929; 5) Stadler 1948; 6) Székessy 1944; 7) Székessy 1950; 8) Walker 1896.

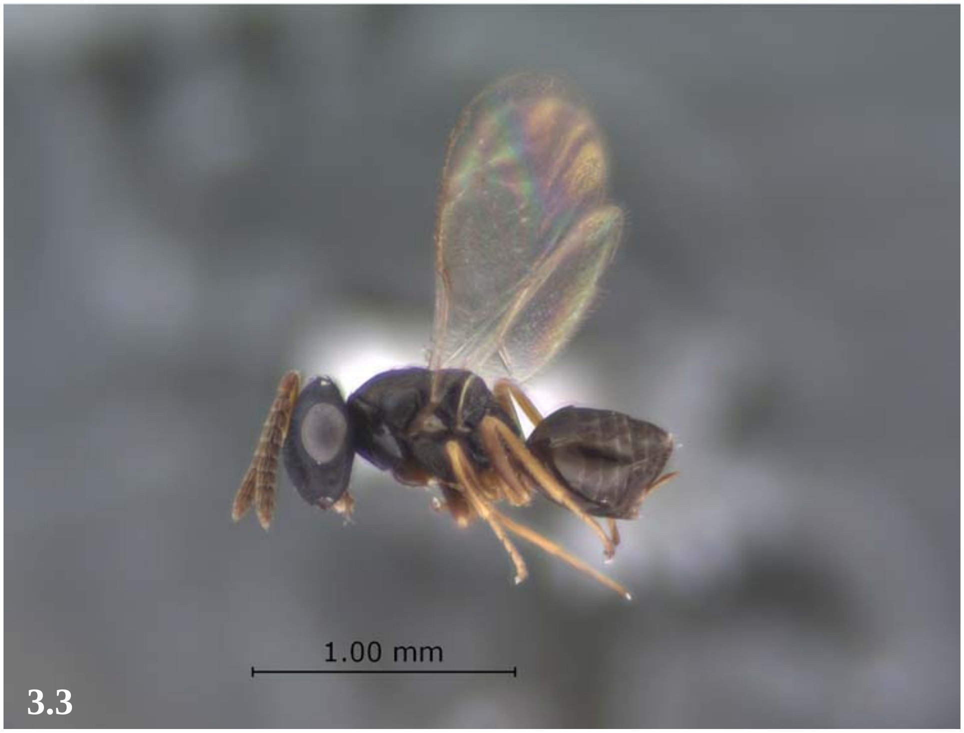
Table 3.5. Endomychid species known to infest stored products.



Endomychid Taxon	Stored products infested	Ref [1]
Merophysiinae		
Holoparamecus caularum	rice, grain	6
	grain	7
	flour, barley, grain, cacao, spices	3
Holoparamecus depressus Curtis	rice, dried mushrooms, chocolate bars, bone sacks, flour, ginger	6
	Indian ground–nuts, wine vats	7
	Brazil nuts, oils seeds, carobs, illipenuts	1
	flour, barley, grain, cacao, spices	3
Holoparamecus ellipticus Wollaston	Unknown (not provided)	4
Holoparamecus ragusae Reitter	wine vats, chocolate	7
Holoparamecus signatus Wollaston	Unknown (not provided)	4
Holoparamecus singularis (Beck)	rice	6
	wine vats	6
	flour, barley, grain, cacao, spices	3
Holoparamecus spp.	licorice apricots, dried bamboo leaves, bean curd, betel, dried chili pods, dried black pepper and dry soup mix	8
Merophysia letourneuxi Pic	flour, barley, grain, cacao, spices	3
Mycetaeinae		
Mycetaea subterranea	wine corks, hay refuse, mouldy sacks, flour, oats, beer drippings, corn, grain, mouldy wood	7
	hay	5
	palm kernels, stored bones	1
Pleganophorinae		
Trochoideus desjardinsi	coconut husks	2
	kapok seeds	1

[1] References: 1) Aitken 1975; 2) Arrow 1925; 3) Attia & Kamel 1965; 4) Biodiversity New Zealand 2007; 5) Buchelos & Athanassiou 1998; 6) Hinton 1941; 7) Hinton 1945; 8) Zimmerman 1990.

Figure 3.1. *Eumorphus micans* Strohecker (smaller, brown specimens) and *Eumorphus fryanus festivus* (Arrow) (larger, black specimens) (Endomychidae: Lycoperdininae) resting on a *Piper* sp. (Piperaceae) in Borneo. Photo courtesy of D. Mann.



Figures 3.2-3.3. Natural enemies of Endomychidae. **2)** Larva of *Eurycoleus* sp. (Carabidae: Lebiinae) feeding on a pupa of *Corynomalus vestitus cinctus* (Endomychidae: Lycoperdininae) on Barro Colorado Island, Panama. Photo courtesy of N. Lord. **3)** *Endomychobius flavipes* (Hymenoptera: Pteromalidae), a host-specific parasitoid that attacks *Endomychus biguttatus* (Endomychidae: Endomychinae). Photo courtesy of M. Gates.

CHAPTER 4

PHYLOGENY OF THE HANDSOME FUNGUS BEETLES (COLEOPTERA: ENDOMYCHIDAE) INFERRED FROM NUCLEAR AND MITOCHONDRIAL GENES: WHO'S HANDSOME AND WHO'S NOT?[1]

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[1] Shockley, F.W., J.A. Robertson, K.B. Miller, J.V. McHugh and M.F. Whiting. To be submitted to Systematic Entomology.

ABSTRACT

Recent phylogenetic studies have recovered conflicting results regarding the monophyly of Endomychidae and its constituent subfamilies. These studies each suffer from different problems that can only be resolved by more extensive analyses. Here we present a phylogenetic study based on eight genes including nuclear ribosomal (18S, 28S), nuclear protein-coding (Wnt, H3), mitochondrial ribosomal (12S, 16S) and mitochondrial protein-coding (COI, COII) genes. The taxon sampling for this analysis included nine outgroup taxa, including one from each of the other Cerylonid-Series families. Trees were rooted to a "distant" outgroup taxon from Erotylidae. Within the in-group, 91 taxa were included, representing 10 of the 12 subfamilies of Endomychidae. Alignment for the protein-coding genes was done manually, while the ribosomal genes were statically aligned using the program MAFFT. Maximum parsimony, maximum likelihood and Bayesian analyses were used for phylogenetic reconstruction. Endomychidae was recovered as paraphyletic in all three analyses with Anamorphinae consistently recovered outside of the remaining endomychid lineages. Anamorphinae, Epipocinae, Leiestinae, Lycoperdininae, Merophysiinae and Pleganophorinae were all recovered as monophyletic. Endomychinae and Stenotarsinae were found to be paraphyletic with respect to each other in all three analyses. Placement of Mycetaeinae and Eupsilobiinae within Endomychidae was confirmed only by the parsimony analysis. They were recovered outside of the remaining endomychid lineages in the likelihood and Bayesian analyses. Pleganophorinae, Leiestinae and Merophysiinae form a monophyletic clade sister to clade comprising Stenotarsinae, Endomychinae, Epipocinae and Lycoperdininae. Internal relationships for all subfamilial, suprageneric and generic clades are discussed.

Key Words: Systematics, phylogeny, evolution, classification, nuclear genes, mitochondrial genes, protein-coding genes, ribosomal genes

INTRODUCTION

Endomychidae, whose members are commonly known as the Handsome Fungus Beetles, is a moderately speciose family of mycophagous beetles. Although cosmopolitan in distribution, much of the family's diversity is concentrated in the tropical regions of the world. Strohecker (1953) provided the first comprehensive keys to the known endomychid genera of the world, but this treatment lacked the phylogenetic context necessary for establishing a stable, natural classification and is now grossly outdated. The family includes 130 genera and 1782 species and subspecies (Shockley *et al.* 2009), making it the second largest family within the Cerylonid Series (CS) and the 4th largest family in the superfamily Cucujoidea. Species of Cucujoidea are generally smaller in size and less charismatic in coloration than other beetles, and many CS taxa serve as taxonomic "dumping grounds" for any small, brown beetles not easily placed elsewhere.

The family Endomychidae has been particularly problematic and considered by some to be a heterogeneous assemblage of highly variable taxa, with some subfamilies sharing closer affinities to other CS taxa than with each other. The family has been difficult to characterize due to a lack of uniform morphological characters that unite it as a natural group. Nonetheless, endomychids are generally recognizable by the presence of a frontoclypeal suture, 3-3-3 or 4-4-4 tarsal formula, anterior pronotal angles produced anteriad along the head, and the presence of lateral or basal sulci on the pronotum of many taxa. Unfortunately, relatively little has been done to investigate the internal relationships within Endomychidae, identify potential synapomorphies for the family and its constituent subfamilies, and determine the relationship of the family as a whole to other CS families.

Although Strohecker (1953) was the first to discuss the potential evolutionary relationships of Endomychidae to other cucujoids (Fig. 4.1), his discussion lacked the cladistic context necessary to formally evaluate the phylogenetic relationship between the endomychid subfamilies. Since then, the internal classification of Endomychidae has changed significantly, and Alexiidae has been elevated to the family-level (Sen Gupta and Crowson 1973, Crowson 1981, Lawrence 1982, Ślipiński and Pakaluk 1991, Lawrence and Newton 1995). Sasaji (1978, 1987, 1990) was the first to propose that Endomychidae might not be a natural group, arguing that Anamorphinae (as Mychothenidae) constituted an independent group outside of the remaining Endomychidae (Fig. 4.2). Ślipiński and Pakaluk (1991) specifically discussed some of the problems with the current classification of the CS and concluded that the inclusion of Anamorphinae, Merophysiinae and Eupsilobiinae renders Endomychidae polyphyletic (Fig. 4.3). However, their conclusions were based on an intuitive phylogenetic hypothesis and not a formal analysis and reconstruction.

Using adult morphological characters, Tomaszewska (2000) performed the first modern phylogenetic analysis of the family. The study recovered the family and its constituent subfamilies as monophyletic but failed to resolve the relationships between the subfamilies (Fig. 4.4). In a follow-up analysis, Tomaszewska (2005) was able to better resolve the relationships between the subfamilial branches and identified a monophyletic clade of "higher" endomychid subfamilies (Endomychinae, Epipocinae, Lycoperdininae and Stenotarsinae) (Fig. 4.5). Unfortunately, both studies assumed a sister-group relationship with Coccinellidae *a priori* rather than including outgroup taxa sampled from throughout the CS, thus rendering both studies inadequate to truly test the monophyly of the family.

Using 3 genes (18S, 16S, COI) in a broader sample of CS taxa, Hunt *et al.* (2007) recovered the clade Alexiidae+Anamorphinae+Coccinellidae as sister to the "higher" Endomychidae of Tomaszewska (2005)(Fig. 4.6). Interestingly, that study did not recover the subfamilies Merophysiinae, Leiestinae and Anamorphinae as monophyletic with the remaining Endomychidae. Unfortunately, the taxon and gene sampling of that study were insufficient to fully resolve the subfamilial relationships within Endomychidae. Nonetheless, the resulting hypotheses raised lingering questions about the monophyly of Endomychidae and the placement of several of the endomychid subfamilies.

Robertson *et al.* (2008) conducted the first formal test of the limits of the CS using molecular sequence data (18S, 28S). Anamorphinae was again recovered outside of Endomychidae, in this case as sister to the family Corylophidae (Fig. 4.7). In addition, the placement of the Leiestinae was uncertain. Parsimony analyses recovered Leiestinae outside of Endomychidae and sister to Coccinellidae, but Bayesian analysis recovered it as basal within Endomychidae sister to the higher endomychid subfamilies. Robertson *et al.* (2008) included exemplars from only six of the 12 subfamilies of Endomychidae and did not include mitochondrial or protein-coding genes.

The goals of this study were three-fold: 1) to rigorously test the monophyly of the family Endomychidae using both nuclear (ribosomal and protein-coding) and mitochondrial (ribosomal and protein-coding) genes; 2) to test for incongruence and heterogeneity between gene partitions and identify conflicts between these partitions; and 3) to investigate the internal relationships of the subfamilies and attempt to resolve their placement relative to each other and to other CS families.

MATERIALS AND METHODS

Taxon Sampling

This analysis included a total of 85 taxa (15 species duplicates; 100 total specimens), representing approximately 1/3 of the known genera (40/126) and most of the subfamilies of Endomychidae (10/12) (Table 4.1). The remaining subfamilies (Danascelinae and Xenomycetinae) are rare North American endemics not often collected and difficult to obtain as fresh DNA-grade material. Because of the uncertain relationship of some endomychid subfamilies to other CS families, 1 outgroup exemplar was selected from each of the remaining seven families in the CS. The enigmatic genus *Akalyptoishion*, which has historically been placed within Latridiidae, was recovered outside of the remaining Latridiidae in a recent phylogenetic study (Lord 2008). Based on the unclear relationship of *Akalyptoishion* to the remaining CS families from the aforementioned study, one exemplar from this genus was also included. The resulting topologies were rooted to *Pselaphacus nigropunctatus* (Erotylidae), a non-CS cucujoid. Primary and secondary voucher specimens are deposited in the University of Georgia Coleoptera Tissue Collection (University of Georgia Collection of Arthropods, Athens, GA, USA), and DNA extracts are deposited in the BYU Insect Genomics Collection (Brigham Young University, Provo, UT, USA).

Data Sampling

DNA was extracted using Qiagen (Valencia, California, USA) DNEasy kit for animal tissues. For smaller specimens (length < 5 mm), the abdomen was removed prior to extraction, and the whole specimen placed in buffer. For larger taxa (length < 5 mm), muscle tissue was extracted through a small incision in the thoracic pleuron using fine-tipped forceps and then placed in buffer. After a 24 hr incubation period during which samples were gently agitated in buffer, whole specimens were rinsed with buffer, placed back in their original vials with clean ethanol and retained as primary vouchers. In the case of larger specimens, excess muscle tissue remaining after incubation was removed prior to purification and amplification.

Eight target genes were amplified and sequenced, including representative nuclear and mitochondrial genes. The specific targets were: 12S ribosomal DNA (12S), 16S ribosomal DNA (16S), 18S ribosomal DNA (18S), 28S ribosomal DNA (28S), Cytochrome Oxidase I (COI), Cytochrome Oxidase II (COII), *wingless* (Wnt) and Histone III (H3). External and internal primers (for larger genes) used for gene amplification are shown in Table 4.2. Polymerase chain reaction (PCR) amplification was run on a DNA Engine DYAD™ Peltier Thermal Cycler (Bio-Rad Laboratories, Hercules, CA). PCR product yield, specificity, and contamination were monitored using agarose gel electrophoresis.

PCR products for 18S and 28S were generated using the following protocol: (i) initial denaturation at 94° for 2 min; (ii) 35 cycles of 94° (60 sec), 50° (60 sec), 72° (75 sec); and (iii) 1 final elongation cycle of 72° for 7 min. PCR products for COI and COII were generated using the following protocol: (i) initial denaturation at 95° for 1 min; (ii) 40 cycles of 94° (60 sec), 50° (60 sec), 72° (3 min); and (iii) 1 final elongation cycle of 72° for 12 min. PCR products for 12S and 16S were generated using the following protocol: (i) initial denaturation at 95° for 2 min;

(ii) 45 cycles of 94° (60 sec), 50° (60 sec), 60° (2 min); and (iii) 1 final elongation cycle of 60° for 7 min. PCR products for H3 and Wnt were generated using the following protocol: (i) initial denaturation at 95° for 5 min; (ii) 55 cycles of 95° (30 sec), 54° (30 sec), 72° (60 sec); and (iii) 1 final elongation cycle of 72° for 15 min.

Products were purified using Montage PCR96 Cleanup Kit (Millipore®). Sequencing reactions were done using ABI Prism Big Dye® (Version 3), and reaction products were purified using Sephadex™ G-50 medium. Sequencing was done with an ABI 3730xl DNA analyzer (BYU DNA Sequencing Center, Provo, Utah, USA). Data editing and contig assembly was performed using Sequencher® 4.2 (GeneCodes Corp., Ann Arbor, MI).

Analytical Methods

Alignment of COI, COII, Wnt and H3 was done in Sequencher based on conservation of the codon reading frame. Alignment of 12S, 16S, 18S and 28S was done using MAFFT 6.0 (Multiple Alignment using Fast Fourier Transformation) (Katoh and Toh 2008**)** as implemented through the European Bioinformatics Institute web server (http://www.ebi.ac.uk/Tools/mafft/index.html) under the default settings. Resulting alignments were then edited to remove terminal gaps and ambiguously aligned characters using GBlocks 0.91b (Castresana 2000, Talavera and Castresana 2007) under the default settings. The number of parsimony-informative characters remaining in each of the curated alignments was determined using WinClada (Nixon 2002), and concatenation of the genes to form a single data matrix was also performed in WinClada.

To test *a priori* whether the different genes contained congruent phylogenetic signal, partition homogeneity tests were performed in PAUP* 4.0b10 (Swofford 2002). Pairwise incongruence length difference (ILD) tests were used on 10 different partitions to test for heterogeneity (Table 4.3). Each test consisted of heuristic searches under the parsimony optimality criterion with 100 replicates, 10 random stepwise-sequence additions, maxtrees = 100, tree bisection-reconnection (TBR) branch swapping, all characters unordered and unweighted, and gaps treated as missing. A significance threshold of $P \leq 0.01$ was used to reject the null hypothesis of congruence between gene sets in each partition.

Phylogenetic reconstruction was performed in T.N.T. (Goloboff *et al.* 2008) under the maximum parsimony criterion (MP) implementing 5000 replicates using a combination of New Technology heuristic algorithms (e.g., sectorial searches, tree drifting, tree fusing, and ratcheting). Gaps were treated as missing data, and all characters were unordered and equally weighted. An analysis based on rapid maximum likelihood inference (ML) was performed in GARLI 0.951 (Zwickl 2006) using the default settings (streefname = stepwise; attachmentspertaxon = 50; genthreshfortopoterm = 10000; numberofprecreductions = 10; treerejectionthreshold = 50) and model of evolution (GTR + Γ + I).

Bayesian analysis was performed using MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003) using the MAFFT alignments with mixed model settings. ModelTest (Posada and Crandall 1998), as implemented through PAUP* 4.0b10, was used to select the appropriate model of evolution (GTR + Γ + I) based on the application of the Akaike Information Criterion (AIC) on the log likelihood scores. The Bayesian analysis comprised four separate runs each utilizing 10 million generations, flat priors, unlinked partitions, four chains (one cold and three hot), and trees sampled every 1000 generations. The first 2500 trees sampled in each run (25%) were discarded as “burn-in,” and the remaining trees from all four runs were combined and used to construct a 50% majority rule consensus tree.

Topological support for T.N.T trees was assessed via nonparametric bootstrap values calculated in T.N.T using 1000 replicates. TreeRot (Sorenson and Franzosa 2007), as implemented in PAUP* 4.0b10, was used to calculate partitioned Bremer support values (Baker & DeSalle 1997) for each node of the T.N.T. consensus tree. Branch support for the Bayesian trees was assessed with posterior probabilities determined via the 50% majority rule consensus percentages.

RESULTS

The concatenated matrix of all 8 genes resulted in 9,086 total aligned characters of which 7,217 (79.4%) were unambiguous and 2,598 (28.6%) were parsimony-informative (Table 4.4). Of all of the partitions tested for heterogeneity, only the mitochondrial, ribosomal genes (12S, 16S) and the nuclear, protein-coding genes (H3, Wnt) were found to be homogeneous *a priori*.

Maximum parsimony analysis recovered 12 equally parsimonious trees (Length = 23783 steps; CI = 0.22; RI = 0.55) from the static alignment analyses in T.N.T. The strict consensus tree was highly resolved, collapsing only 5 terminal nodes to form polytomies (Fig. 4.8). Bootstrap and partitioned Bremer support values for the T.N.T. tree are given in Table 4.5. The partitioned Bremer support values for the nodes of the T.N.T. consensus tree revealed the source of the heterogeneity between gene partitions to be largely due to 3 genes—28S, COI and COII. While the remaining 5 genes all positively and strongly supported the MP topology, 28S, COI and COII did not support this topology (Tables 4.3, 4.5). As a result, many of the basal nodes are very poorly supported. Exclusion of these genes yielded a similar topology with increased support for the basal nodes but decreased resolution at nodes corresponding to the suprageneric and generic levels. Nonetheless, the same general topology was recovered in the maximum parsimony, maximum likelihood and Bayesian analyses, suggesting that there was still sufficient phylogenetic signal to fully resolve most of the internal nodes.

All Bayesian runs reached stationarity by 100000 generations. To insure adequate "burn-in," sampled trees from the first 2,500,000 generations (2500 per run, 10,000 trees total) were discarded. The remaining 30,000 sampled trees were combined and used to construct a 50% majority rule consensus tree (Fig. 4.9). The maximum likelihood tree was nearly identical to the Bayesian tree so it was not separately figured. However, the ML tree was more fully resolved compared to the MP and Bayesian topologies, but nodal support at additionally resolved nodes was very low. Conflicting nodes between the ML, MP and Bayesian topologies are indicated on both the MP (Fig. 4.8) and Bayesian trees (Fig. 4.9).

The topological support for the trees recovered from the three different analyses showed the same general pattern: high support values (i.e., bootstrap values, Bremer supports and posterior probabilities) corresponding to generic clades. Most deep nodes corresponding to subfamilial clades are also strongly supported with several notable exceptions. The subfamilies Stenotarsinae and Endomychinae render each other paraphyletic. There was also very low support in terms of bootstrap and Bremer values for the node subtending Lycoperdininae, but it had a high posterior probability. Low posterior probabilities on the Bayesian tree were generally associated with clades that collapsed into polytomies in the T.N.T. consensus tree, demonstrating the overall agreement between the topologies at these nodes.

All three analyses recovered a paraphyletic Endomychidae. These data also supported the following endomychid subfamilies as monophyletic: Anamorphinae, Epipocinae, Leiestinae, Lycoperdininae, Merophysiinae and Pleganophorinae. All three analyses recovered

Endomychinae and Stenotarsinae as paraphyletic with respect to one another. Only one species each of Mycetaeinae and Eupsilobiinae were included so the monophyly of those subfamilies could not be rigorously tested.

DISCUSSION

"Endomychidae" and Outgroup Taxa

The results of the present study corroborate those of previous studies (Tomaszewska 2005, Hunt *et al.* 2007, Robertson *et al.* 2008), suggesting a close affinity between the different endomychid lineages and the families Coccinellidae and Corylophidae. Overall, there was a high degree of congruence between the topologies generated by the parsimony, likelihood and Bayesian analyses, especially for many of the nodes containing endomychid lineages (Figs. 4.10-4.12). Although the analyses varied in their placement of some endomychid lineages relative to outgroup taxa, all three analyses failed to recover Endomychidae as monophyletic but shared similar patterns of relationship for the endomychid subfamilies: 1) Anamorphinae was consistently recovered outside of Endomychidae; 2) Mycetaeinae and Eupsilobiinae are sister taxa; 3) Pleganophorinae, Merophysiinae and Leiestinae were recovered as a strongly supported clade (the "PML clade") basal and sister to a clade that included Endomychinae, Epipocinae, Lycoperdininae and Stenotarsinae (the "SEEL" clade) which corresponds to the "Higher" Endomychidae of Tomaszewska (2005); 4) Endomychinae and Stenotarsinae are paraphyletic with respect to each other; 5) Epipocinae and Lycoperdininae are sister taxa.

The relationships between the outgroup taxa differed significantly between the MP analysis and the ML and Bayesian analyses, with poor support for all recovered relationships. The MP and ML/Bayesian analyses all recovered a relationship between Bothrideridae, Cerylonidae and Discolomatidae. A relationship between these three families was also recovered and discussed by Robertson *et al.* (2008). In the present study, parsimony analysis recovered Bothrideridae as basal within this clade with an internal sister grouping of Cerylonidae and Discolomatidae, corroborating their relative placements in the Bayesian analysis of Robertson *et al.* (2008). Interestingly, both likelihood and Bayesian analyses in this study recovered Cerylonidae as the most basal member of this clade with a strongly supported (PP = 92) internal sister grouping of Bothrideridae and Discolomatidae. This placement was unexpected and represents a novel hypothesis of relationship within the CS.

Although *Akalyptoishion* was recently proposed for elevation to family-level by Lord (2008), in both the ML and Bayesian analyses *Akalyptoishion* was recovered as sister to the other latridiid included in this study, *Cartodere*. *Akalyptoishion* was recovered as sister to Alexiidae in the MP analysis. Lord (2008) provided morphological evidence for exclusion of *Akalyptoishion* from being placed within Alexiidae. However, a sister group relationship can not be ruled out based on the present work.

Anamorphinae

Most of the genera currently included in Anamorphinae were historically placed within Mycetaeinae. Anamorphinae is a relatively well-defined group of small, rounded, coccinellid-like fungus beetles first defined by Strohecker (1953) as the tribe Anamorphini within the Mycetaeinae and including the genera *Anamorphus*, *Micropsephus*, and *Rhymbomicrus*. Sasaji (1978) elevated this tribe to the subfamilial level as Mychotheninae, arguing that these genera form a unique assemblage based on their broadly, externally-closed mesocoxal cavities and the condition of the tentorium with anterior arms not fused medially. Pakaluk (1986) suggested that

Mychotheninae should probably be removed from the remainder of Endomychidae, and Sasaji (1987) subsequently elevated Mychotheninae to the family-level. This classification was followed by Sasaji (1990), but it was never widely accepted and more recent treatments continued placing it as a subfamily of Endomychidae (Ślipiński and Pakaluk 1991, Lawrence and Newton 1995, Tomaszewska 2000, Tomaszewska 2005, Skelley and Leschen 2002). Lawrence and Newton (1995) pointed out that Anamorphinae Strohecker, 1953 has priority for the subfamilial name and synonymized Mychotheninae Sasaji, 1978 under it. Pakaluk and Ślipiński (1995) erected a new subfamily, Acritosomatinae, to accommodate the genus *Acritosoma* from Peru, which they considered related to, but distinct from Anamorphinae. Tomaszewska (2000) later synonymized Acritosomatinae under Anamorphinae based on phylogenetic analysis of adult morphology.

Although previous phylogenetic analyses based on morphology (Tomaszewska 2000, Tomaszewska 2005) have consistently recovered Endomychidae as monophyletic with Anamorphinae placed basal, but within it, Hunt *et al.* (2007) and Robertson *et al.* (2008) provided the first phylogenetic hypotheses suggesting that Anamorphinae may lie outside of Endomychidae, recovering it as sister to Alexiidae and Corylophidae, respectively. Robertson *et al.* (2008) argued for the elevation of Anamorphinae to the family-level as preferable to transferring the subfamily from Endomychidae to Corylophidae. Interestingly, a recent study (Ślipiński *et al.* 2009) of Corylophidae based on adult and larval morphology recovered Anamorphinae as sister to Discolomatidae but with an unresolved relationship to Coccinellidae and Corylophidae.

Despite a much broader sampling of taxa within Endomychidae and inclusion of outgroup exemplars from all CS families, the placement of Anamorphinae could not be fully resolved. In this study, Anamorphinae was strongly supported as monophyletic, but was variably recovered as sister to Corylophidae+Coccinellidae (MP) or Coccinellidae only (ML, Bayesian). Nodal support for these proposed sister group relationships was conflicting between the two analyses with poor support in the MP analysis (BS = <50, BrS = 1) but relatively strong support in the Bayesian analysis (PP = 94). These results also suggest that Anamorphinae should be recognized as its own family, Anamorphidae, albeit with uncertain sister-group relationships to the remaining CS families.

Within Anamorphinae, *Symbiotes* was recovered as the basal most anamorphine genus in all three analyses. The placement of *Micropsephodes* varied between the analyses, resulting in the only major disagreement between topologies. Parsimony analysis placed *Micropsephodes* as sister to *Anamorphus*, while the ML/Bayesian analyses recovered it as sister to the remaining anamorphines (excluding *Symbiotes*, *Papuella*, *Clemmus* and *Mychothenus*). In addition, the node containing *Papuella*+*Clemmus*+*Mychothenus* collapsed to form a polytomy in the MP analysis, but was fully resolved in the ML and Bayesian analyses. The two anamorphine genera for which multiple taxa and terminals were included, *Anamorphus* and *Bystus*, were strongly supported as monophyletic, and *Bystus* was recovered as the most derived anamorphine genus in all three analyses.

Mycetaeinae and Eupsilobiinae

As discussed above, only a single species from each of these subfamilies was included in this analysis; therefore, it was impossible to test the monophyly of either of these subfamilies. Nonetheless, these two subfamilies were consistently recovered as sister taxa. Tomaszewska

(2005) also pointed out that these two subfamilies are united by the common larval morphological character of having a prostheca in the form of a rigid tooth.

In the MP analysis, the Mycetaeinae+Eupsilobiinae clade is the basal most clade within the Endomychidae, sister to the remaining endomychid lineages (excluding Anamorphinae). However, in the Bayesian analysis the same node includes Corylophidae, Mycetaeinae+Eupsilobiinae and the remaining endomychid subfamilies in an unresolved trichotomy. This node was fully resolved in the likelihood analysis with the Mycetaeinae+Eupsilobiinae clade being excluded from the PML+ SEEL clade. Instead, Corylophidae was recovered as the sister taxon to the PML + SEEL clade. The placement of these two subfamilies relative to the other endomychid subfamilies can not clearly be defined based solely on the results of this study as it varies slightly in all three analyses.

PML clade—Merophysiinae, Leiestinae and Pleganophorinae

The subfamilies Merophysiinae, Leiestinae and Pleganophorinae form a strongly supported clade (“PML clade”) that is sister to a clade identical in its constituency to the “Higher” endomychid subfamilies discussed by Tomaszewska (2005) and Robertson *et al.* (2008). This node is the most basal node that was consistently recovered within Endomychidae in all three analyses. The Pleganophorinae were recovered as the basal subfamily within this clade, and an internal sister group relationship between Merophysiinae and Leiestinae was recovered in all three analyses.

Tomaszewska (2000) suggested that the Merophysiinae and Pleganophorinae share the morphological feature of having the mesotrochantin concealed while the mesocoxal cavity is narrowly closed externally (as opposed to broadly closed externally, one of the synapomorphic characters for Anamorphinae). Tomaszewska (2005) later suggested that Merophysiinae was the most basal subfamily of Endomychidae, presenting morphological evidence suggesting possible relationships between Pleganophorinae and Anamorphinae and between Leiestinae and Mycetaeinae. Although this study corroborates Tomaszewska's observation that Merophysiinae is basal within Endomychidae *sensu stricto*, the internal relationships proposed by Tomaszewska (2005) are not supported by these results.

SEEL clade—Endomychinae, Stenotarsinae, Epipocinae and Lycoperdininae

The relationship between these four subfamilies has been repeatedly recovered using both morphology (Tomaszewska 2000, 2005) and molecular sequence data (Hunt *et al.* 2007, Robertson *et al.* 2008). Not surprisingly, this clade (the "SEEL" clade) was strongly supported as a monophyletic group in the present study as well. Members of this group of subfamilies are generally recognizable within the family by the presence of pseudotrimerous tarsi, a feature shared with Coccinellidae, as well as their much larger size compared to the "lower" Endomychidae. Tomaszewska (2005) recovered a clade comprising Endomychinae, Stenotarsinae and Epipocinae that was sister to the Lycoperdininae, and included an internal sister grouping of Stenotarsinae and Epipocinae. None of the analyses in the present study support this hypothesis of relationship. The Endomychinae+Stenotarsinae clade was consistently recovered as sister to the Epipocinae+Lycoperdininae clade, a pattern identical to that recovered by Robertson *et al.* (2008).

Endomychinae and Stenotarsinae were recovered as paraphyletic with respect to one another, with MP analysis recovering a sister group relationship between *Endomychus* (Endomychinae) and the *Danae*+*Saula* clade and the ML and Bayesian analyses recovering a sister group relationship between *Endomychus* and the *Chondria*+*Paniegena*+*Stenotarsus* clade. In all three analyses, the remaining Endomychinae (*Meilichius*, *Cyclotoma*) were recovered as sister to the Stenotarsinae+*Endomychus* clade. In the absence of a total evidence analysis that includes morphology and sequence data, we are unwilling to formally synonymize Stenotarsinae under Endomychinae, particularly in light of the results of this study which failed to recover the same relationship between the two subfamilies in all three analyses.

Of the genera for which multiple species and terminals were included, most endomychine and stenotarsine genera were recovered as monophyletic, including *Stenotarsus* (7 spp., 13 terminals). However, one notable exception involves the placement of *Saula*, which is primarily Indomalaysian in distribution, nested within *Danae*, which is primarily Afrotropical. There are insufficient data at present to evaluate the validity of this placement, but this relationship was recovered in all three analyses albeit with only modest nodal support for the internal relationship for the internal grouping (BS = 69, BrS = 8, PP = 100).

Lycoperdininae and Epipocinae were both monophyletic and sister to each other, although only Epipocinae was strongly supported in the parsimony analysis, while all three nodes (Epipocinae, Lycoperdininae, Epipocinae+Lycoperdininae) were strongly supported in the ML and Bayesian analyses (PP = 100). The relationship between these two subfamilies is supported by several adult features discussed and subsequently discarded as unconvincing by Tomaszewska (2005). However, this analysis, as well as that of Robertson *et al.* (2008), recovered strong support for the sister-group association of these two subfamilies.

Within Epipocinae, *Epipocus* was recovered as basal and sister to an internal grouping of *Anidrytus*+*Epopterus*. *Epopterus* was recovered nested within *Anidrytus* in all three analyses. The validity of *Epopterus* was first questioned by Strohecker (1997), based on the structure of the aedeagus. However, since this work was published posthumously, no formal action to synonymize them was taken. Early endomychid workers generally tended to group the larger, unicolorous taxa under the genus *Anidrytus* and the smaller, more colorful forms under the genus *Epopterus*. These results support the conclusion of Strohecker (1997) that the two genera should be synonymized.

Many of the internal nodes of Lycoperdininae were very poorly supported, largely resulting from a conflict in the placement of *Aphorista* and the *Acinaces*+*Beccariola*+*Corynomalus* clade relative to each other and to the remaining lycoperdinines. In all three analyses, *Mycetina* was recovered as the most basal genus, sister to the remaining Lycoperdininae. Tomaszewska (2005), based on adult and larval morphology, concluded that *Mycetina* belongs within the "*Amphix*-group" of Lycoperdininae closely allied with *Aphorista*. However, this suprageneric grouping was based on a single larval synapomorphy: labrum with apical margin sinuate or multidenticulate. Further, the relationship between *Mycetina* and *Aphorista* as one of the distinct lineages within the group were not supported by any synapomorphies, and there is no evidence from the present study to support such a grouping. The consistent placement of *Aphorista* and *Mycetina* outside of the "*Amphix*-group" make this group paraphyletic in all three analyses. However, the remaining members of the "*Amphix*-group" (*Beccariola*, *Acinaces* and *Corynomalus*) were recovered as a strongly supported monophyletic group in all three analyses.

The "*Amphisternus*-group" and "*Eumorphus*-group" of Tomaszewska (2005) were recovered as paraphyletic due to consistent recovery of *Trycherus* ("*Eumorphus*"-group) as sister to *Amphisternus* ("*Amphisternus*-group"), a strongly supported monophyletic grouping in all three analyses. The remaining members of the "*Eumorphus*-group" (*Encymon*, *Eumorphus*, *Indalmus*, *Ancylopus* and *Callimodapsa*) were always recovered as a monophyletic group. The basal placement of *Encymon* and *Eumorphus* within this group by Tomaszewska was confirmed by this analysis, as were the internal relationships between *Ancylopus*, *Callimodapsa* and *Indalmus*. Interestingly, of the three genera within the "*Eumorphus*-group" which included multiple species in this analysis, only *Encymon* was recovered as monophyletic.

Indalmus was never recovered as monophyletic due to *Indalmus lineellus*, an Australian endemic, which was consistently recovered as sister to *Ancylopus bisignatus*. The remaining two African species of *Indalmus* were recovered together in all three analyses. *Indalmus lineellus* was originally described by Chapuis (1876) and placed in its own genus *Mycella*, which was subsequently synonymized under *Indalmus* by Strohecker (1953). Strohecker (1979) later questioned that synonymy, suggesting that *Mycella* should probably be recovered as a valid genus with *I. lineellus* and *I. lachrymosus* transferred to it, reflecting the dissimilarity between these species and other Asiatic and African species of *Indalmus*. Based on these results, which corroborate the conclusions of Strohecker (1979), *Indalmus lineellus* is probably not a true *Indalmus*. *Mycella* should be recovered as a valid genus, which in the current analysis is placed sister to *Ancylopus*, and *I. lineellus* should be transferred to *Mycella.*

Similarly, *Eumorphus* was also not recovered as monophyletic in any of the analyses, despite being one of the most distinctive and recognizable of the lycoperdinine genera. This finding is the result of the variable placement of *E. drescheri*, which was recovered in an unresolved polytomy with *Callimodapsa* and *Indalmus* (in part) in the MP analysis but was fully resolved as sister to the *Indalmus*+*Callimodapsa*+*Ancylopus* clade in the ML and Bayesian analyses. In the absence of a total evidence analysis, the monophyly of *Eumorphus* can not be fully resolved based on this study. This placement is likely erroneous as there is strong adult and larval morphological evidence to support the monophyly of *Eumorphus*.

CONCLUSIONS

The Handsome Fungus Beetles, as currently defined, do not constitute a natural group. Endomychidae *sensu stricto* is comprised of two distinct lineages that are sister taxa, including seven subfamilies—the "lower" Endomychidae (i.e., Pleganophorinae, Merophysiinae and Leiestinae) and the "higher" Endomychidae (i.e., Stenotarsinae, Endomychinae, Epipocinae and Lycoperdininae).

The subfamily Anamorphinae is monophyletic but should not be classified within Endomychidae. Although there is some morphological evidence to corroborate this conclusion, we are hesitant to formally elevate it to the family-level based solely on molecular sequence data. Total evidence analyses that utilize both morphology and sequence data are needed before the placement of Anamorphinae can be clarified and formal action taken, if necessary. Furthermore, studies incorporating sequence data from the two subfamilies not included in this study (Danascelinae and Xenomycetinae) should be performed to rule out the possibility of a sister-group relationship between Anamorphinae and either Xenomycetinae or Danascelinae. Previous analyses based on morphology and including all 12 subfamilies (Tomaszewska 2000, Tomaszewska 2005) placed Xenomycetinae and Danascelinae sister to each other and together form a clade sister to the "higher" Endomychidae.

The placement of Mycetaeinae and Eupsilobiinae could be not resolved based on the present study. Parsimony analysis recovered them as basal within Endomychidae, sister to the remaining endomychid subfamilies as described above. However, the ML analysis recovered these two subfamilies outside of Endomychidae with Corylophidae (an outgroup taxon) as sister to the remaining endomychid subfamilies, while Bayesian analysis recovered them in an unresolved trichotomy with Corylophidae and the remaining endomychid subfamilies. Unfortunately, Mycetaeinae and Eupsilobiinae were each represented in the present study by a single species so they could not be tested for monophyly. The relationship between the Stenotarsinae and Endomychinae should be more thoroughly explored in the context of a total evidence analysis including all subfamilies and both morphological and molecular data before formal action can be taken to synonymize Stenotarsinae under Endomychinae.

This type of study is a necessary precursor to total evidence analyses that combine morphological (adult and larval) and molecular character data, allowing future exploration of ecological and behavioral evolutionary patterns within the family. With the reasonably-sized DNA library now available for Endomychidae, it is possible to develop a molecular clock to estimate approximate divergence times of the major endomychid lineages. Among the CS families, Endomychidae is among the best represented families in the fossil record, with 6 of the 12 extant subfamilies represented. Calibration of the endomychid molecular clock using fossils should not only provide greater accuracy in estimating relative divergence times within Endomychidae, but will have the downstream effect of providing initial estimates for the minimum divergence times of other CS families that share common ancestry with one or more endomychid lineages (e.g., Corylophidae, Coccinellidae).

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Table 4.1. Taxa included in this study with corresponding GenBank accession numbers for eight gene sequences (VID = BYU Tissue Voucher specimen identification number). The symbol "--" indicates missing sequences for those terminals included in the analysis.

				Mitochondrial genes				Nuclear genes			
Family	**Subfamily**	**Taxon**	**VID**	**12S**	**16S**	**COI**	**COII**	**18S**	**28S**	**H3**	**Wnt**
Erotylidae	Tritominae	*Pselaphacus nigropunctatus*	CO515	EU164568	EU164590	EU164678	EU164712	EU164627	EU164657	EU164744	--
Alexiidae	Alexiinae	*Sphaerosoma* sp. 1	CO899	GQ302083	GQ302155	GQ302372	GQ302434	GQ302220	GQ302290	GQ302496	--
Bothrideridae	Bothriderinae	*Bothrideres geminatus*	CO680	--	EU164600	GQ302326	--	EU145597	EU145658	EU164735	GQ30196
Cerylonidae	Ceryloninae	*Cerylon unicolor*	CO599	GQ302022	GQ302109	GQ302314	GQ302389	EU145600	EU145661	--	GQ30195
Coccinellidae	Coccinellinae	*Hippodamia convergens*	CO627	EU164553	EU164588	EU164681	EU164707	EU164617	EU164644	EU164743	GQ30195
Corylophidae	Corylophinae	*Clypastraea fasciata*	CO603	GQ302023	GQ302110	--	--	EU145622	EU145681	--	GQ30195
Discolomatidae	Aphanocephalinae	*Aphanocephalus* sp. 1	CO600	EU164554	EU164591	EU164675	EU164711	EU145628	EU145687	EU164734	--
Latridiidae	Latridiinae	*Akalyptoishion atrichos*	CO699	EU164560	--	EU164684	--	EU164620	EU164660	EU164741	GQ30197
Latridiidae	Latridiinae	*Cartodere constrictus*	CO596	EU164580	EU164606	EU164690	EU164714	EU164640	EU164655	EU164750	GQ30195
Endomychidae	Anamorphinae	*Anamorphus tenuicornis*	CO778	GQ302054	GQ302130	GQ302345	GQ302409	GQ302191	GQ302261	--	--
Endomychidae	Anamorphinae	*Anamorphus* sp. 1	CO649	GQ302025	--	--	--	EU145636	EU145694	--	--
Endomychidae	Anamorphinae	*Anamorphus* sp. 2	CO786	GQ302062	GQ302138	--	--	GQ302199	GQ302269	GQ302479	--
Endomychidae	Anamorphinae	*Bystus fibulatus*	CO782	GQ302058	GQ302134	GQ302349	--	GQ302195	GQ302265	GQ302476	GQ30198
Endomychidae	Anamorphinae	*Bystus pallidulus*	CO784	GQ302060	GQ302136	GQ302351	GQ302414	GQ302197	GQ302267	GQ302477	GQ30198
Endomychidae	Anamorphinae	*Bystus piceus*	CO319	GQ302008	GQ302095	GQ302305	GQ302384	EU145631	EU145689	--	GQ30195
Endomychidae	Anamorphinae	*Bystus piceus*	CO320	GQ302009	GQ302096	GQ302306	--	EU145632	EU145690	--	GQ30195
Endomychidae	Anamorphinae	*Bystus piceus*	CO321	GQ302010	GQ302097	GQ302307	GQ302385	GQ302164	GQ302234	--	GQ30195
Endomychidae	Anamorphinae	*Bystus piceus*	CO783	GQ302059	GQ302135	GQ302350	GQ302413	GQ302196	GQ302266	--	GQ30198
Endomychidae	Anamorphinae	*Bystus ulkei*	CO719	GQ302051	--	GQ302342	GQ302406	GQ302188	GQ302258	--	--
Endomychidae	Anamorphinae	*Bystus vestitus*	CO785	GQ302061	GQ302137	GQ302352	GQ302415	GQ302198	GQ302268	GQ302478	GQ30198
Endomychidae	Anamorphinae	*Bystus* sp. nov.	CO787	GQ302063	GQ302139	GQ302353	GQ302416	GQ302200	GQ302270	GQ302480	--
Endomychidae	Anamorphinae	*Catapotia* kuhneli	CO983	GQ302089	--	GQ302379	GQ302442	GQ302228	GQ302298	GQ302502	--
Endomychidae	Anamorphinae	*Clemmus minor*	CO713	GQ302047	--	GQ302338	--	GQ302185	--	--	--
Endomychidae	Anamorphinae	*Geoendomychus glaber*	CO974	GQ302084	GQ302156	GQ302373	GQ302435	GQ302221	GQ302291	GQ302497	--
Endomychidae	Anamorphinae	*Idiophyes brevis*	CO975	GQ302085	GQ302157	GQ302374	GQ302436	GQ302222	GQ302292	--	--
Endomychidae	Anamorphinae	*Micropsephodes lundgreni*	CO705	GQ302040	GQ302119	GQ302331	--	GQ302178	GQ302248	GQ302470	GQ30197
Endomychidae	Anamorphinae	*Mychothenus tropicalis*	CO715	GQ302049	GQ302126	GQ302340	GQ302404	--	GQ302256	--	--
Endomychidae	Anamorphinae	*Papuella birolecta*	CO804	GQ302076	GQ302150	GQ302366	GQ302428	GQ302213	GQ302283	GQ302490	GQ30200
Endomychidae	Anamorphinae	*Symbiotes gibberosus*	CO986	GQ302091	GQ302162	GQ302381	GQ302444	GQ302230	GQ302300	GQ302504	--
Endomychidae	Endomychinae	*Cyclotoma cingalensis*	CO980	GQ302087	--	GQ302377	GQ302439	GQ302225	GQ302295	GQ302500	--
Endomychidae	Endomychinae	*Endomychus biguttatus*	CO657	GQ302032	GQ302115	GQ302321	GQ302390	EU145643	EU145701	GQ302462	GQ30196
Endomychidae	Endomychinae	*Endomychus gorhami*	CO789	GQ302065	GQ302141	GQ302355	GQ302418	GQ302202	GQ302272	GQ302481	GQ30198
Endomychidae	Endomychinae	*Meilichius apicicornis*	CO800	GQ302073	GQ302147	GQ302363	--	GQ302210	GQ302280	GQ302488	GQ30199

Table 4.1. Taxa included, cont'd.

				Mitochondrial genes				Nuclear genes			
Family	**Subfamily**	**Taxon**	**VID**	**12S**	**16S**	**COI**	**COII**	**18S**	**28S**	**H3**	**Wnt**
Endomychidae	Epipocinae	*Anidrytus ephippium*	CO779	GQ302055	GQ302131	GQ302346	GQ302410	GQ302192	GQ302262	GQ302475	GQ30198
Endomychidae	Epipocinae	*Anidrytus nigricans*	CO654	GQ302029	GQ302113	GQ302319	--	EU145640	EU145698	GQ302459	--
Endomychidae	Epipocinae	*Anidrytus trinitatis*	CO780	GQ302056	GQ302132	GQ302347	GQ302411	GQ302193	GQ302263	--	GQ30198
Endomychidae	Epipocinae	*Epipocus tristis tristis*	CO790	GQ302066	GQ302142	GQ302356	GQ302419	GQ302203	GQ302273	GQ302482	GQ30199
Endomychidae	Epipocinae	*Epipocus gorhami*	CO791	GQ302067	GQ302143	GQ302357	GQ302420	GQ302204	GQ302274	GQ302483	GQ30199
Endomychidae	Epipocinae	*Epopterus testudinarius*	CO656	GQ302031	GQ302114	--	--	EU145642	EU145700	GQ302461	GQ30196
Endomychidae	Epipocinae	*Epopterus testudinarius*	CO792	GQ302068	GQ302144	GQ302358	GQ302421	GQ302205	GQ302275	--	GQ30199
Endomychidae	Eupsilobiinae	*Chileolobius cekalovici*	CO982	--	--	--	GQ302441	GQ302227	GQ302297	GQ302501	--
Endomychidae	Eupsilobiinae	*Chileolobius cekalovici*	CO1014	GQ302093	--	--	GQ302446	GQ302232	GQ302302	GQ302506	--
Endomychidae	Leiestinae	*Phymaphora californica*	CO987	GQ302092	--	GQ302382	GQ302445	GQ302231	GQ302301	GQ302505	--
Endomychidae	Leiestinae	*Phymaphora pulchella*	CO659	--	--	GQ302323	--	EU145645	EU145703	GQ302464	GQ30196
Endomychidae	Leiestinae	*Phymaphora pulchella*	CO806	GQ302077	--	GQ302367	GQ302429	GQ302214	GQ302284	GQ302491	GQ30200
Endomychidae	Leiestinae	*Rhanidea unicolor*	CO708	GQ302043	GQ302121	GQ302334	GQ302399	GQ302181	GQ302251	GQ302471	GQ30197
Endomychidae	Lycoperdininae	*Acinaces laceratus*	CO660	GQ302034	--	GQ302324	GQ302391	EU145646	EU145704	GQ302465	GQ30196
Endomychidae	Lycoperdininae	*Amphisternus vomeratus*	CO658	GQ302033	--	GQ302322	--	EU145644	EU145702	GQ302463	GQ30196
Endomychidae	Lycoperdininae	*Amphisternus* sp. 1	CO777	GQ302053	GQ302129	GQ302344	GQ302408	GQ302190	GQ302260	--	GQ30198
Endomychidae	Lycoperdininae	*Ancylopus bisignatus*	CO776	GQ302052	GQ302128	GQ302343	GQ302407	GQ302189	GQ302259	GQ302474	GQ30198
Endomychidae	Lycoperdininae	*Aphorista morosa*	CO781	GQ302057	GQ302133	GQ302348	GQ302412	GQ302194	GQ302264	--	--
Endomychidae	Lycoperdininae	*Aphorista vittata*	CO700	GQ302036	--	GQ302327	GQ302393	GQ302174	GQ302244	--	--
Endomychidae	Lycoperdininae	*Beccariola papuensis*	CO717	GQ302050	GQ302127	GQ302341	GQ302405	GQ302187	GQ302257	GQ302473	GQ30197
Endomychidae	Lycoperdininae	*Callimodapsa hova*	CO704	GQ302039	GQ302118	GQ302330	GQ302396	GQ302177	GQ302247	GQ302469	--
Endomychidae	Lycoperdininae	*Corynomalus laevigatus*	CO318	EU164558	EU164597	EU164679	EU164709	EU164639	EU164646	EU164731	GQ30195
Endomychidae	Lycoperdininae	*Corynomalus tarsatus*	CO661	GQ302035	GQ302116	GQ302325	GQ302392	EU145647	EU145705	GQ302466	GQ30196
Endomychidae	Lycoperdininae	*Corynomalus vestitus cinctus*	CO317	GQ302007	GQ302094	GQ302304	GQ302383	GQ302163	GQ302233	GQ302447	GQ30194
Endomychidae	Lycoperdininae	*Encymon bipustulatus*	CO081	GQ302006	--	GQ302303	--	AY310600	AY310659	--	GQ30194
Endomychidae	Lycoperdininae	*Encymon bipustulatus*	CO124	--	--	--	--	AY310608	AY310669	--	--
Endomychidae	Lycoperdininae	*Encymon gorhami*	CO648	GQ302024	--	GQ302315	--	EU145635	EU145693	--	GQ30195
Endomychidae	Lycoperdininae	*Encymon immaculatus*	CO788	GQ302064	GQ302140	GQ302354	GQ302417	GQ302201	GQ302271	--	GQ30198
Endomychidae	Lycoperdininae	*Eumorphus quadriguttatus*	CO794	GQ302069	GQ302145	GQ302359	GQ302422	GQ302206	GQ302276	GQ302484	GQ30199
Endomychidae	Lycoperdininae	*Eumorphus drescheri*	CO795	GQ302070	GQ302146	GQ302360	GQ302423	GQ302207	GQ302277	GQ302485	GQ30199
Endomychidae	Lycoperdininae	*Indalmus graphicus*	CO797	GQ302071	--	GQ302361	GQ302424	GQ302208	GQ302278	GQ302486	GQ30199
Endomychidae	Lycoperdininae	*Indalmus lineellus*	CO714	GQ302048	GQ302125	GQ302339	GQ302403	GQ302186	GQ302255	--	GQ30197
Endomychidae	Lycoperdininae	*Indalmus oblongulus*	CO798	GQ302072	--	GQ302362	GQ302425	GQ302209	GQ302279	GQ302487	GQ30199

Table 4.1. Taxa included, cont'd.

				Mitochondrial genes				Nuclear genes			
Family	**Subfamily**	**Taxon**	**VID**	**12S**	**16S**	**COI**	**COII**	**18S**	**28S**	**H3**	**Wnt**
Endomychidae	Lycoperdininae	*Lycoperdina ferruginea*	CO650	GQ302026	--	GQ302316	--	EU145637	EU145695	--	--
Endomychidae	Lycoperdininae	*Mycetina amabilis*	CO807	GQ302078	GQ302151	GQ302368	GQ302430	GQ302215	GQ302285	GQ302492	GQ30200
Endomychidae	Lycoperdininae	*Mycetina cyanipennis*	CO803	GQ302075	GQ302149	GQ302365	GQ302427	GQ302212	GQ302282	GQ302489	GQ30199
Endomychidae	Lycoperdininae	*Mycetina horni*	CO655	GQ302030	--	GQ302320	--	EU145641	EU145699	GQ302460	GQ30196
Endomychidae	Lycoperdininae	*Mycetina trimaculata*	CO802	GQ302074	GQ302148	GQ302364	GQ302426	GQ302211	GQ302281	--	GQ30199
Endomychidae	Lycoperdininae	*Trycherus fryanus*	CO703	GQ302038	GQ302117	GQ302329	GQ302395	GQ302176	GQ302246	GQ302468	GQ30197
Endomychidae	Lycoperdininae	*Trycherus nitidus*	CO810	GQ302081	GQ302153	GQ302370	GQ302433	GQ302218	GQ302288	--	GQ30200
Endomychidae	Merophysiinae	*Holoparamecus depressus*	CO976	--	GQ302158	GQ302375	GQ302437	GQ302223	GQ302293	GQ302498	--
Endomychidae	Merophysiinae	*Holoparamecus integer*	CO710	GQ302045	GQ302123	GQ302336	GQ302401	GQ302183	GQ302253	--	GQ30197
Endomychidae	Mycetaeinae	*Mycetaea subterranea*	CO984	GQ302090	GQ302161	GQ302380	GQ302443	GQ302229	GQ302299	GQ302503	--
Endomychidae	Pleganophorinae	*Trochoideus boliviensis*	CO711	GQ302046	GQ302124	GQ302337	GQ302402	GQ302184	GQ302254	--	GQ30197
Endomychidae	Pleganophorinae	*Trochoideus desjardinsi*	CO977	GQ302086	GQ302159	GQ302376	GQ302438	GQ302224	GQ302294	GQ302499	--
Endomychidae	Pleganophorinae	*Trochoideus goudoti*	CO809	GQ302080	GQ302152	GQ302369	GQ302432	GQ302217	GQ302287	GQ302494	GQ30200
Endomychidae	Pleganophorinae	*Trochoideus goudoti*	CO981	GQ302088	GQ302160	GQ302378	GQ302440	GQ302226	GQ302296	--	--
Endomychidae	Stenotarsinae	*Chondria armipes*	CO084	--	--	--	--	AY310609	AY310670	--	--
Endomychidae	Stenotarsinae	*Chondria armipes*	CO652	GQ302027	GQ302111	GQ302317	--	EU145638	EU145696	--	GQ30196
Endomychidae	Stenotarsinae	*Chondria nigra*	CO653	GQ302028	GQ302112	GQ302318	--	EU145639	EU145697	GQ302458	GQ30196
Endomychidae	Stenotarsinae	*Danae androgyna*	CO702	GQ302037	--	GQ302328	GQ302394	GQ302175	GQ302245	GQ302467	GQ30197
Endomychidae	Stenotarsinae	*Danae testacea*	CO709	GQ302044	GQ302122	GQ302335	GQ302400	GQ302182	GQ302252	GQ302472	GQ30197
Endomychidae	Stenotarsinae	*Paniegena baloghi*	CO831	GQ302082	GQ302154	GQ302371	--	GQ302219	GQ302289	GQ302495	--
Endomychidae	Stenotarsinae	*Saula japonica*	CO808	GQ302079	--	--	GQ302431	GQ302216	GQ302286	GQ302493	GQ30200
Endomychidae	Stenotarsinae	*Stenotarsus blatchleyi*	CO706	GQ302041	GQ302120	GQ302332	GQ302397	GQ302179	GQ302249	--	--
Endomychidae	Stenotarsinae	*Stenotarsus cuprivestis*	CO324	GQ302013	GQ302100	GQ302308	--	GQ302165	GQ302235	GQ302450	--
Endomychidae	Stenotarsinae	*Stenotarsus cuprivestis*	CO326	GQ302014	GQ302101	--	--	GQ302166	GQ302236	GQ302451	--
Endomychidae	Stenotarsinae	*Stenotarsus cuprivestis*	CO328	GQ302016	GQ302103	GQ302310	--	GQ302168	GQ302238	GQ302453	--
Endomychidae	Stenotarsinae	*Stenotarsus cuprivestis*	CO329	GQ302017	GQ302104	GQ302311	--	GQ302169	GQ302239	GQ302454	GQ30195
Endomychidae	Stenotarsinae	*Stenotarsus hispidus*	CO707	GQ302042	--	GQ302333	GQ302398	GQ302180	GQ302250	--	--
Endomychidae	Stenotarsinae	*Stenotarsus lemniscatus*	CO322	GQ302011	GQ302098	--	--	EU145633	EU145691	GQ302448	--
Endomychidae	Stenotarsinae	*Stenotarsus lemniscatus*	CO331	GQ302019	GQ302106	--	--	GQ302171	GQ302241	--	--
Endomychidae	Stenotarsinae	*Stenotarsus lemniscatus*	CO332	GQ302020	GQ302107	GQ302313	GQ302388	GQ302172	GQ302242	GQ302456	--
Endomychidae	Stenotarsinae	*Stenotarsus lemniscatus*	CO333	GQ302021	GQ302108	--	--	GQ302173	GQ302243	GQ302457	--
Endomychidae	Stenotarsinae	*Stenotarsus obtusus*	CO323	GQ302012	GQ302099	--	--	EU145634	EU145692	GQ302449	--
Endomychidae	Stenotarsinae	*Stenotarsus panamanus*	CO330	GQ302018	GQ302105	GQ302312	GQ302387	GQ302170	GQ302240	GQ302455	--
Endomychidae	Stenotarsinae	*Stenotarsus subtilis*	CO327	GQ302015	GQ302102	GQ302309	GQ302386	GQ302167	GQ302237	GQ302452	--

Table 4.2. Primers (5’ to 3’) used to amplify nuclear and mitochondrial gene sequences in the present study.

Gene	Primer	Direction	Sequence (5’- 3’)	Length	Ref.[1]
12S	*ai*	Forward	AAACTACGATTAGATACCCTATTAT	25	6
	bi	Reverse	AAGAGCGACGGGCGATGTGT	20	6
16S	*16SA*	Forward	CGCCTGTTTATCAAAAACAT	20	11
	16SB	Reverse	CTCCGGTTTGAACTCAGATCA	21	11
COI	*COI_F1*	Forward	CCTACTATGATTGGTGGTTTTGGTAATTG	29	3
	COI_F3	Forward	TGAGCTCACCATATGTATACAGTAGG	26	3
	Mtd6	Forward	GGAGGATTTGGAAATTGATTAGTTCC	26	7
	Ron	Forward	GGATCACCTGATATAGCATTCCC	23	7
	Jerry	Forward	CAACATTTATTTTGATTTTTTGG	23	7
	Nancy	Reverse	CCCGGTAAAATTAAAATATAAACTTC	26	7
	Pat	Reverse	TCCAATGCACTAATCTGCCATATTA	25	7
	COI_R3	Reverse	CAATGTAGAGCAAAAATAACTAAATC	26	3
COII	*F-leu*	Forward	TCTAATATGGCAGATTAGTGC	21	9
	R-lys	Reverse	GAGACCAGTACTTGCTTTCAGTCATC	26	9
18S	*1F*	Forward	TACCTGGTTGATCCTGCCAGTAG	23	2
	ai	Forward	CCTGAGAAACGGCTACCACATC	22	10
	a2.0	Forward	ATGGTTGCAAAGCTGAAAC	19	10
	b5.0	Reverse	TAACCGCAACAACTTTAAT	19	10
	bi	Reverse	GAGTCTCGTTCGTTATCGGA	20	10
	9R	Reverse	GATCCTTCCGCAGGTTCACCTAC	23	2
28S	*28S1a*	Forward	CCCSCGTAAYTTAGGCATAT	20	8
	28SA	Forward	GACCCGTCTTGAAGCACG	18	10
	4.5a	Forward	AAGTTTCCCTCAGGATAGCTG	21	9
	3A	Forward	AGTACGTGAAACCGTTCAGG	20	8
	28SB	Reverse	TCGGAAGGAACCAGCTAC	18	10
	5b	Reverse	CCACAGCGCCAGTTCTGCTTAC	22	9
	4b	Reverse	CCTTGGTCCGTGTTTCAAGAC	21	8
	7b1	Reverse	GACTTCCCTTACCTACAT	18	9
H3	*H3F*	Forward	ATGGCTCGTACCAAGCAGACVGC	23	5
	H3R	Reverse	ATATCCTTRGGCATRATRGTGAC	23	5
Wnt	*Wg1*	Forward	GARTGYAARTGYCAYGGYATGTCTGG	26	1
	Wg2a	Reverse	ACTICGCARCACCARTGGAATGTRCA	26	1

[1] References: 1) Brower & DeSalle 1998; 2) Giribet *et al.* 1996; 3) Kanzaki & Futai 2002; 4) Magnacca & Danforth 2007; 5) Ogden & Whiting 2003; 6) Ogden & Whiting 2005; 7) Simon *et al.* 1994; 8) Terry & Whiting 2005; 9) Whiting 2002; 10) Whiting *et al.* 1997; 11) Xiong & Kocher 1991.

Table 4.3. Results of Partition Homogeneity tests on 10 different partitions.

Partitions	***P* value**
Mitochondrial Ribosomal: 12S x 16S	0.66
Nuclear Ribosomal: 18S x 28S	0.01*
Mitochondrial Protein-Coding: COI x COII	0.01*
Nuclear Protein-Coding: H3 x Wnt	0.84
All Ribo: (12S+16S) x (18S+28S)	0.01*
All PC: (COI+COII) x (H3+Wnt)	0.01*
All Mito: (12S+16S) x (COI+COII)	0.01*
All Nuc: (18S+28S) x (H3+Wnt)	0.01*
Ribo-PC: (12S+16S+18S+28S) x (COI+COII+H3+Wnt)	0.01*
Mito-Nuc: (12S+16S+COI+COII) x (18S+28S+H3+Wnt)	0.01*

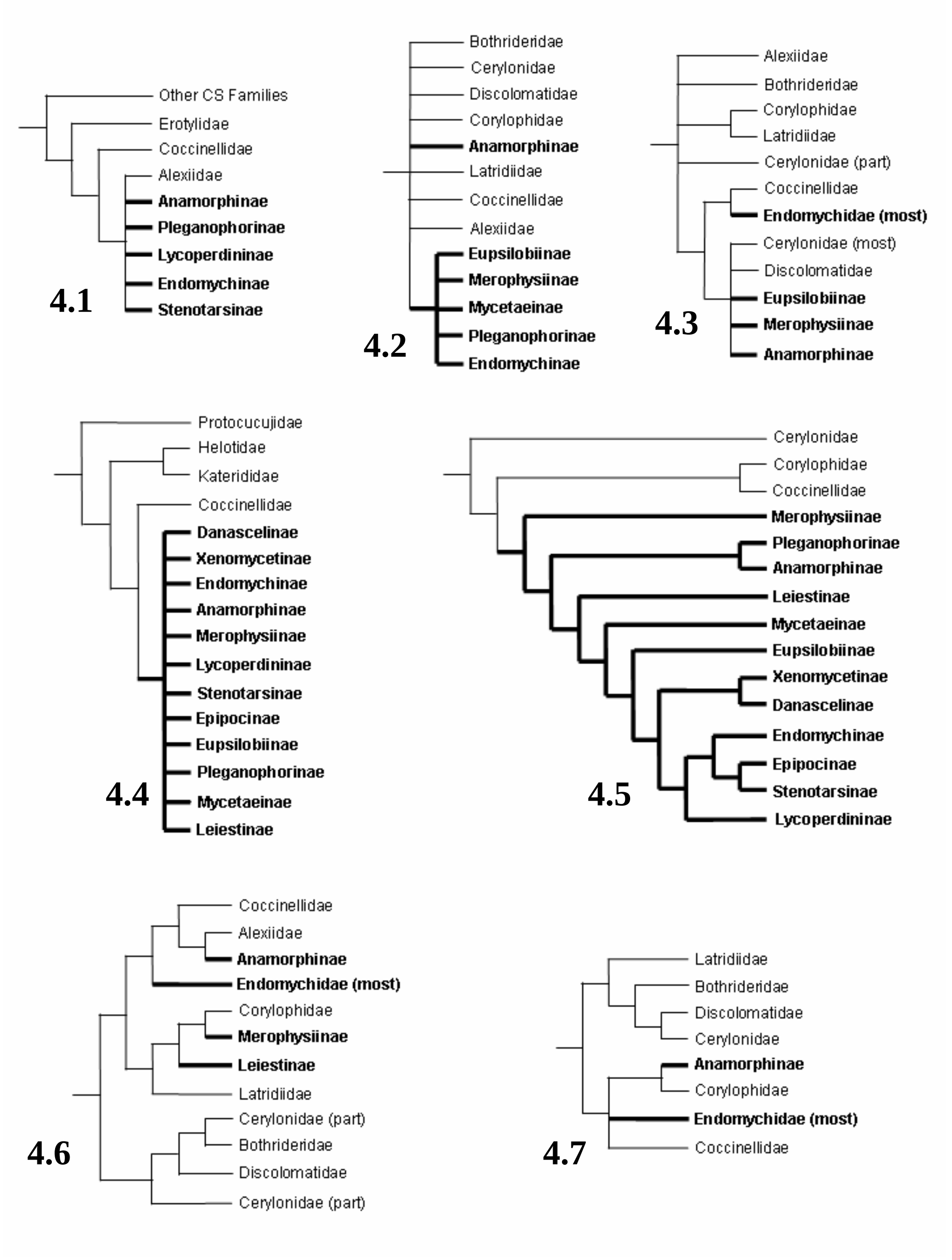
* Significant heterogeneity at the 99% confidence level

Table 4.4. Genes targeted for amplification and included in this study. Number of Parsimony-Informative Characters (PIC) determined using WinClada.

Genes	# of Aligned bp	% of Alignment	# of Unambiguous	% of Unambiguous	# of PIC	% of PIC
12S	378	4.2%	324	4.5%	203	7.8%
16S	529	5.8%	528	7.3%	255	9.8%
18S	1995	22.0%	1869	25.9%	266	10.2%
28S	3156	34.7%	2181	30.2%	658	25.3%
COI	1388	15.3%	841	11.7%	386	14.9%
COII	736	8.1%	717	9.9%	449	17.3%
H3	390	4.3%	326	4.5%	133	5.1%
Wnt	514	5.7%	431	6.0%	248	9.5%
Total	**9086**		**7217**		**2598**	

Table 4.5. Nonparametric bootstrap (BS) values, Bremer support (BrS) values, and partitioned Bremer support (pBrS) values for all nodes from the combined MP topology generated in T.N.T. Partition Bremer supports have been rounded to the nearest whole number.

			pBrS											**pBrS**							
Node	**BS**	**BrS**	**12S**	**16S**	**18S**	**28S**	**COI**	**COII**	**H3**	**Wnt**	**Node**	**BS**	**BrS**	**12S**	**16S**	**18S**	**28S**	**COI**	**COII**	**H3**	**Wnt**
1	100	100+	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	47	69	8	7	7	10	-15	-17	2	14	1
2	<50	2	8	1	8	-29	-5	8	6	5	48	<50	3	2	0	2	-4	1	1	0	1
3	<50	5	4	-5	12	-36	-3	26	-2	9	49	100	47	6	27	4	10	0	0	0	0
4	<50	2	8	1	8	-29	-5	8	6	5	50	83	7	9	5	9	-19	-9	8	3	1
5	<50	1	15	6	21	2	-15	-49	4	17	51	53	4	16	5	18	-2	-16	-39	6	16
6	<50	2	8	1	8	-29	-5	8	6	5	52	100	31	2	8	4	4	5	1	6	1
7	<50	3	13	21	6	9	-20	-41	12	3	53	100	48	0	9	7	0	8	16	8	0
8	<50	1	15	6	21	2	-15	-49	4	17	54	50	6	9	2	7	-28	-1	7	9	1
9	<50	4	13	22	6	9	-20	-41	12	3	55	98	12	18	12	21	9	-23	-50	6	19
10	99	53	2	10	15	22	-10	-1	4	11	56	<50	1	0	0	0	-2	0	1	2	0
11	<50	3	13	22	6	9	-20	-42	12	3	57	100	18	0	3	0	1	0	1	8	5
12	63	9	0	0	2	-1	6	1	1	0	58	56	8	8	1	7	-24	-5	4	11	6
13	<50	1	15	6	21	2	-15	-49	4	17	59	100	58	2	4	5	14	0	2	22	9
14	<50	5	-2	4	-7	13	-2	0	-5	4	60	100	48	2	7	1	14	1	3	8	12
15	<50	3	15	12	13	5	-19	-40	9	8	61	53	6	4	4	3	-12	-11	1	15	2
16	100	140	6	23	7	23	28	3	22	28	62	100	66	19	26	28	11	-35	-38	34	21
17	<50	1	15	6	21	2	-15	-49	4	17	63	100	40	3	2	14	-17	-1	28	2	9
18	99	33	12	7	36	8	-9	-42	16	5	64	100	43	16	16	19	31	-17	-43	6	15
19	94	12	1	2	4	-5	0	1	9	0	65	68	5	0	1	0	1	2	0	0	1
20	100	45	20	37	15	30	-20	-41	14	0	66	<50	5	3	4	0	-6	1	-1	5	-1
21	92	15	3	5	8	19	-10	-4	0	-6	67	100	14	0	3	0	10	-3	-1	1	4
22	100	91	0	19	28	9	16	18	1	0	68	<50	2	8	1	8	-29	-5	8	6	5
23	100	31	15	11	26	13	-15	-49	5	25	69	100	21	4	-5	28	-36	-3	26	-2	9
24	99	21	10	5	11	-18	-4	8	7	2	70	98	18	4	12	2	-1	-5	3	4	-1
25	100	51	6	-4	13	-28	0	43	3	18	71	93	15	1	-2	2	17	-4	0	1	0
26	58	4	14	10	13	1	-17	-33	8	8	72	<50	1	2	4	2	1	-5	-2	2	-3
27	<50	2	1	1	-1	1	5	-6	-1	2	73	<50	2	0	1	-1	-6	-1	0	6	3
28	<50	6	0	6	-8	16	-5	-1	-3	1	74	99	21	9	16	13	-22	-16	5	13	3
29	100	74	8	35	15	4	-5	6	6	5	75	<50	3	3	4	1	-3	-2	-1	3	-2
30	<50	1	15	6	21	2	-15	-49	4	17	76	94	14	3	3	0	3	-2	0	4	3
31	<50	4	12	1	15	12	-16	-46	12	14	77	<50	2	14	6	16	21	-23	-50	11	7
32	99	33	1	-10	11	34	-8	-2	4	3	78	100	45	7	12	15	-13	-13	25	3	9
33	100	84	10	25	9	23	-10	18	12	-3	79	81	7	1	2	0	-1	3	2	0	0
34	99	26	2	5	3	-9	12	1	9	3	80	<50	2	3	4	1	-4	-2	-1	3	-2
35	92	23	14	10	12	0	-18	-20	17	8	81	<50	4	13	8	17	-7	-12	-30	4	11
36	100	53	4	13	9	4	9	5	2	7	82	100	14	4	-5	21	-36	-3	26	-2	9
37	91	19	17	15	24	0	-11	-48	5	17	83	99	5	0	0	5	0	0	0	0	0
38	100	97	14	21	18	30	12	-13	8	7	84	92	9	4	-5	16	-36	-3	26	-2	9
39	99	17	7	2	8	-23	4	8	6	5	85	66	4	0	1	4	-1	0	0	0	0
40	94	23	20	13	13	-6	-8	-37	9	19	86	100	14	13	22	17	9	-20	-42	12	3
41	51	12	8	-2	10	-18	-10	12	0	12	87	73	3	8	5	11	-1	-7	-21	3	5
42	100	63	5	3	3	33	-1	10	11	-1	88	100	8	0	0	8	0	0	0	0	0
43	86	14	8	10	9	-15	-16	-2	12	8	89	78	10	14	6	18	26	-16	-52	0	14
44	<50	6	4	4	1	12	-9	-17	5	6	90	81	16	2	2	0	3	3	1	1	4
45	100	63	4	7	10	13	-2	3	8	20	91	<50	4	10	0	9	-18	-6	-2	5	6
46	88	13	21	14	28	8	-28	-53	2	21	92	100	70	4	5	0	26	9	19	7	0
												Total pBrS		661	650	904	-8	-567	-794	538	590



Figures 4.1-4.7. Previous hypotheses of relationship within Endomychidae and between endomychid lineages and the remaining Cerylonid Series families. Clades corresponding to endomychid taxa are highlighted in bold. Taxon names have been updated to reflect their current classification. **4.1)** Strohecker (1953); **4.2)** Sasaji (1987); **4.3)** Ślipiński & Pakaluk (1991); **4.4)** MP analysis of adult morphology by Tomaszewska (2000b); **4.5)** MP analysis of combined adult and larval morphology by Tomaszewska (2005); **4.6)** Bayesian analysis of 18S, 16S and COI in Hunt *et al.* (2007); **4.7)** Bayesian analysis of 18S and 28S genes by Robertson *et al.* (2008). Figures 4.1-4.3 are intuitive relationships only and not based on any formal analysis. Figures 4.4-4.7 represent tests of relationship using modern phylogenetic methods.

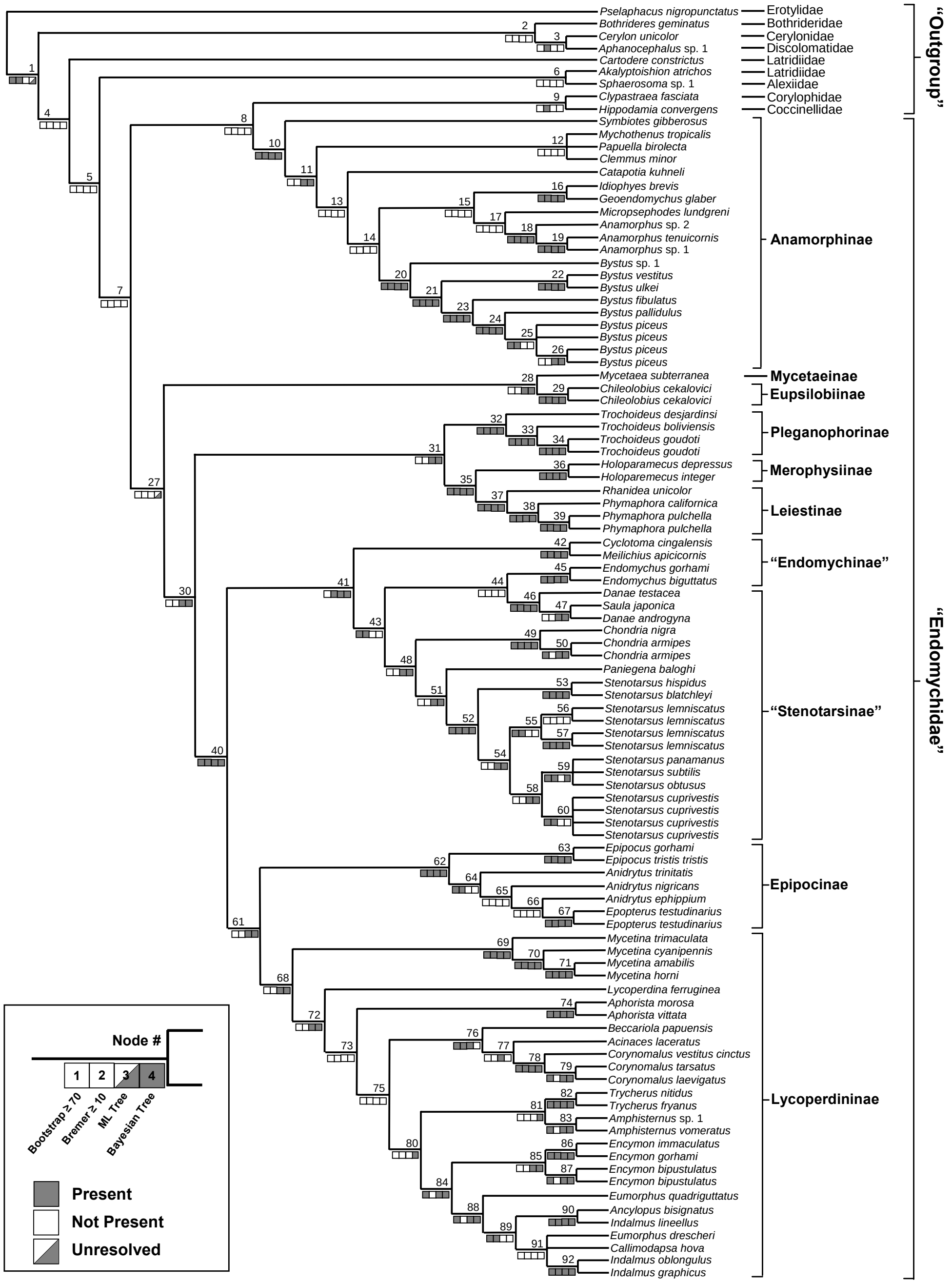


Figure 4.8. Strict consensus of 12 most parsimonious trees recovered in T.N.T. using the concatenated static alignments of 8 genes. Length = 23783, CI = 0.22, and RI = 0.55. Taxonomic names in quotation marks represent paraphyletic taxa. Shaded or unshaded boxes beneath each node reflect the general amount of branch support for that node. The first box reflects the bootstrap support value with full shading indicating a bootstrap value ≥70. The second box reflects the Bremer support for that node with full shading indicating Bremer support ≥10. The 3rd and 4th boxes indicate the presence or absence of that node in the ML tree and the Bayesian tree, respectively. Nodes are numbered, and exact bootstrap, Bremer, and partitioned Bremer support values are given in Table 4.5.

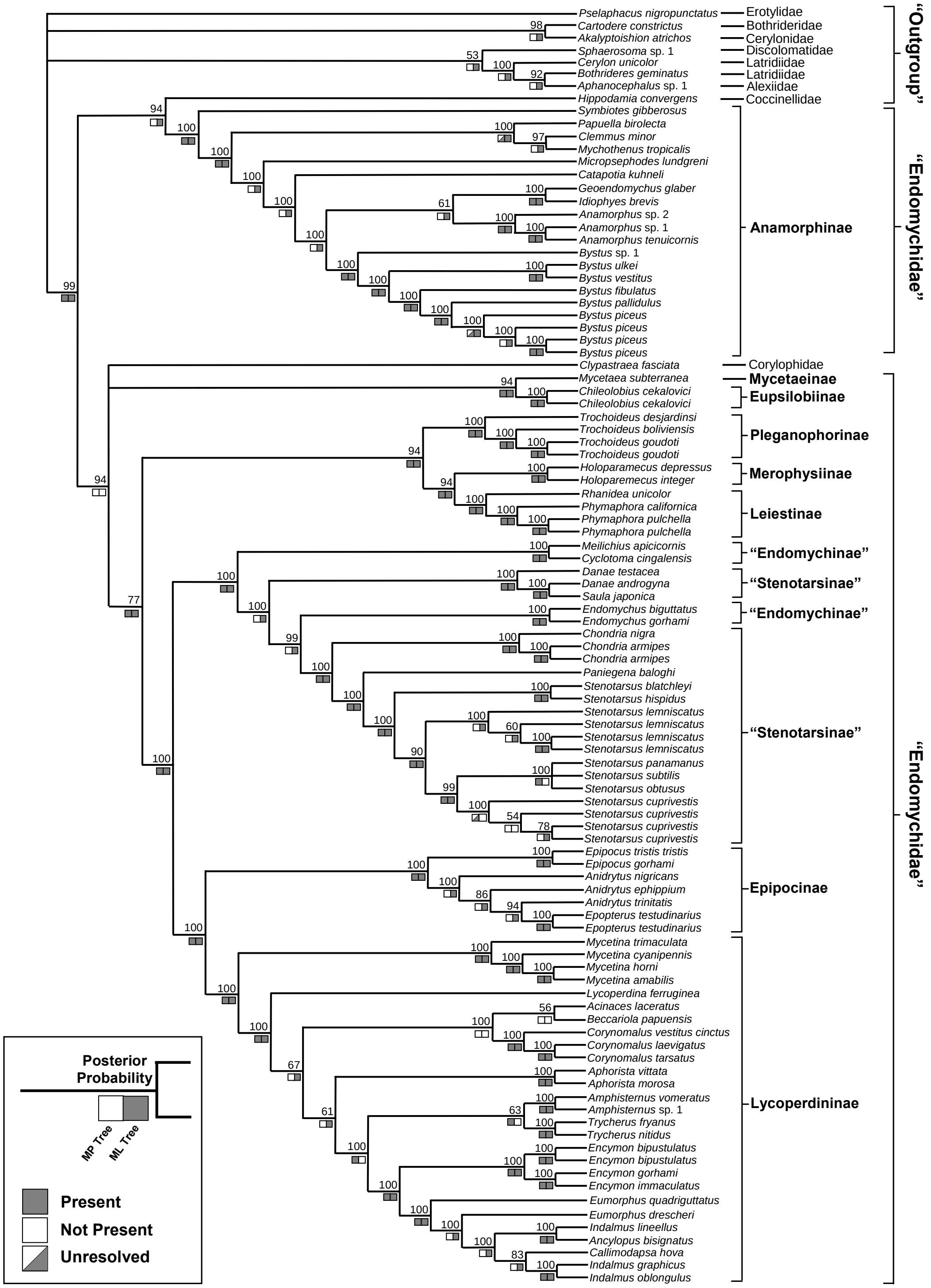
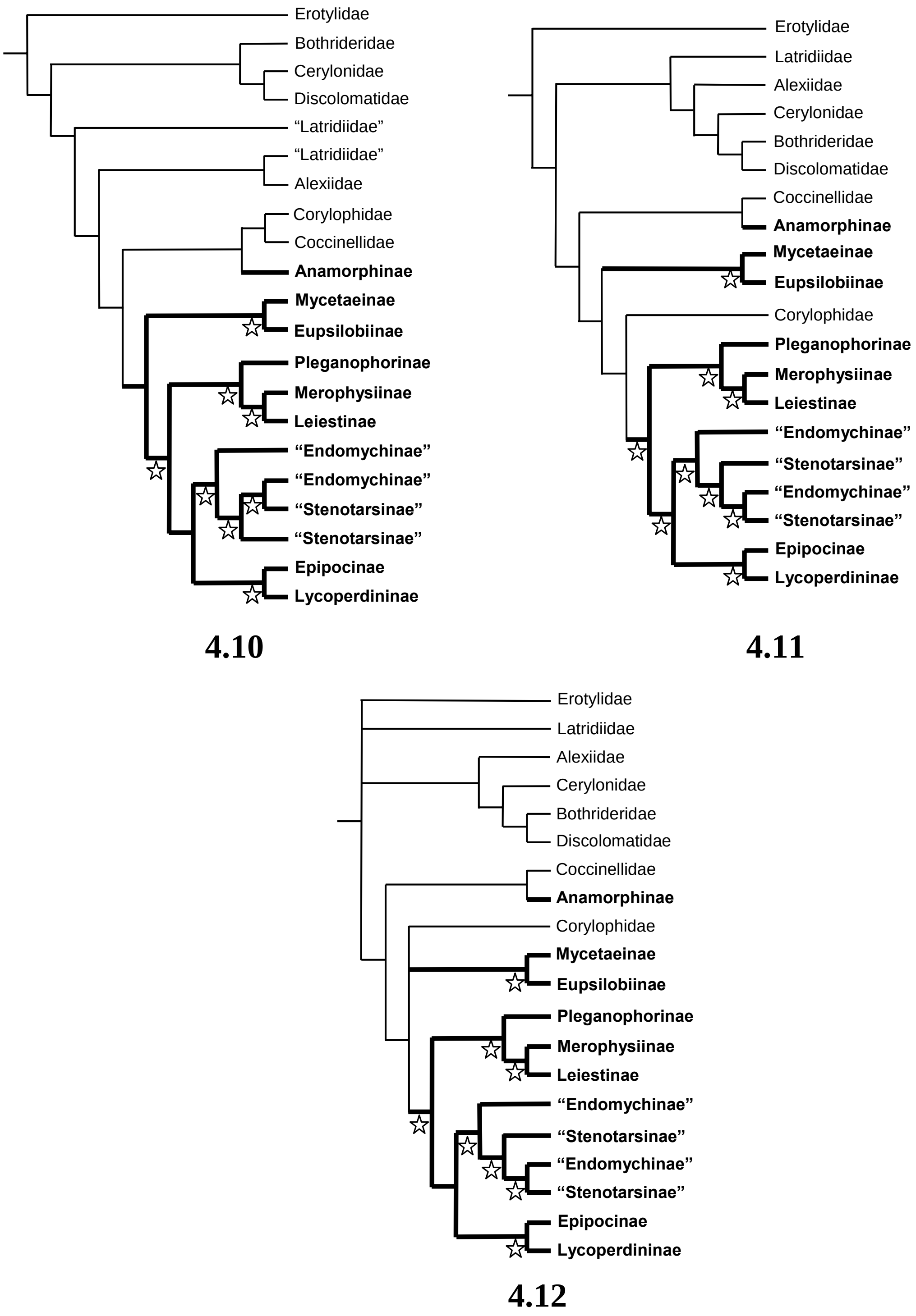


Figure 4.9. Bayesian analysis tree generated by taking a 50% majority rule consensus of 30,000 trees remaining after discarding the "burn-in" (first 25% of trees in each of 4 separate runs). Taxonomic names in quotation marks represent paraphyletic taxa. Posterior probabilities are indicated for each node. The boxes beneath the node indicate the presence (shaded) or absence (unshaded) of that node in the MP tree and the ML tree, respectively.



4.10 **4.11**

4.12

Figures 4.10-4.12. Summary of hypotheses of relationship recovered for the major endomychid lineages in the present study. Current endomychid clades are highlighted in bold. Taxonomic names in quotation marks represent paraphyletic taxa. Nodes common to all three hypotheses are indicated (stars). **4.10)** Maximum parsimony; **4.11)** Maximum likelihood; **4.12)** Bayesian analysis.

CHAPTER 5

A STUDY OF ADULT MORPHOLOGY IN *BYSTUS PICEUS* (GORHAM), 1887-99 (COLEOPTERA: ENDOMYCHIDAE: ANAMORPHINAE)[1]

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[1] Shockley, F.W. and J.V. McHugh. To be submitted to *Annales Zoologici (Warszawa)*.

ABSTRACT

Based on recent family-level phylogenetic analyses of Endomychidae which consistently recover Anamorphinae as independent from the remaining endomychid lineages, extensive morphological studies looking for additional evidence to support the removal of Anamorphinae from Endomychidae are necessary. Many anamorphine genera are badly in need of revision. As more species are discovered, original species descriptions become less reliable for differentiating between morphologically similar species, and detailed illustrations are often lacking entirely. One exemplar species of the New World genus *Bystus*, *B. piceus* (Gorham), is completely described and illustrated, including all primary external and internal anatomical features. This study serves as an important anatomical reference for discussing and homologizing the morphology of Anamorphinae and Endomychidae, and morphological features are discussed in light of what is known in other beetle taxa.

Key Words: Endomychidae, Anamorphinae, *Bystus*, morphology, anatomy.

INTRODUCTION

The family Endomychidae currently includes 130 genera and 1782 species and subspecies arranged within 12 subfamilies (Shockley *et al.* 2009a). The family is represented in all biogeographical regions of the world, but it is particularly speciose in the tropics. The family as a whole is generally considered to be mycophagous; however, predaceous and phytophagous members are also known (Shockley *et al.* 2009b). In recent years, several significant treatments of endomychid morphology have been published which greatly expand our knowledge of the anatomy of the family (Tomaszewska 2000a, 2000b, 2005). The subfamily Anamorphinae is of particular interest because recent phylogenetic studies have yielded conflicting hypotheses regarding the placement of this subfamily in relation to the remaining endomychid subfamilies, with morphology suggesting it is within Endomychidae (Tomaszewska 2000a, 2005) and molecular sequence data suggesting that it is not (Hunt *et al.* 2007, Robertson *et al.* 2008).

Unfortunately, even though previous studies included exemplars from Anamorphinae, the subfamily remains poorly known and inadequately described in the literature. Thus, additional studies are needed to clarify the morphology before attempting to resolve the subfamily's phylogenetic relationship to other endomychid subfamilies. Anamorphines have historically been diagnosed by a combination of the following features: 3-3-3 or 4-4-4 tarsi; claws simple/modified; tarsi linear; tentorium with anterior arms not fused medially; antenna 9-11 segmented; procoxal cavity open posteriorly; mesocoxal cavity closed outwardly by the meso & metasterna; frontoclypeal suture distinct; abdomen with six visible sternites; and elytral epipleuron flat, wide. In fact, the combination of these characters led some workers to conclude that anamorphines are so unusual that they should be treated separately from other endomychids (Sasaji 1978, 1987, 1990).

Extensive morphological studies on individual species are becoming increasingly rare in the literature in light of comparative and phylogenetic studies (for examples see Straus-Durckheim 1828 [*Melolontha vulgaris* (Hanneton)], Hopkins 1909 [*Dendroctonus valens* LeConte], Doyen 1966 [*Tenebrio molitor* L.], and McHugh *et al.* 1997 [*Megalodacne heros* (Say)]). However, a complete study of a single taxon often serves as an important reference point for subsequent larger-scale projects and provides for a much more thorough exploration of the morphological characters before attempting a search for phylogenetic patterns that would explain how those characters evolved.

Bystus Guérin–Méneville is an ideal candidate to serve as a morphological reference for Anamorphinae because of its high diversity (18 species), relatively large size (compared to other anamorphines), and shared suite of diagnostic characters for Anamorphinae. Unfortunately, incomplete or inaccurate descriptions in the literature necessitate a detailed morphological study before any subsequent descriptive work could be attempted on *Bystus* or any phylogenetic work on Anamorphinae. *Bystus piceus* (Gorham) was selected for this study based on: 1) the availability of several large series of fresh specimens of both sexes for dissection; 2) its average size and typical coloration compared to other *Bystus* spp.; and 3) its distribution (Costa Rica & Panama), which lies near the geographic center of the distribution of *Bystus*.

Since this work is a morphological study, the text accompanying the images and illustrations has been expanded from the typical telegraphic style of taxonomic publications. A formal redescription of the genus is provided in the taxonomic revision of *Bystus* (Chapter 6).

TAXONOMIC HISTORY

General diagnoses for the genus *Bystus* (and its junior synonym *Rhymbus*) and taxonomic descriptions of its constituent species were provided by Guérin–Méneville (1857), Gerstaecker (1858), Crotch (1873), Gorham (1873, 1875, 1887-99, 1898), Weise (1903), Strohecker (1957), and Leschen and Carlton (1993). Guérin–Méneville (1857) erected the genus *Bystus* for a distinct new species, *B. coccinelloides*, collected by Dejean and Reiche from Colombia. Gerstaecker (1858) later erected the genus *Rhymbus* for three species: *R. hemisphaericus* (from Costa Rica), *R. apicalis* (from Colombia) and *R. pallidulus* (from Brazil). Despite the general acknowledgement that *Bystus* had priority over *Rhymbus*, subsequent workers continued using *Rhymbus* for new species descriptions, and listed it in most subsequent catalogues (*e.g.*, Blackwelder 1945; Blatchley 1910; Bruch 1914; Csiki 1910; Fattig 1937; Guérin 1953; Leng 1920, 1927, 1933; Leng & Mutchler 1914). Strohecker (1953) formally synonymized *Rhymbus* under *Bystus*.

Rhymbus piceus was described by Gorham (1887-99) from a small series of eight specimens collected by Champion from the caldera of Volcan de Chiriqui in Panama. The description consisted of a discussion of color, punctation of the elytra and the general shape of the lateral sulci, accompanied only by a small dorsal habitus illustration. Strohecker (1953) used *B. piceus* as the model for his redescription of *Bystus*; however, subsequent examination of Gorham’s type series and fresh specimens collected by the authors showed that some of Strohecker's figures were inaccurate and several key anatomical features were not illustrated at all, necessitating the present study.

BIOLOGY

The mandibles of many anamorphines, including *Bystus*, have a bifid apical incisor lobe, a brushy prostheca and a well-developed mola, making them well-adapted for feeding on spores (Pakaluk 1986, Lawrence 1991, Leschen and Carlton 1993, Tomaszewska 2000a, Skelley and Leschen 2002). *Bystus* species are exophagous as adults and larvae, preferring to feed externally on their host fungi, and are often collected from the underside of old basidiocarps of bracket fungi. Whether they are feeding on the spores of the basidiocarps themselves or on microfungi growing on the decaying fruiting bodies remains unknown. Shockley *et al.* (2009b) reported *Bystus* from seven different genera of basidiomycete and ascomycete fungi, mostly encrusting fungi on logs or standing dead trees.

Like many other endomychids, the digestive system of *Bystus* includes delicate gastric caecae which often contain endosymbiotic bacteria and yeasts. McHugh *et al.* (1997) speculated that endosymbionts in the gastric caecae of *Megalodacne heros* (Erotylidae) were playing a role in fungal tissue digestion. Shockley *et al.* (2009b) suggested a similar function in endomychids, listing all known yeast species recovered from endomychids, including several from *B. piceus*. The digestive enzymes of mycophagous beetles are usually directed towards starch (a storage polysaccharide) and collagen (an important animal protein) and display very little enzymatic activity against chitin (the primary structural polysaccharide of fungi) (Martin *et al.* 1981). This finding suggests that chitin may not be nutritionally important for fungivores, but whether the enzymes are produced by the beetles or their gut endosymbionts remains unknown.

Given the inconsistent treatment of adult morphology in the literature, it is not surprising that the immature stages of *Bystus* also are poorly known. *Bystus decorator* Leschen & Carlton is the only species for which the pupal and egg stages have been described (Leschen and Carlton 1993). Descriptions and/or illustrations were provided for the larvae of *B. decorator* (Leschen and Carlton 1993), *B. pallidulus* (Costa *et al.* 1988) and *B. ulkei* (Crotch) (Boving and Craighead 1930). Another *Bystus* species was illustrated by Lawrence (1991), but the species was left undetermined. However, the caption accompanying the illustration noted that the specimen was collected from Barro Colorado Island (BCI), Panama. Since the most common species of the appropriate size class collected on BCI is *B. piceus*, this dorsal habitus likely represents that species.

MATERIALS AND METHODS

Field-collected adults of *Bystus piceus* were identified by comparison with specimens in the Strohecker collection at the Florida State Collection of Arthropods (FSCA) and later confirmed by direct comparison to the Gorham syntypes borrowed from the Natural History Museum, London (BMNH). Voucher specimens are deposited in the University of Georgia Collection of Arthropods (UGCA). Collection data for these specimens are: COSTA RICA: Heredia Prov.; La Selva Biological Station, 38m; 10°25’55”N, 84°00’35”W; 15-16.VI.2004, F. Shockley; Hand collected from fungus.

Specimens were collected into Dietrich’s solution (80 mL distilled water, 15 mL 95% ethanol, 6 mL formalin, 1 mL glacial acetic acid). Many of these specimens were later dissected in 75% EtOH. Prior to disarticulation, specimens were relaxed in a warm 10% solution of KOH and then teased apart. Removal of mouthparts often led to damage to the head capsule, so the cleared head capsule was drawn first with mouthparts *in situ* and then mouthparts were removed for individual examination and illustration. Fully disarticulated specimens were placed in a liquid mount of glyerine on a deep-well depression slide for examination and storage. Partially dissected specimens were stored in 75% EtOH for subsequent viewing.

The reproductive system was first examined and illustrated *in situ* and then the genital capsules excised and dissected. In several specimens, the median lobe was stained (500 mL distilled water, 25 mL 10% hydrochloric acid, and 1 gram of acid fuschin) to allow examination and illustration of the smaller, delicate internal structures associated with the internal sac. For several specimens, the internal sac was everted for examination. The median lobe was placed in a warm solution of soapy water (9 mL of distilled water, 1 mL of Ultra Dawn® dishwashing liquid). The internal sac was then everted using hook-tipped pins, one holding the base of the median lobe while the other was used to gently squeeze the lobe from base to apex. Once everted, the internal sac was photographed and then fixed using the method described in Nation (1983). Tissues were transferred to 1% glutaraldehyde in 0.1 M sodium cacodylate buffer (pH 7.0) for 5 min, washed in distilled water for 5 min., and then dehydrated through an ethanol series (25%, 75%, 95% and 100% (three washes) at 5 min. each). Finally, the internal sac was immersed in hexamethyldisilazane (Applied Sciences, Inc.) for 5 min. and then sputter-coated for imaging with an SEM.

All SEM micrographs were taken on a Zeiss 1450EP digital environmental scanning electron microscope (Carl Zeiss MicroImaging, Inc., One Zeiss Drive, Thornwood, NY 10594) with a variable pressure sample chamber that allows imaging from high vacuum mode to 2,600 Pa and equipped with a cold stage, water injection system, and an Oxford INCA EDS system (Oxford Instruments X-Ray Technology, Inc., 275 Technology Circle, Scotts Valley, CA 95066). For some structures (*e.g.*, mouthparts, elytra and wings), a second set of micrographs were taken at higher magnificiation after sputter-coating with gold-palladium using an SPI Module sputter coater (Structure Probe, Inc., 569 East Gay Street, West Chester, PA 19380).

Non-SEM photographs were taken using a Canon EOS-1DS digital camera attached to an ML-1000 Digital Imaging System (Microptics, Inc., Ashland, VA). Line drawings were made using either a Leica MZ8 stereomicroscope (< 50x magnification) or a Leitz Labor Lux S laboratory microscope (> 50x magnification), each fitted with a camera lucida. Illustrations have been labeled to aid the identification of primary structures. Abbreviations used in the figures are explained in Supplemental Material 5.1.

MORPHOLOGY

General Description (Figs 5.1-5.3, 5.61). The body is oval in dorsal view and strongly convex, measuring 3.0-3.2 mm long, 2.7-3.0 mm wide, and 1.6-1.9 mm high. The head is retracted into the prothorax and deflected downward (hypognathous). When viewed dorsally, the head is almost completely concealed by the pronotum. The dorsum is shiny and smooth and covered with dense, fine punctures, each of which bears a single, long erect pale-colored seta. The setae on the head are shorter than those on the pronotum and elytra and are conspicuously directed mesad, whereas the setae on the pronotum and elytra are typically directed posteriad and/or laterad. Dorsal surfaces are light yellowish or reddish brown in color in teneral specimens and dark brown in mature specimens. The venter has a vestiture of short, stout, decumbent setae. Ventral surfaces are generally dark brown; however, the pronotal hypomera, elytral epipleura, and the appendages are generally lighter in color. The antennal club is black while the remaining antennal segments are reddish brown.

Head Capsule (Figs 5.4-5.8, 5.10-5.11). Snodgrass (1928, 1947, 1960) and Duporte (1957) reviewed the evolutionary origins of the sutures and internal inflections of the insect head. Stickney (1923) included two endomychids, *Phymaphora pulchella* Newman (Leiestinae) and *Endomychus biguttatus* Say (Endomychinae), in an extensive study of the head capsule of Coleoptera. The head capsules of four anamorphines, *Symbiotes gibberosus* (Lucas), *Mychothenus asiaticus* Sasaji, *Micropsephodes serraticornis* Champion and *Erotendomychus lawrencei* Tomaszewska, were illustrated by Tomaszewska (2000a), and, not surprisingly, the head capsule of *B. piceus* agrees more with these latter taxa in general appearance. The head capsule of *B. piceus* is broadly round and almost trapezoidal when viewed dorsally or ventrally

(Figs. 5.4-5.5), and it is weakly compressed dorsolaterally when viewed anteriorly or posteriorly (Figs. 5.6-5.7). In lateral view (Fig. 5.7), the head capsule is relatively flat ventrally but dorsally is steeply angled from anterior to posterior. The compound eyes are large, oval, and finely faceted with ~250-300 hexagonal facets.

The head capsule of *B. piceus* lacks antennal grooves. The antennal socket bears along its anteroventral margin a small, acute antennifer, giving the socket a somewhat heart-shaped appearance. The antennal sockets are partially obscured from above by a short epistomal ridge, which fuses posterolaterally with the dorsal surface of the circumocular sclerite and becomes indistinct anteromedially (Fig. 5.10). The fronto-clypeal suture has been internalized and is indistinct medially, only represented externally at the anterolateral margins of the frons near the anterior tentorial pits (Fig. 5.11). Internally, the fronto-clypeal suture is represented by a thin transverse ridge between the frons and the clypeus. The clypeus is transverse, weakly convex, and anteroventrally excavated to receive the basal ridge of the labrum.

The occipital foramen (Figs. 5.5, 5.7) is large and ovoid in shape, taller than wide, bordered dorsally by a narrow postocciput and ventrally by the gular ridge. The oral foramen (Figs. 5.5-5.6) is relatively small and oval in shape, bordered dorsally by the clypeus, laterally by the subgenal brace and ventrally by the anterior submentum. The subgenal braces are large, narrow medially and expanding anterolaterally where each bears a distinct lateral mandibular articulation at the apex. The submentum and pregula are incompletely divided by a poorly, developed submental suture, represented externally only as a short transverse ridge.

The tentorium (Figs. 5.5-5.8) is typical for the subfamily. The anterior arms are not fused medially and diverge anteriorly to fuse with the lateral edges of the fronto-clypeal ridge. The anterior arms each bear near the midline a small process along their ventrolateral surface. The posterior arms diverge posteriorly to fuse with the lateral edges of the gular suture, forming the posterior tentorial pits. The corpotentoria diverge posterodorsally from the posterior arms of the tentorium, abruptly curving anterodorsally near midlength and converging to fuse ventromedially.

Head Appendages (Figs. 5.9, 5.12-5.24). Gorham (1887-99) was the first to suggest using the number of antennomeres (9 or 10) to separate *Bystus* spp. (as *Rhymbus*). Strohecker (1953) described *Bystus* as having 9-segmented antennae, but noted that some species have 10-segmented antennae. In *B. piceus*, the antennae are 9-segmented and relatively long (1.5x length of head), extending just beyond the base of the pronotum (Figs. 5.9, 5.12). The scape is elongate, curving laterad near its midpoint. The pedicel is elongate-oval and swollen distally. Antennomere III is narrow and elongate, generally twice as long as IV. Antennomeres IV-VI are subequal in length. Antennomeres VII-IX expand apically to form a conspicuous, 3-segmented dark club. Antennomere IX is elongate and rectangular in shape. The club antennomeres lack sensorial pits, but each bears 10-20 long trichoid sensilla and a thick vestiture of short setae (Fig. 5.12).

The mouthparts of *B. piceus* (Fig. 5.19) are well-adapted for sporophagy, with the mandibular mola forming a large broad surface for grinding spores and large tracts of medial maxillary and dorsal labial setae for manipulating ground spore debris and directing it posteriorly to the mouth. The terminology used for describing and labeling the mouthparts was adapted from Crampton (1923, 1928), Denis and Bitsch (1973) and Nel and Scholtz (1990). The labrum (Figs. 5.13-5.14, 5.20) is very transverse, expanded laterally, but broadly rounded anteriorly and constricted posteriorly. The dorsal surface is moderately punctured and densely setose. The apical margin of the labrum is fringed with stout labral bristles directed ventromedially. The ventral surface of the labrum has a paired series of medially directed stout setae along the anterolateral margin and a cluster of basomedial placoid sensilla. At its base, the lateral edges of the labral ridge are attached to the epipharyngeal braces, which are directed posteromedially to form the epipharyngeal process, and to the tormae, which are directed posterodorsally and connect at their bases with the suspensory sclerites. The epipharyngeal process is visible in ventral aspect only as a thick fringe of posteromedially-directed setae. The anterior margin of the suspensory sclerite bridge bears two acute arms directed anteroventrally (Figs. 5.13-5.14). The oral braces project posterolaterad from the bridge of the suspensory sclerites and are associated at their bases with tendons connecting to the small ventrolateral processes of the anterior tentorial arms.

The basal membrane that supports the hypopharynx runs between the anterior arms of the suspensory sclerite bridge. The hypopharynx (Fig. 5.15) is very simple in structure and lies along the midline between the mandibles and the maxillae, separating the preoral cavity into a dorsal cibarium and a ventral salivarium. The hypopharynx is lobed with two fleshy lateral superlinguae and a smaller median lingua, the latter of which has a dorsal groove that widens and deepens basally to form the ventral floor of the cibarium. The median lingua also has a narrower ventral channel that forms the dorsal ceiling of the salivarium.

The mandibles are asymmetrical in relation to one another and heavily sclerotized, with the apices fitting tightly together at rest. Each mandible (Figs. 5.16, 5.21) bears a pair of distidentes (or incisor teeth) at the apex and a second pair of subapical teeth, all curved mesad. The dorsal surface of the mandible has a narrow band of setae along the lateral margin, all directed anterolaterad. The mola is large and triangular when viewed mesally, with the distal angle pointing anterodorsally and the proximal angles pointing posteroventrally. The molar surface is heavily sculptured and sclerotized, made up of powerful grinding molar cusps. The membranous prostheca is separated from the rest of the mandible by a proximal mandibular groove and bears a fringe of erect setae which are all bent near their midpoint and directed mesad. Each mandible has a dorsal and ventral condyle near the proximolateral margin which articulate with the apex of their respective subgenal brace.

Williams (1938) discussed the comparative morphology of the maxillae and labium across Coleoptera, including two endomychids. Of the endomychids included in Williams' study, the maxilla of *B. piceus* more closely resembles that illustrated for *Mycetaea subterranea* (Fabricius), but in *B. piceus* the distigalea and basigalea are distinguishable, the terminal maxillary palpomere is not abruptly tapered apically and the palpifer is much reduced. The labium of *B. piceus* does not correspond well with either of the species illustrated by Williams (1938). In overall structure, the mouthparts of *B. piceus* agree with those illustrated for other anamorphines by Tomaszewska (2000a), but differences in the articulation of the lacinia to the mediostipes, the condition of the galea, the size of the palpifer and the shape of the palpomeres suggest that each of the mouthparts may be phylogenetically important and taxonomically useful.

The maxillae of *B. piceus* are similar to those illustrated for *B. decorator* (Leschen and Carlton 1993). Each maxilla (Figs. 5.17, 5.22) is elongate, with a distinct, narrow 4-segmented palpus. The cardo has a rounded proximal lobe, which has a mesal finger-like process and a smaller lateral spiniform process, and a triangular-shaped distal lobe that broadly articulates with the basistipes. The triangular basistipes and the rectangular mediostipes are separated by a distinct dorsal groove which traverses from the proximomedial articulation of the mediostipes and the lacinia to the lateral margin of the maxilla posterior of the palpifer. The elongate lacinia is narrow proximally, but flattens and expands mesad near midlength before narrowing again distally. The apex of the lacinia is armed with a large tuft of stout setae and a small fringe of delicate subapical setae, all directed anteromesad. The basigalea is separated from the mediostipes by a distinct, angled transverse groove running from the lateral margin to the medial margin. The distigalea is fused with the basigalea, the transition now marked externally only by the presence of two distinct rows of long erect setae which bear conspicuous hooks distally, all of which are directed mesad. The maxillary palpus consists of a small, laterally curved palpomere I, a subcylindrical palpomere II, a triangular palpomere III that is partially retracted into II along its proximomedial margin, and an elongate conical terminal palpomere.

The labium (Figs. 5.18, 5.23-5.24) is trapezoidal in shape, widening distally, with a pair of large 3-segmented palpi. Basoventrally, the labium includes a rounded, transverse mentum, the dorsal surface of which serves as an attachment for the internal musculature of the labium (easily viewable upon removal of the mentum). The prementum consists of a submembranous ligula, the proximal palpomeres, their respective palpigers and the glossae. The glossae are fused with the mesal margin of the proximal palpomere and are no longer visible externally. The ligula is concave distomedially and widens distolaterally to form the two broadly rounded paraglossae. The ventral paraglossal setae extend beyond the apex of the ligula, while the dorsal paraglossal setae are directed mesad and form a pair of fringes that converge basally to create a channel, the ventral surface of the preoral cavity. The labial palpus consists of a small, subconical palpomere I, a transverse and laterally-curved palpomere II that forms a right angle with respect to I, and a large subquadrate, distomedially-curved terminal palpomere. The apex of palpomere III is truncate and covered with fine microsculpture and a fringe of fine setae. An apical sensorium is lacking.

Cervical Region (Figs. 5.25-5.27). Martin (1916) discussed the reduction of the size and number of cervical sclerites in Coleoptera, proposing that in many groups they may be lost entirely or indistinguishably fused to the anterior margin of the prothorax. The cervix in *B. piceus* consists of a long basal cervical membrane which extends anteriad through the occipital foramen where it is attached inside the base of the head capsule. The membrane extends posteriad deep into the pronotum. The membrane bears a pair of lateral rows of short stout setae directed anterodorsad. The membrane is further delineated by an obvious constriction near the basal end of the ventral cervepisterna to form an anterior cervinotum. The cervix in most polyphagans typically also includes two pairs of narrow cervical sclerites embedded in the cervical membrane for ventrolateral support of the head (Lawrence and Britton 1991). The cervepisterna (Figs. 5.26-5.27) are wider apically and narrow basally, and each sclerite is angled posterolaterad basally. Lateral to the cerviepisterna, there are two stout anterolaterally-directed setae, which appear to be ventromedial to the cerviepisterna when viewed laterally. The cerviepimera have been lost entirely in *Bystus* and are also absent from the endomychid species illustrated by Stickney (1923), so the cerviepimera may have been lost in all Endomychidae.

Prothorax (Figs. 5.28, 5.31-5.33, 5.61-5.62, 5.65-5.66). The major features and evolution of the thorax were extensively reviewed by Snodgrass (1909), Crampton (1926), Hlavac (1972) and Matsuda (1970). The pronotum of *B. piceus* (Figs. 5.28, 5.31) is strongly transverse and laterally-rounded with the lateral margins narrowed posteriorly and widened anteriorly. Each anterolateral margin contains a central, longitudinal groove housing a row of pores (Figs. 5.32-5.33), many of which are also associated with a single seta. The pores exude a viscous, sticky exudate. Skelley and Leschen (2002) listed *Bystus* among endomychids which do not reflex bleed; however, they were referring to reflex bleeding from the femoro-tibial joint, the most common site for reflex bleeding in beetles. When grooming, *B. piceus* adults often rub the prothoracic tarsi along the anterolateral margin of the pronotum, so the exudate may include a compound used for chemical defense or as a pheromone. In many specimens, the groove also collects debris, including host fungal spores.

The anterior angles of the pronotum are broad and rounded, extending alongside the head to a point near the posterior margin of the compound eyes. The pronotal disc is gently convex, covered in a vestiture of short, erect setae that are directed posteriad. The lateral sulci are narrow but distinctly impressed and abruptly curved anteromesad. There is no external basal sulcus. The basomedial margin of the pronotum is expanded posteriorly to form a broad lobe, which contains an internal transverse channel (the internalized basal sulcus) connecting laterally to antebasal foveae located mesad of the lateral sulci.

The pleural region of the pronotum (Fig. 5.61) is represented externally by the ventrolateral hypomera and internally by the cryptopleura (Hlavac 1972), also called proendosternites by Chamorro-Lacayo and Konstantinov (2004). Each cryptopleuron consists of a short stalk that extends dorsomesad from the medial margin of the procoxal cavity and abruptly widens apically to form a round, flat posteriorly acute projection. The prothoracic spiracle has been lost entirely.

The prosternum (Fig. 5.62) is rounded laterally and has a broad medial prosternal process. The prosternal process extends posteriad beyond the procoxae, broadening to form a weakly rounded apex, and has a thickened lateral margin, forming a medial declivity (Figs. 5.65-5.66). The posterior margin of the prosternum forms the anterior wall of the procoxal cavity. The posterior margin extends posterolaterad to form an acute posterior angle, as well as serving as the lateral wall of the procoxal cavity. However, this posterior angle is anterior of the midlength of the prothoracic coxa, creating an externally- and posteriorly-open cavity. The lateral margins of the prosternum are tightly fused to the margins with the prothoracic hypomera (Fig. 5.61) and form acute anterior angles at the lateral ends of the thickened anterior margin of the prosternum. This thickened anterior margin is all that remains externally of the prothoracic sternacosta.

The base of the prosternum medially has a pair of anteriorly diverging carinae which delimit a triangular elevated area containing a thick conspicuous patch of elongate setae and deep pores. Faustini and Halstead (1982) suggested that similar structures in other beetles are often setiferous sex patches, especially in males. In *B. piceus*, the presence of this patch is not sexually dimorphic, although it is usually smaller in females.

Mesothorax (Figs. 5.29, 5.61, 5.64-5.67). The mesonotum (Fig. 5.29) is relatively small compared to the pronotum and metanotum. It bears anterolateral processes to brace against the posterior edge of the pronotum as the elytra are raised for flight and posterolateral processes for articulation of the elytra. The mesothoracic prescutal membrane is incompletely divided into two parts by the posteromedial margin of the mesothoracic prephragma and the anteromedial margin of the mesothoracic prescutum. The mesoscutellum is small and triangular with a weakly rounded, acute apex.

In *B. piceus*, much of the mesopleuron is submembranous. The mesopleuron (Fig. 5.61) includes a large, anterodorsally expanded mesepisternum and a narrow, posteriorly-rounded mesepimeron (Fig. 5.64). The mesepisternum has a thickened vertical ridge posteriorly which narrowly articulates with the anterior apex of the mesepimeron posteroventrally (Fig. 5.61). The mesothoracic spiracle is shifted anteriorly to the anterior margin of the mesothorax and is obscured by the pronotum when viewed dorsally and laterally.

The mesosternum (Fig. 5.64) has two anteriorly convergent carinae extending from the posterior margin to the anterior margin, creating a declivity for reception of the prosternal process (Fig. 5.66). The mesofurca is narrow, lacks lateral arms, and runs transversely across the mesosternum near its anterior margin. The intercoxal process (Fig. 5.67) is transverse and broad, forming the anteromedial margin of the mesocoxal cavities. The mesosternal-metasternal articulation is nearly straight with a weakly curved metasternal apex fitting tightly against the posteromedial margin of the mesosternum. The anterolateral margins of the mesosternum bear a pair of large, slightly depressed circular “pits” (Fig. 5.66) just mesad of the mesepisternum. These shallow depressions represent thickened areas of the cuticle associated with internal apodemes and have no other internal structures associated with them to suggest glandular or mycangial function.

Metathorax (Figs. 5.30, 5.61, 5.63-5.64, 5.67). The complex metanotum (Fig. 5.30) is delimited anteriorly by a narrow transverse ridge formed by the metathoracic prephragma, the posterior margin of which has a medial acute process extending posteriorly into the metathoracic prescutal membrane. The metanotum has a bilobed anterolateral notal wing process which articulates directly with the humeral plate, the 1st axillary sclerite and the 3rd axillary sclerite, all embedded in the membrane at the base of the hind wing. The 2nd axillary sclerite transects the base of the wing, narrowing posteriorly, and articulating with posterolateral end of the 3rd axillary sclerite. The metathoracic scutellar groove is formed by the alar ridges which expand medially and have acute posteromedial processes. The ventral ridges of the metascutellum arch posterolaterad from the posterior margins of the alar ridges, and are connected at their base by a transverse suspensory sclerite anterior to their articulation with the posteromedial ends of the metathoracic laterophragmites. The large, rounded anterolateral ends of the metathoracic laterophragmites form the posterior notal wing processes. The membranous postnotal cleft is formed anteriorly by the transverse suspensory sclerite and posteriorly by the metathoracic mediophragmites.

The metapleuron (Fig. 5.61), like the mesopleuron, is mostly submembranous but includes a large, vertical, oblique basalar disc which narrows anterodorsally. The basalare is a small, narrow, vertical sclerite lying in the membrane just anterior of the basalar disc. The subalare is small and narrow, curving posteriad just past midlength. The subalare is located posterior of the basalar disc and ventral of the anterolateral margin of the metascutum. The large metepisternum appears teardrop-shaped in lateral view, rounded anteriorly, and transected by a longitudinal ridge. The metepimeron is small and located immediately dorsad of the metepisternum, and it is articulated at its posterior end with the anterolateral margin of the first abdominal tergite. The metepimeron is not visible when viewed ventrally. The metathoracic spiracle is located in an invagination of the membrane inside the posteroventral margin of the basalar disc (and not visible laterally), lying just posterior to the mesepimeron.

The metasternum (Fig. 5.64) is transverse, more than twice as wide as long, and moderately convex. The margins are thickened and heavily sclerotized, particularly along the anterior margin. A row of large conspicuous punctures runs along the anterior margin, ending near the lateral margin of the mesocoxal cavities (Fig. 5.67). Each puncture bears a short stout seta. The anterolateral margins of the metasternum bear a pair of large, oval pits mesad of the posterior mesepimeron and anterior metepisternum. As with the mesosternal “pits”, these shallow depressions are also associated with internal apodemes and further exaggerated by the greatly thickened anterior margin of the metasternum.

The posteromedial margin of the metasternum has a conspicuous metendosternite which projects anterodorsad. Crowson (1938, 1944) conducted extensive studies of the metendosternite in Coleoptera and argued their phylogenetic value. However, only the latter study (1944) included an endomychid, *Holoparamecus caularum* Aubé (Merophysiinae), which is not representative of the family. Tomaszewska (2000a) included illustrations of the metendosternite of many endomychids, including several anamorphines; however, none of these illustrations resemble the metendosternite of *B. piceus.* At the base, the metendosternite of *B. piceus* (Fig. 5.63) includes a pair of medial membranous laminae, which are shallow and separated by a narrow medial flange. Each lamina extends anterolaterad along the mesal margins of the anteriorly-diverging arms of the metafurcae. The metafurcal arms have at their distal ends three fingerlike processes: a posterolateral arm, an anterolateral arm, and an anteromedial apodeme for attachment of the metafurcal tendons.

Elytra (Figs. 5.34-5.48, 5.61). The strongly convex elytra (Figs. 5.34-5.36) are elongate, hemisphaerical, and densely punctured with a thick vestiture of long, pale-colored, decumbent setae. There are no striae or scutellary strioles on the elytra. In cross-section, the elytral microstructure consists of a relatively thin epicuticle, a thicker exocuticle in alternating thin and thick areas to form disks, and very thin endocuticle and epidermal (epithelial) layers. Similar architecture has been found in other Coleoptera (Krzelj 1969), where it increases rigidity and hardness of the elytra after sclerotization. The thick exocuticular disks are difficult to see using light microscopy but are easily visible when the elytra are viewed ventrally using an SEM (Figs. 5.37-5.39, 5.43). Each disk lies directly underneath a much smaller dorsal puncture and its accompanying seta.

The convexity of the elytra creates a deep subelytral cavity (Fig. 5.61). Heberdey (1938) and Draney (1993) discussed several possible functions of this cavity. The sutural margins of the elytra form a tongue-in-groove locking system similar to that described in *Megalodacne heros* (McHugh *et al.* 1997) and *Tenebrio molitor* (Doyen 1966). The basal margin of each elytron includes a prominent medial process for articulation with the notal elytral processes of the mesonotum. The humerus is only weakly produced. The elytral epipleuron (Figs. 5.37-5.39) is broadly margined and flat basally, curving ventromesad just anterior of the humerus and narrowing apically to form an incomplete apex.

The elytral epipleuron has three distinct forms of setae along its inner surface. Setae near the apex of the elytron (Fig. 5.40) are arranged in compact rows of alternating large and small setae. Setae located near midlength (Fig. 5.41) are much less dense and are arranged in small, random clusters of 3-4 medium-sized stout setae. While setae located near the base of the elytron (Fig. 5.42) are uniformly-sized and spaced, arranged individually and consisting of a single short stout, decumbent seta. The functions of each of these setal morphologies and distribution patterns along the elytral epipleuron remain unknown.

The ventral surface of the sutural margin of each elytron bears three conspicuous wing-binding patches (Fig. 5.43) made up of squamous setae (Fig. 5.48). A basal patch (Fig. 5.44) is located directly on the margin near the basal process of each elytron. A second, small patch is located on the inner surface of the subelytral cavity (Fig. 5.45), mesad of the sutural margin and anteriad of the groove of the elytral locking mechanism (Fig. 5.46). Each elytron also has a large subapical patch (Fig. 5.47), which lies just beyond 2/3 length directly mesad of the sutural margin. The location of this patch corresponds with a complementary patch on the dorsal surface of the hind wing (Fig. 5.50). Although these complementary patches serve primarily to bind the wing, Gahan (1900) and Wessel (2006) both suggested that this type of structure may be an alary-elytral stridulatory organ. Ohya (1996) and McHugh *et al.* (1997) described a similar structure in Erotylidae. Shockley *et al.* (2009b) reported that this "organ" had been found in most endomychids examined, although sometimes in highly reduced form.

Wings (Figs. 5.49-5.60). Many authors have discussed wing venation and folding mechanisms comparatively across Insecta (Comstock and Needham 1898-99; Hamilton 1971, 1972a, b, c), as well as within Coleoptera (Kempers 1900, 1901, 1902, 1903; d'Orchymont 1920, 1921; Forbes 1922, 1924, 1926a, b; Graham 1922; Bernet Kempers 1923, 1924; Rüschkamp 1927; Balfour-Browne 1944; Ponomarenko 1972; Wallace and Fox 1975, 1980). Wing venation in particular has been historically difficult to homologize because authors have based their respective nomenclatural systems on different structural assumptions related to the ancestral wing condition, freely modifying previous systems to fit their own interpretations. Kukalova-Peck and Lawrence (1993) thoroughly reviewed the different systems and homologized the vein nomenclature, as it applies to the hind wing in Coleoptera. Browne and Scholtz (1994) provided additional clarification regarding structures associated with the wing articulation and wing base in Coleoptera.

For the purposes of this study, Forbes (1926a, b) was used to describe the folds of the wing, and Kukalova-Peck and Lawrence (1993) was used to describe the wing venation and fields. The hind wing of *B. piceus* lacks a jugal lobe. The wing displays reduced venation and has several areas of dark melanization (Fig. 5.54); both conditions are typical of endomychid hind wings.

Forbes (1926b) described the wing folding mechanism in two endomychids, *Aphorista vittata* (Fabricius) (Lycoperdininae) and *Endomychus biguttatus* (Endomychinae); however, these two taxa both represent the more advanced "higher" Endomychidae (Tomaszewska 2005) and differ significantly from *Bystus*. The hind wing of *B. piceus* contains 18 distinct folds—11 dorsal and 7 ventral (Fig. 5.51). Dorsal folds act to cause sections of the wing distad of the fold to pivot ventrally, while ventral folds cause distal sections to pivot dorsally. There are two primary transverse folds that cross the wing, and both folds are dorsal and composite, created by two or more folds acting in concert. The longer of the two folds, which is located near the wing midlength, is composed of the D1, A3 and G4 folds. This fold separates the central and apical fields from the basal fields of the wing. The central field is large and rectangular, delimited by the dorsal composite transverse folds proximally (D1+A3+G4) and distally (E1+E2+H4). The apical field is relatively small, somewhat triangular in shape, and delimited proximally by the distal transverse fold (E1+E2+H4). The second transverse fold is closer to the apex and is composed of the fused E1+E2 and the H4 folds. This fold separates the apical field from the central field.

The wing also contains three primary dorsal longitudinal folds (F1+G2, H3, E3). Longitudinal folds act to cause the wing to twist anteroventrally. This twisting motion is accomplished by the small anterior convex and concave pivots (B2, B3, C2 and D2) and the dorsal transverse folds working together to move the apex of the wing anteroventrally as it pivots toward the base of the wing. The two longitudinal ventral folds in the basal half of the wing (A2, J2) define the narrow radial, medial and anal fields. These folds also assist in twisting the wing to compact the apical field during its ventral rotation, but are primarily responsible for providing torque needed for anteroventral folding of the central field.

There is an additional longitudinal ventral fold (I1) in the apex of the hind wing of *B. piceus* for which no homologous fold could be identified. This fold repositions the apices of the E3 and H5 folds, bringing them together during anteroventral twisting and folding of the apex. When folded, the wing forms an elongate triangle (Figs. 5.49-5.50) with the apical field first folded ventrally, the central field also folded ventrally (thus pivoting the apical field back into the dorsal position), and the narrow anal field folded and resting on top of the medial field.

Bernet Kempers (1923) illustrated the wing venation of five endomychids, one from Endomychinae (*Endomychus* Panzer) and four from Lycoperdininae (*Corynomalus tarsatus* Erichson, *Eumorphus bipunctatus* Perty, *E. marginatus* Fabricius) and *E. quadriguttatus* (Illiger). Tomaszewska (2000a, 2005) demonstrated that wing venation varies significantly across the family. Although Tomaszewska (2000a) did not illustrate a *Bystus* wing, the wings of three other anamorphines were illustrated—*Symbiotes gibberosus* (Lucas), *Mychothenus asiaticus* Sasaji and *Micropsephodes serraticornis* Champion. The wing of *B. piceus* (Fig. 5.52) differs significantly from each of these, suggesting that the wing may be of taxonomic value and may contain important phylogenetic characters.

In *B. piceus*, the cubito-anal vein (CuA) is reduced and conspicuous only near the wing base. The CuA vein becomes obsolete distally where it becomes lost in a field of melanization that continues a short distance before ending in a very faint rounded, subcubital fleck. The media posterior (MP_{1+2}) is long and dark, extending nearly to the A3 fold near the midpoint of the wing before abruptly curving posteriorly and merging with the posterior margin at the claval furrow. The radius posterior (RP) has been lost entirely. The radius anterior (RA) is divided. The proximal section of the RA is fused at its base to the short subcosta (Sc). The distal section of the RA runs parallel to the anterior margin of the wing, between the costa (C) and a sharply, defined transverse fleck, ending proximad of the D1 fold. The medial bridge is absent, and the radial cell is reduced and indistinct. The posterior margin of the wing contains a conspicuous medial fleck proximad of the claval furrow.

The dorsal surface of the wing is covered with a fine vestiture of short stout setae (Fig. 5.53). There is an abrupt transition at the edge of the medial fleck (Figs. 5.55-5.58) where the setae change shape and the setal field becomes denser. The setae at the edge of the medial fleck (Fig. 5.59) change from trichoid to triangular within the fleck (Fig. 5.60). The size and location of the fleck on the hind wing match that of the large subapical wing-binding patch of the elytra. The setae on the dorsal surface of the fleck are a close match for the intersetal spaces of the squamous setae on the elytral binding patch. The interactions of the ventral wing-binding patches of the elytra and the dorsal wing-binding patches of the wings inside the subelytral cavity of Coleoptera were reviewed by Heberdey (1938).

Legs (Figs. 5.68-5.79). Strohecker (1953) described *Bystus* as having a 4-4-4 tarsal formula; however, the illustration that he provided correctly depicted the prothoracic tarsus of *B. piceus* as 3-segmented. Although male tarsal heteromerism is known within the Cucujiformia, the reduction is usually in the metathoracic tarsus and is more often associated with families of the Tenebrionoidea. Heteromerism in *Bystus* is not sexually dimorphic. Within Cucujoidea, heteromerism in both sexes is limited to three genera of anamorphine endomychids—*Bystus* (3-4-4), *Asymbius* Gorham (3-3-4) and *Exysma* Gorham (3-4-4). The only similar reduction in the prothoracic tarsus within the Cucujiformia is found in the tenebrionoid family Mycetophagidae, but in that example the heteromerism is sexually dimorphic with 3-4-4 males and 4-4-4 females.

The trochantins of all the legs are indistinguishably fused to the coxae. The prothoracic legs (Figs. 5.68-5.69) have weakly oval procoxae that are housed in externally-open procoxal cavities. The trochanter is concealed laterally by the femur but is visible in ventral view. The trochantero-femoral articulation is oblique. The femur is moderately swollen, widest at midlength, and has a shallow ventral depression for reception of the tibia. The tibia is narrow and straight, curving mesad near the femoro-tibial articulation and weakly widening apically. Bayer (1924) argued the importance of this articulation above all others in the insect leg for locomotion by providing necessary structural stability and rotational flexion of the leg. The tibia lacks apical spurs, but it has an apical notch on the dorsal surface, armed with a row of stout setae along the margins of the notch.

Although the number of tarsomeres on the prothoracic leg does not differ between males and females, the structure of tarsomere I exhibits a sexual dimorphism (Figs. 5.74-5.76). Tarsomere I in males is dilated and triangular, bearing a pectinate comb with teeth directed dorsolaterad. In the female (Fig. 5.77), tarsomere I is not dilated and is similar in shape and size to II. Both tarsomeres I and II have narrow lobes projecting distoventrad, concealing the base of the next tarsomere when viewed ventrally. Tarsomere III in both sexes is long, narrow and gently curved ventrad. The apex of tarsomere III bears a simple pretarsus consisting of a pair of ungues (claws) and a small medial empodium. The empodium is articulated at its base with a slender unguitractor plate located inside the apex of tarsomere III and bears a pair of long slender setae projecting laterad (Fig. 5.79). The ungues are simple and not appendiculate. The ventral surface of each unguis is excavated to produce a rectangular process at the base of the unguis, but this process is never acute and does not form a tooth.

Strohecker (1953) is the first to mention the modified male protarsus in *Bystus*. Modification of the male protarsus in Coleoptera usually serves some role in mating (Crowson 1981). According to Leschen and Carlton (1993), the basitarsis served no obvious role during observation of copulating pairs of *B. decorator*. Leg modifications in Coleoptera are often also used as grooming devices (Beutel and Lawrence 2005), although this type of modification is primarily known found in adephagan families. Valentine (1973) reviewed autogrooming behaviors in beetles. Within beetle families known to have grooming structures on the legs, the "comb" varies both in structure and location, appearing on the tarsus (Hlavac 1971), the tibia (Beutel 1997), or the femur (Beutel *et al.* 2006). However, if this structure is indeed a grooming device, the reason that it would be found only in males remains unknown. Observation of copulating pairs of *B. piceus* suggests that the male basitarsus may be involved in solicitation or grooming of the female by the male during precopulatory courtship (Shockley pers. obs.).

The mesothoracic and metathoracic legs (Figs. 5.70-5.71) are generally similar in structure and are not sexually dimorphic. The mesocoxae are spherical in appearance and bear a rounded process dorsally that projects into the body cavity. The trochanter is of the "normal" type and is exposed and visible. The trochantero-femoral junction is oblique. The femur is moderately swollen and widest at midlength with a deep ventral furrow for reception of the tibia. The tibia is narrow and nearly straight, curving mesad at the femoro-tibial junction and weakly widening apically. The mesothoracic tarsi (Figs. 5.72-5.73, 5.78) are simple and 4-segmented, with tarsomeres I-III similar in size and shape, each with narrow, ventral lobes. Tarsomere IV appears identical to that of the protarsus.

The metacoxae are transverse, widest medially and narrowing laterally to form a "teardrop" shaped coxa. The trochanter is subconical and exposed. The trochantero-femoral junction is transverse. The femur is less dilated than in the pro- and mesofemora and is widest proximad of the midpoint. The ventral surface of the metathoracic femur also has a deep ventral furrow for reception of the tibia. Tibiae are similar to the pro- and mesotibiae; however, the metathoracic tibiae are not dilated apically. The tarsus appears identical to the mesotarsus.

Abdomen (Figs. 5.61, 5.80-5.81). Verhoeff (1895), Jeannel and Paulian (1944) and Matsuda (1976) discussed the morphology and evolution of the abdomen. The abdominal tergum (Figs. 5.61, 5.80) consists of eight transverse submembranous tergites which gradually shorten apically. Tergites I and III-V each have a pair of spiracles embedded near their anterolateral margins. The spiracles on tergite II are located near midlength of the lateral margin and are partially obscured by a longitudinal ridge when viewed dorsally. Tergites VI-VIII lack spiracles. Tergites II-VII are margined laterally by the pleural parasternites. Tergite I is partially obscured medially by the metathoracic postnotum when viewed dorsally. Tergite VIII is not fully articulated with tergite VII and is connected only by membrane. The abdominal tergites are mostly glabrous; however, tergite VIII has a fringe of short setae and a median tuft of longer setae along the anterior margin and a second fringe of setae along the posterior margin.

The abdominal venter (Figs. 5.61, 5.81) consists of five freely articulated ventrites corresponding to abdominal sternites III-VII. Sternites I and II have been internalized, forming a thickened internal ridge at the anterior margin of the abdominal venter (Fig. 5.97). All ventrites are much wider than long, each margined laterally by a pleural laterosternite embedded in a narrow band of membrane. The ventral surface is covered in a vestiture of decumbent setae which are directed laterad near the lateral margins and mesad near the center of each ventrite. Ventrite I has two large, circular glabrous areas posterolateral of the metathoracic coxal cavity. Along the midline, ventrite I is as long as II-IV combined. The anteromedial intercoxal process of ventrite I is heavily sclerotized and slightly curved and has a broad articulation with the metasternal intercoxal process. Ventrites II-V are subequal in length. The anterior margin of ventrite V is slightly curved anteriad, while the posterior margin bears a concave semicircular notch lined with a thick fringe of setae, all directed mesad.

Reproductive System (Figs. 5.82-5.94). In male and female *B. piceus*, the reproductive system spans much of the abdomen (Figs. 5.82-5.83). Tanner (1927) included three endomychids in a comparative study of female genitalia in Coleoptera, providing illustrations of *Aphorista laeta* (LeConte) (Lycoperdininae). Tomaszewska (2000a) also illustrated the female genitalia of Endomychidae, including four anamorphines. The female genitalia of *B. piceus* are similar in general structure, but vary sufficiently to suggest that they may have important phylogenetic significance. The ovipositer (Fig. 5.84) is weakly sclerotized and comprises a dorsal epiproct, sternite VIII, and a pair of short, lateral paraprocts concealed by sternite VIII when viewed ventrally. Gonocoxites arise from paraprocts, which are contiguous at their base and are apically divergent. Each gonocoxite bears a small finger-like apical gonostylus. Both the gonocoxites and the gonostyli have elongate setae extending posteriorly. The vagina is a short broad chamber posterior to the dilated bursa copulatrix creating a mushroom-shaped genital chamber. The paired ovaries are positioned on either side of the gut. The ovarioles are bundled in a common membrane opening posteriorly into the swollen end of the lateral oviducts. Mature oocytes are white to light yellow in color, elongate oval in shape, 0.5 mm in length and 0.3 mm in width, and lacking conspicuous microsculpturing. The lateral oviducts lead into a common median oviduct which empties into the anterior end of the bursa copulatrix. The spermatheca is small, oval and membranous, attached anterodorsally to the bursa copulatrix and narrowly connected to a delicate leaf-like spermathecal gland dorsad of the spermatheca.

The male terminalia in beetles are well known as useful sources of taxonomic and phylogenetic characters. Sharp and Muir (1912) provided one of the first large comparative studies to establish affinities between the families of Coleoptera based on the male genitalia. That study included four endomychids, but *Bystus* differs significantly from all of these. Likewise, the anamorphine aedeagi illustrated by Tomaszkewsa (2000a) agree with *B. piceus* only in the general shape of the median lobe. The tegmen is highly variable in form between species. Prior to this work, the only illustration of any part of the male reproductive system for any *Bystus* species was that of the median lobe of *B. decorator* by Leschen and Carlton (1993).

In males of *B. piceus* (Fig. 5.85), the genital capsule is formed by the proctiger posteriorly, the paraprocts laterally, abdominal tergite VIII dorsally and the spiculum gastrale ventrally. The spiculum gastrale is partially obscured beneath sternite VIII when viewed ventrally. The proctiger is short and broadly emarginate anteriorly, with the apex truncate and bearing a fringe of setae directed posteroventrad. The spiculum gastrale is composed of a pair of bifurcated posterior struts that fuse anteriorly to form a rounded brace. The tegmen (Figs. 5.88-5.90) is reduced to a ring-like structure fused apically with the parameres so there is no median strut. The tegmen is supported anterodorsally by a tendon-like bifurcated aedeagal apodeme. The curved parameres overlap asymmetrically and are fused basally and apically with a narrow band of clear membrane between them. Each paramere bears at its apex a small fringe of stout setae directed posteriad. The tegmen wraps transversely around the dorsal surface of the median lobe and then projects anteroventrally around the lateral edges of the median lobe before fusing apically to the parameres. The base of the fused tegmen and parameres is expanded to form a large flat, rounded basal piece, extending posteriorly to the midlength of the median lobe.

When viewed *in situ*, the aedeagus rests on its side. During eversion and copulation, the aedeagus rotates 90º counterclockwise. The median lobe (Figs. 5.86, 5.88-5.90) is long, stout, and weakly curved, abruptly narrowing apically and curving ventrad with a membranous elongate subapical gonopore. The lobe is connected anteriorly to a large, dilated upper ejaculatory duct bearing a long, narrow apical flagellum. The penis is supported at its base by a posterior sclerite and two sclerites of the internal sac. The lower ejaculatory duct fuses with the convergent vasa deferentia leading from the paired testes mesad of the base of the medial struts of the spiculum gastrale to form a common ejaculatory duct.

At rest, the internal sac lies inside the median lobe. The apex of the everted internal sac (Figs. 5.87, 5.91-5.94) bears a large subapical ventral lobe and a pair of much smaller basolateral lobes. The teeth of the internal sac vary in size and shape based on their position. The teeth on the ventral lobe are long and capitate, appearing to be flat to slightly convex on the apical side of the tooth. The teeth located at midlength of the sac and on the basolateral lobe form wide flat plates, each with a fringe of apical setae. The setae on the teeth at midlength are short and blunt, while the setae on the basal lobe are long and apically acute. During copulation, the apex of the internal sac swells to fill the cavity inside the bursa copulatrix, with the capitate teeth providing additional stability against the inside wall of the bursa.

Muscular System (Figs. 5.95-5.97). Evans (1960-61) and Larsen (1966) provided exhaustive treatments of the morphology of the muscular system in Coleoptera, particularly of the thorax and abdomen, and these references were used as a guide for homologizing and labeling the muscles.

The head muscles include a series of dorsal, ventral and tergo-sternal muscles that attach to various apodemes and condyles on the mandibles and maxillae, as well as to internal ridges of the head, including the tentorium, to affect the shape of the cibarium. The dorsal longitudinal muscles in the meso- and metathorax and the metathoracic tergo-sternal muscles are involved in flight and are the largest muscles in the body. The coxae are operated by smaller ventral and oblique muscles that connect either to the laterally to the furcae or medially to the internal ridges formed at the intercoxal, intersegmental articulation. The pro- and mesothoracic coxae are also each attached to a narrow band of muscles which run to the internal dorsal phragma at the posterior margin of the preceding tergite. This internal phragma is formed by the fusion of the postnotum of the preceding tergite and the succeeding acrotergite. The metathoracic coxae lack these additional muscles most likely because these coxae are fixed in place and are largely immovable.

The dorsal longitudinal muscles of the abdominal segments are arranged into dense sheets which extend the entire length and width of each segment. The longer dorsal and shorter ventral longitudinal muscles compress the abdomen longitudinally, causing the apex to curve ventrad during copulation and oviposition. This motion is reversed by relaxation of the dorsal longitudinal muscles, followed by relaxation of the ventral longitudinal muscles, and then by contraction of the lateral tergosternal muscles bridging the abdominal pleura.

Respiratory System (Figs. 5.98, 5.100). The respiratory system is associated laterally with the external spiracles. The 1st thoracic spiracle has been lost. The 2nd thoracic spiracle is sitting at the anterolateral margin of the mesonotum and is obscured from above by the posterior margin of the prothorax. The 3rd thoracic spiracle is obscured in lateral view by the anterolateral margin of the basalar disc. The 1st abdominal spiracle is the largest spiracle, with a conspicuous spiracular sclerite surrounding it. Abdominal spiracles 2-5 are distinctly smaller than spiracle 1, gradually reducing in size. As previously noted, abdominal spiracle 2 is partially obscured when viewed dorsally by a marginal ridge that traverses the entire length of abdominal tergite 2.

Internally, the respiratory system is closely associated with all of the other body systems. In the head and prothorax, the respiratory system consists of dorsal and ventral trunks which cross each other inside the head and wrap laterally around the cerebral ganglion and anterior alimentary canal. These trunks then pass posteriorly through the thorax, running parallel to each other and meeting only at their common connection just mesad of the thoracic spiracles. In addition to the lateral trunks, there are a series of transverse connectives which provide additional oxygen to the digestive system and the locomotory muscles of the pterothorax. In the abdomen, the ventral trunk has been lost, but the dorsal trunk continues posteriorly where it connects to each of the 5 external spiracles.

Nervous System (Figs. 5.99-5.100). The cephalic ganglion (brain) consists of a large dorsal protocerebrum and much smaller ventral deuto- and tritocerebra, the latter two completely concealed by the protocerebrum when viewed dorsally. The optic nerve innervates laterally with a large optic lobe just mesad of the ommatidial disk of the compound eye and medially with the protocerebrum. Posteroventrad to the protocerebrum and connected to it via cucumoesophageal connectives is the large, subquadrate suboesophageal ganglion. The ventral nerve “cord” actually consists of a pair of ventral nerve connectives that run just laterad of the midline, extending posteriorly to the thoracic and abdominal ganglia.

The thoracic and abdominal ganglia rest inside the thickened anterior margins of the intercoxal process of the thoracic and 1st abdominal segments. Each of the thoracic segments has an individual ganglion innervating it, whereas the abdominal ganglia have fused to form a single, large ganglion. The lateral connectives in the abdomen extend posterolaterally to the approximate original position of the abdominal ganglia that innervated each segment. Fusion of ganglia varies widely across Coleoptera. The ganglia are all associated with transverse connectives of the respiratory system.

Niven *et al.* (2008) studied the evolution of the ventral nerve cord and found that Coleoptera was the most diverse order in terms of neuromere fusion of any insect order. Peyerimhoff (1903) reported four abdominal ganglia in *Endomychus coccineus* (L.). Unfortunately, this study did not indicate the degree of fusion of abdominal ganglia in *E. coccineus*, if any. The number and location of ganglia in *B. piceus* also differ significantly from *Megalodacne heros* (Erotylidae) (McHugh *et al.* 1997), but closely resembles those of *Leptinotarsa decimlineata* (Say) (Chrysomelidae) (Pavlovskii and Teravskii 1958). Unfortunately, so few studies have included examination of the ventral nerve cord and ganglionic fusion varies so widely within Coleoptera that it is impossible presently to evaluate the phylogenetic utility of the structure of the nervous system.

Digestive System (Figs. 5.100-5.101). The mouth is located at the dorsal and posterior margin of the preoral cavity, connecting to the oesophagus ventrad of the brain. The oesophagus arches posterodorsad and passes through a channel formed by the protocerebrum dorsally, the circumoesophageal connectives laterally and the suboesophageal ganglion ventrally. The oesophagus is long and thin, reaching to the posterior of the prothorax before emptying into a moderately-sized crop just inside the anterior margin of the mesothorax. The crop extends posteriad for the length of the mesothorax, terminating at the anterior proventriculus. The junction between the crop and proventriculus is only recognizable externally by a shallow, but conspicuous constriction.

The midgut is widest anteriorly, narrowing posteriorly, its apex marked by the pyloric valve. The surface of the midgut is covered with short, thick gastric caecae. McHugh *et al.* (1997) suggested that these gastric caecae serve as storage sites for endosymbiotic bacteria and yeasts in *Megalodacne heros* (Erotylidae). Shockley *et al.* (2009b) speculated similar function in endomychids. The pyloric valve is recognizable externally by the area of the midgut where the gastric caecae stop and the long Malgiphian tubules are attached at their anterior ends. The location and size of the gastric caecae and Malpighian tubules vary between individuals, but their respective attachment points to the midgut do not. The Malpighian tubules wrap variably around the digestive and reproductive systems, moving through the large, abdominal fat body before curving posteriad and coming into close contact with the posterior ileum to form a short cryptonephridium.

The anterior ileum curves anterodorsad to form a short loop before abrupting curving posteroventrad. The ilium is closely associated with the reproductive system. The anterior loop of the ilium curves around the anterodorsal surface of the reproductive system then passes along its ventral surface before wrapping dorsolaterally around the right side, ultimately coming to rest dorsad of the genital chamber. The rectum includes both the short anterior cryptonephridium and a posterior chamber that is longitudinally scleritized to form distinct rectal pads. The rectum abruptly tapers posteriorly where it fuses with the inner margin of the aperature forming the external anus.

Vascular System (Figs. 5.100, 5.102). The vascular system in *B. piceus* is very simple in structure and is an open system. The heart and aorta are dorsad of the rest of the body systems, lying embedded along the midline in the fasciae of the dorsal longitudinal muscles, just ventrad of the tergites. The heart is housed entirely in the abdomen, consisting of 6 lobes positioned near midlength of each of abdominal tergites I-VI. The aorta is long and slender, extending from the anterior margin of abdominal tergite I through the prothorax and terminating inside the posterior head capsule. This arrangement allows hemolymph to be actively pumped from posterior to anterior where it bathes the brain and then is drawn back through the prothorax and into the abdomen by passive convection.

CONCLUSIONS

The uncertain placement of Anamorphinae relative to the remaining Endomychidae continues to be plagued by contradictory character evidence from different data sources. This uncertainty suggests that detailed morphological studies are needed on the remaining anamorphine genera to clarify the generic definitions within Anamorphinae, and to help resolve the relationship of the subfamily to other endomychids. The overall resemblance of *B. piceus* morphology to other anamorphine taxa, confirms that *Bystus* is indeed a good model to serve as an anatomical reference for the subfamily. While some morphological features appear to be shared by all anamorphines, much more work is needed.

Although *Bystus* is the most diverse genus and one of the most recognizable genera within the Anamorphinae, very little was known about its biology, morphology and diversity prior to this work. *Bystus* species display remarkable variety in morphological adaptations for such a seemingly homogeneous genus. This study corrects several errors and misconceptions from the literature, while expanding the knowledge of *Bystus* anatomy to cover aspects that had previously been overlooked or ignored. Some features of the mouthparts and wing were discovered during this study that will serve as valuable additional sources of reliable species-level characters. Other features such as the form of the lateral sulci, non-sexually dimorphic tarsal heteromerism and the presence of the anterolateral groove of the pronotal lateral margin, while interesting, are not restricted to *Bystus*. Even the form of the male basitarsus, arguably one of the most diagnostic characters for *Bystus*, may not be present in all *Bystus* species since several species are only known from the female. Furthermore, males having a modified prothoracic basitarsus may not be a character exclusive to *Bystus*. Unfortunately, inadequate knowledge of the morphology of the remaining anamorphines prevents direct comparison at this time.

Extensive anatomical treatments are becoming increasingly rare. However, these studies are necessary to establish baseline understanding of the morphology at the generic level before subsequent taxonomic revisions can be attempted. Likewise, studies like this one serve as important references for generalized studies on other aspects of the biology such as physiology, ecology and behavior.

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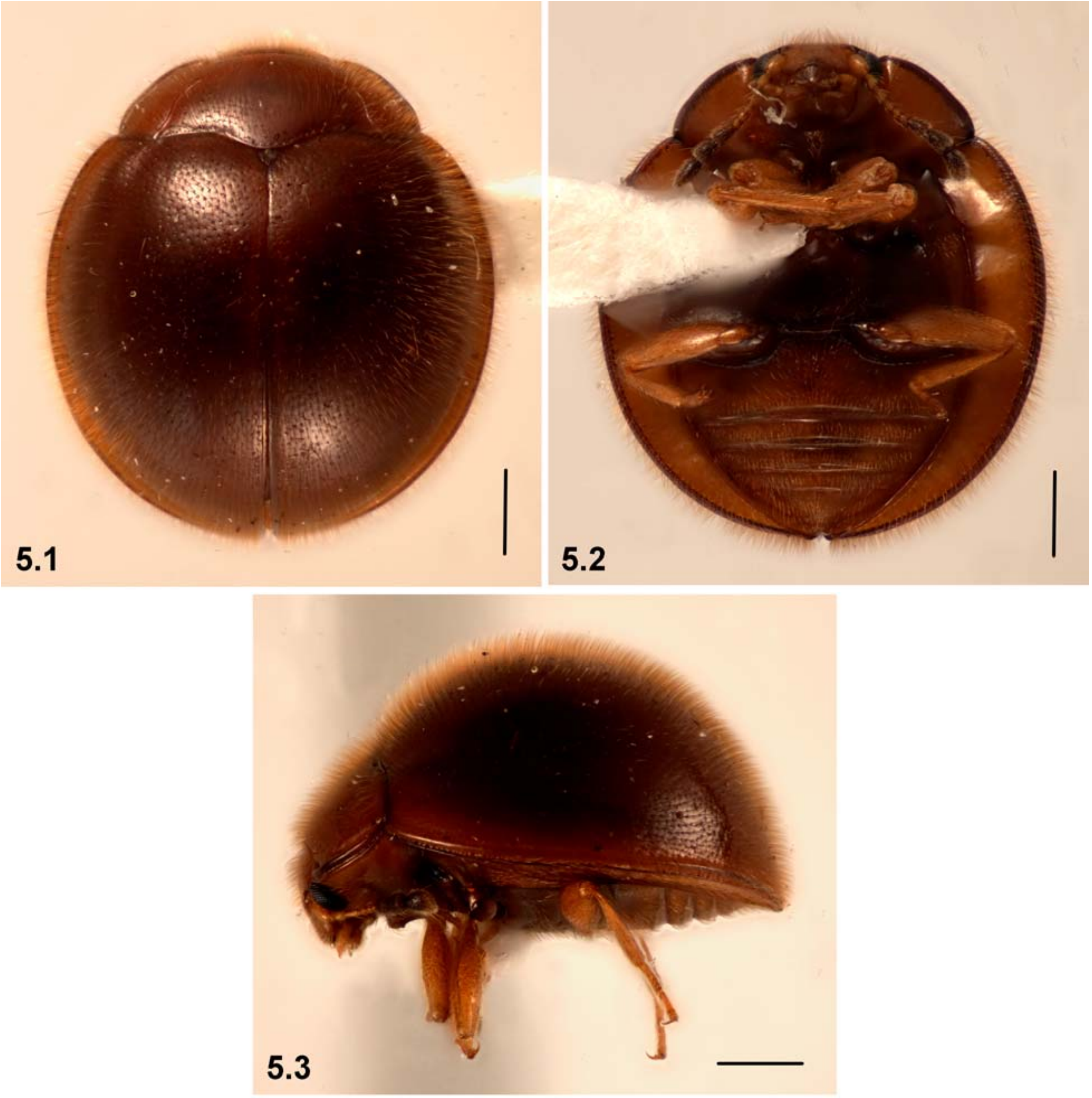
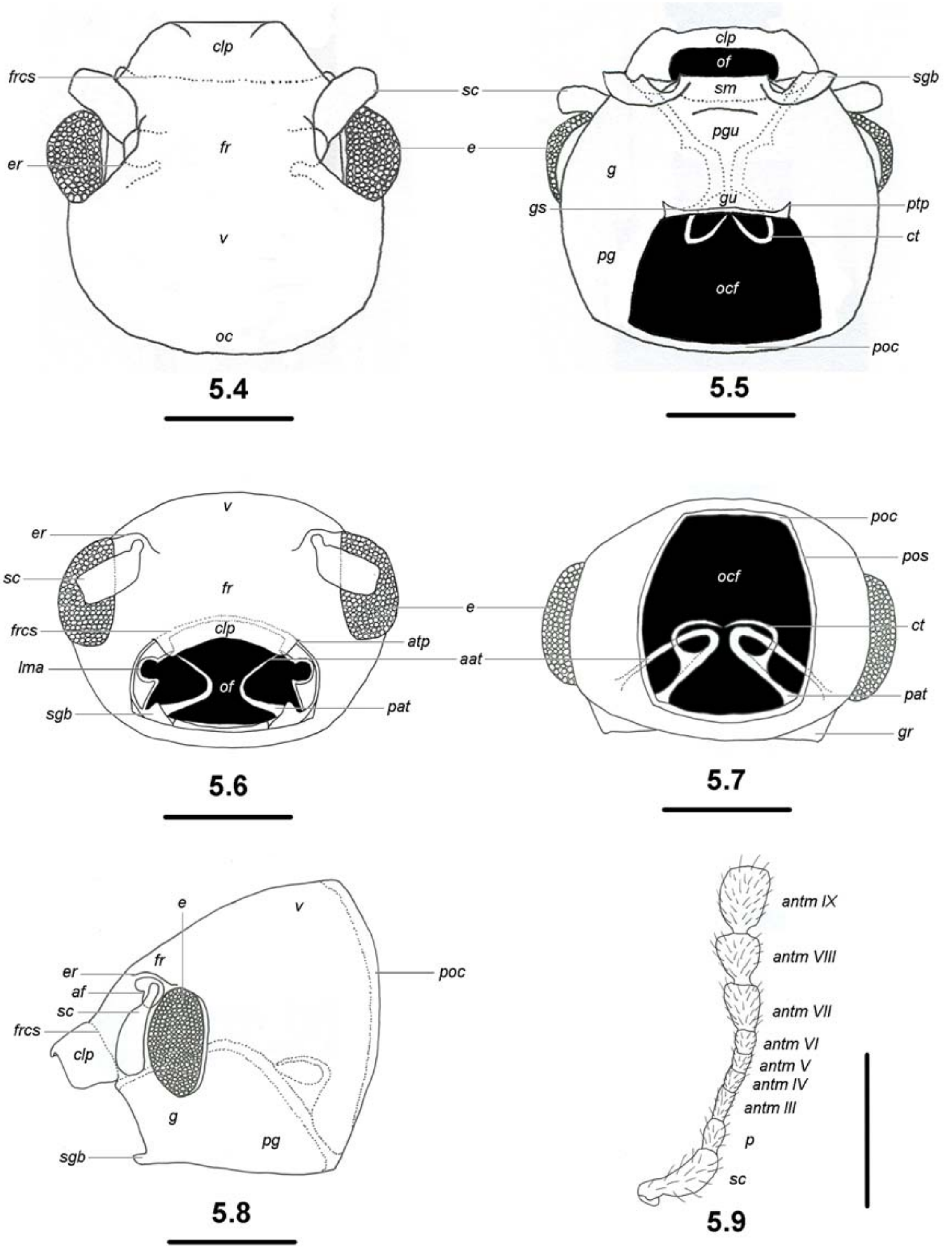
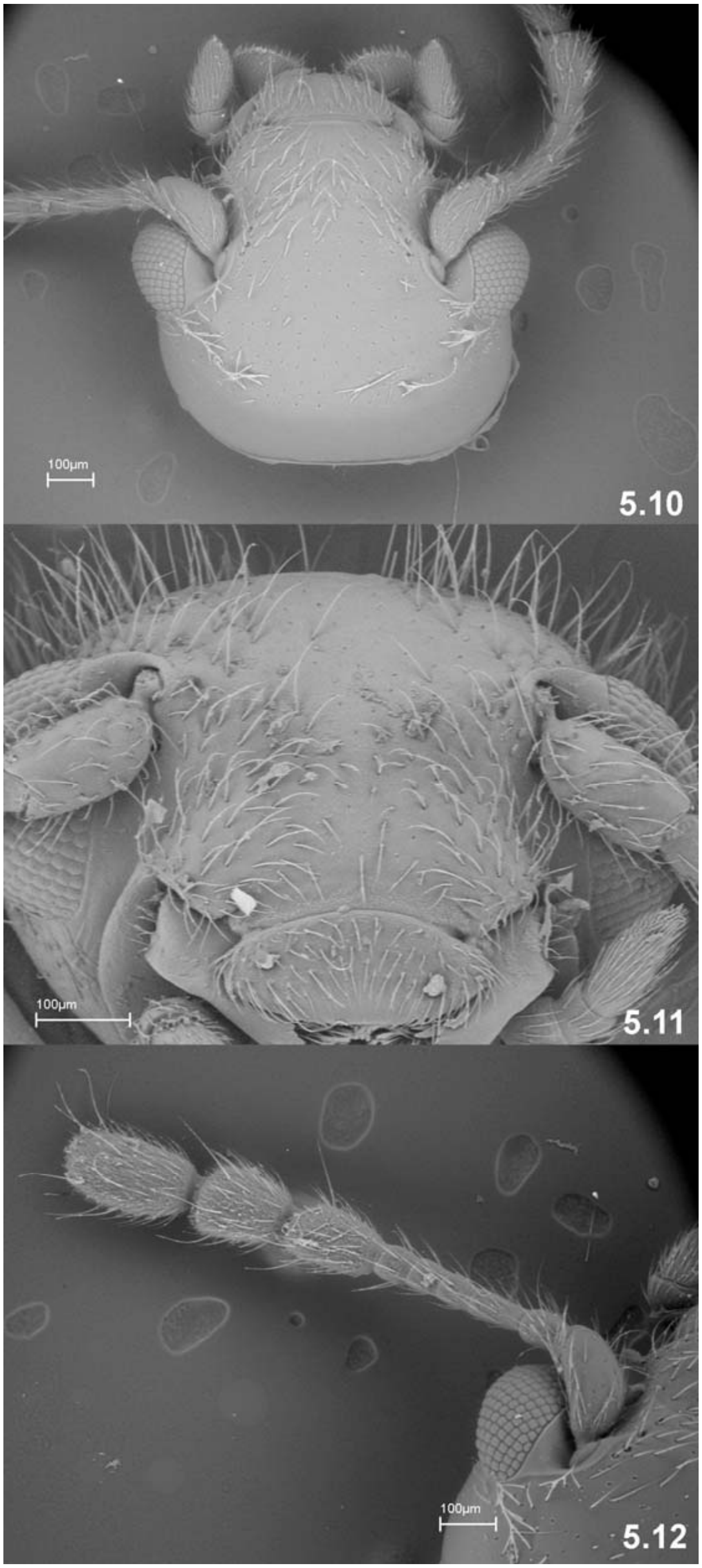


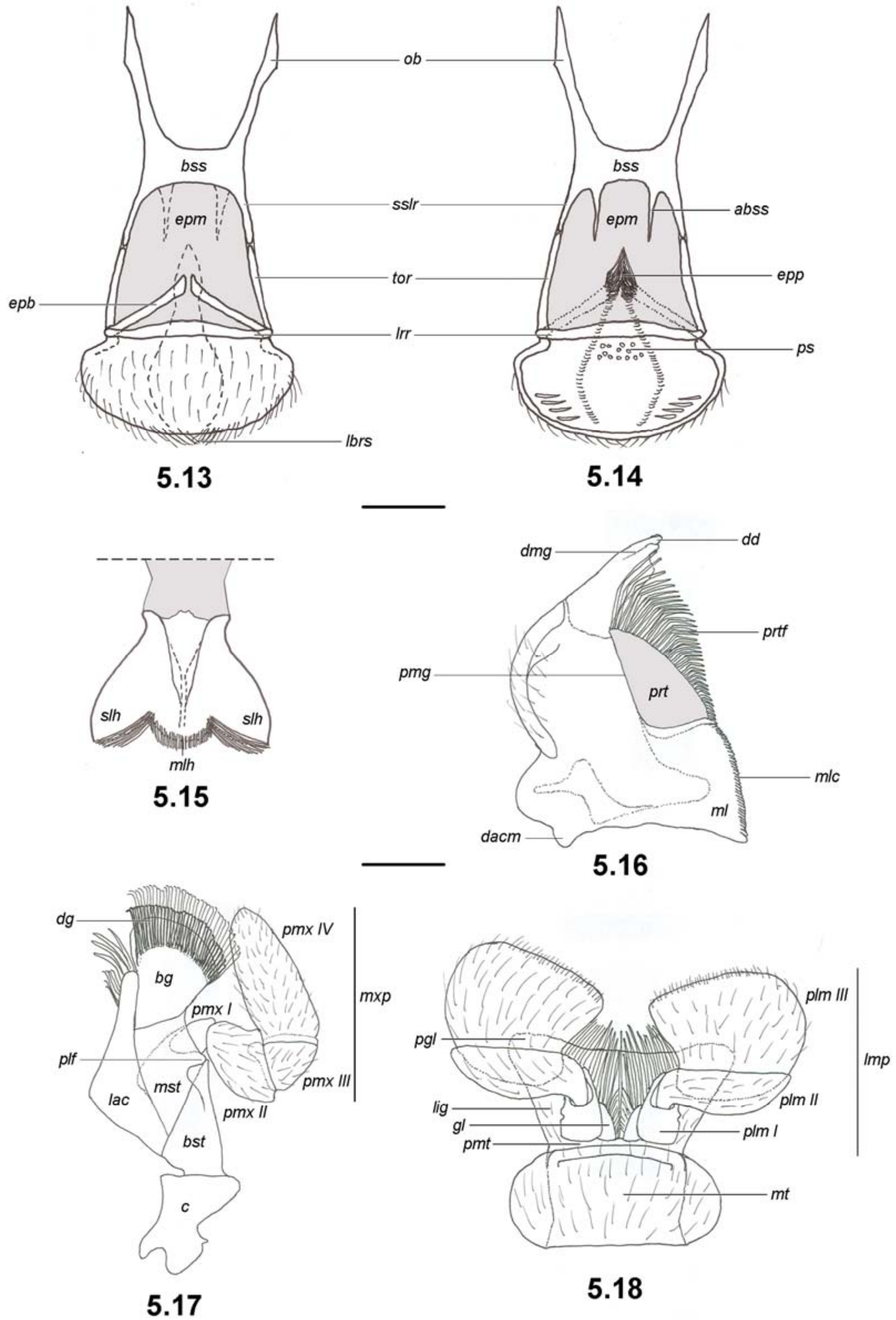
Figures 5.1-5.3. Habitus of *B. piceus* (female). **5.1)** Dorsal; **5.2)** Ventral; **5.3)** Lateral. Scale bars = 0.5 mm.



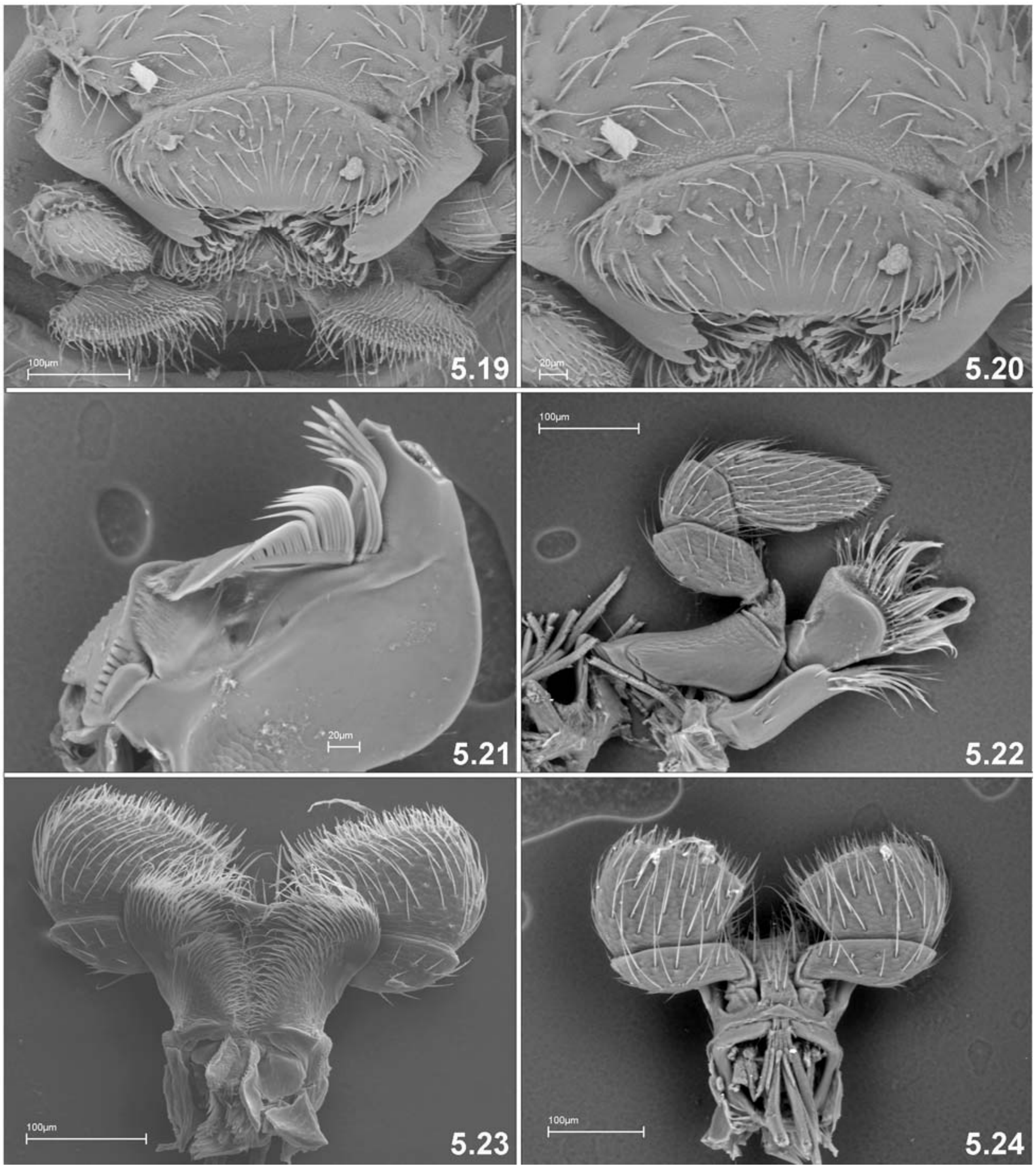
Figures 5.4-5.9. Head and antenna of *B. piceus* (mouthparts and setae removed). **5.4)** Head, dorsal; **5.5)** Head, ventral; **5.6)** Head, anterior; **5.7)** Head, posterior; **5.8)** Head, lateral; **5.9)** Antenna, dorsal (setae intact). Scale bar = 0.5 mm.



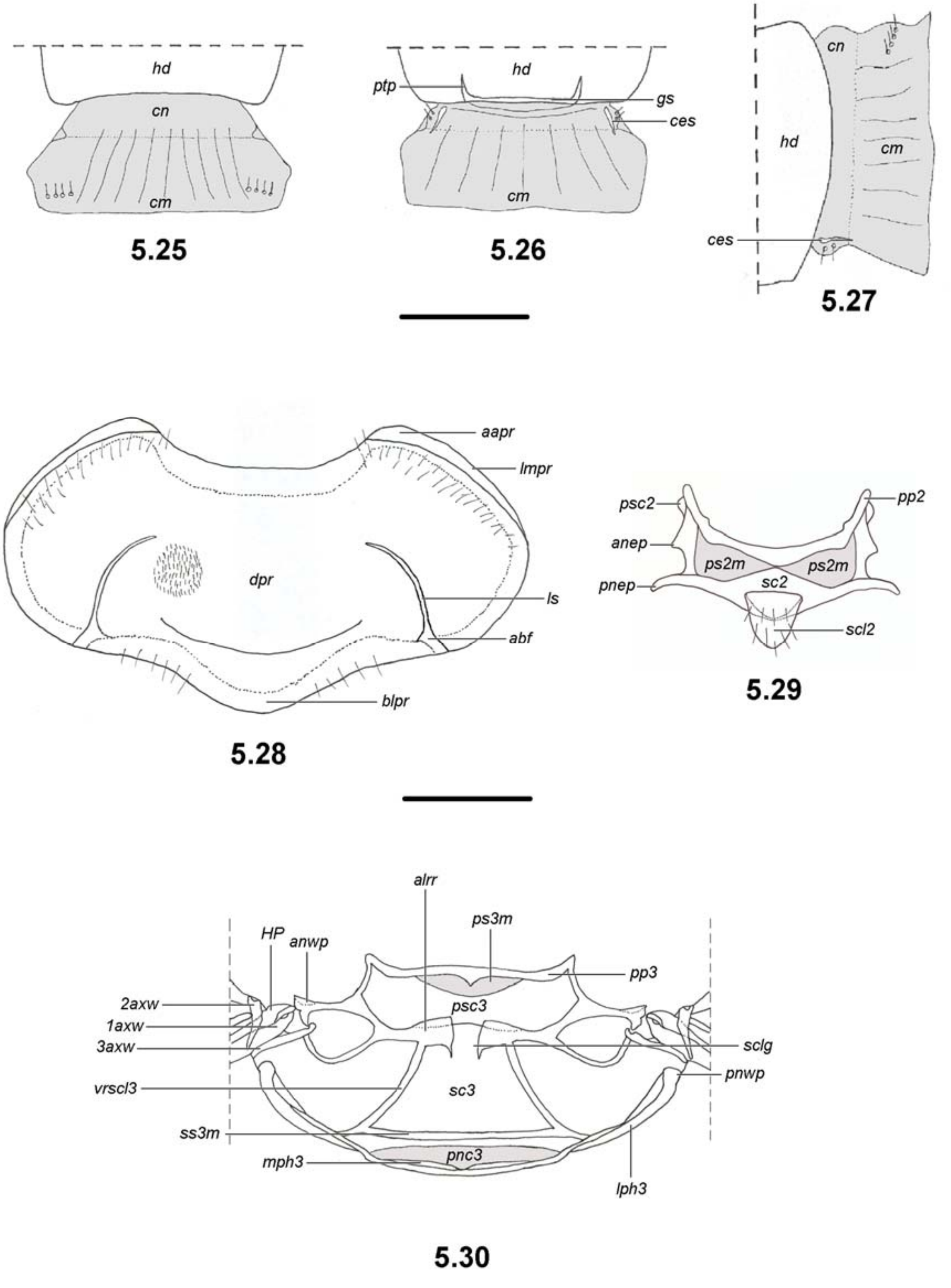
Figures 5.10-5.12. SEM of the head of *B. piceus*. **5.10)** Head, dorsal; **5.11)** Head, anterior; **5.12)** Antenna, dorsal.



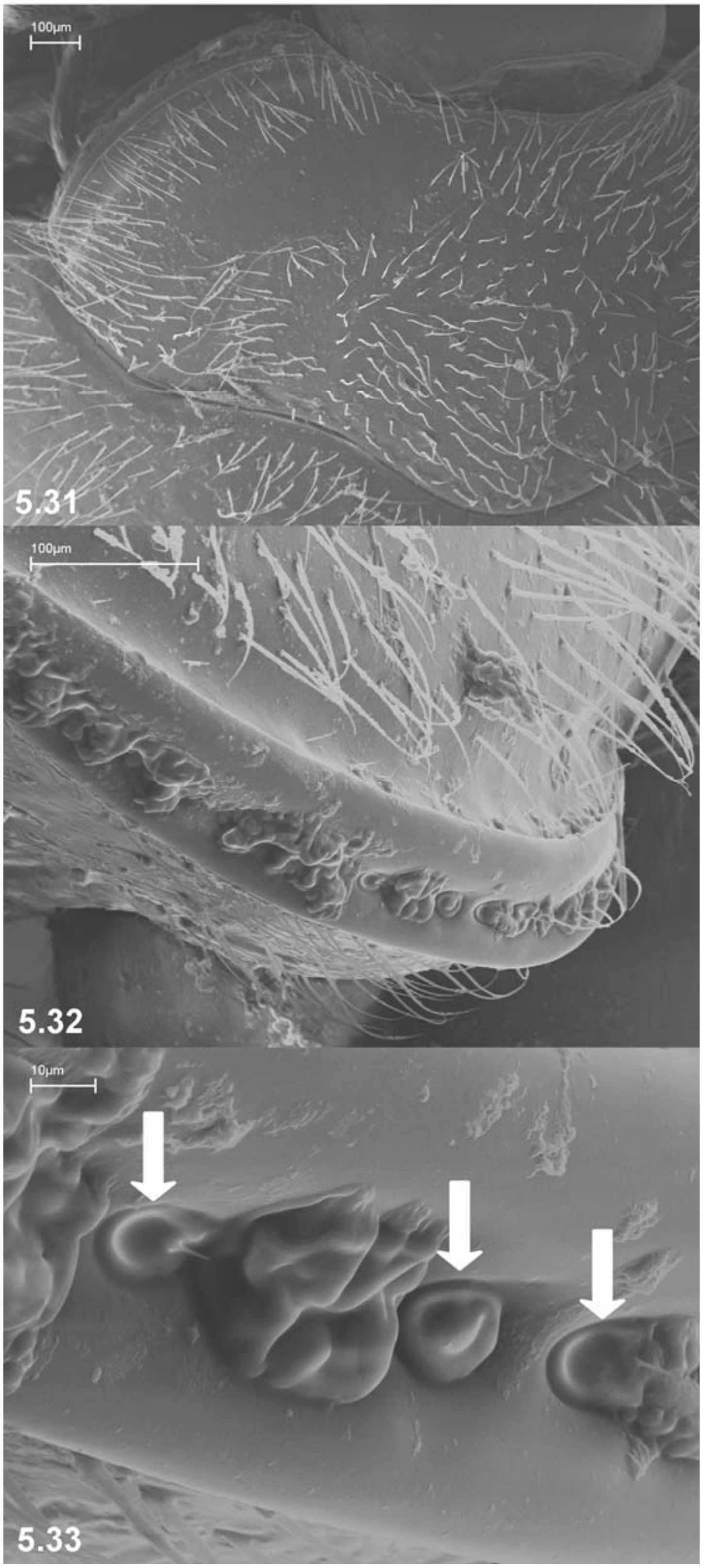
Figures 5.13-5.18. Mouthparts of *B. piceus* (membrane shaded gray). **5.13)** Labrum, dorsal; **5.14)** Labrum, ventral; **5.15)** Hypopharynx, dorsal; **5.16)** Mandible, dorsal; **5.17)** Maxilla, dorsal; **5.18)** Labium, ventral. Scale bars = 0.1 mm.



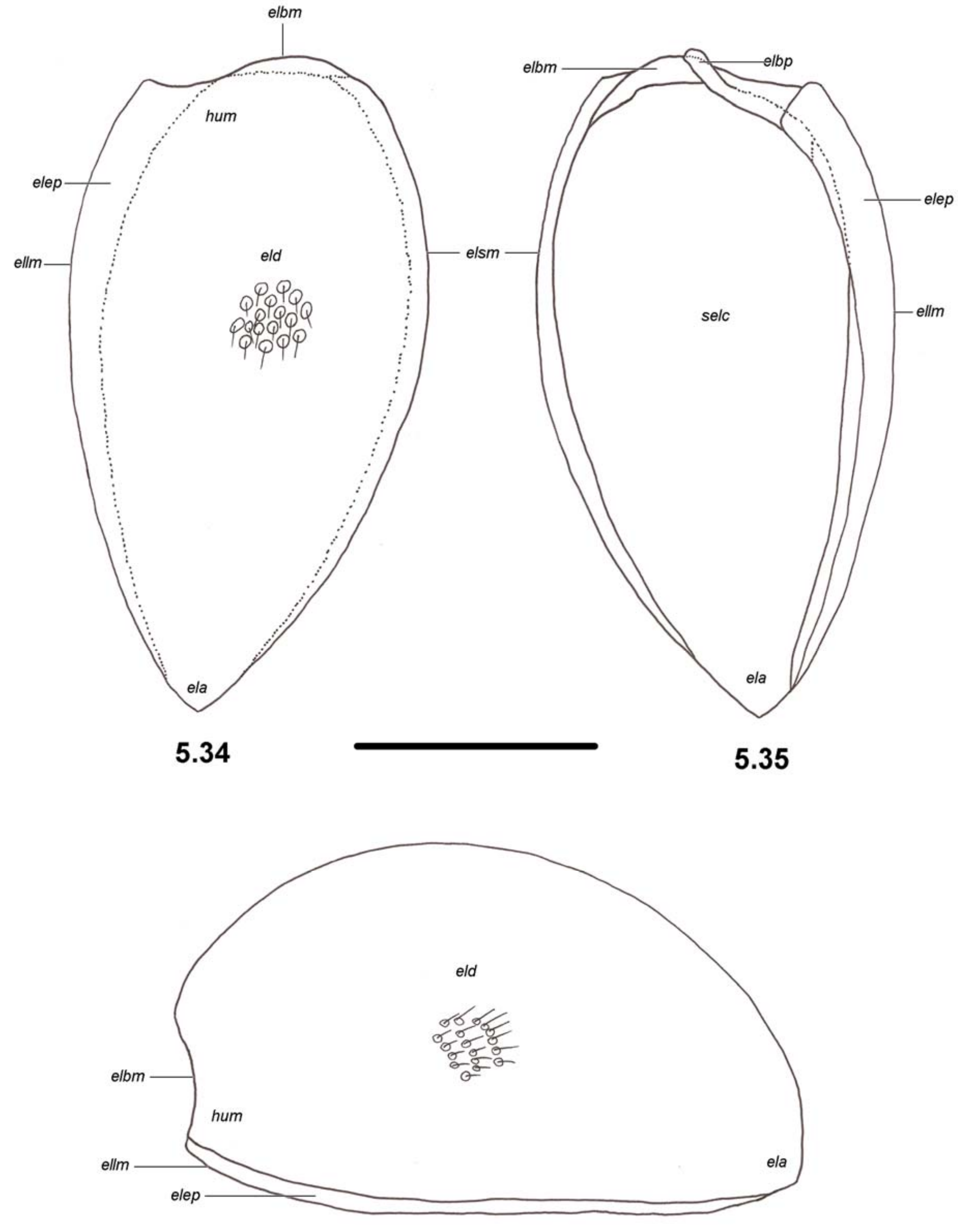
Figures 5.19-5.24. SEM of *B. piceus* mouthparts. **5.19)** Mouthparts *in situ*, anterior; **5.20)** Labrum, dorsal; **5.21)** Mandible, ventral; **5.22)** Maxilla, ventral; **5.23)** Labium, dorsal; **5.24)** Labium, ventral (mentum removed).



Figures 5.25-5.30. Cervical region and thoracic tergites of *B. piceus* (membrane shaded gray). **5.25)** Cervix, dorsal; **5.26)** Cervix, ventral; **5.27)** Cervix, lateral; **5.28)** Pronotum, dorsal; **5.29)** Mesonotum, dorsal (elytra removed); **5.30)** Metanotum, dorsal (wings transected at base). Scale bar = 0.5 mm.



Figures 5.31-5.33. SEM of the pronotum of *B. piceus*. **5.31)** Pronotum, dorsal; **5.32)** Anterolateral margin, lateral; **5.33)** Marginal pits/pores, lateral (arrows).



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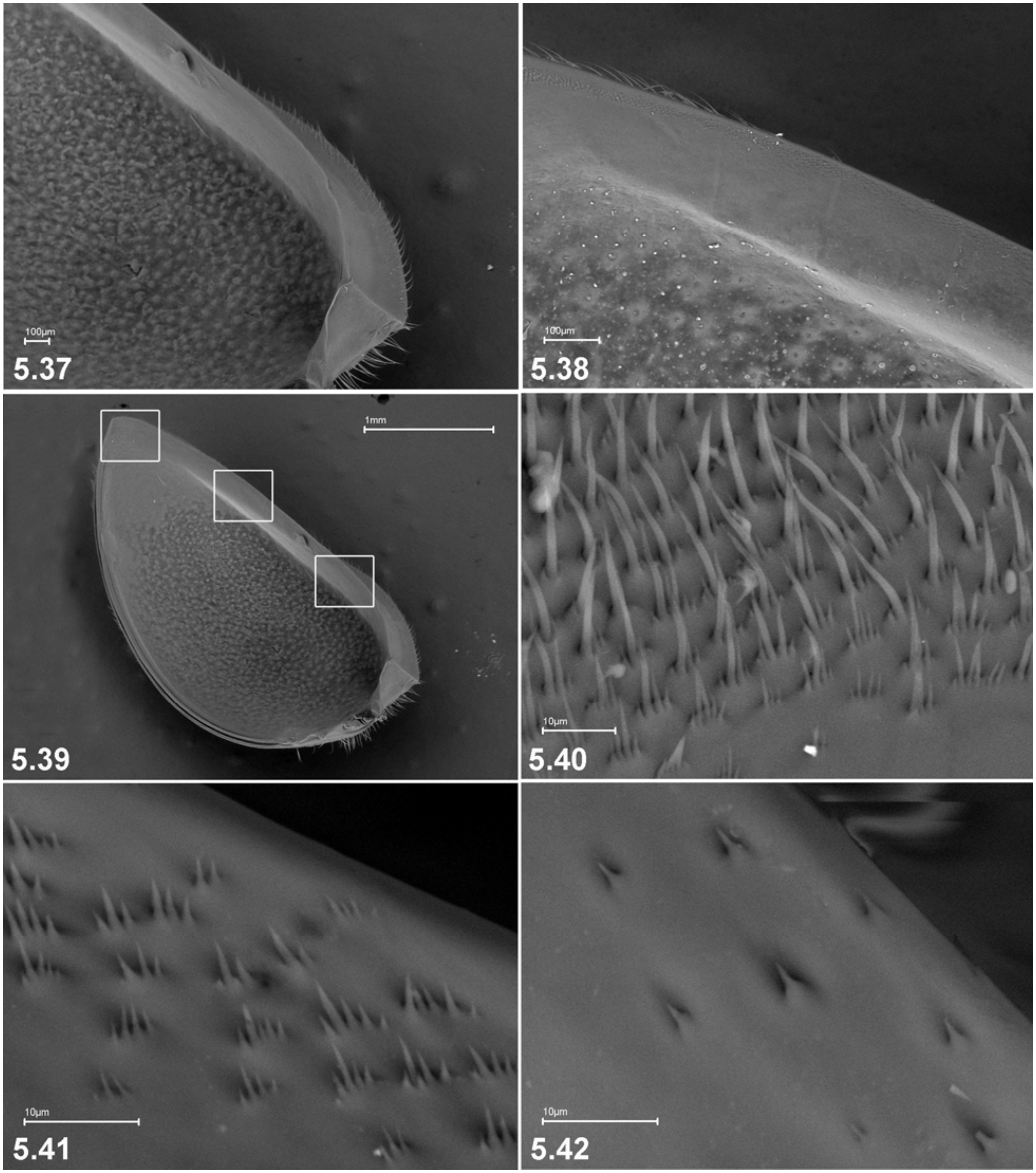
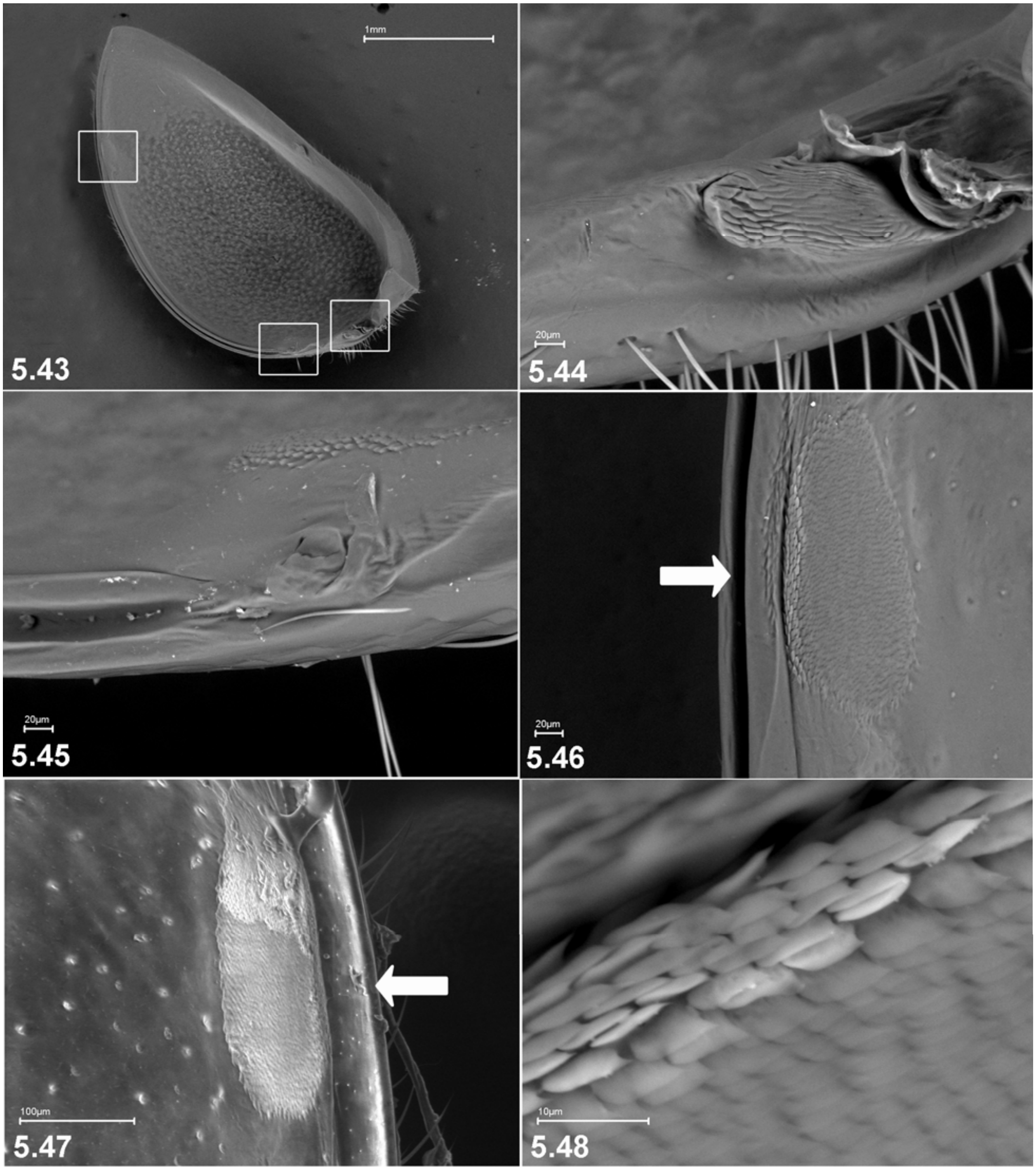
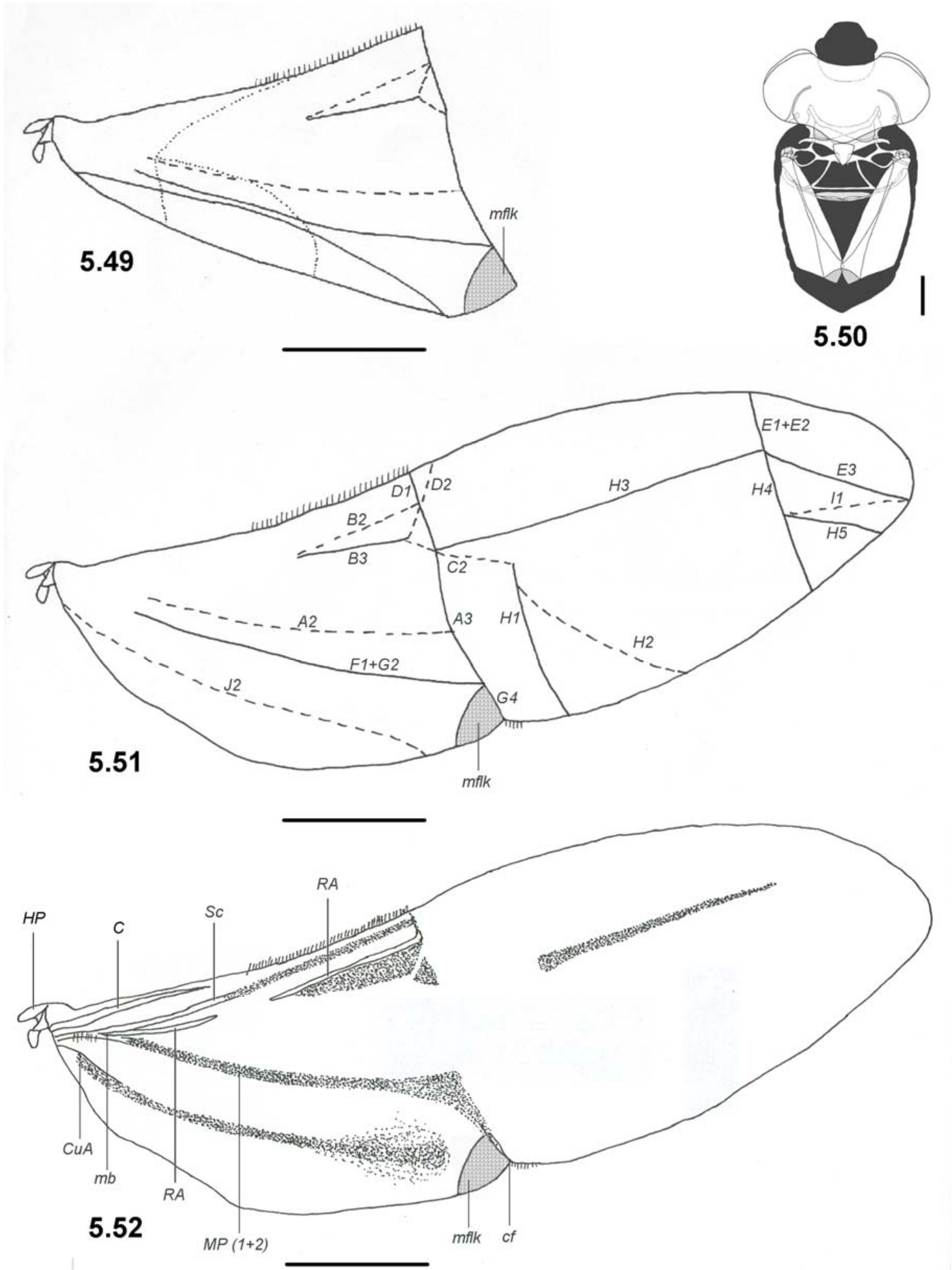
Figures 5.34-5.36. Elytron of *B. piceus*. **5.34)** Dorsal; **5.35)** Ventral; **5.36)** Lateral. Scale bar = 1.0 mm.



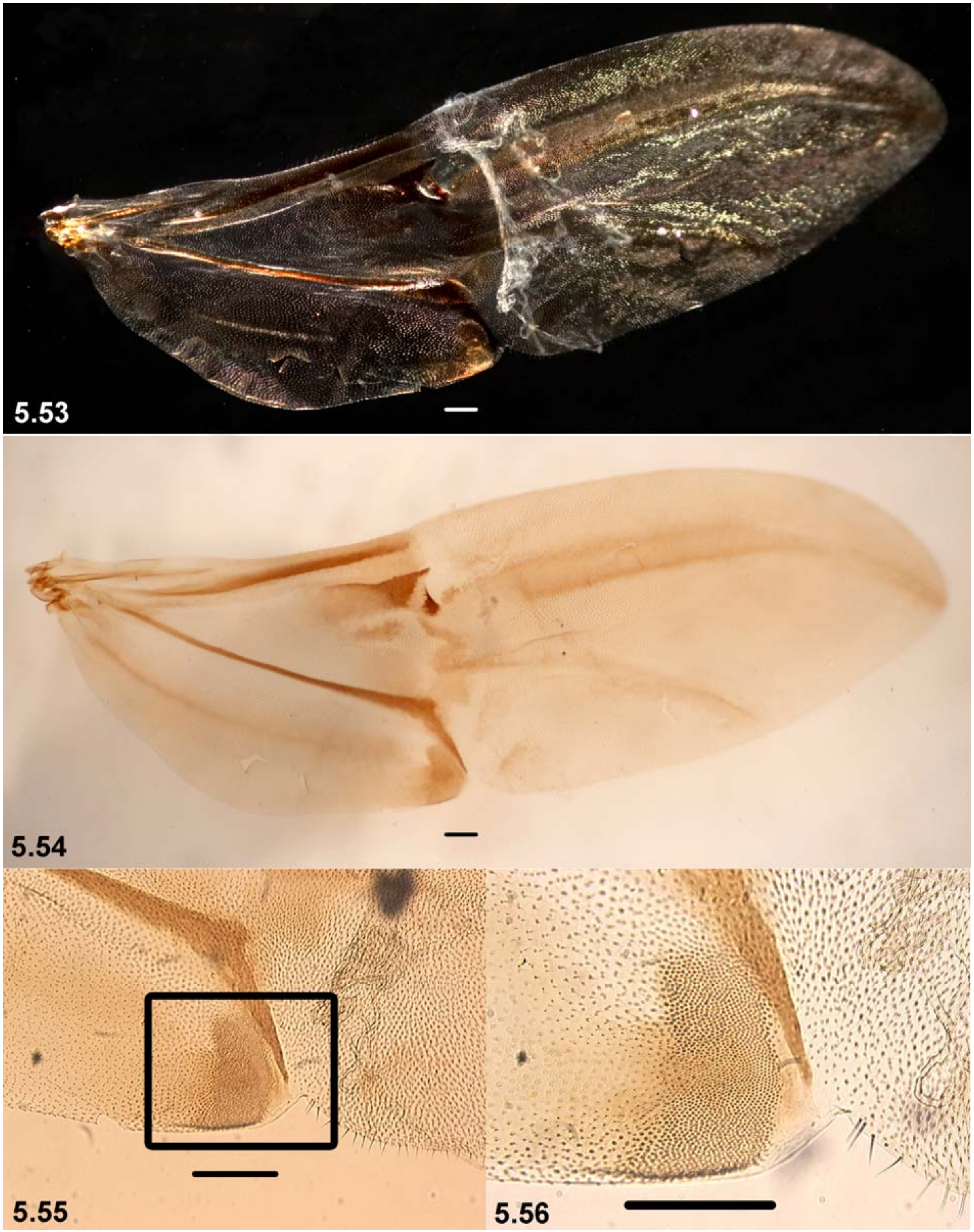
Figures 5.37-5.42. SEM of elytral epipleuron of *B. piceus*. **5.37)** Anterior near humerus, ventral; **5.38)** Near midlength, ventral; **5.39)** Right elytron, ventral (white boxes = areas examined at higher magnification); **5.40)** Setae near apex; **5.41)** Setae near midlength; **5.42)** Setae near base.



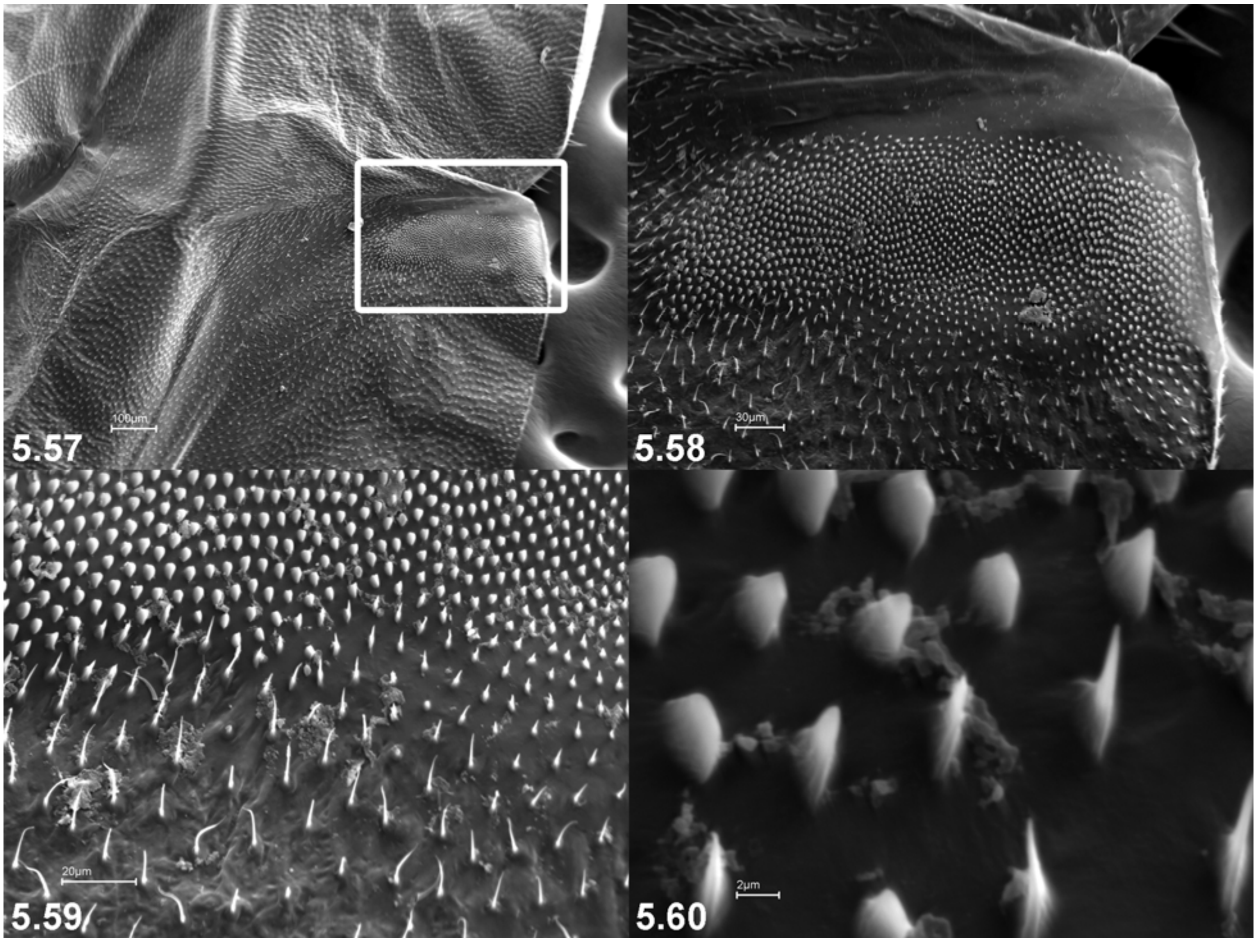
Figures 5.43-5.48. SEM of wing binding patches on elytron of *B. piceus*. **5.43)** Right elytron, ventral (white boxes = areas examined at higher magnification); **5.44)** Basal shagreened patch; **5.45)** Shagreened patch near end of groove in elytral locking mechanism; **5.46)** Posterior shagreened patch mesad of the groove of the elytral locking mechanism (white arrow); **5.47)** Posterior shagreened patch of opposing elytron mesad of the tongue of the elytral locking mechanism (white arrow); **5.48)** Microtrichiae of the posterior shagreened patch.



Figures 5.49-5.52. Wing of *B. piceus*, dorsal. **5.49)** Wing folded; **5.50)** Wings folded, *in situ*; **5.51)** Wing unfolded showing primary folds (dorsal folds = solid lines; ventral folds = dotted lines); **5.52)** Wing unfolded showing veins and areas of melanization. Scale bar = 0.5 mm.



Figures 5.53-5.56. Wing and wing binding patch (WBP) of *B. piceus*, dorsal. **5.53)** Wing, entire, side illumination; **5.54)** Wing, entire, top illumination; **5.55)** WBP (black box = area examined at higher magnification); **5.56)** Close-up of WBP. Scale bars = 0.1 mm.



Figures 5.57-5.60. SEM of wing binding patch (WBP) of *B. piceus*, dorsal. **5.57)** WBP (white box = area examined at higher magnification); **5.58)** Close-up of WBP; **5.59)** Transition between two different forms of microtrichiae at edge of WBP; **5.60)** WBP microtrichiae.

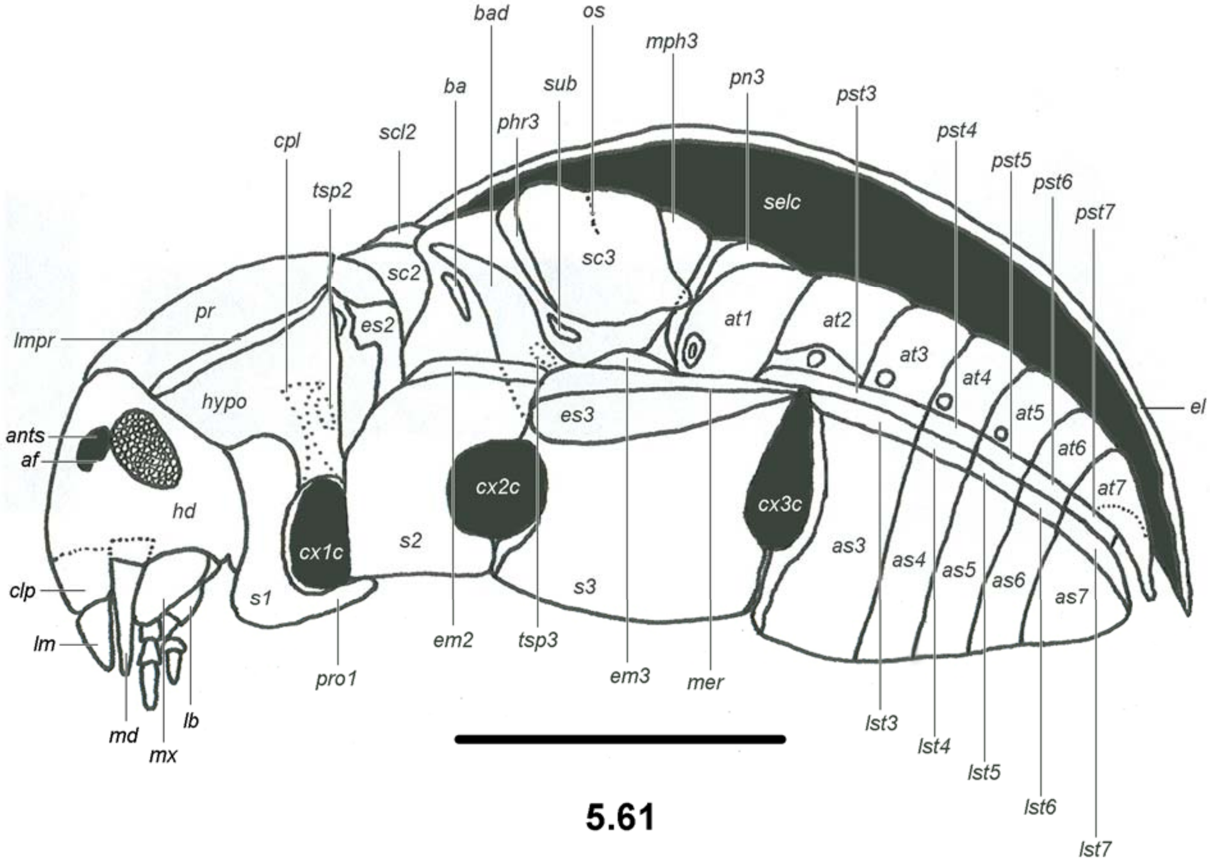


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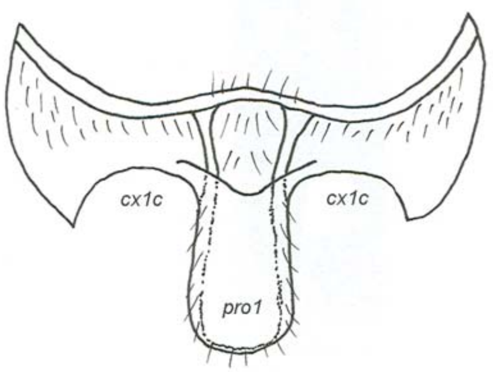
Figure 5.61. Lateral habitus of *B. piceus* (left antenna, elytron and legs excised). Scale bar = 1.0 mm.



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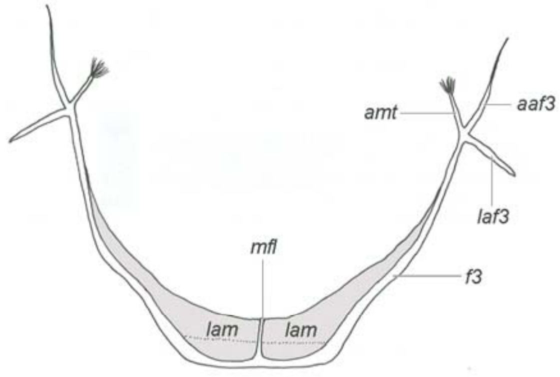

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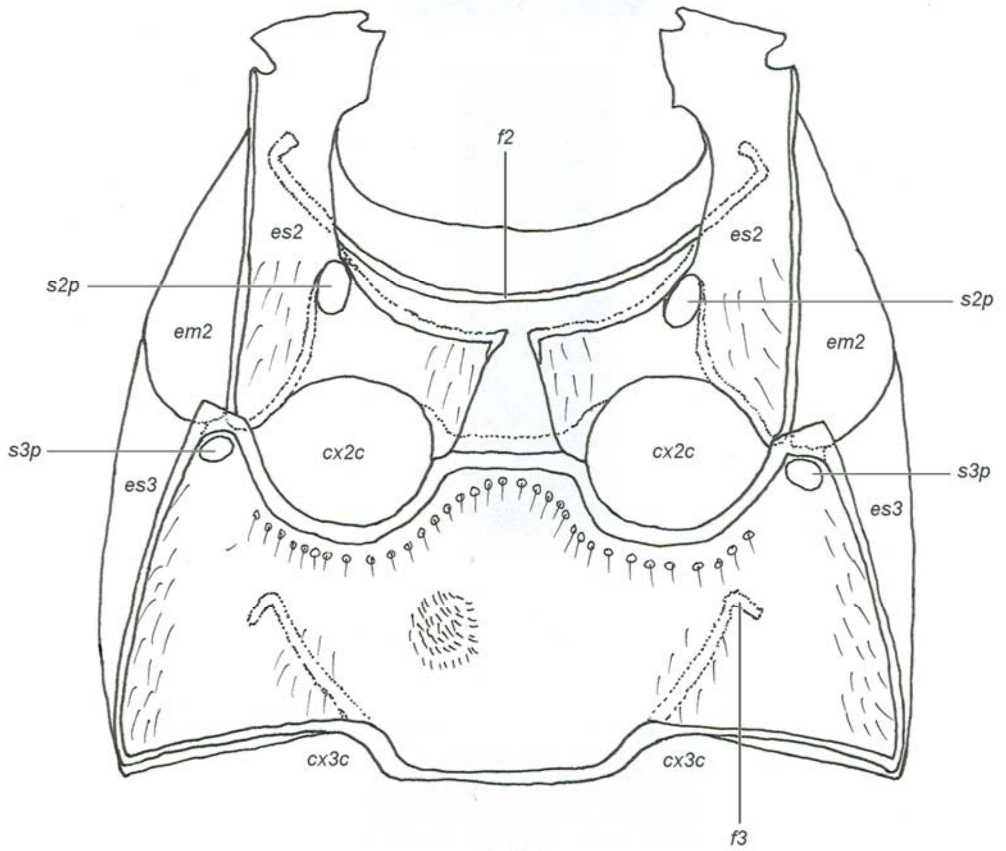

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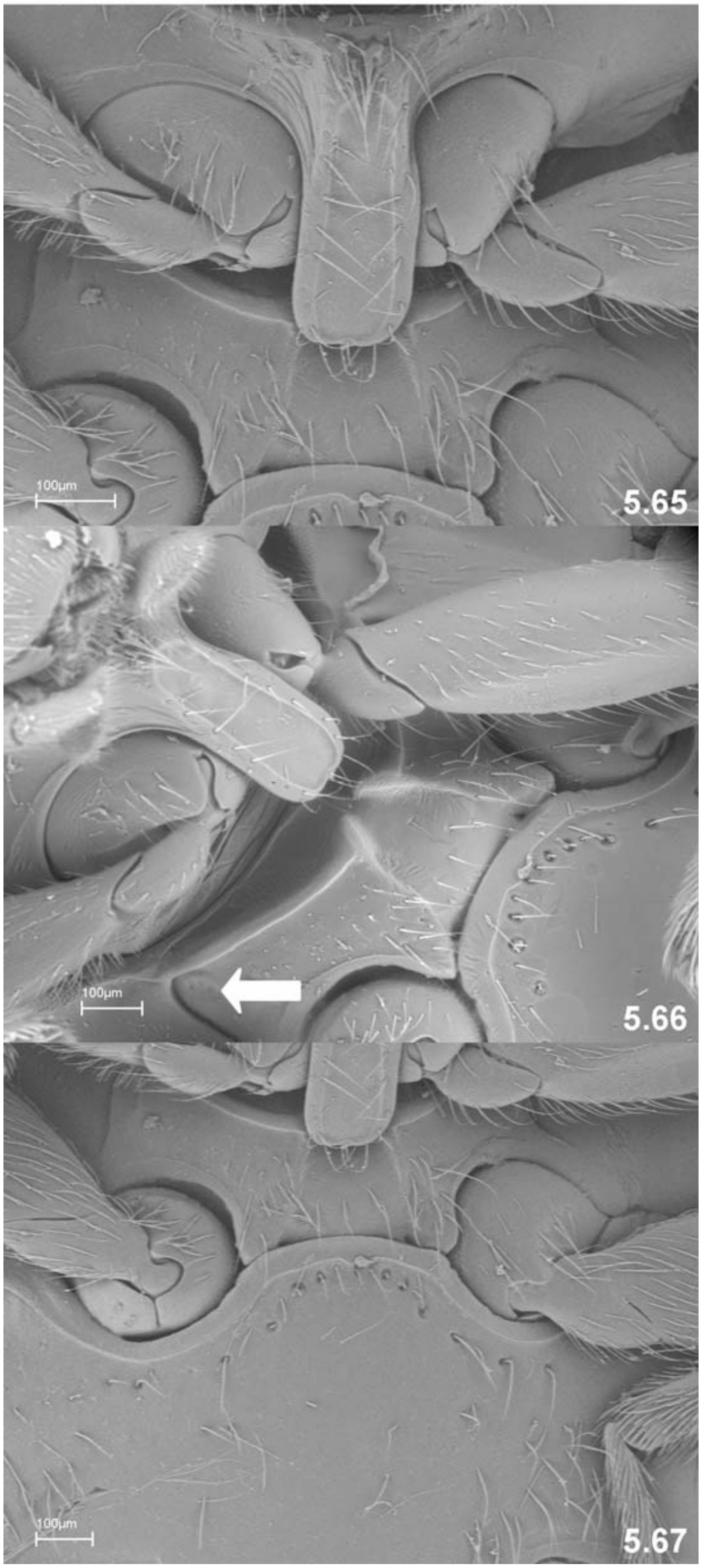
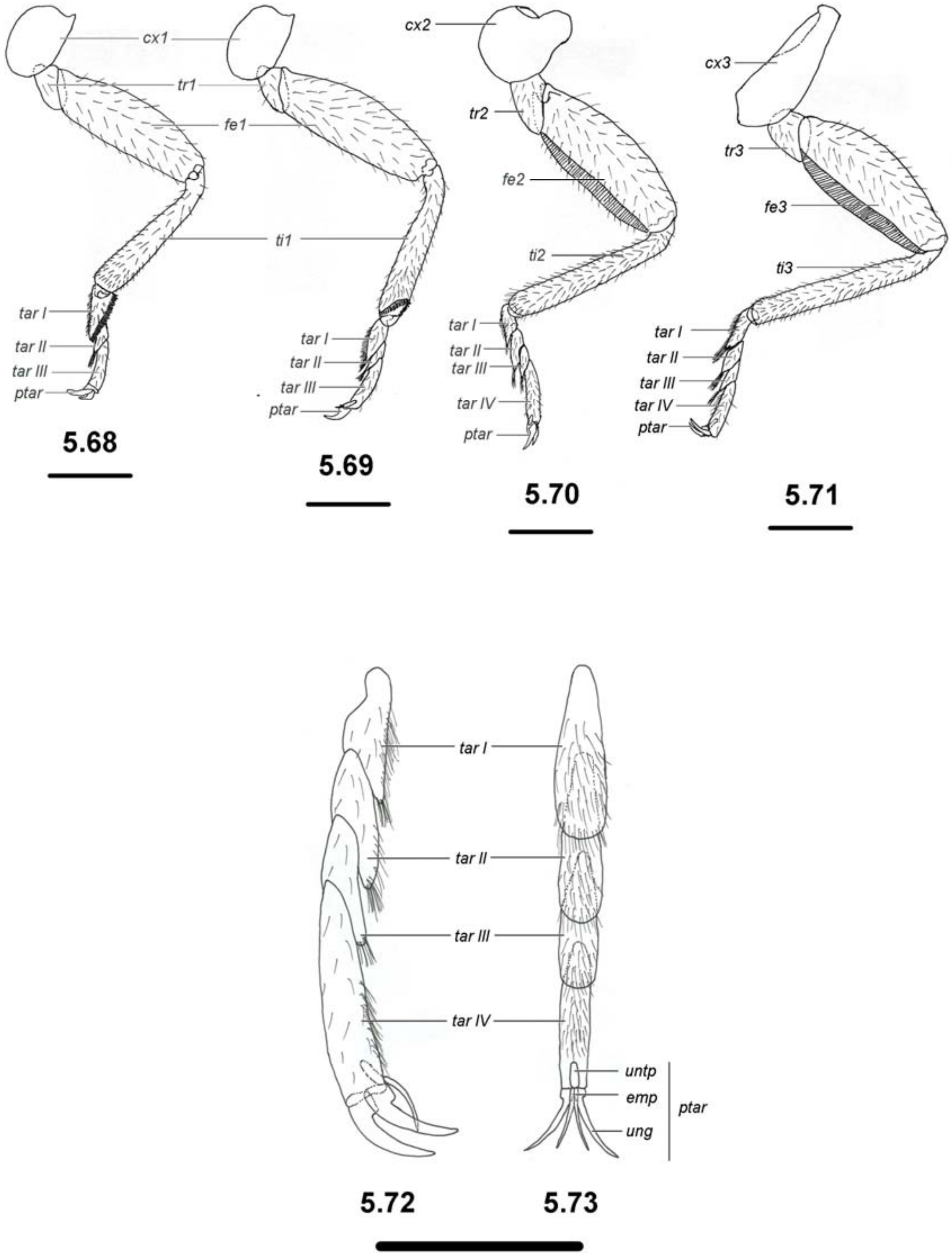
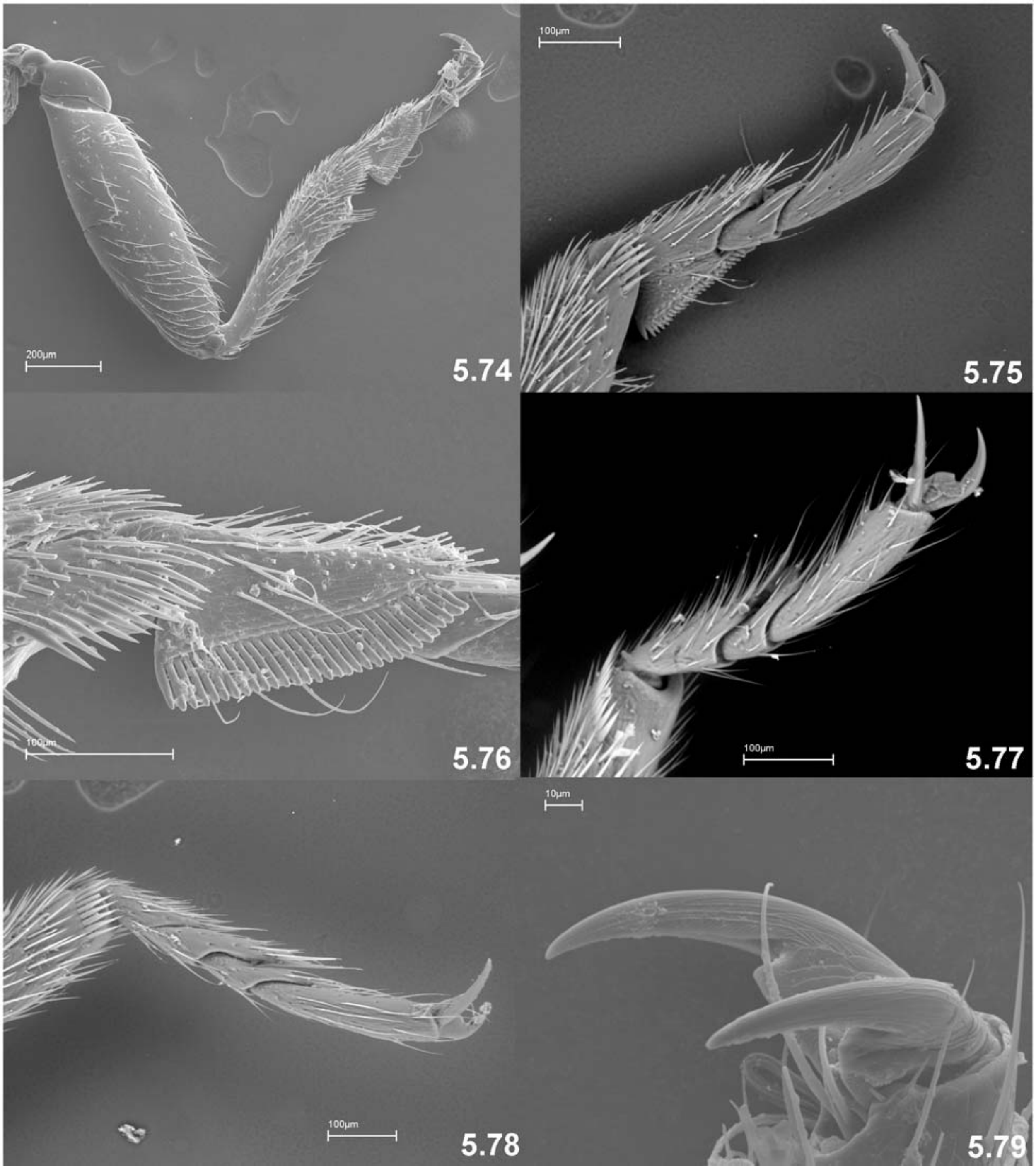
Figures 5.62-5.64. Thoracic sternites of *B. piceus*, ventral (membrane shaded gray). **5.62)** Prosternum; **5.63)** Metendosternite; **5.64)** Meso- and Metasternum. Scale bar = 0.5 mm.



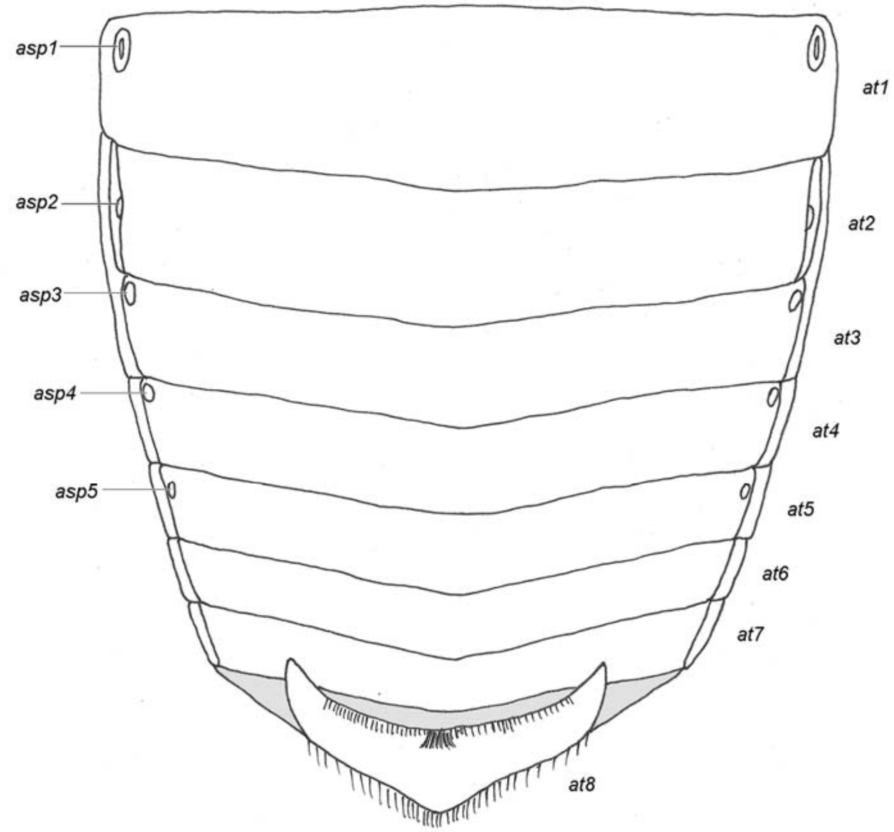
Figures 5.65-5.67. SEM of thoracic venter of *B. piceus*, ventral. **5.65)** Prosternum and mesosternum; **5.66)** Mesosternal “pit” (white arrow); **5.67)** Metasternum.



Figures 5.68-5.73. Legs and tarsi of *B. piceus*. **5.68)** Prothoracic leg, male; **5.69)** Prothoracic leg, female; **5.70)** Mesothoracic leg; **5.71)** Metathoracic leg; **5.72)** Mesothoracic tarsus, lateral; **5.73)** Mesothoracic tarsus, ventral. Scale bars = 0.5 mm.



Figures 5.74-5.79. SEM of legs and tarsi of *B. piceus*. **5.74)** Prothoracic leg, male; **5.75)** Prothoracic tarsus, male; **5.76)** Pectinate comb of male basitarsus; **5.77)** Prothoracic tarsus, female; **5.78)** Mesothoracic tarsus; **5.79)** Pretarsus.



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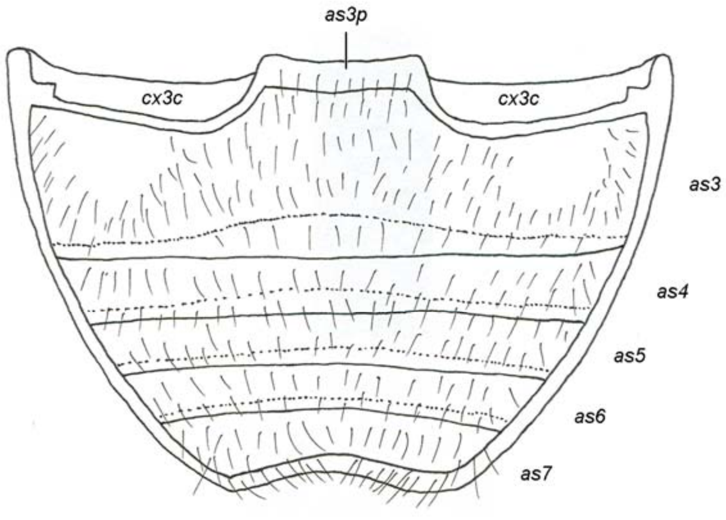

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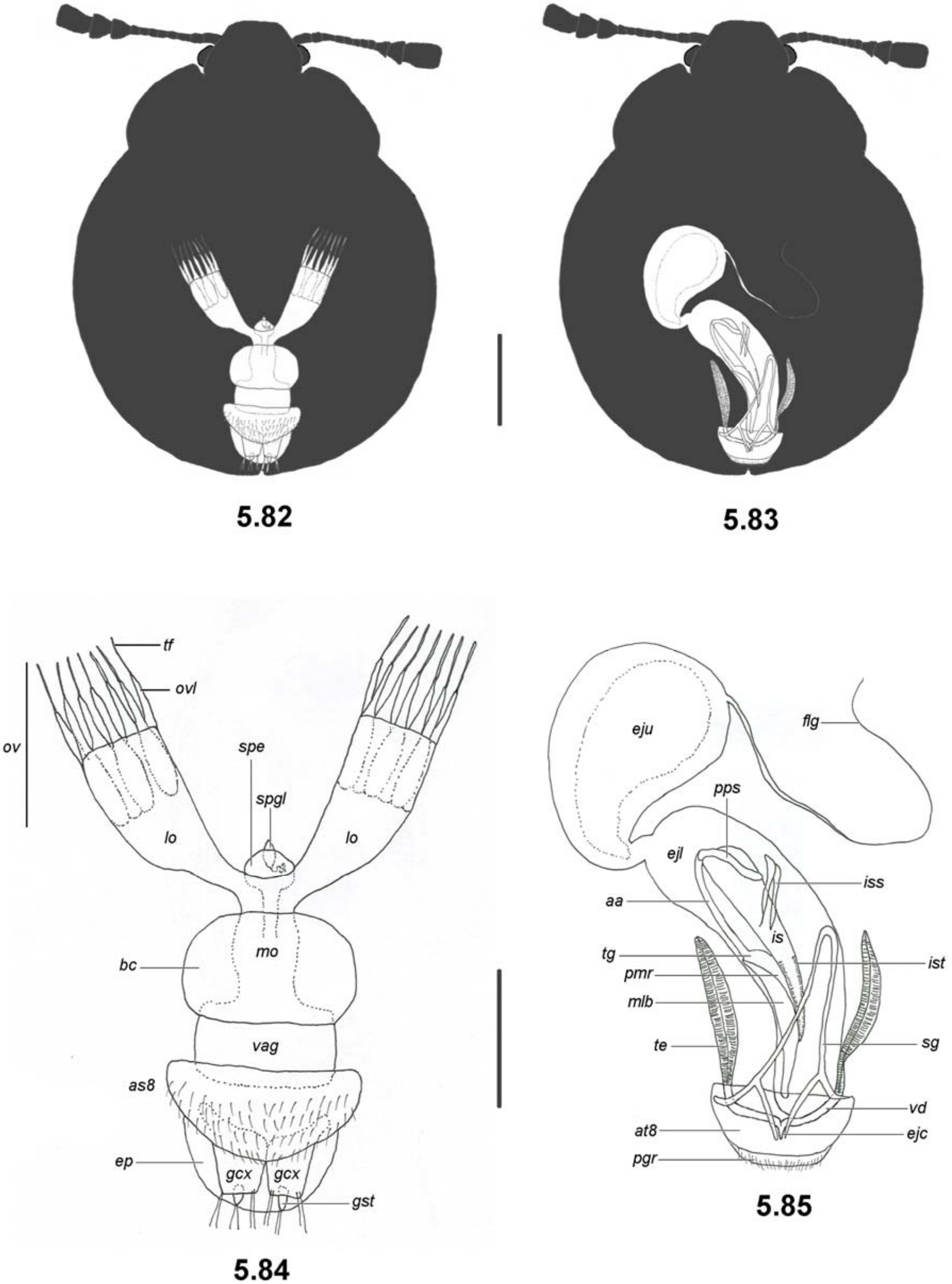
Figures 5.80-5.81. Abdomen of *B. piceus* (membrane shaded gray). **5.80)** Dorsal; **5.81)** Ventral. Scale bar = 0.5 mm.



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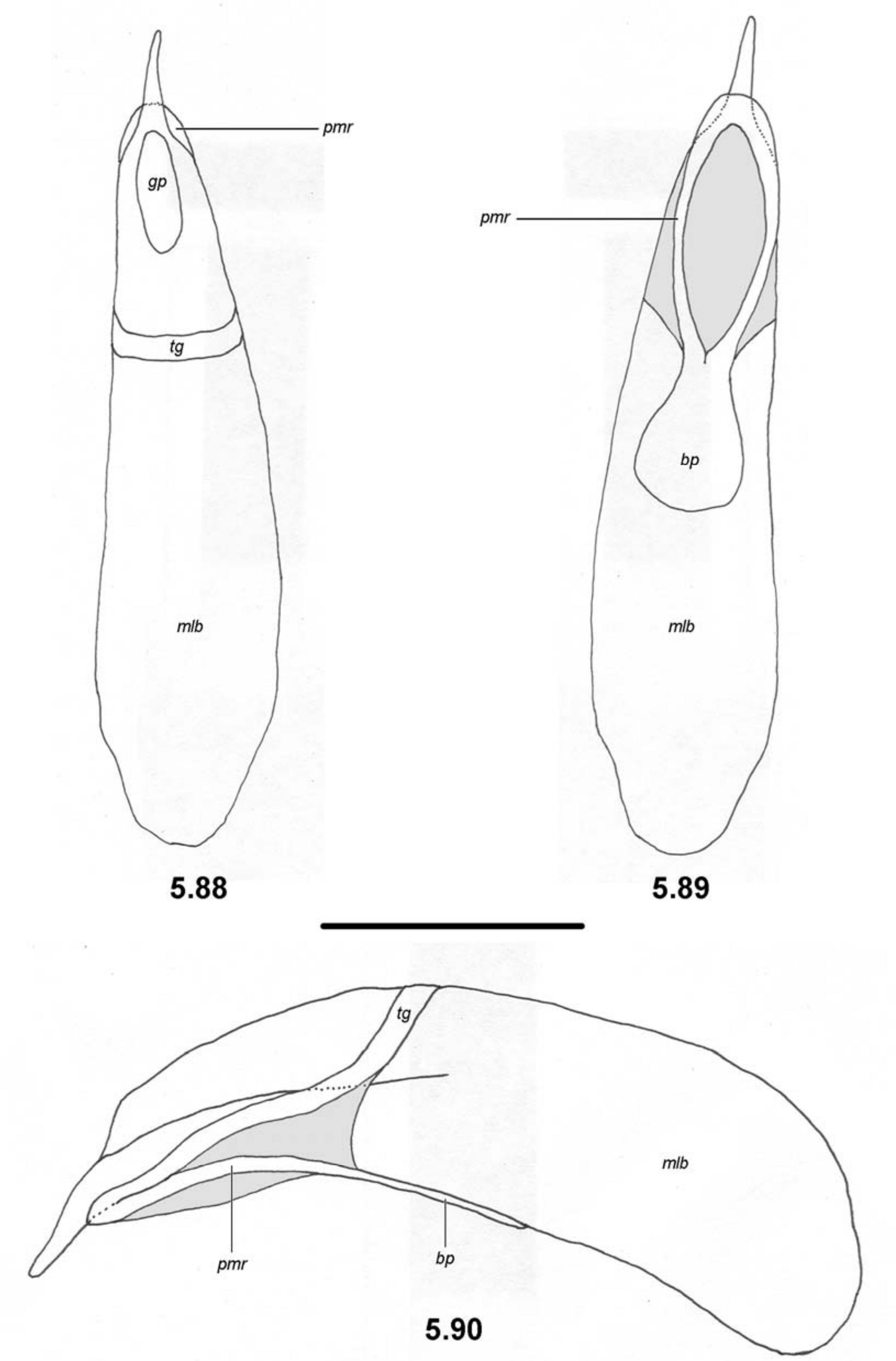
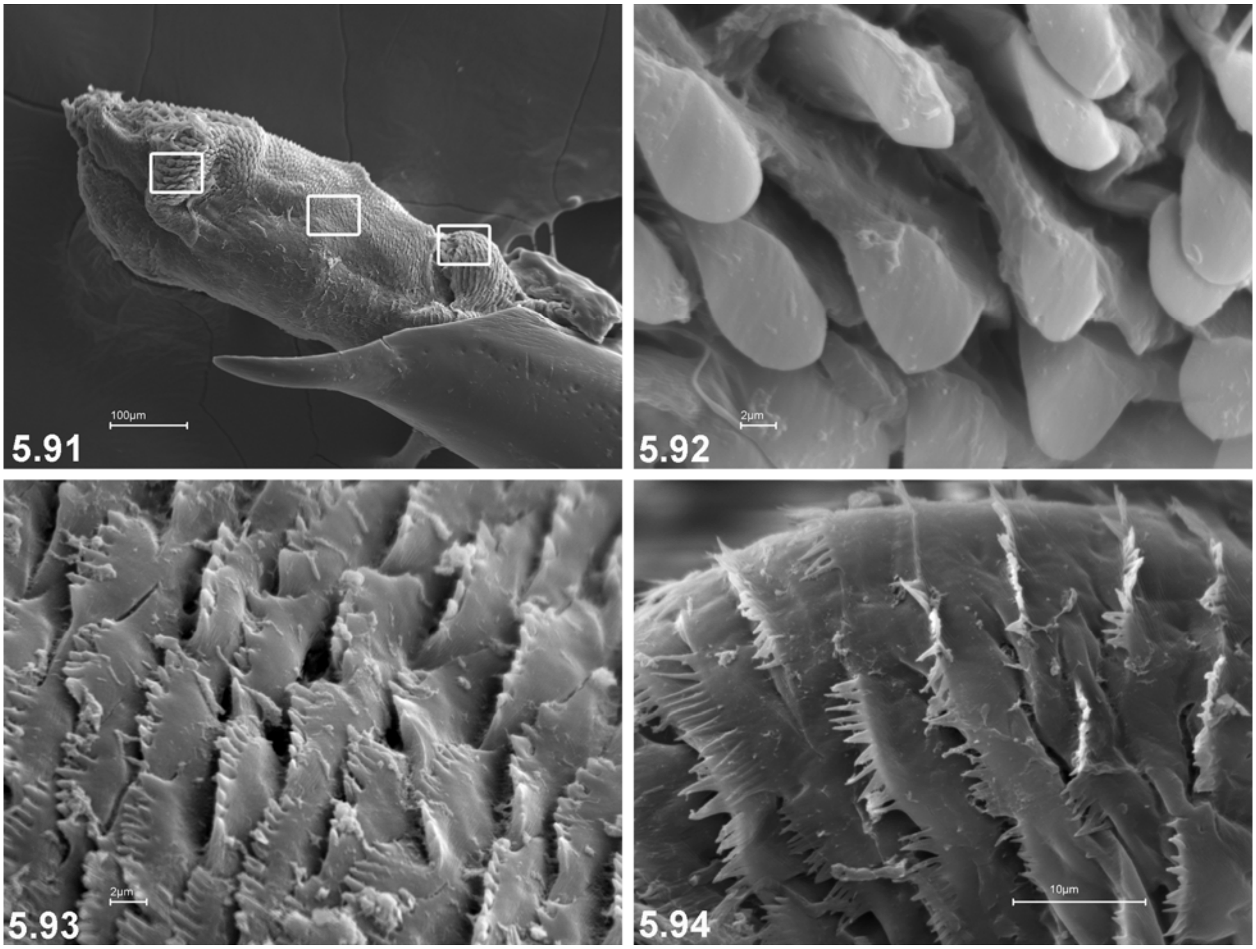
Figures 5.82-5.85. Reproductive Systems of *B. piceus*, ventral. **5.82)** Female, *in situ*; **5.83)** Male, *in situ*; **5.84)** Female; **5.85)** Male. Scale bars = 0.5 mm.

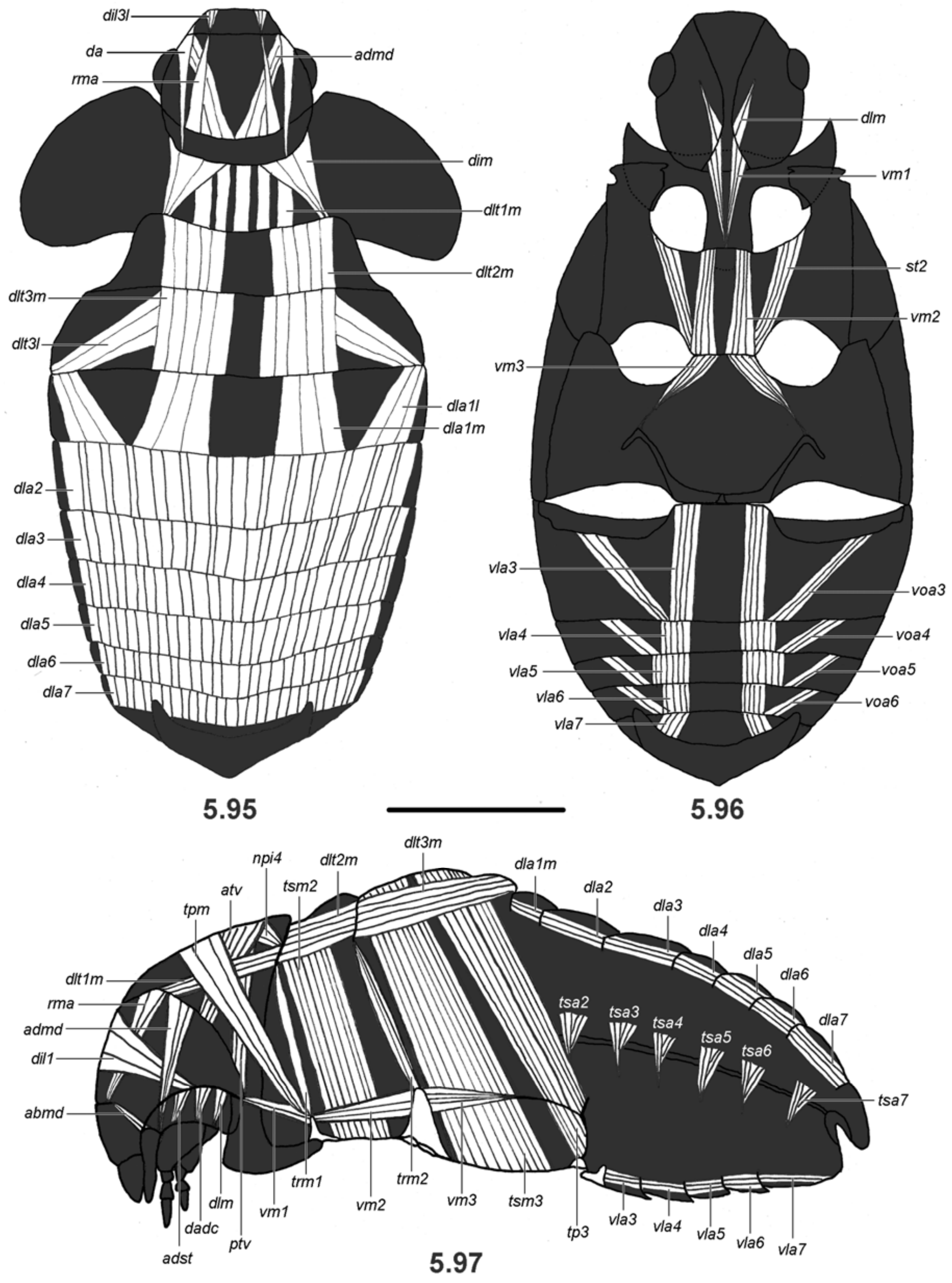
Figure 5.86-5.87. Aedeagus of *B. piceus*, lateral. **5.86)** Median lobe, internal sac not everted; **5.87)** Tip of median lobe, with internal sac everted. Scale bar = 0.5 mm.



Figures 5.88-5.90. Median lobe of *B. piceus* (membrane shaded gray). **5.88)** Dorsal; **5.89)** Ventral; **5.90)** Lateral. Scale bar = 0.5 mm.



Figures 5.91-5.94. SEM of the internal sac of *B. piceus*, lateral. **5.91)** Entire (white boxes = areas examined at higher magnification); **5.92)** Clavate teeth on ventrolateral lobe near apex; **5.93)** Lamellate teeth near midlength; **5.94)** Lamellate teeth near base with apical fringe of stout setae.



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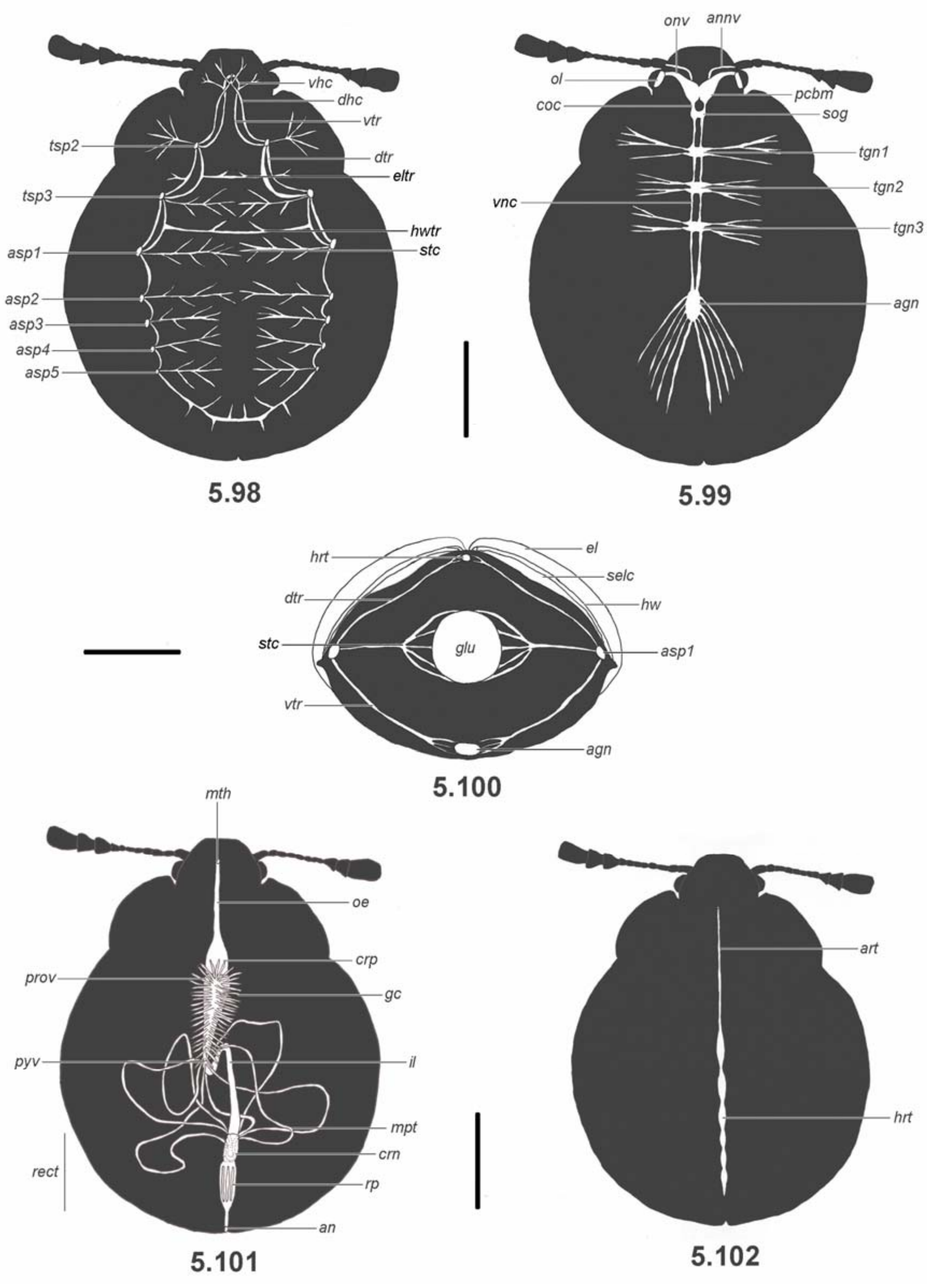

Figures 5.98-5.102. Internal organ systems of *B. piceus, in situ* (diagrammatic). **5.98)** Respiratory, dorsal; **5.99)** Nervous, dorsal; **5.100)** Respiratory, anterior, cross-section at junction between metathorax and abdominal segment 1; **5.101)** Digestive, dorsal; **5.102)** Vascular, dorsal. Scale bars = 1.0 mm.

Supplemental Material 5.1. List of abbreviations used in figures (abd. = abdominal, interseg. = intersegmental, m. = muscle).

1axw	1st axillary sclerite
2axw	2nd axillary sclerite
3axw	3rd axillary sclerite
A2	cubital fold
A3	median fold
aa	aedeagal apodeme
aaf3	anterior arm of metafurca
aapr	anterior angle of pronotum
aat	anterior arms of tentorium
abf	antebasal fovea
abmd	abductor m. of mandible
abss	anterior arm of suspensory sclerites
admd	adductor m. of mandible
adst	adductor m. of stipes
af	antennifer
agn	abdominal ganglion
alrr	alar ridge of metascutellum
amt	anterior metafurcal tendons
an	anus
anep	anterior notal elytral process
annv	antennal nerve
antm	antennomere
ants	antennal socket
anwp	anterior notal wing process
art	aorta
as	abdominal sternite
as3p	intercoxal process of abd. sternite 3
asp	abdominal spiracle
at	abdominal tergite
atp	anterior tentorial pit
atv	anterior tergo-ventral m. of prothorax
B2	proximal convex pivot fold
B3	proximal concave pívot fold
ba	basalare
bad	basalar disc
bc	bursa copulatrix
bg	basigalea
blpr	basal lobe of pronotum
bp	basal piece of tegmen
bss	posterior bridge of suspensory sclerites
bst	basistipes
C	costa
c	cardo
C2	antemedial fold
ces	cervepisternum
cf	claval furrow
clp	clypeus
cm	cervical membrane
cn	cervinotum
coc	circumesophageal connective
cpl	cryptopleuron (proendosternite)
crn	cryptonephridium
crp	crop
ct	corpotentorium
CuA	cubitoanal
cx1	prothoracic coxa
cx1c	procoxal cavity
cx2	mesothoracic coxa
cx2c	mesocoxal cavity
cx3	metathoracic coxa
cx3c	metacoxal cavity
D1	distal concave pivot fold
D2	distal convex pivot fold
da	depressor m. of antenna
dacm	dorsal articulatory condyle of mandible
dadc	dorsal adductor m. of cardo
dd	distidentes
dg	distigalea
dhc	dorsal head commissures
dil1	dilator m. of cibarium
dil3l	lateral dilator m. of anterior pharynx
dim	dorsal intersegmental m. of prothorax
dla	dorsal longitudinal m. of abd. segment
dla1l	lateral dorsal longitudinal m. of abd. seg. 1
dla1m	medial dorsal longitudinal m. of abd. seg. 1
dlm	dorsal m. of labium
dlt1m	medial dorsal longitudinal m. of prothorax
dlt2m	medial dorsal longitudinal m. of mesothorax
dlt3l	lateral dorsal longitudinal m. of metathorax
dlt3m	medial dorsal longitudinal m. of metathorax
dmg	distal mandibular groove
dpr	disc of pronotum
dtr	dorsal trunk
e	compound eye
E1+E2	1st costo-apical
E3	2nd costo-apical
ejc	common ejaculatory duct
ejl	lower ejaculatory duct
eju	upper ejaculatory duct
el	elytron
ela	elytral apex
elbm	basal margin of elytron
elbp	basal elytral process
eld	elytral disc
elep	elytral epipleuron
ellm	lateral margin of elytron
elsm	sutural margin of elytron
eltr	elytral tracheal bridge
em2	mesepimeron
em3	metepimeron
emp	empodium
ep	epiproct
epb	epipharyngeal brace
epm	epipharyngeal membrane

epp	epipharyngeal process
er	epistomal ridge
es2	mesepisternum
es3	metepisternum
F1+G2	anal folds
f2	mesofurca of mesendosternite
f3	metafurca of metendosternite
fe1	prothoracic femur
fe2	mesothoracic femur
fe3	metathoracic femur
flg	flagellum
fr	frons
frcs	fronto-clypeal suture
g	gena
G4	claval fold
gc	gastric caeca
gcx	gonocoxa
gl	glossa
glu	gut lumen
gp	gonopore
gr	gular ridge
gs	gular suture
gst	gonostylus
gu	gula
H1-5	principle folds
hd	head
HP	humeral plate
hrt	heart
hum	humerus
hw	hind wing
hwtr	hind wing tracheal bridge
hypo	hypomeron
I1	apical convex pivot fold
il	ilium
is	internal sac
iss	sclerites of the internal sac
ist	teeth of internal sac
J2	axillary fold
lac	lacinia
laf3	lateral arm of metafurca
lam	metafurcal lamina
lb	labium
lbrs	labral bristles
lig	ligula
lm	labrum
lma	lateral mandibular articulation
lmp	labial palp
lmpr	lateral margin of pronotum
lo	lateral oviduct
lph3	metapostnotal laterophragmite
lrr	basal labral ridge
ls	lateral sulcus
lst	laterosternite
mb	medial bridge
md	mandible
mer	metepisternal ridge
mfl	medial flange
mflk	medial fleck
ml	mola
mlb	median lobe
mlc	molar cusps
mlh	median lingua of hypopharynx
mo	median oviduct
MP	medius posterior
mph3	metapostnotal mediophragmite
mpt	malpighian tubules
mst	mediostipes
mt	mentum
mth	mouth
mx	maxilla
mxp	maxillary palp
npi4	noto-prephragmal interseg. m. of prothorax
ob	oral brace
oc	occiput
ocf	occipital foramen
oe	oesophagus
of	oral foramen
ol	optic lobe
onv	optic nerve
os	oblique suture of metascutum
ov	ovary
ovl	ovariole
p	pedicel
pat	posterior arms of tentorium
pcbm	protocerebrum
pg	postgena
pgl	paraglossa
pgr	proctiger
pgu	pregula
plf	palpifer
plm	labial palpomere
pmg	posterior mandibular groove
pmr	paramere
pmt	prementum
pmx	maxillary palpomere
pn3	metathoracic postnotum
pnc3	metanotal postnotal cleft
pnep	posterior notal elytral process
pnwp	posterior notal wing process
poc	postocciput
pos	postoccipital suture
pp2	mesothoracic prephragma
pp3	metathoracic prephragma
pps	posterior sclerite of the penis
pr	pronotum
pro1	prosternal process
prov	proventriculus
prt	prostheca
prtf	prosthecal fringe
ps	placoid sensilla
ps2m	mesonotal prescutal membrane
ps3m	metanotal prescutal membrane

psc2	mesothoracic prescutum
psc3	metathoracic prescutum
pst	parasternite
ptar	pretarsus
ptp	posterior tentorial pit
ptv	posterior tergo-ventral m. of prothorax
pyv	pyloric valve
RA	radius anterior
rect	rectum
rma	retractor m. of mouth angles
rp	rectal pad
s1	prosternum
s2	mesosternum
s2p	mesosternal “pit”
s3	metasternum
s3p	metasternal “pit”
Sc	subcosta
sc	scape
sc2	mesoscutum
sc3	metascutum
scl2	mesoscutellum
sclg	scutellar groove
selc	subelytral cavity
sg	spiculum gastrale
sgb	subgenal brace
slh	superlingua of hypopharynx
sm	submentum
sog	suboesophageal ganglion
spe	spermatheca
spgl	spermathecal gland
ss3m	suspensory sclerites of metanotum
sslr	suspensory sclerites of labrum
st2	sterno-trochanteral m. of mesothorax
stc	stomadeal connectives
sub	subalare
tar	tarsomere
te	testis
tf	terminal filament
tg	tegmen
tgn	thoracic ganglion
ti1	prothoracic tibia
ti2	mesothoracic tibia
ti3	metathoracic tibia
tor	torma
tp3	tergal promoter m. of metacoxa
tpm	tergopleural m. of prothorax
tr1	prothoracic trochanter
tr2	mesothoracic trochanter
tr3	metathoracic trochanter
trm1	tergal remoter m. of prothorax
trm2	tergal remoter m. of mesothorax
tsa	lateral tergo-sternal m. of abd. segment
tsm2	tergo-sternal m. of mesothorax
tsm3	tergo-sternal m. of metathorax
tsp	thoracic spiracle
ung	unguis
untp	unguitractor plate
v	vertex
vag	vagina
vd	vas deferens
vhc	ventral head commissures
vla	ventral longitudinal m. of abd. segment
vm1	ventral m. of prothorax
vm2	ventral m. of mesothorax
vm3	ventral m. of metathorax
vnc	ventral nerve connective
voa	ventral oblique m. of abd. segment
vrscl3	ventral ridges of metascutellum
vtr	ventral trunk

CHAPTER 6

REVISION OF THE NEW WORLD GENUS *BYSTUS* GUÉRIN–MÉNEVILLE, 1857 (COLEOPTERA: ENDOMYCHIDAE: ANAMORPHINAE) WITH DESCRIPTIONS OF FOUR NEW SPECIES[1]

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[1] Shockley, F.W. and J.V. McHugh. To be submitted to *Zootaxa.*

ABSTRACT

This paper represents a review of the genus *Bystus* Guérin–Méneville (Coleoptera: Endomychidae: Anamorphinae), which now includes 22 species. This treatment includes notes on the distribution and biology of *Bystus*, descriptions of the immature stages, and descriptions or redescriptions of the adults of all species. The following species are included: *B. apicalis* (Gerstaecker), *B. ashei* Shockley and McHugh, **new species**, *Bystus coccinelloides* Guérin–Méneville, *Bystus decipiens* (Gorham), *Bystus decorator* Leschen and Carlton, *Bystus drakei* (Weise), *Bystus fibulatus* (Gorham), *Bystus foveatus* Strohecker, *Bystus globosus* (Gorham), *Bystus hemisphaericus* (Gerstaecker), *Bystus humeralis* Shockley and McHugh, **new species**, *Bystus limbatus* (Gorham), *Bystus marginatus* Shockley and McHugh, **new species**, *Bystus pallidulus* (Gerstaecker), *Bystus rodmani* Shockley and McHugh, **new species**, *Bystus piceus* (Gorham), *Bystus rhizobioides* (Gorham), *Bystus rufus* (Weise), *Bystus seminulum* (Gorham), *Bystus ulkei* (Crotch), *Bystus unicolor* (Gorham), and *Bystus vestitus* (Gorham). Lectotypes and paralectotypes are designated for the following species: *B. apicalis*, *B. decipiens*, *B. drakei*, *B. fibulatus*, *B. globosus*, *B. hemisphaericus*, *B. pallidulus*, *B. piceus*, *B. rhizobioides*, *B. seminulum* and *B. vestitus*. Keys to the adults and known larvae of *Bystus* are provided.

Key Words: Endomychidae, Anamorphinae, *Bystus*, morphology, life history, distribution.

INTRODUCTION

The family Endomychidae, whose members are known as the Handsome Fungus Beetles, is a group of primarily tropical mycophagous beetles with 130 genera and 1782 species and subspecies distributed among 12 subfamilies (Shockley *et al.* 2009a). Historically, family-level treatments of the Endomychidae were limited to regional checklists and individual species descriptions. The family Endomychidae occurs in all biogeographical regions of the world, but they are particularly speciose in the New World tropics, equatorial Africa, and Southeast Asia. Anamorphinae, the subfamily to which *Bystus* Guérin–Méneville belongs, contains 37 genera and 175 species distributed across all biogeographical regions, except the Antarctic (Table 6.1). Of the 37 anamorphine genera, 12 occur in the New World, 8 occur exclusively there (including *Bystus*). In terms of species diversity, *Bystus* is the largest genus in the Anamorphinae (Fig. 6.1).

Many members of the subfamily Anamorphinae are most likely specialists on spores and hyphae of microfungi (Skelley and Leschen 2002). The mandibles of many adult anamorphines, including *Bystus*, have a bifid apical incisor lobe, a brushy prostheca and a well-developed mola which make them well-adapted for a lifestyle as obligate spore feeders (Pakaluk 1986, Lawrence 1991, Leschen and Carlton 1993, Tomaszewska 2000). *Bystus* species are exophagous as adults and larvae, preferring to feed externally on their host fungi (Fig. 6.2). To date, there have been very few treatments of the fungal-host associations for Endomychidae, in general, and the few host records that do exist tend to be largely uninformative or inaccurate.

Shockley *et al.* (2009b) reported *Bystus* species have been recovered from seven genera of basidiomycete and ascomycete fungi (Table 6.2). Leschen and Carlton (1993) reported *B. decorator* from Peru from an encrusting type of ascomycete fungus with white mycelia and a dark red spore field. Dissections of *B. decorator* revealed that the gut was filled with spores, confirming sporophagy as the primary mode of nutrition for *Bystus.* Lawrence and Milner (1996) list *Bystus* among surface grazing endomychids on ascomycetes, suggesting that at least some *Bystus* species feed facultatively on ascomycetes. *Bystus* adults and larvae are often collected in association with encrusting fungi on logs or standing dead trees and can be found grazing during the day or night (though populations tend to be greater at night). Individuals display no apparent preference for old or new fungal growth (Shockley pers. obs.). Lawrence (1991) also reported that *Bystus* has been associated with various polypore bracket fungi, citing Donisthorpe (1935) and Weiss and West (1920). However, neither of these studies made any mention of *Bystus* or its junior synonym *Rhymbus*. *Bystus* species can often be collected from the underside of old basidiocarps of bracket fungi (Shockley pers. obs.), though it is unclear if they are feeding on the spores of the basidiocarps themselves or on microfungi growing on the decaying fruiting bodies.

In addition to their associations with their host fungi, *Bystus* species, like many other endomychids, have been documented to have endosymbiotic yeasts associated with their digestive systems, typically housed in thick gastric caecae associated with the anterior midgut, but found secondarily throughout the midgut. McHugh *et al.* (1997) speculated that endosymbiotic yeasts in *Megalodacne heros* (Say) (Erotylidae) were likely playing a role in digestion of fungal tissue. Shockley *et al.* (2009b) suggested the same function for endosymbiotic yeasts in endomychids and listed all described yeast species that have been recovered from endomychids, including several from *B. piceus* (Table 6.3). At present, the mode of transmission/inoculation of the beetle midgut by these endosymbionts remains unknown.

Although *Bystus* adults and larvae are sometimes found in small clusters (5-10 beetles), true gregariousness has never been formally proposed. Leschen and Carlton (1993) noted the unusual nature of their discovery of a large population of *B. decorator* at the type locality in Peru, compared to the typical behavior exhibited by other anamorphines. Large aggregations in other *Bystus* species have not been documented. It is unclear what benefit the beetles experience by clustering in small groups, but it seems more likely an artifact of the beetles' feeding on the spatially-limited spore fields of their primary host fungi. *Bystus* adults, like many anamorphines and endomychids in general, generally prefer to scramble from the exposed feeding surface when disturbed, but will readily retract their legs and antennae and drop from the substrate if escape is otherwise prevented. Larvae tend to aggregate near the edges of the fungal substrate, near the fungus/wood interface. They do not usually drop from the substrate when disturbed, instead fleeing to cracks and crevices in the wood or remaining immobile.

Unlike some species of Endomychidae, *Bystus* species do not reflex bleed (Leschen and Carlton 1993) although they do exude a viscous secretion from pores located along the anterior half of the lateral margin of the pronotum. No studies have yet been done to isolate and identify these compounds so it is unclear what purpose they may serve, perhaps defensive. Other endomychids have been reported to have some form of defensive chemistry (*e.g.*, stenotarsol isolated from *Stenotarsus subtilis*; Laurent *et al.* 2005), but the physiological function and mode of synthesis/sequestration of these compounds remains unknown. Leschen and Carlton (1993) described a behavior in the larvae of *B. decorator* whereby the larvae actively cover themselves with debris from the host, although they were hesitant to speculate on its function as a defense against predation. Within Endomychidae, this specific debris cloaking mechanism appears to be unique to *Bystus decorator*, though debris cloaking in one form or another, is known for a variety of other beetle families. Leschen (1994) speculated that this behavior in *Bystus* allows larvae to avoid predation by potential visual or tactile predators. The only specific record of potential predation on *Bystus* involved adults recovered from a bivouac of the Army ant, *Eciton hamatum*, on Barro Colorado Island, Panama, in which Wheeler (1925) speculated that the beetles' presence indicated potential predation by the ants. However, Mann (1925) dismissed their presence in the bivouac as only incidental (*e.g.*, they were already on the branch as the bivouac was being assembled).

Hoffmann *et al.* (2004) recorded an unidentified species (as *Rhymbus*) from a cave (Cueva de Sambulha) in the Merida District of the Yucatan State in Mexico. Unfortunately, they did not list the number of specimens collected, nor did they speculate on whether or not they believed the collection record to be incidental. Cavernicolous species are known in other anamorphine genera that superficially resemble *Bystus* (*e.g.*, *Anamorphus*, *Clemmus*) so it seems more likely that these specimens belonged to a genus other than *Bystus* or were only incidental.

TAXONOMIC HISTORY

Guérin–Méneville (1857) erected the genus *Bystus* for a distinct new species, *B. coccinelloides*, collected by Dejean and Reiche from Colombia. This new genus was readily distinguished from other endomychids by its small size, highly convex and nearly hemispherical habitus, vestiture of long decumbent setae, and the presence of long, narrow, anteromedially-curved lateral sulci. Gerstaecker (1858) later erected the genus *Rhymbus* for three species: *R. hemisphaericus* (from Costa Rica), *R. apicalis* (from Colombia) and *R. pallidulus* (from Brazil).

Subsequent workers acknowledged that *Bystus* had priority but continued using *Rhymbus* for new species descriptions, and most regional catalogues followed this classification (*e.g.*, Blatchley 1910, Csiki 1910, Bruch 1914, Leng and Mutchler 1914, Leng 1920, Leng 1927, Leng 1933, Fattig 1937, Blackwelder 1945, Guérin 1953). Strohecker (1953) transferred *Rhymbus minor* (Crotch, 1873) to the genus *Clemmus* Hampe, synonymized *Rhymbus pilosus* Casey, 1916 under *Symbiotes duryi* Blatchley, 1910, and then formally synonymized *Rhymbus* under *Bystus*.

Strohecker (1953) listed three African species described by Weise (1903) under both *Bystus* and *Pararhymbus* Arrow and an Argentinian species described by Weise (1906) under both *Bystus* and *Austroclemmus* Strohecker. Strohecker (1959) later transferred the African species to *Geoendomychus* (*G. csikii* and *G. partitus*) and *Dialexia* (*D. thoracicus*). Unfortunately, Strohecker (1959) only synonymized the original *Rhymbus* combinations, ignoring the new *Bystus* and *Pararhymbus* combinations which he had created (Strohecker 1953). After examining the Weise types, Shockley *et al.* (2009a) confirmed the new placements and corrected these discrepancies.

Similarly, Csiki (1901) incorrectly transferred *Alexia hirtula* Kirsch, 1876 to the genus *Rhymbus*, and Strohecker (1953) retained this placement when synonymizing *Rhymbus* under *Bystus*. Examination of the Kirsch types from Staatliches Museum fur Tierkunde (SMTD) revealed that this species does not belong in *Bystus* and is not even an endomychid. The type series consists of four specimens representing two different species of Coccinellidae. The transfer of *A. hirtula* (and all associated synonyms) from Endomychidae to Coccinellidae is the subject of a separate manuscript (Shockley and Vandenberg *in prep*). This species, along with the previous four discussed above, will not be treated further.

PHYLOGENETIC RELATIONSHIPS

Anamorphinae was first defined by Strohecker (1953) as a tribe within the subfamily Mycetaeinae. Sasaji (1978) elevated this tribe to the subfamilial level as Mychotheninae, including twelve genera. Pakaluk (1986) suggested that Mychotheninae should be removed from the remainder of Endomychidae. A year later, Sasaji (1987) elevated Mychotheninae to the family-level as Mychothenidae, though this classification was never widely accepted. Most recent treatments continued classifying it as a subfamily of Endomychidae, albeit under the name Anamorphinae Strohecker, 1953, which has priority over Mychotheninae Sasaji, 1978 (Pakaluk *et al.* 1994, Lawrence and Newton 1995). Pakaluk and Ślipiński (1995) erected a new subfamily, Acritosomatinae, to accommodate the genus *Acritosoma* from Peru, which they considered related to but distinct from Anamorphinae. However, Tomaszewska (2000) later synonymized Acritosomatinae under Anamorphinae based on a phylogenetic analysis using adult morphology.

Among phylogenetic analyses of Endomychidae employing modern methods, only Tomaszewska (2005), Robertson *et al.* (2008) and Shockley *et al.* (in prep; Chapter 4) included representatives of *Bystus*. The phylogenetic analysis of Tomaszewska (2005) was based on a combined matrix of adult and larval characters and included three anamorphine genera: *Symbiotes*, *Mychothenus* and *Bystus*. When adult characters alone were used to reconstruct the phylogeny, Anamorphinae was not recovered as monophyletic. The inclusion of larval characters, however, consistently led to the recovery of a monophyletic Anamorphinae, but the relationship between the three genera included in that analysis was unresolved.

Using two ribosomal genes (18S, 28S), Robertson *et al.* (2008) recovered a monophyletic Anamorphinae under both maximum parsimony and Bayesian optimality criteria while testing the monophyly of the Cerylonid Series (CS) and the familial limits of the CS families. Endomychidae was recovered as polyphyletic in both analyses with Anamorphinae recovered as sister taxon to Corylophidae. In both trees, *Bystus* was also recovered as monophyletic and sister to *Anamorphus*, albeit based on the inclusion of only two unidentified exemplars that were later determined to be conspecific.

Shockley *et al.* (in prep; Chapter 4) performed a more thorough phylogenetic analysis of Endomychidae based on 8 genes, including 10 anamorphine genera and 6 different *Bystus* species. Anamorphinae was recovered outside of Endomychidae sister to either Coccinellidae+Corylophidae or Coccinellidae alone in the parsimony and ML/Bayesian analyses, respectively. *Bystus* was consistently recovered as monophyletic and placed within Anamorphinae. In the parsimony analysis, *Bystus* was recovered as sister to the clade comprising *Geoendomychus* Lea, *Idiophyes* Blackburn, *Micropsephodes* Champion and *Anamorphus* LeConte. The same sister group relationship was recovered in the ML and Bayesian analyses except that *Micropsephodes* was not recovered within the aforementioned clade.

MATERIALS AND METHODS

Specimens for the Taxonomic Studies

This revision is based on the examination of types and material from the following institutions and private collections (codens follow those of Arnett *et al.* 1997 and Evenhuis 2007):

AMNH - American Museum of Natural History, New York, NY, USA.
BMNH - Natural History Museum, London, United Kingdom.
CMNH - Carnegie Museum of Natural History, Pittsburgh, PA, USA.
CUIC - Cornell University, Ithaca, NY, USA.
CZUG - Centro de Estudios en Zoología, Universidad de Guadalajara, Jalisco, México.
EGRC - E.G. Riley, College Station, TX, USA.
EMEC - Essig Museum of Entomology, University of California, Berkeley, CA, USA.

FSCA - Florida State Collection of Arthropods, Gainesville, FL, USA.

FWSC - F.W. Shockley, Athens, GA, USA.

KSUC - Kansas State University, Manhattan, KS, USA.

LSAM - Louisiana State University, Baton Rouge, LA USA.

MAIC – Michael A. Ivie, Bozeman, MT, USA.

MTEC – Entomological Collection, Montana State University, Bozeman, MT, USA.

NHRS - Swedish Museum of Natural History, Stockholm, Sweden.

NZAC - NZ Arthropod Collection, Landcare Research, Auckland, New Zealand.

OSUC - C.A. Triplehorn Insect Collection, Ohio State University, Columbus, OH, USA.

PESC - P.E. Skelley, Gainesville, FL, USA.

RALC - R.A.B. Leschen, Landcare Research, Auckland, New Zealand.

RHTC - R.H. Turnbow, Jr., Fort Rucker, AL, USA.

SEMC - Snow Entomological Museum, University of Kansas, Lawrence, KS, USA.

SMTD - Staatliches Museum fur Tierkunde, Dresden, Germany.

TAMU - Texas A & M University, College Station, TX, USA.

UADE - University of Arkansas, Fayetteville, AR, USA.

UGCA - University of Georgia Collection of Arthropods, Athens, GA, USA.

USNM - United States National Museum, Washington, DC, USA.

ZMHB - Museum fur Naturkunde der Humboldt-Universitat, Berlin, Germany.

Immatures of *B. decorator* and *B. hemisphaericus* were borrowed from RABL, and specimens of *B. ulkei* larvae were borrowed from USNM. The *B. decorator* specimens were fixed in Trump's Solution and later transferred to 70% ethanol. They bear the following collection label data: “PERU: Tambopata Prov., Madre de Dios Dpto.; 15 km NE. Puerto Maldonaldo, Reserva; Cuzco Amazonica, 12°33’S, 69°03’W, 200m.; Terraform Forest Plot#Z1U13; coll. 10,15 July 1989, ex., red fungal spore-field; #476 22 larvae (mostly early), 8 teneral, 23 nonteneral adults Richard A. Leschen; *Bystus* sp.” The *B. hemisphaericus* specimens were received in 70% ethanol (it is unknown if they were fixed prior to transfer into the ethanol). These specimens bear the following collection label data: “HONDURAS: Dept. Lempira; 13.1 km NE & 7.3 km E; Gracias, lower slopes of; Montana Puca 1320m.; 18 June 1994; S. Ashe, R. Brooks #143; ex: encrusting fungus below log.” The *B. ulkei* larvae and pupal specimens were also in 70% ethanol and bear the following collection label data: “*Rhymbus ulkei*, Cr.; on fungus; E. Falls Church, Va. Aug.24.1923; E.A. Chapin.” These specimens were extremely fragile and in poor condition, so they were first gently rehydrated using warm soapy water before examination.

Imaging and Illustration

Images were taken using a Canon EOS-1DS digital camera attached to an ML-1000 Digital Imaging System (Microptics, Inc., Ashland, VA). In cases where punctation was important, a light diffuser made of wax paper was used. Line drawing illustrations were drawn using either a Leica MZ8 stereomicroscope (< 50x magnification) and a Leitz Labor Lux S laboratory microscope (> 50x magnification) both fitted with a camera lucida.

Mapping

Because of the preliminary nature of this study, maps were produced demonstrating the general distribution of species based either on specimens examined in this study or based on the literature. Several species are only known from the type locality, and plotting a single point on a map may not reflect the actual distribution of that species. Plotting points in the center of a defined area (*e.g.*, Mexico) is commonly used for this type of record, but this method is generally uninformative and ultimately misleading in regard to the species' true distributions. We have elected to avoid this problem for now and concentrate on the general distributions rather than point-based distributions.

***BYSTUS* ADULTS**

Diagnosis:

Bystus species can readily be distinguished from other similar coccinelloid-like members of the subfamily Anamorphinae by combination of the following characters: basal tarsomere of the prothoracic legs of the males modified; anteromedially curved lateral sulci reaching only to the middle of the pronotal disc; antennae 9- or 10-segmented with a 3-segmented club; pronotum rounded laterally, narrowly margined, and posteromedially lobate; tarsal formula 3-4-4 in both sexes.

Description:

Body oval to elongate oval (Fig. 6.4), strongly convex. Length 1.0 – 4.0 mm; width 1.0 – 3.2 mm. Dorsal vestiture consisting of suberect setae, varying from very short in some species to very long in others. Ventral vestiture always comprised of short, decumbent setae. Pronotum and elytra similar in color and lateral margins of both often lighter in color than the disc. Each elytron typically light reddish brown to dark brown or black in color, rarely with a conspicuous light yellow or black macula on the disc.

Head globose or weakly transverse, retracted and hypognathous. Compound eyes large, oval, and prominent; finely- to moderately-faceted. Antennal sockets partially obscured from above by ridge formed by anterolateral region of the frons. The fronto-clypeal suture always present but difficult to see in some species, varying from conspicuous to completely obliterated externally (still viewable when head capsule cleared and viewed with transmitted light). Tentorium with anterior arms widely divergent anteriorly, convergent medially but not fused; corpotentorium curved medially. Antennae 9- or 10-segmented, relatively long (1.5 - 2.5x length of head) with a loose, but conspicuous 3-segmented club varying in length from shorter or subequal to the stalk to much longer than the stalk. Basal antennomeres yellowish to brownish in color; terminal antennomeres dark brown to black, sometimes with terminal antennomere partially (apically) or wholly lighter in color. Antennomere III narrow and elongate; antennomeres IV-VI (VII in 10-segmented species) vary in shape from short, almost bead-like in appearance to rather narrow and elongate. Club antennomeres expanded apically, varying from being subequal in length to their greatest width to being much longer than their greatest width. Terminal antennomere elongate and either rectangular or elliptical in shape, sometimes concave to give the terminal antennomere a curved appearance. Clypeus transverse, weakly convex, and concave to weakly bisinuate along anterior margin. Labrum is transverse, rounded anteriorly and constricted posteriorly; relatively uniform in overall shape, punctation, and pubescence across species. Mandibles asymmetrical, heavily sclerotized and bearing 2-3 apical and subapical teeth; mola varying in size between species but always armed with multiple rows of sharp, stout denticles; prostheca present, prominent, submembranous with a distinct and variably setose prosthecal fringe. Maxillae highly conserved in structure across the genus with no discernible interspecific variation. Labium with transverse to rectangular mentum, which may be rounded laterally and distally or angulate (hexagonal); paraglossae expanded distolaterally to form broad lobes which are variable in shape; labial palpi 3-segmented with small, subconical palpomere I, transverse palpomere II, large palpomere III with apex truncate bearing thick fringe of fine setae and varying from securiform to broadly subcylindrical.

Pronotum strongly transverse and laterally rounded, lateral margins expanded anteriorly but narrow posteriorly. Lateral sulci narrow near the middle of the disc but gradually expanded basally, anteriorly curved mesad with degree of curvature ranging from slight to moderate. Basal margin of the pronotum broadly lobed medially, may or may not contain shallow antebasal depressions or foveae at the base and mesad of the lateral sulci. Prosternum similar in overall shape across all species, bearing a variable number of large, deep punctures along its anteromedial margin. Scutellum small and triangular. Elytra varying from moderately to strongly convex, elongate and hemispherical in shape; humeral region may be weakly to strongly produced; epipleuron weakly to broadly margined basally and incomplete (not reaching apex of the elytron). Mesosternum with transverse intercoxal process broadly separating mesocoxae. Hind wing with reduced venation and similar in overall appearance and venation across species; degree of melanization varying from completely transparent to almost completely melanized and dark brown; small to medium sized medial and subcubital flecks varying intraspecifically in shape but interspecifically in size and exact location. Metasternum transverse bearing a row of large conspicuous punctures of variable number extending to the midpoint of the mesocoxal cavities, beyond the mesocoxal cavities in some; metendosternite with stalk fused to posterior margin of the metasternum, anterior arms widely separated, anteriorly divergent with length of the arms varying from short to moderately long.

Abdomen with five freely articulated ventrites corresponding to abdominal segments III-VII; all segments transverse; ventrite I always larger than ventrites II-IV, often larger than II-IV combined, with anteromedial intercoxal process varying in width from 0.1 – 0.3x the width of ventrite I; intersegmental membranes separating II-V straight or slightly curved anteriorly to slightly curved posteriorly; posterior margin of ventrite V bearing a broad semicircular notch (somewhat narrowly sinuate in females), rarely with an additional distinct notch medially. Male genitalia very similar in overall appearance across species and highly reduced; tegmen reduced to membraneous, ring-like structure connected to the base of the parameres and through which the median lobe projects; median lobe long, stout, and weakly curved, narrowing apically with an almost straight to distinctly hooked apex, often with a short to relatively long groove running from the midline extending laterad, creating a ridge of variable length and elevation along the lateral surface of the median lobe.

Legs similar in form across all species; tarsal formula 3-4-4; males with prothoracic tarsomere I triangular to elongate in form bearing a conspicuous straight to highly concave pectinate comb directed dorsally. Females lack such a modification (Fig. 6.101) and there is no sexual or interspecific variation in the form of the mesothoracic and metathoracic legs (Figs. 6.102-6.103).

Etymology:

The name appears to be a Latinized reference to an obscure name from Greek mythology (Booth 1814, Michaud and Michaud 1832, Jacobi and Bernard 1854, Vollmer 1874). *Βύστος* or Bystos (Greek), Bystus (Latin) and Byste (French) all appear to refer to the same historical figure. Bystus was the father of Hippodamia (herself the inspiration for a genus of

Coccinellidae), whose wedding to Pirithous, King of the Lapiths in Thessaly, was disrupted by drunken centaurs trying to abduct and rape her and the other women and children, leading to a legendary battle between the Lapiths and the Centaurs. This battle (called the Centauromachy) is a common theme in early Greek sculpture and relief, often as a metaphor for the battle between civilization and barbarism (Vollmer 1874). Bystus was the maternal grandfather of Polypoites, who led the armies of Thessaly on the side of the Greeks during the Trojan War and was one of the men selected to infiltrate the walls of Troy inside the Trojan horse (Smith 1867).

Although Pirithous, Hippodamia and Polypoites all appear as characters featured in Homer's *The Iliad*, there is no mention of a figure named Bystus. However, Grimal (1990) listed Adrastus, the legendary king of Argos, as Hippodamia's father, suggesting that Bystus may be a transliteration of Butes, the rarely used common name for Adrastus. Adrastus figures prominently in *The Iliad*, both in the stories of the interrupted marriage feast of Pirithous and Hippodamia and as the main hero of the celebrated 'Seven against Thebes' war.

Distribution:

The genus extends into northeastern North America (*B. ulkei*), throughout Central America, and into south temperate South America (*B. drakei*, *B. rufus*). Species often have relatively large and overlapping distributions across temperate and tropical forests. In addition, there are two endemic species (*B. globosus* and *B. unicolor*) found exclusively in the Caribbean (Table 6.4).

Additional Notes:

Because of the relatively homogenous morphology of *Bystus* species, the generic description above follows closely the morphological treatment of adult *B. piceus* presented in Shockley and McHugh (in prep; Chapter 5). If a feature was not explicitly mentioned, then it does not vary significantly among species. Adults of different species may generally be separated by the following features: 1) shape and condition of the male prothoracic basitarsus; 2) modifications of the terminal antennomere and the antennal club; 3) pronotal and elytral color pattern; and 4) structure of the median lobe. Most species are easily identifiable, but several morphologically similar sympatric species exist which are more difficult to differentiate.

***BYSTUS* PUPAE**

Introduction/Background:

Pupae are known for only a handful of Endomychidae with illustrations/descriptions scattered randomly throughout the literature (Bates 1862, Kemner 1924, Pakaluk 1984, Costa *et al.* 1988, Leschen and Carlton 1988, Leschen and Carlton 1993). Leschen and Carlton (1993) provided the first and only published description of a pupa of any *Bystus* species for *B. decorator*. However, this description was relatively short and lacked sufficient detail for diagnosis of *Bystus* pupae. Pupae of *Bystus*, like other endomychid pupae, are not found in pupal chambers. Instead, they are generally found suspended by their pygopods from the surface of the feeding substrate, albeit generally in a protected location on the underneath side of decaying logs (Leschen and Carlton 1993, Shockley pers. obs.) (Fig. 6.3). When disturbed, pupae of *B. decorator* pivot on their pygopod (Leschen and Carlton 1993). The last larval exuvium is typically attached to the abdomen near the point of attachment to the substrate. The following is modified from the description and illustration of *B. decorator* pupae (Leschen and Carlton 1993) and based on additional observations of pupae of *B. decorator* and *B. ulkei* by the first author.

Description:

Pupa (Figs. 6.5-6.8) exarate, adecticous, and similar in length to the adult (~2 mm). Body typically white to light yellowish in color, elongate oval in habitus, and somewhat flattened dorsoventrally. Shape and dimensions of the head and pronotum similar to those of the adult. Dorsum covered with short, fine, erect setae.

Head strongly deflexed ventrally, appearing nearly opisthognathous and not visible dorsally. Antennae relatively long, extending perpendicular from the midline of the body; club directed posteriad, lying dorsad of the prothoracic femora. Labrum large and trapezoidal, extending beyond the apex of the mandibles, thus obscuring all remaining mouthparts. Maxillary palps extend beyond anterolateral margin of the labrum.

Pronotum transverse and extending laterally beyond the edge of the body. The meso- and metathoracic wingpads relatively long and tapering; mesothoracic wingpads (protelytra) subequal in length to adult elytra; metathoracic wingpads (protowings) narrower and shorter than the adult wing. Protelytra and protowings obliquely angled posterolaterally. Mesothoracic scutellum large and conspicuous. Abdomen approximately half of total length; last larval exuvium attached to abdomen by a pair of semilunar papillae located on the pygopod. Urogomphi, pedunculate setae and terminal abdominal processes absent. Spiracles annular in shape, located at the anterolateral margins of abdominal tergites II-V.

Legs long, visible, and weakly sclerotized (submembranous) with femora extending perpendicular to the midline of the body. Tibiae angled posteromedially, obscuring the femoro-coxal articulation of the subsequent segments. Tarsi are directed posteriormedially along a sagittal plane half of their length from the midline of the body.

Additional Notes:

The pupae of *B. ulkei* and *B. decorator* differ in the shape of the abdomen, which is somewhat rounded in *B. decorator* but is relatively elongate in *B. ulkei*. However, the pupae of *B. ulkei* examined in this study were quite old and poorly preserved causing visible distortion of the specimens. Multiple attempts to rehydrate the specimens were made to try and correct this distortion, all unsuccessful. In most other features, the pupae of these two species generally agree.

***BYSTUS* LARVAE**

Introduction/Background:

The first illustration of the larva of any *Bystus* species was published by Boving and Craighead (1931) for *B. ulkei* (as *Rhymbus ulkei*), but this illustration was not accompanied by a description. Costa *et al.* (1988) described *B. pallidulus* (as *Rymbus pallidus* and *Rhymbus pallidus*). Another *Bystus* species was illustrated by Lawrence (1991) from BCI in Panama, but the specimen was not identified to species. Shockley and McHugh (in prep; Chapter 5) later identified this larva as *B. piceus*. Again, no description accompanies the illustration. Leschen and Carlton (1993) provided the only estimate of the number of larval instars for any *Bystus* sp., four (in *B. decorator*), based on calculations of head capsule width and Dyar's Law. In that treatment, they included a thorough description of the 4th instar larva including a discussion of the setae and thoracic musculature involved in debris-cloaking, a behavior that is only known within Endomychidae to occur in this species but is known in other beetle families and non-Coleoptera taxa. In that treatment, they questioned the accuracy of the description of *B. pallidulus* by Costa *et al.* (1988) while comparing it to their own description of the last instar larva of *B. decorator*. The following description is based on the published illustrations/descriptions of the larvae of *B. ulkei* (Boving and Craighead 1931), *B. pallidulus* (Costa *et al.* 1988) and *B. decorator* (Leschen and Carlton 1993), as well as preserved specimens of *B. decorator*, *B. fibulatus*, *B. hemisphaericus*, and *B. ulkei* (Figs. 6.9-6.12).

Description (based on 4th instar):

Length varies from 1.3 mm in the smaller species to nearly 5.0 mm in the larger species. Body is white to slightly yellowish in color; dorsum, venter and appendages very lightly pigmented in early instars; dorsum densely pigmented in later instars. Body (Fig. 6.15) elongate-oval in shape; widest anteriorly; dorsoventrally flattened; urogomphi absent. Thoracic and abdominal segments transverse, often with medium to large tubercles along their dorsolateral margins. Dorsal vestiture densely pubscent and consisting of long, erect, pale setae. Vestiture on ventral surfaces and legs consisting of short, fine sparse setae.

Head hypognathous, triangular in shape (Fig. 6.13), partially obscured by the anterior margin of the pronotum dorsally. Stemmata absent or with a single stemma positioned dorsolaterally near base of the antennal articulation. Epicranial, frontal and frontoclypeal sutures absent. Gular suture short, gula membranous (Fig. 6.14). Antennae shifted posteriorly, 3-segmented with a transverse antennomere I. Antennomere II very long (4-5x longer than antennomere I), bearing an elongate sensory appendage (Fig. 6.20). Antennomere III short (shorter than the sensory appendage of antennomere II) with short sensillae. Labrum distinct and transverse with rounded anterior angles. Mandibles (Fig. 6.16) symmetrical with two dorsolateral setae, lacking a distomedial incisor lobe and prostheca. Anterior region of the mandibles distad of the mola rarely produced with additional hyaline processes and lobes (*e.g.*, *B. decorator*) (Fig. 6.17). Mola comprised of several staggered rows of sharp teeth. Maxillae (Fig. 6.18) elongate, with a triangular cardo and elongate stipes. Mala with 2 stout distal spines and 3 subapical setae. Maxillary palps 3-segmented with palpomere I short and stout, palpomere II elongate and cylindrical, and palpomere III shorter and narrower than palpomere II. Apical sensory field with a variable number of setae and stout papillae. Labium (Fig. 6.19) with fused mentum – submentum, variable in shape, respectively appearing square and transverse (*e.g.*, *B. decorator*), elongate and rectangular (*e.g.*, *B. ulkei*) or almost lyriform (*e.g.*, *B. pallidulus*). Labial palps 2-segmented with a stout palpomere I and a shorter, narrower palpomere II, bearing papillar sensillae apically.

Thoracic segments with well-developed lateral projections, especially in later instars. Tubercles larger in the prothorax and mesothorax and smaller in the metathorax, all segments densely setose. Prothorax longer than the meso- and metathorax combined, subequal to the mesothorax in some species (*B. ulkei*). Thorax with single pair of annular spiracles located on the prothorax posteroventrad from the lateral lobe. Abdomen with nine visible segments dorsally. Each segment with a pair of pleural tubercles directed laterally each bearing a tuft of long, erect setae. Abdominal segments I-III subequal to or wider than the metathorax. Abdominal segments I-VII often with additional dorsal strumae. Abdominal segments VIII-IX with two pairs of posterolateral lobes, one near the anterior margin of the segment and one near the posterior margin of the segment. The mesal lobes are absent in some species (*e.g.*, *B. ulkei*, *B. decorator*). Spiracles located on each segment dorsad of the pleural lobes. Segment IX narrow and lacking urogomphi. Segment X developed into a short, 3-lobed pygopod, directed posteroventrally and not visible dorsally.

Legs (Fig. 6.21) of all thoracic segments similar in shape and length, with coxae widely separated basally; coxae triangular and nearly as long as the trochanter and femur combined. Femora cylindrical and elongate, more than 2x as long as wide. Tibiotarsus is relatively long, longer than the femur and trochanter combined. Tarsungulus with a single long claw and a single short subapical seta ventrally.

Additional Remarks:

The triangular head and posteriorly shifted antennae are similar to those found in other larval endomychids. Beutel *et al.* (2000) postulated that these characters may be important for defining the family, but noted their absence in Mycetaeinae, Merophysiinae, Leiestinae and some Lycoperdininae. Both features are present in all known anamorphine larvae, including those of *Bystus* (Shockley and Tomaszewska 2007).

The dorsal and lateral habiti of *B. ulkei* (Boving and Craighead 1931) and *B. decorator* (Leschen and Carlton 1993) are quite different than those for *B. pallidulus* (Costa *et al.* 1988) and *Bystus piceus* (Lawrence 1991). The primary differences are in the reduction/absence of the dorsal lobes on the abdominal segments of *B. ulkei* and the lack of the mesal pair of lobes on abdominal segments VIII and IX in both *B. ulkei* and *B. decorator*. This is similar to the condition in larvae of other genera of Anamorphinae (*Idiophyes* in Hayashi 1986; *Mychothenus* in Sasaji 1978).

BYSTUS EGGS

Leschen and Carlton (1993) provided the only published description of *Bystus* egg structure from eggs of *Bystus decorator* collected in Peru. *Bystus decorator* eggs (Fig. 6.22) are 0.55 mm long and 0.31 mm long. This is consistent with measurements of mature ova dissected from gravid females of *B. piceus* by the first author (see Shockley and McHugh in prep; Chapter 5). *Bystus* females lay their eggs singly on the surface of the feeding substrate rather than in clutches. Eggs of *Bystus* are white to slightly yellowish in color depending on their age, and are structurally simple without any conspicuous microsculpturing.

KEY TO THE ADULTS OF *BYSTUS*

Because of the uniformity in morphology across the genus, diagnostic characters are limited. The most reliable character for species recognition is in the shape of the median lobe. However, this structure is often difficult to extract without damaging the remainder of the specimen (in the case of pinned specimens). The following key should allow for the differentiation of the species included in this study.

1. Length > 2.5 mm; antennae 9-segmented (*coccinelloides*-group)..................................2

– Length < 2.5 mm; antennae 10-segmented (*ulkei*-group)...13

2. Terminal antennomere partially/entirely light brown to white..3

– Terminal antennomere dark brown or black..4

3. Larger species (>3.0 mm), antennomere IX with only the tip red........*B. hemisphaericus*

– Medium-sized species (2.5-3.0 mm), antennomere IX entirely red .... *B. apicalis*

4. Pronotum and elytra both reddish brown, brown or yellowish in color 5

– Pronotum black, elytra dark red to reddish brown in color ....*B. rodmani*

5. Elytral disc and margin similarly colored...6

– Elytral with disc black and margins light yellow to brown .... *B. limbatus*

6. Elytral margins narrow and flattened laterally 7

– Elytral margins widely expanded and reflexed laterally ....*B. marginatus*

7. Antennal club longer than the remaining segments combined.......................................8

– Antennal club distinctly shorter than the remaining segments combined 10

8. Antennomere III distinctly longer than IV 9

– Antennomere III subequal to IV .... *B. rhizobioides*

9. Antennomere VII triangular...*B. decipiens*

– Antennomere VII subcylindrical ....*B. coccinelloides*

10. Antennal club segments gradually enlarging apically 11

– Antennomere VIII wider than VII or IX, as wide as long ....*B. drakei*

11. Antennomere IV distinctly shorter than III...12

– Antennomere IV elongate, subequal or longer than III ....*B. pallidulus*

12. Antenna long and slender; antennomere IX longer and wider than VIII............*B. piceus*

– Antenna short and stout; antennomere VIII longer and wider than IX ....*B. rufus*

13. Head, pronotum and elytra the same color 14

– Head and pronotum black, elytra reddish brown...*B. globosus*

14. Pronotum uniform in color 15

– All lateral areas of pronotum (lateral to sulci) lighter in color than disc..............*B. ashei*

15. Elytra bicolored with conspicuous maculae 16

– Elytra uniformly dark brown to reddish brown (epipleura may be lighter)...................17

16. Elytra with yellow maculae near the sutural margin .... *B. decorator*

– Elytra with orangish yellow maculae on the humeri ....*B. seminulum*

17. Elytra with margin and disc the same color..18

– Elytra with margin lighter than disc .... *B. ulkei*

18. Lateral sulci typical and not edged laterally by a carina..19

– Lateral sulci edged laterally by a distinct carina...*B. vestitus*

19. Antennae with only last 3 segments black...20

– Antennae with last 4 segments black...*B. fibulatus*

20. Antebasal foveae poorly developed; antennal segment X as wide as long 21

– Pronotal foveae well-developed; antennal segment X longer than wide..........*B. foveatus*

21 Prosternal process normal; humerus only weakly developed.......................... *B. unicolor*

– Prosternal process with a medial carina; humerus well-developed...............*B. humeralis*

KEY TO 4th INSTAR LARVAE OF *BYSTUS*

Shockley and Tomaszewska (2007) provided the first key to the larvae of Anamorphinae, including three species of *Bystus*. The following key has been modified from Shockley and Tomaszewska (2007) to include *B. hemisphaericus*, *B. piceus* and *B. fibulatus*. *Bystus* larvae are recognizable from the larvae of other anamorphines by having antenna with antennomere II very long, at least 4 times as long as broad (Fig. 6.20).

1. Number of stemmata 0...2

– Number of stemmata 1 ....……………….....3

2. Mandible w/premolar membranous processes (Fig. 6.17)............................ *B. decorator*

– Mandible lacking premolar membranous processes (*e.g.*, Fig. 6.16) ... *B. hemisphaericus*

3. Dorsal tuberculate lobes absent on last two abdominal segments. 4

– Dorsal tuberculate lobes present on last two abdominal segments. 5

4. Prothorax as long as meso- and metathorax combined.................................. *B. fibulatus*

– Prothorax subequal in length to mesothorax.. *B. ulkei*

5. Metanotum with a dorsomedial sclerotized tubercle (Fig. 6.15) .... *B. pallidulus*

– Metanotum without such a dorsomedial sclerotized tubercle............................. *B. piceus*

SPECIES ACCOUNTS

Bystus is remarkable for its intraspecific morphological uniformity, despite large differences in size, coloration and distribution. Species accounts have been presented in a way that provides descriptions of only those morphological features that vary between them. Features showing little or no variation across species have been removed to avoid unnecessary redundancy. Some features which show intraspecific variation such as melanization of the wing and structure of the male prothoracic basitarsus have been included for most species; however, it is still unclear how plastic these characters are within species so they should not yet be considered truly diagnostic and included in species keys.

***Bystus apicalis* (Gerstaecker)**

Bystus apicalis (Gerstaecker) Strohecker, 1953: 21.

Rhymbus apicalis Gerstaecker, 1858: 350.

Diagnosis: This species is most similar to *B. hemisphaericus* but can be separated from it based on its smaller size and the antenna which has the club dark except for the apical antennomere, which is lighter in color, appearing almost completely white in some specimens (Fig. 6.23).

Redescription: Length = 2.75 – 3.0 mm. Body (Fig. 6.23) elongate-oval, less convex dorsally. Dorsal surfaces uniformly reddish brown. Vestiture comprised of fine erect pale-colored setae. Antenna (Fig. 6.45) 9-segmented, reddish brown, antennomeres VII-VIII black, terminal antennomere pale yellow (almost white in some specimens); antennomeres III-VI very narrow; antennal club subequal in length to preceding segments combined; antennomere IX elongate, rounded apically. Pronotum with narrow but distinctly impressed lateral sulci, antebasal foveae poorly developed. Elytron densely and finely punctate, regularly rounded apically. Hind wing (Fig. 6.67) with modest melanization. Prothoracic basitarsus of male forming long, triangular lobe with narrow pectinate comb (Fig. 6.87). Aedeagus with apex of median lobe asymmetrical, bearing well-developed hook (Fig. 6.104).

Etymology: Derived from the combination of the Latin root “apic-,” meaning “apex” or “tip,” + “al-,” meaning “towards,” and the general suffix “-is,” referring to the terminal antennomere which is pale compared to the remaining black club segments.

Type(s): **Lectotype (here designated):** SYN- TYPE / Co- Type / apicalis Gerst (type) / Gorham Coll. 91-50 [BMNH]. **Paralectotype (here designated):** 21876 / His.-Coll. (Coleoptera) Nr. 21876 Rhymbus apicalis Gerst. x Columb., Moritz Zool. Mus. Berlin / ? SYNTYPUS? Rhymbus apicalis Gerstaecker, 1858 labelled by MNHUB 2005 / apicalis Gerst. * Columb. Mor. / Museum fur Naturkunde Humboldt-Univ. Berlin (MNHUB) [ZMHB].

Additional Specimens Examined: **VENEZUELA:** Venezuela Aragua El Limon 450m. 8-V-1978 / En la Luz. / J. A. Clavijo col / Venezuela-Inst. Zool. Agricola Fac. Agronomia Univ. Central [1: FSCA]; Sta. Clara Venezuela-Cara-bobo 1200m. 31-VII-1968 / J.&B. Bechyne leg. / Venezuela-Inst. Zool. Agricola Fac. Agronomia Univ. Central [3: FSCA].

Distribution (Fig. 6.117): Colombia, Guatemala, Mexico, Venezuela.

***Bystus ashei* Shockley and McHugh, new species**

Bystus ashei Shockley and McHugh, new species

Diagnosis: This species is readily recognizeable by the light lateral areas of the pronotum, appearing yellow or orange in most specimens, and contrasting with the brown disc.

Description: Length = 1.75-1.95 mm. Body (Fig. 6.24) hemispherical, highly convex dorsally. Dorsal surfaces dark brown with areas of the pronotum laterad of lateral sulci yellowish or orangish. Vestiture uniformly reddish, conspicuously longer on lateral areas of elytron. Antenna (Fig. 6.46) 10-segmented, reddish brown, club segments conspicuously darker; antennomere III subequal to IV; antennomeres IV-VII subequal in length; antennomere X triangular, almost hatchet-shaped. Pronotum with lateral areas strongly reflexed, lighter in color than disc; sulci narrowly but distinctly impressed; antebasal foveae poorly developed. Hind wing (Fig. 6.68) with distinct melanization. Prothoracic basitarsus of male long and narrow, not triangular, but with conspicuous narrow comb (Fig. 6.88). Aedeagus (Fig. 6.105) with median lobe expanded dorsolaterally with fleshy lobe near gonopore; apex not conspicuously hooked.

Etymology: Patronym for J.S. Ashe, one of the primary collectors of the type series.

Type(s): **Holotype (here designated):** VENEZUELA: Aragua Rancho Grande Biol. Stn. 10º21’0”N,67º41’0”W, 1200-1300 m 12 MAY 1998; J.Ashe,R.Brooks,R.Hanley VEN1ABH98 003 ex: fungusy log [SEMC]. **Paratypes (here designated):** Same data as the holotype [7: SEMC, 2: FSRC, 3: UGCA, 3: USNM, 2: FSCA]; Same data as the holotype but dated 13 May 1998 [1: SEMC]; Same data as the holotype but collected from “white gilled mushroom” [1: FSRC].

Additional Specimens Examined: **VENEZUELA:** VENEZUELA: Aragua Rancho Grande Biol. Stn. Pico Periquitos, 1100-1300 m 10º20’32”N,67º41’46”W 13 MAY 1998; J.Ashe,R.Brooks,R.Hanley VEN1ABH98 009 ex: fungusy log [2: SEMC]; VENEZUELA: Aragua Rancho Grande Biol Stn. 10º20’N,67º41’W, 1450m “La Cumbre”,26 Feb 1995 R. Brooks#001, ex: crustose polypore under log [5: SEMC]; Same data as previous but dated 28 Feb 1995 [4: SEMC]; VENEZUELA: Aragua Rancho Grande Biol. Stn. 10º21’0”N,67º41’0”W, 1200-1300 m 13 MAY 1998; J.Ashe,R.Brooks,R.Hanley VEN1ABH98 016 ex: tree fall litter [1: SEMC]; VENEZUELA: Aragua Rancho Grande Biol. Stn., 1450 m 10º21’38”N,67º40’38”W 14 MAY 1998; J.Ashe,R.Brooks,R.Hanley VEN1ABH98 046 ex: fungusy log [3: SEMC]; VENEZUELA: Aragua Rancho Grande Biol. Stn., 1300 m 10º21’0”N,67º41’0”W 12-14 MAY

1998; J.Ashe,R.Brooks,R.Hanley VEN1ABH98 027 ex: flight intercept trap [1: SEMC]; VENEZUELA: Aragua Rancho Grande Biol. Stn., 1700 m 10º21’0”N,67º41’0”W 14 MAY 1998; J.Ashe,R.Brooks,R.Hanley VEN1ABH98 049 ex: fungusy log [1: SEMC]; VENEZUELA: Aragua Rancho Grande Biol. Stn., 1400 m 10º21’38”N,67º41’38”W 14 MAY 1998; J.Ashe,R.Brooks,R.Hanley VEN1ABH98 047 ex: fungusy log [2: SEMC]; VENEZUELA: Aragua Rancho Grande Biol. Stn. 10º21’N,67º41’W, 1370m 8 Mar 1995, R. Brooks #067, ex: crustose polypore on underside of log [2: SEMC]; VENEZUELA: Tachira San Cristobol, 10 km. SE P.N. Chorro El Indio 1320 m 7º44’3”N,72º13’1”W 29 MAY 1998; R. Anderson VEN1A98 049E ex: upper montane forest litter. **SURINAME:** SURINAME: Marowijne Palumeu, ca 160 m 3º20’56”N,55º6’18”W 8 JUL 1999; Z.H. Falin SUR1F99 180; ex: fungusy log (pyrethrum fogging) [1: SEMC]. **FRENCH GUIANA:** FRENCH GUIANA Cayenne, 33.5 km S, 30 m 4º48’18”N,52º28’41”W 21 MAY 1997; J.Ashe,R.Brooks FG1AB97 004 ex: fungusy log [1: SEMC]; FRENCH GUIANA Saul, 7 km N, Les Eaux Claires 3º39’46”N,53º13’19”W, 220 m 31 MAY 1997; J.Ashe,R.Brooks FG1AB97 094 ex:fungusy log [1: SEMC]; FRENCH GUIANA Saul, 7 km N, 0.5 km ESE Les Eaux Claires, Mt. La Fumee 3º39’46”N,53º13’19”W, 300 m 4-8 JUN 1997; J.Ashe,R.Brooks FG1AB97 164 ex:flight intercept trap [1: SEMC]; FRENCH GUIANA Saul, 7 km N, 3 km NW Les Eaux Claires, along Mt. La Fumee trail, 230-400 m 3º39’46”N,53º13’19”W 1 JUN 1997; J.Ashe,R.Brooks FG1AB97 103 ex:fungusy log [1: SEMC].

<u>Distribution (Fig. 6.118):</u> French Guiana, Suriname and Venezuela.

***Bystus coccinelloides* Guérin–Méneville**

Bystus coccinelloides Guérin–Méneville, 1857: 270 + pl. 13, fig. 22.

Diagnosis: The large size and antenna with the club entirely black readily differentiates *B. coccinelloides* from the remaining larger species.

Redescription: Length = 3.0-3.5 mm. Body (Fig. 6.25) hemispherical, strongly convex dorsally. Dorsal surfaces yellow to light brown in color. Vestiture long and thick, comprised of erect pale yellow setae. Antenna (Fig. 6.47) 9-segmented, yellowish, club antennomeres black; antennomere III conspicuously longer than IV; IV-VI subequal in length; antennomeres VII-IX forming loose 3-segmented club longer than the remaining segments combined; antennomere IX elongate, narrowly rounded apically. Pronotal sulci narrowly but distinctly impressed; antebasal foveae poorly developed. Elytron with very fine punctation. Hind wing (Fig. 6.69) extremely well melanized. Prothoracic basitarsus of male forming very elongate, narrow lobe with narrow pectinate comb dorsally. Aedeagus (Fig. 6.106) with apex of median lobe bearing subapical dorsal ridge and conspicuous hook.

Etymology: Derived from the combination of the Latin root “coccinell-“ + the Latinized form (“-oides”) of the original Greek suffix “eides, ” meaning “resembling” or “similar in form,” based on general resemblance to some Coccinellidae.

Type(s): The Guérin–Méneville type could not be located or examined in time to be included in this study.

Specimens Examined: **COLOMBIA**: Poima Colombia Santan-der del Norte, 1900m. 28-V-1965. / J.&B. Bechyne leg. / Venezuela-Inst. Zool. Agricola Fac. Agronomia Univ. Central [1: FSCA]; COLOMBIA: Magdalena; Sierra de Perija Socorpa Mission / Elev. 1350-1400m. VIII:14-20,1968 leg. B. Malkin [1: FSCA]. **UNDETERMINED LOCATION:** Bystus coccinelloides Dej. / R. coccinelliodes Guer. [1: FSCA].

Distribution (Fig. 6.119): Colombia.

Bystus decipiens **(Gorham)**

Bystus decipiens (Gorham) Strohecker, 1953: 21.

Rhymbus decipiens Gorham, 1875: 21.

Diagnosis: The antennae with the last 5 segments dark separates this species from similar species.

Redescription: Length = 1.5-1.75 mm. Body (Fig. 6.26) elongate-oval, subhemispherical, less convex dorsally. Dorsal surfaces yellowish or reddish brown, shiny. Vestiture comprised of moderately long golden-colored setae. Antenna (Fig. 6.48) 9-segmented, reddish brown, club antennomeres dark almost black; antennomere III distinctly longer than IV; IV-VI subequal in length; antennomeres VII-IX forming loose, 3-segmented club distinctly shorter than preceding segments combined; antennomere IX subquadrate, rounded apically. Pronotum with very fine punctation, very shiny; pronotal sulci narrowly but distinctly impressed; antebasal foveae poorly-developed. Elytron also very finely punctured. Hind wing (Fig. 6.70) moderately well melanized. Males unknown.

Etymology: Epithet derived from the Latin word “decipiens,” meaning “deceptive” or “misleading,” a possible reference to the close resemblance of this species to its congener *B. rhizobioides*, which occurs in the same geographical region.

Types: **Lectotype (here designated):** SYN- TYPE / Gorham Type / Fry Rio San. / Fry Coll. 1905.100 / 9023 / Rhymbus decipiens, Gorh / Lectotype Bystus decipiens Shockley 2008 [BMNH]. **Paralectotype (here designated)**: Same data as holotype [BMNH].

Additional Specimens Examined: **BRAZIL:** Rio Grande 84.8 [1: FSCA].

Distribution (Fig. 6.120): Brazil.

***Bystus decorator* Leschen and Carlton**

Bystus decorator Leschen and Carlton, 1993: 37-41.

Diagnosis: This species can easily be distinguished from its congeners by the presence of a light yellow macula on each elytron near the medial suture.

Redescription: Length = 1.7 – 2.5 mm. Body (Fig. 6.27) hemispherical, less convex dorsally. Dorsal surfaces light to dark brown, bearing vestiture of long erect setae; mouthparts, legs and elytral epipleura yellow. Antenna (Fig. 6.49) 10-segmented, antennomeres I-II and V-X dark brown, III-IV yellow; antennomeres III-VII subequal in length; antennal club shorter than preceding segments combined; antennomere X asymmetrical, slightly longer than IX. Pronotal sulci deeply impressed; antebasal foveae well-developed. Elytron densely punctate with large punctures; elytron with light-colored macula near midlength approximate to medial suture; humerus often also light in color (Fig. 6.27). Hind wing (Fig. 6.71) modestly melanized. Prothoracic basitarsus of male forming elongate, curved lobe (Fig. 6.90). Aedeagus (Fig. 6.107) with distinct curve apically.

<u>Etymology:</u> Derived from the combination of the Latin root "decor-," meaning "elegant," + the suffix "-ator," meaning "having the property of". Based on the original description, it is unclear whether this is a reference to the yellow maculae on the elytra of the adults, or the unusual behavior of the larvae which cloak themselves with debris to avoid predation. The former seems more likely.

<u>Type(s):</u> **Holotype:** PERU: Dpt. Madre de Dios Prv. Tambopata, Reserva Cuzco Amazónico, 15 km NE Puerto Maldonado 12º33'S, 69º03'W, 200m / 10 July 1989, J. Ashe & R. Leschen ex: red imperfect fungus [SEMC]. **Paratypes:** PERU: Dpt. Madre de Dios Prv. Tambopata, Reserva Cuzco Amazónico, 15 km NE Puerto Maldonado 12º33'S, 69º03'W, 200m / 10 July 1989, J. Ashe & R. Leschen ex: red imperfect fungus / PARATYPE Bystus decorator Leschen & Carlton 1993 [27: SEMC, 4: FSCA]; PERU: Tambopata Prov. Madre de Dios Dpto. 15km NE Puerto / Maldonado Reserva Cuzco Amazonico 12º33'S, 69º03'W 200m, Z1E13 / 1 July 1989, J.S. Ashe, R.A. Leschen #340 ex., red imperfect / PARATYPE Bystus decorator Leschen &

Carlton 1993 [6: SEMC, 4: USNM]; PERU: Tambopata Prov., 15km NE Puerto Maldonado, Reserva Cuzco Amazónica / 12º33'S, 69º03'W, 200m, 13 July 1989, ex., red imperfect fungi J.S. Ashe & R.A. Leschen / PARATYPE Bystus decorator Leschen & Carlton 1993 [1: SEMC, 3: PESC]; PERU: Tambopata Prov. 15km NE Pto. Maldonado 13 July 1989, 200m J. Ashe,R.Leschen#513 ex: Red imperfect / PARATYPE Bystus decorator Leschen & Carlton 1993 [1: SEMC].

Additional Specimens Examined: PERU: Tambopata Prov., 15km NE Puerto Maldonado, Reserva Cuzco Amazónica / 12º33'S, 69º03'W, 200m, 13 July 1989, ex., red imperfect fungi J.S. Ashe & R.A. Leschen [2: LSAM].

Distribution (Fig. 6.121): Peru.

Additional Notes: The pupa, larva and egg of *B. decorator* were described by Leschen and Carlton (1993). All known specimens were collected from the same site in Peru during July and found feeding on the red spore field of an undetermined fungus at the type locality.

***Bystus drakei* (Weise)**

Bystus drakei (Weise) Strohecker, 1953: 21.

Rhymbus drakei Weise, 1903: 206.

Diagnosis: The raised humerus, male prothoracic basitarsus shape and the shape of the median lobe separate this species from the other two species that occur in its native range.

Redescription: Length = 2.8 – 3.0 mm. Body (Fig. 6.28) elongate oval, less convex dorsally. Dorsal surface yellowish to reddish brown, shiny. Vestiture dense, comprised of long gray setae. Antenna (Fig. 6.50) 9-segmented, yellowish brown, club dark brown; antennomere III not conspicuously longer than IV; antennomeres IV-VI subequal in length; antennal club distinctly shorter than preceding segments combined. Prothorax and elytra finely, distinctly punctured; humerus raised, often lighter than elytral disc. Hind wing (Fig. 6.72) very poorly melanized. Prothoracic basitarsus of male triangular, projecting apically and basally (Fig. 6.99). Aedeagus (6.108) relatively simple with single shallow groove dorsally.

Etymology: Patronym honoring the original collector of this species, who provided it to Weise for description.

Type(s): **Lectotype (here designated):** Paraguay Drake / Coll. J. Weise Coll. J. Weise / Rhymbus drakei m. / SYNTYPUS Rhymbus drakei Weise, 1903 labelled by MNHUB 2005 [ZMHB]. **Paralectotypes (here designated):** Same data as holotype [2: ZMHB].

Additional Specimens Examined: BRAZIL: Rep BRASIL Minus 190 C. Bruch / 10. [2: FSCA].

Distribution (Fig. 6.122): Brazil, Paraguay.

***Bystus fibulatus* (Gorham)**

Bystus fibulatus (Gorham) Strohecker, 1953: 22.

Rhymbus fibulatus Gorham, 1887-99: 144.

Diagnosis: The fine punctation, body uniformly dark brown to black and the long, narrow antennae with the last five antennomeres dark separate this species from similar species.

Redescription: Length 2.0 – 2.2 mm. Body (Fig. 6.29) elongate-oval, subhemispherical, less convex dorsally. Dorsal surfaces uniformly dark brown to black, somewhat shiny. Antenna (Fig. 6.51) 10-segmented, reddish brown, last five antennomeres partially to completely dark brown to black, terminal antennomere occasionally lighter in color; antennomere III distinctly longer than IV; IV-VII subequal in length; antennal club subequal to preceding segments combined; antennomere X oblong, rounded apically. Pronotum with basal sulcus running between narrow, distinctly impressed lateral sulci; antebasal foveae poorly developed. Pronotum and elytron sparsely and finely punctate. Hind wing (Fig. 6.73) relatively well-melanized. Prothoracic basitarsus of male forming narrow, triangular lobe (Fig. 6.91). Aedeagus damaged during dissection.

Etymology: Derived from the combination of the Latin root “fibula-,” meaning “clasp” or “buckle,” and the suffix “-us.”

Type(s): **Lectotype (here designated):** SYN- TYPE / Type / Toxpam / Mexico Salle Coll. / 2204 / Rhymbus fibulatus, Gor / B.C.A.,Col.,VII. R. fibulatus Gorh [BMNH]. **Paralectotype**

(here designated): SYN- TYPE / 2287 / Mexico Salle Coll. / Rhymbus fibulatus Gorh / B.C.A.,Col.,VII. R. fibulatus Gorh [BMNH].

Additional Specimens Examined: **MEXICO:** Tezonapa, Veracruz, MEX. VIII:3:41 / Col. by Henry S. Dybas [5: FSCA].

Distribution (Fig. 6.123): Mexico.

Bystus foveatus Strohecker

Bystus foveatus Strohecker, 1957: 259 + fig. 1.

Diagnosis: The deep antebasal fovae and the elongate antennae readily separate this species from similar small species.

Redescription: Length = 2.4 – 2.6 mm. Body (Fig. 6.30) nearly hemispherical, strongly convex dorsally. Dorsal surfaces light to dark brown. Pronotum and elytra minutely punctured, covered with semi-erect, coppery setae. Antenna (Fig. 6.52) 10-segmented, yellow brown, club black; antennomeres III-VII subequal in length, progressively stouter apically; VIII-IX longer than broad; X widened from base, longer than wide, apex slightly emarginated. Pronotum with well-developed antebasal foveae. Hind wing (Fig. 6.74) conspicuously melanized. Males unknown.

Etymology: Derived from the combination of the Latin root “fove-,” meaning “pit,” + the suffix “-atus,” meaning “having the property of.” This is likely a reference to the prominent round foveae found just mesad of the base of the lateral sulci on the pronotum, a feature especially prominent in this species.

Type(s): **Holotype:** Suapure VENEZ. Caura River July 3-13, 1900. E.A. Klages / Bystus foveatus Strohecker Holo-TYPE Cornell U. 2952 [CUIC].

Additional Specimens Examined: **VENEZUELA:** Venezuela-Aragua Rancho Grande 1500m.19-VII-64 / J.&B.Bechyne leg. / Venezuela-Inst. Zool. Agricola Fac. Agronomia Univ. Central [3: FSCA].

Distribution (Fig. 6.124): Venezuela.

Additional Notes: The sex of the holotype was not determined by Strohecker (1957) but appears to be female.

Bystus globosus **(Gorham)**

Bystus globosus (Gorham) Strohecker, 1953: 22.

Rhymbus globosus Gorham, 1898: 337.

Diagnosis: Similar to *B. unicolor*, but with the head and pronotum black.

Redescription: Length = 1.65 – 1.85 mm. Body (Fig. 6.31) hemispherical, very convex, shiny. Vestiture relatively thick, comprised of moderately long, suberect setae, grey on the head and thorax and reddish on the elytra. Head, antennae, mouthparts and thorax uniformly black, elytra reddish in color (Fig. 6.31). Antenna (Fig. 6.53) 10-segmented, stout; antennomere III subequal to IV; antennomeres IV-VI subequal in length; antennal club subequal to preceding antennomeres combined; antennomere X rounded apically, with oblique angle laterally. Pronotum with lateral margins narrow, reflexed; sulci widely separated basally, strongly convergent apically; antebasal foveae poorly developed. Elytron with very fine punctation. Hind wing (Fig. 6.75) very weakly melanized. Male unknown.

Etymology: Epithet derived from the combination of the Latin root "globos-," meaning "ball-like," with the latin suffix "-us," a likely reference to the extremely round habitus of this species.

Type(s): **Lectotype (here designated):** SYN- TYPE / Type / Type / Chantilly Est. (Windward side) Grenada. W.I. H.H. Smith. 63 / W. Indies 98.237. / Rhymbus globosus, Gor [BMNH]. **Paralectotypes (here designated):** Same data as the holotype [2: BMNH]. All types are female.

Distribution (Fig. 6.125): Grenada.

Bystus hemisphaericus **(Gerstaecker)**

Bystus hemisphaericus (Gerstaecker) Strohecker, 1953: 22.

Rhymbus hemisphaericus Gerstaecker, 1858: 349 + pl. 3, fig. 6.

Diagnosis: The terminal antennomere light-colored only at its apex readily distinguish this species from *B. coccinelloides* and *B. apicalis*.

Redescription: Length 3.0-4.0 mm. Body (Fig. 6.32) elongate-oval, subhemispherical, strongly convex dorsally. Dorsal surfaces uniformly reddish brow, lateral margins of pronotum and elytra often lighter. Vestiture relatively dense, comprised of long, suberect yellow setae. Antenna (Fig. 6.54) 9-segmented, elongate, reddish or yellowish brown, club dark with apex of terminal antennomere lighter; antennomere III distinctly longer than IV; IV-VI subequal in length; antennal club not as long as preceding segments combined; antennomere IX elongate, narrow, apically pointed. Pronotal sulci finely but deeply impressed; antebasal foveae poorly developed. Elytra and pronotum finely punctured. Hind wing (Fig. 6.76) very well melanized. Prothoracic basitarsus of male with lobe elongate in appearance with thick pectinate comb (Fig. 6.92). Aedeagus (Fig. 6.109) with median lobe bearing strong curving hook apically.

Etymology: Epithet derived from the combination of the Greek roots “hemi-,” meaning “half,” + “sphaero-,” meaning “sphere,” + the Latinized suffix “-icus,” an apparent reference to the notably round and strongly convex habitus of this species.

Type(s): **Lectotype (here designated):** 21874 / His.-Coll. (Coleoptera) Nr. 21874 Rhymbus hemisphaericus Gerst. Costa Rica, Wagner Zool. Mus. Berlin / SYNTYPUS Rhymbus hemisphaericus Gerstaecker, 1858 labelled by MNHUB 2005 / hemisphaericus Gerst. Costa Rica. Wagn. / Museum fur Naturkunde Humboldt-Univ. Berlin (MNHUB) [ZMHB].

Specimens Examined: **GUYANA:** Mackenzie Demerara R. BRIT.GUIANA June 22’27 / Cornell U. Lot 760 Sub 103 / Bystus hemisphericus Gerst. det.H.F.Strohecker [1: CUIC].

PANAMA: PANAMA, Chiriqui Prov. 2km N Sta. Clara,1300m,8º51'N, 82º36'W Hartmann's Finca 30-31.V.77 H. & A. Howden [1: FSCA].

Distribution (Fig. 6.126): Belize, Costa Rica, Guatemala, Guyana, Mexico, Panama.

Additional Notes: Gorham (1887-99) attributed a short series of 3 specimens from Belize to *B. pallidulus*. Based on our studies of the available material, this conclusion appears to be erroneous. Those specimens belong to *B. hemisphaericus*. Wheeler (1925) reported this species as recovered as a prey item from the bivouac of the Army ant *Eciton hamatum*. Mann (1925) later questioned this conclusion, dismissing their presence as only incidental.

Bystus humeralis **Shockley and McHugh, new species**

Bystus humeralis Shockley and McHugh, new species

Diagnosis: The smaller size, well-developed, raised humerus and the presence of a medial carina on the prosternal intercoxal process readily separate this species from similar species.

Description: Length = 1.5-1.75 mm. Body (Fig. 6.33) hemispherical, highly convex dorsally. Dorsal surfaces light brown to dark brown, elytron darker near humerus. Vestiture comprised of relatively short, pale-colored setae. Antenna (Fig. 6.55) 10-segmented, dark brown, club antennomeres black; antennomere III subequal to IV; IV-VII subequal in length; antennal club longer than preceding segments combined; antennomere X subquadrate. Prosternal process medially carinate. Elytra and pronotum finely, sparsely punctured. Hind wing (Fig. 6.77) very poorly melanized. Male unknown.

Etymology: Epithet based on the inflation of the humeral region of the elytra, which appears darker than the rest of the elytra in intact specimens.

Type(s): **Holotype (here designated):** GUAYANA: Region 8 Iwokrama Forest, Pakatau hills 4º44’54”N,59º1’36”W, 70 m 28 MAY 2001; R. Brooks, Z. Falin GUY1BF01 049 ex: fogging fungusy logs [SEMC]. **Paratypes (here designated):** Same data as the holotype [4: SEMC]; GUYANA: Region 8 Iwokrama Forest, Turtle Mt. base camp, 50 m, 4º43’5”N,58º43’5”W 31 MAY 2001; R. Brooks, Z. Falin GUY1BF01 077 ex: fogging fungusy logs [1: SEMC, 1: FSRC]; GUYANA: Region 8 Iwokrama Forest, Turtle Mt. base camp, 50 m, 4º43’5”N,58º43’5”W 1 JUN 2001; R. Brooks, Z. Falin GUY1BF01 099 ex: fogging fungusy logs [1: SEMC]; GUAYANA: Region 8 Iwokrama Forest, Pakatau hills 4º44’54”N,59º1’36”W, 70 m 27 MAY 2001; R. Brooks, Z. Falin GUY1BF01 039 ex: fogging fungusy logs [1: SEMC]; GUAYANA: Region 8 Iwokrama Forest, 1 km W Kurupukari, Iwokrama Field Stn. 60 m 4º40’19”N,58º41’4”W, 21 MAY 2001 R.Brooks,Z.Falin GUY1BF01 004 ex: fogging fungusy logs [1: SEMC]; GUAYANA: Region 8 Iwokrama Forest, 26 km SW Kurupukan, Iwokrama Mt. base camp, 60 m. 4º20’17”N,58º48’38”W 23 MAY 2001; R.Brooks, Z.Falin GUY18F01 013 ex: fogging fungusy logs [1: SEMC]; GUYANA Region 8 Iwokrama Forest, Kabocalli Field Stn 4º17’4”N,58º30’35”W, 60 m 4 JUN 2001, R.Brooks,Z.Falin GUY1BF01 125 ex. fogging fungusy log [1: SEMC].

Additional Specimens Examined: **FRENCH GUIANA:** FRENCH GUIANA Saul, 7 km N, Les Eaux Claires 3º39’46”N,53º13’19”W, 220 m 31 MAY 1997; J.Ashe,R.Brooks FG1AB97 094 ex: fungusy log [1: SEMC]; FRENCH GUIANA Roura, 13.0 km SSE, 240 m 4º38’38”N,52º17’56”W 13 JUN 1997; J.Ashe,R.Brooks FG1AB97 196 ex:misc.collecting [1: SEMC].

Distribution (Fig. 6.127): French Guiana, Guyana.

Bystus limbatus **(Guérin in Gorham)**

Bystus limbatus (Guérin in Gorham) Strohecker, 1953: 22.

Rhymbus limbatus Guérin in Gorham, 1873: 63.

Diagnosis: The black elytra margined in yellow or light brown make this species easily recognizeable.

Redescription: Length = 3.5 – 4.0 mm. Body (Fig. 6.34) elongate-oval, subhemispherical, highly convex. Dorsal surfaces black, shiny, pronotal and elytral margins yellowish or reddish. Vestiture fine, sparse. Antenna (Fig. 6.56) 9-segmented, brownish; antennomere III longer than IV; IV-VI subequal in length; antennal club nearly as long as preceding segments combined; antennomere IX elongate, narrowly rounded apically. Pronotal and elytral discs black, narrowly margined in yellow or red; pronotal sulci narrowly impressed; antebasal foveae poorly developed. Elytron deeply, sparsely punctured. Hind wing (Fig. 6.78) very well melanized. Prothoracic basitarsus of male forming long, curved lobe with narrow pectinate comb (Fig. 6.93).

Aedeagus (Fig. 6.110) with median lobe strongly curved medially, tapering to elongate tip apically.

Etymology: Derived from the combination of the Latin root "limb-," meaning "edge," and the suffix "atus," meaning "having the property of." This name likely refers to the light brown-red margins of the pronotum and the elytra which have black maculate discs.

Type(s): **Holotype:** Holo- type / Type / R. limbatus Gorham Type / Gorham Coll. 91-50 / Bystus limbatus Guerin. (type) Mexique / Type Guerin Men [BMNH].

Additional Specimens Examined: **MEXICO:** Mex / Estado de Vera Cruz / Casey bequest 1925 / R. Hanover [1: USNM]; Tezonapa, Ver., MEX. VIII:8:41 / Col. by H. S. Dybas [5: FSCA]; San Juan de la Punta,Ver.,MEX. VII 13 41 / Col. by Henry S. Dybas [1: FSCA]; 7.5 mi. S.W. Tamazunchale S.L.P., MEX. / VI-27-65 F.G. Thompson [1: FSCA]; Jalapa, Mexico. Hoege. / Rhymbus limbatus, Gorh. co-type / B.C.A.,Col.,VII. R. limbatus Gorh [2: FSCA].

Distribution (Fig. 6.128): Mexico.

Additional Notes: Gorham originally attributed the name *R. limbatus* to Guérin because he claimed to have examined a specimen with Guérin's type label, although he noted that Guérin had not formally described it. Nonetheless, Gorham is generally credited with describing this species.

Bystus marginatus **Shockley and McHugh, new species**

Bystus marginatus Shockley and McHugh, new species

Diagnosis: The distinctly widened lateral margins of the elytra, which give the beetle a heart-shaped appearance, readily distinguishes *B. marginatus* from its congeners.

Description: Length = 2.75-3.0 mm. Body (Fig. 6.35) broadly oval, heart-shaped, less strongly convex dorsally. Dorsal surfaces uniformly dark brown. Vestiture comprised of suberect, pale setae. Antenna (Fig. 6.57) 9-segmented, light to dark brown, club antennomeres darker; antennomere III subequal to IV; antennal club longer than preceding segments combined; antennomere IX elongate, very narrow basally, greatly expanded apically. Pronotal sulci narrowly, distinctly impressed; antebasal foveae poorly developed. Lateral margin of elytron widened, reflexed for most of length, narrowing only at apex. Body widest at elytral humeri rather than at midlength, the more common condition among *Bystus* species. Hind wing (Fig. 6.79) modestly melanized. Prothoracic basitarsus of male forming smaller, more triangular lobe (Fig. 6.94). Aedeagus (Fig. 6.111) with median lobe thick for entire length, narrowing abruptly only at apex.

Etymology: Derived from the combination of the Latin stem “margin-,” meaning “edge,” and the general suffix “-atus,” meaning “having the property of.” This is a reference to the explanate margins of the pronotum which differentiate this species from other similar species.

Type(s): Holotype (here designated): PERU: Dept. Loreto 1.5 km N. Teniente Lopez 2º35.66'S, 76º06.92'W 26 July 1993, 210-240 m Richard Leschen #224 ex:fogging fungusy log [SEMC]. Paratypes (here designated): PERU: Dept. Loreto Teniente Lopez 2º35.66'S, 76º06.92'W 24 July 1993, 210-240 m Richard Leschen #193 ex:flight intercept trap [1: SEMC]; PERU: Dept. Loreto 1.5km N Teniente Lopez 2º35.66'S, 76º06.92'W 18 July 1993, 210-240 m Richard Leschen #119 ex: flight intercept trap [1: SEMC]; PERU: Dept. Loreto 1.5km N Teniente Lopez 2º35.66'S, 76º06.92'W 17 July 1993, 210-240 m Richard Leschen #122 [1: SEMC]; PERU: Dept. Loreto 1.5km N Teniente Lopez 2º35.66'S, 76º06.92'W 22 July 1993, 210-240 m Richard Leschen #164 ex: flight intercept trap [1: SEMC]; PERU: Dept. Loreto Campamento San Jacinto 2º18.75'S, 75º51.77'W 3 July 1993, 175-215 m Richard Leschen, #12 ex: flight intercept trap [1: SEMC]; PERU: Dept. Loreto Campamento San Jacinto 2º18.75'S, 75º51.77'W 9 July 1993, 175-215 m Richard Leschen, #68 ex:flt intcpt. trap, Qd.20 [1: SEMC].

Additional Specimens Examined: ECUADOR: ECUADOR: Pichincha Rio Palenque Science Center 200 m; 0º36'0"S, 79º21'0"W 25 MAY-6 JUL 1996; P.Hibbs ECU2H96 007B; ex: malaise trap [1: SEMC]; ECUADOR: Pichincha Maquipucuna For. Res. 50 km NW Quito 21 Dec. 1991, 1650 m C.Carlton, R.Leschen #37 ex: fungusy log [2: SEMC]; ECUADOR: Pichincha Maquipucuna For. Res. 50 km NW of Quito 1350-1600 m, 23 Dec. 1991, C.Carlton R.Leschen #70 [1: SEMC]; ECUADOR: Sucumbios Sacha Lodge, 270 m 0º28'14"S, 76º27'35"W 24 MAR 1999; R.Brooks ECU1B99 030 ex:fungus covered log [1: SEMC].

Distribution (Fig. 6.129): Ecuador and Peru.

***Bystus pallidulus* (Gerstaecker)**

Bystus pallidulus (Gerstaecker) Strohecker, 1953: 22.

Rymbus pallidus Costa, Vanin and Casari-Chen, 1988: plate 96.

Rhymbus pallidus Costa, Vanin and Casari-Chen, 1988: 201.

Rhymbus pallidulus Gerstaecker, 1858: 351.

Diagnosis: The light colored margins of the elytra and the black antennal club help distinguish this species from sympatric species.

Redescription: Length = 3.0-3.5 mm. Body (Fig. 6.36) elongate-oval, subhemispherical, less convex dorsally. Dorsal surfaces reddish brown, somewhat shiny. Vestiture relatively thick, comprised of very pale almost white setae. Antenna (Fig. 6.58) 9-segmented, light brown, club antennomeres black; antennomeres III-IV subequal in length, each longer than segments V-VIII; antennal club not longer than preceding segments combined; antennomere IX elongate oval, narrowed apically. Elytron densely punctured, pronotum widely punctured. Hind wing (Fig. 6.80) well melanized. Prothoracic basitarsus of male forming large triangular lobe, the largest in the genus (Fig. 6.95). Aedeagus (Fig. 6.112) with median lobe very slender, the tip abruptly, narrowly constricted to form small hook.

Type(s): **Lectotype (here designated):** SYN- TYPE / Co- Type / Caracas / pallidulus (Gerst. – type) / Gorham Coll. 91-50 [BMNH]. **Paralectotypes (here designated):** S. Paulo Brasil / 10.073 / Rhymbus pallidulus Seroa. [1: NHRS]; Sao Paolo Thering / 10.073 / Rhymbus pallidulus Seroa. [2: NHRS].

<u>Specimens Examined:</u> **BRAZIL:** Petropolis 22-8-98 / Bystus pallidulus (Gerst.) (over) det.H.F.Strohecker {on reverse side of label: from study of co-type ♂ Br. Mus.}[1: FSCA]; **PERU:** TINGO MARIA (PERU) 670 M. LEG. WEYRAUCH / WKW 121 [1: FSCA]; **UNDETERMINED LOCATION:** 8. / Rhymbus pallidulus G. Am. mer. {on reverse side of label: Rhymbus sent to Chapuis} / R. pallidulus Gerst. [1: FSCA].

<u>Etymology:</u> Derived from combination of the Latin root "pallidus-," meaning "pale in color," and the diminutive suffix "-ulus," an apparent reference to the whitish-yellowish pubescence of this species.

<u>Distribution (Fig. 6.130):</u> Brazil, Peru.

<u>Additional notes:</u> The larva of this species was described by Costa *et al.* (1988), although it was variably referred to as *Rhymbus pallidus* and *Rymbus pallidus*. Shockley *et al.* (2009a) synonymized both names under *B. pallidulus*.

***Bystus piceus* (Gorham)**

Bystus piceus (Gorham) Strohecker, 1953: 22.

Rhymbus piceus Gorham, 1887-99: 143 + pl. 8, fig. 13.

<u>Diagnosis:</u> The dark brown color of this species and the abruptly curved median lobe differentiates this species from similarly sized sympatric species.

Redescription: Length = 3.0-3.2 mm. Body (Fig. 6.37) hemispherical, highly convex dorsally. Dorsal surfaces, legs, antennae dark reddish brown. Vestiture dense, comprised of long suberect, pale reddish setae. Antenna (6.59) 9-segmented, dark reddish brown, club antennomeres darker; antennomere III distinctly longer than IV; IV-VI subequal in length; antennal club not longer than preceding segments combined. Hind wing (6.81) well melanized. Prothoracic basitarsus of male forming short, stout, triangular lobe (Fig. 6.96). Aedeagus (Fig. 6.113) with median lobe abruptly, strongly curving ventrad near 2/3 length, narrowing rapidly to form acute apex.

Etymology: Epithet derived from the combination of the Latin root "pice-," meaning "pitch black," and the suffix "-us," an apparent reference to the darker, "pitchy" color of this species.

Type(s): **Lectotype (here designated):** SYN- TYPE / Type / Sp. figured. / V. de Chiriqui 25-4000 ft. champion / Rhymbus piceus Gorh / basal joint of front tarsi enlarged ♂,? joints of club long. / B.C.A, Col., VII. R. piceus, Gorh [BMNH]. **Paralectotypes (here designated):** Same data as holotype [4: BMNH]; SYN- TYPE / Caldera 1200 ft. Champion / Rhymbus piceus, Gorh. / B.C.A, Col., VII. R. piceus, Gorh [2: BMNH].

Additional Specimens Examined: **PANAMA:** PANAMA, Chiriqui Prov. 2km N Sta. Clara,1300m,8º51'N, 82º36'W Hartmann's Finca 30-31.V.77 H. & A. Howden [1: FSCA]; V. de Chiriqui, 25-4000 ft. Champion. / Rhymbus piceus Gorh. co-type ♀ / B.C.A.,Col.,VII. R. piceus, Gorh [1: FSCA]. **COSTA RICA:** COSTA RICA: Heredia Prov.; La Selva Biological Station, 38m; 10°25’55”N, 84°00’35”W; 15-16.VI.2004, F. Shockley; Hand collected from fungus [2: UGCA].

Distribution (Fig. 6.131): Costa Rica, Panama.

Additional Notes: Shockley and McHugh (in prep; Chapter 5) conducted an exhaustive morphological study of this species and pointed out that the *Bystus* larva illustrated by Lawrence (1991) was most likely this species.

***Bystus rhizobioides* (Gorham)**

Bystus rhizobioides (Gorham) Strohecker, 1953: 22.

Rhymbus rhizobioides Gorham, 1875: 20.

Diagnosis: The short antennae with a greatly elongate club readily separate this species from similarly sized congeners.

Redescription: Length = 2.5-2.75 mm. Body (Fig. 6.38) elongate-oval, subhemispherical, highly convex dorsally. Dorsal surfaces reddish brown, shiny. Vestiture comprised of very fine, short, gold-colored setae. Antenna (Fig. 6.60) 9-segmented, relatively short, dark brown to almost black; antennomere III subequal to IV; IV-VI subequal in length; antennal club elongate, much longer than preceding segments combined; antennomere IX elongate, narrowly rounded apically. Elytron convex, thickly and finely punctured. Hind wing (Fig. 6.82) fairly melanized. Prothoracic basitarsus of male wide basally, curving dorsad before narrowing apically (Fig.

6.97). Aedeagus (Fig. 6.114) simple, with median lobe bearing short distal groove and straight, unhooked apex.

Etymology: Possibly derived from the combination of the coccinellid generic name *Rhizobius* with the suffix "-oides," meaning "resembling in appearance," perhaps a reference to the similarity in overall appearance between this species and some species of *Rhizobius*.

Type(s): **Lectotype (here designated):** 20434 / SYN- TYPE / TYPE H.T. / Gorham Type / Fry Rio San. / Fry Coll. 1905.100. / Rhymbus Rhyzobioides, Gorh. [BMNH]. **Paralectotype (here designated):** SYN- TYPE / Gorham Type / Co- Type / Fry Rio San. / Gorham Coll. 91-50 / Rhyzobioides Gorh [BMNH].

Additional Specimens Examined: **BRAZIL:** Sao Paulo, Bras. Muus u.Melzer / Dtsch.Entomol. Institut Berlin [1: FSCA]; S. Paulo. / Coll. E. Csiki [1: FSCA]; Carácas O. Thieme / Bystus coccinellides det. H.F. Strohecker [1: FSCA].

Distribution (Fig. 6.132): Brazil.

Bystus rodmani **Shockley and McHugh, new species**

Bystus rodmani Shockley and McHugh, new species.

Diagnosis: The combination of black pronotum and dark red elytra readily separate this species from any other similar species.

Description: Length = 3.0-3.2 mm. Body (Fig. 6.39) hemispherical, highly convex dorsally. Dorsal surface of pronotum black, elytra dark red. Vestiture relatively long on head and prothorax, shorter on elytra and consisting of golden-colored setae. Antenna (Fig. 6.61) 9-segmented, elongate, yellowish with club light to dark brown; antennomere III distinctly longer than IV; IV-VI subequal in length; antennal club highly elongate and subequal to preceding segments combined; antennomere IX narrowly rounded apically. Hind wing (Fig. 6.83) weakly melanized. Prothoracic basitarsus of male with broader pectinate comb than congeners (Fig. 6.98). Aedeagus (Fig. 6.115) highly modified, median lobe with weak external sclerotization.

Etymology: Patronym honoring Dr. Jim Rodman, one of the pioneers of the National Science Foundation Partnerships for Enhancing Expertise in Taxonomy (PEET) program.

Type(s): **Holotype (here designated):** BOLIVIA: La Paz 9.4 km E Chulumani, Apa Apa Ecol. Reserve, 2100-2400m, 16º20.99'S 67º30.30'W 17-I-2001, J.S. Ashe, R.S. Hanley ex. fungus covered log, BOL1AH01 001 [SEMC]. **Paratypes (here designated):** Same data as the holotype [10: SEMC]; BOLIVIA: La Paz 9.4 km E Chulumani, Apa Apa Ecol. Reserve, 2100-2400m, 16º20.99'S 67º30.30'W 19-I-2001, J.S. Ashe, R.S. Hanley ex. fungus covered log, BOL1AH01 018 [3: SEMC].

Distribution (Fig. 6.133): Bolivia.

***Bystus rufus* (Weise)**

Bystus rufus (Weise) Strohecker, 1953: 22.

Rhymbus rufus Weise, 1903: 206.

Diagnosis: This is the only smaller species (<2.5 mm) to have a 9-segmented antenna.

Redescription: Length = 2.2-2.5 mm. Body (6.40) elongate-oval, less convex dorsally. Dorsal surfaces reddish brown. Vestiture relatively long, especially along margins of pronotum and elytra, consisting of golden-colored setae. Antenna (6.62) 9-segmented, short, stout, brown; antennomere III distinctly longer than IV; IV-VI subequal in length; antennal club greatly expanded apically and not longer than preceding segments combined; antennomere IX subquadrate. Hind wing (6.85) well melanized. Male unknown.

Etymology: Derived from the combination of the Latin "ruf-," meaning "red," with the general suffix "-us," referring to the deep red color of this species.

Type(s): **Holotype:** Paraguay Drake / Coll. J. Weise Coll. J. Weise / Rhymbus rufus m ♀ / SYNTYPUS Rhymbus rufus Weise, 1903 labelled by MNHUB 2005 [ZMHB].

Additional Specimens Examined: **ARGENTINA:** Rep ARGENTINA Prov. Cordoba A.G. 190 C. Bruch [1: FSCA]; **BRAZIL:** S. Catharina Rio Capivary Fruhstorfer 1888 / Coll. Kraatz / Dtsch. Entomol. Institut Berlin [1: FSCA].

Distribution (Fig. 6.134): Argentina, Brazil and Paraguay.

Bystus seminulum **(Gorham)**

Bystus seminulum (Gorham) Strohecker, 1953: 22.

Rhymbus seminulum Gorham, 1873: 56.

Diagnosis: The almost glabrous appearance with a black elytral disc and a raised humerus with a reddish or orangish macula make this species easily recognizeable.

Redescription: Length = 1.3-1.5 mm. Body (Fig. 6.41) hemispherical, highly convex dorsally. Dorsal surfaces black, very shiny. Vestiture very short, sparse. Antenna (Fig. 6.63) 10-segmented, yellowish brown, club antennomeres dark brown, apex of terminal antennomere lighter; antennomere III subequal to IV; IV-VII subequal in length; antennal club not longer than preceding segments combined; antennomere X subquadrate. Pronotum very transverse, pronotal sulci narrowly impressed, antebasal foveae poorly developed. Elytron highly convex with disc black, humerus raised, bearing yellow or orange macula. Single available specimen from Gorham's type series was not dissected.

Type(s): **Lectotype (here designated):** SYN- TYPE / Type / Not Fig' / Rhymbus seminulum,Gorha / Gorham Coll. 91-50 / Gorham Type {underneath side of label = eminulum Type} [BMNH].

Etymology: Epithet derived from the combination of the Latin root "semin-," meaning "seed," and the diminutive suffix "-ulum," meaning "like," perhaps a reference to the small, dark, shiny appearance of this distinctive species.

Distribution (Fig. 6.135): French Guiana.

Bystus ulkei **(Crotch)**

Bystus ulkei (Crotch) Strohecker, 1953: 22.

Rhymbus granulatus Poole and Gentili, 1996: 266.

Exysma ulkei Arrow, 1920: 78.

Rhymbus ulkei granulatus Blatchley, 1910: 535.

Parexysma ulkei Csiki, 1905: 573.

Symbiotes ulkei LeConte and Horn, 1883: 121.

Rhymbus ulkei Horn, 1875: 132.

Alexia ulkei Crotch, 1873: 362.

Diagnosis: The 4-4-4 tarsal formula and the reduced male prothoracic basitarsus readily distinguishes this species from all other congeners.

Redescription: Length = 1.75-2.0 mm. Body (Fig. 6.42) subhemispherical, highly convex dorsally. Dorsal surface dark brown to black with vestiture of long, erect, pale-colored setae, moderately to coarsely punctate. Elytron with disc very dark, almost black, with lateral and sutural margins light brown to yellow. Antebasal pronotal foveae poorly developed. Antenna

(Fig. 6.64) 10-segmented, reddish to brownish, club antennomeres forming loose, dark-colored club; antennomere III subequal to IV; antennal club not longer than preceding segments combined; antennomere X elongate, rounded apically. Hind wing (6.85) weakly melanized. Prothoracic basitarsus of male reduced compared to other species; pectinate comb very small (Fig. 6.100); prothoracic tarsus appearing 4-segmented. Aedeagus (Fig. 6.116) very narrow and reflexed apically.

Etymology: Patronym honoring Henry Ulke, who first collected this species and provided it to Crotch for description.

Type(s): **Neotype (designated by Strohecker 1981):** DC, Ulke Coll. [CMNH].

Additional Specimens Examined: **ALABAMA:** Ala. Dale Co. Ft Rucker Mil. Res. 5 Aug. 1992 R. Turnbow; Bystus ulkei (Crotch) det. R. Turnbow [21: RHTC]. **ARKANSAS:** USA AR Washington Co. 1 mi SW of Fayetteville So. of Hwy 16 / 5 Oct 1987 Dead-Oak Berlesate R. Leschen / Bystus ulkei Crotch [1: UADE]; AR, Logan Co. nr. Charleston / Oct. 1977 Berlesate IDClass [1: UADE]; USA, AR, Polk Co. Caney Crk. Wild. Ar. 3.5 mi. N. Bard Spgs. Beech-maple berlesate Carlton/Robison 15 Nov. 1991 [2: UADE, 4: LSAM]; USA, AR, Mont. Co. 1.5 mi. E. Crystal Rec. Area along FS 177K 19 Dec. 1991 Carlton/Robison Decid. berlesate [1: UADE]. **DISTRICT OF COLUMBIA:** D.C. [1: FSCA]; DC / Carn. Mus. Acc. 349 / Bystus ulkei (Crotch) [From series det. by J. Pakaluk][1: CMNH]; DC / Henry Ulke Beetle Coll. CMNH Acc. No. 1645 / Bystus ulkei (Crotch) [From series det. by J. Pakaluk][1: CMNH]; D.C. / Collection C. V. Riley [2: USNM]. **FLORIDA:** Fla. Walton Co. Eglin AFB 21 Nov. 1998 R.

Turnbow / berlese beech/magnolia litter / Bystus ulkei (Crotch) det. A. D. Allen [1: RHTC]; FLORIDA: Jackson Co. 4.mi.N.Marianna on Chipola R. floodplain 26-V-1994 P.E. Skelley / Bystus ulkei Det: F. W. Shockley 2005 [1: PESC]; FLORIDA:Alachua Co. Gainesville;nr.Doyle Conner Building 30-V-1987 Skelley & Lundgren at light [1: PESC]; Crescent City Fla / Coll Hubbard & Schwarz [2: USNM]; Enterprise Fla 29.5 / CollHubbard &Schwarz [3: USNM]; Bark 2 aquatica / Entprise Fla 1.1 / 708 / C.W.Leng Collection [1: EMEC]; Entprise Fla 11/10 / Bark 2 aquatica / 87I / C.W.Leng Collection [1: EMEC]; Enterprise Fla. 11-15 / C.W.Leng Collection [1: EMEC]. **GEORGIA:** Rabun Co. Ga. July / C.W.Leng Collection / Rhymbus ulkei (Cr.) 10744 [1: EMEC]. **ILLINOIS:** Falling Springs St. Clair Co. ILL June 1.1919 / Cornell U. Lot. 908 Sub. 1528 / Bystus ulkei Cr. det Strohecker [3: CUIC]. **INDIANA:** Crawford Co. Ind. W.S.B. 8-10-09 / Rhymbus ulkei Cr. Edith W. Mank Collection / Bystus ulkei (Crotch) det.H.F.Strohecker [1: CUIC]. **IOWA:** Iowa City Wickham / WICKHAM Collection 1933 / Symbiotes ulkei Cr. 3175 [1: USNM]. **KANSAS:** Oct 31 / TopekaKs Popenoe / Symbiotes [1: USNM]; Nov 1 / TopekaKs Popenoe / 3175 [1: KSUC, 2: USNM]; Nov 3 / TopekaKs Popenoe [1: USNM]; 35. / Benedict. Ks., W. Knaus. / 10744 [1: KSUC]; Kan / 3175 [1: KSUC]; Kans 2047 / Alexia [1: FSRC]; Kans 2047 / 3175 / From Collection Wickham / Acc. No. 36 Dept. No. 200 Collection L.B Walton Kenyon College / Brit Mus. 1949-175 / Bystus ulkei (Crotch) det. Strohecker [1: BMNH]; Kans. / 35 [2: USNM]; Kans 2047 / Wickham Collection 1933 [1: USNM]; Onaga Kan. / Wickham collection 1933 [1: USNM]; RileyCoKs Popenoe / 87 / Horn det. [1: USNM]; Kans. / C.W.Leng Collection [1: EMEC]; USA: Kansas: Douglas Co. Cinton Lake Area / June 2 1993 ex fungusy wood R. Leschen [1: RALC]; Kansas: Crawford Co 2W Pittsburg, 9-27 May 2008, flight intercept trap G A Salsbury [1: SEMC]; USA: Kansas: Crawford Co. 3 mi NE Pittsburg 37º26.64’N 94º37.04’W 13-V-1-VI-2005 G.A. Salsbury, ex.

canopy trap KAN1S05 084 [1: SEMC]; USA: Kansas: Labette Co. Big Hill Reservoir, NW of dam 37º16.55'N 95º28.43'W 13-26-VII-2005 G.A. Salsbury ex. canopy trap KAN1S05 157 [1: SEMC]. **KENTUCKY:** Ky. / Casey Bequest 1925 / Rhymbus ulkei [1: USNM]; Ky. / Casey Bequest 1925 / Casey determ. ulkei [3: USNM]; Ky. / Collection C. V. Riley [1: USNM]; Ky. / 2455 / Collection C. V. Riley / Collection Belfrage [1: USNM]; Rockhaven Ky July 2 1893 / Collection H. Soltau [10: USNM]; Rockhaven Ky July 22 1894 / Collection H. Soltau [2: USNM]; Ky / H.W. Wenzel Collection [1: OSUC]; Ky. / C.W.Leng Collection [1: EMEC]. **MARYLAND**: MARYLAND: Calvert Co. Flag Ponds area 3 km SE Long Beach 9 September 1990 W.E.Steiner, J.M.Hill [1: USNM]; PlummersI Md 25.8.07 / EASchwarz Collector [3: USNM]; PlummersI Md VII-07 / WmPalmer Collector [2: USNM]; Plummers I 4.VII.09 Md / EASchwarz Collector [1: USNM]; freshet drift / Plummer's I 2.IX.11 Md / Barber& SchwarzColl [1: USNM]. **MISSISSIPPI:** Meridian Miss 12.7 / Collection H. Soltau / Rhymbus ulkei granulatus Blatchley 1910.Coleop.Indiana,p.535 [1: USNM]. **MISSOURI:** St.Louis Mo. (1: KSUC); MISSOURI: St. Louis Co.; Creve Coeur Lake 11 July 1903 coll: G. W. Bock [14: FSRC]; New. / 26 Jun 76 / Collection of C. V. RILEY St. Louis, MO. / Alexia Ulkei Crotch Lec. Jun76 [1: USNM]. **OHIO:** Ohio / Symbiotes ulkei / Alexia ulkei / BROOKLYN MUSEUM COLL. 1929 / Cornell U. Lot 908 Sub 1528 Schaeffer Coll. [1: FSCA]; Cincinatti, Ohio IX/13/00 C. Dury, Collr. / Cin. O. 9/13/00 3175 [2: AMNH]; Cincinatti, Ohio IX/13/00 C. Dury, Collr. / Collection ANicolay / Rhymbus ulkei Cr. [1: USNM]; Ohio / Coll MLLinell [3: USNM]; Cincinatti Oh July 25 1897 / Collection H. Soltau [2: USNM]; Ohio / Collection Anicolay [1: USNM]; Cincin. Ohio / Wickham Collection 1933 [2: USNM]; Ohio [1: USNM]; Ohio. / 3175 / C.W.Leng Collection [1: EMEC]; OHIO: Jackson Co. Lake Katherin 2-15 July 1989 R.S. Miller family / Malaise trap in hillside woods [1: MAIC]. **OKLAHOMA:** OKLAHOMA: Latimer Co., 5 mi W. Red Oak, Oct. 1980, K. Stephan / Bystus [1: USNM, 4: FSCA]; USA OK Latimer Co. 10 mi. SW of Red Oak / 3 Nov. 1987 under bark R. Leschen [1: UADE]; OKLAHOMA:LATIMER CO. XI-1987 KARL STEPHAN [2: OSUC]; ; USA OK Latimer Co 5 mi SW of Red Oak / 15 Feb 1988 under bark Richard Leschen [1: RALC]; USA OK Latimer Co. 10 mi. SW of Red Oak / Ex Hericium 3 Nov. 1987 Ramosum RL877 Richard A. B. Leschen [1: RALC]. **PENNSYLVANIA:** Jeannette 10-14 Pa. H.G. Klages / J. Pakaluk Collection [1: USNM]; Jeannette X-14 Pa. H.G. Klages. / H.G. Klages Collection. Carnegie Museum Accession 11414 / Bystus ulkei (Crotch) [From series det. by J. Pakaluk][1: CMNH]; Jeannette VIII-28 Pa. H.G. Klages. / 31751 / H.G. Klages Collection. Carnegie Museum Accession 11414 / Bystus ulkei (Crotch) [From series det. by J. Pakaluk][1: CMNH]; St. Vinc. Penn. / REV. JEROME SCHMITT COLLECTION St. Vincent College Carnegie Museum Accession # 31,800 [5: CMNH]; Allegheny Co. VIII-7-91 PA. E.A. Klages / Symbiotes minor Cr. E.A. Klages Collection / Bystus ulkei Cr. det Strohecker [1: CUIC]; Allegheny Co. VIII-7-91 PA. E.A. Klages / Symbiotes minor Cr. E.A. Klages Collection / Bystus ulkei (Crotch) det.H.F.Strohecker [1: CUIC]; PENNSYLVANIA: Westmoreland Co. Greensburg St. Vincent College [2: CMNH]; 9/17.96 / PA / Bystus ulkei (Crotch) det. J. Pakaluk 1986 [1: CMNH]. **SOUTH CAROLINA:** S.C. / Henry Ulke Beetle Coll. CMNH Acc. No. 1645 / Bystus ulkei (Crotch) [From series det. by J. Pakaluk][2: CMNH]. **TENNESSEE:** Ten / Henry Ulke Beetle Coll. CMNH Acc. No. 1645 / Bystus ulkei (Crotch) [From series det. by J. Pakaluk][4: CMNH]; Tenn. / Casey Bequest 1925 / Casey determ. ulkei [1: USNM]; Ten / J. Pakaluk Collection [2: USNM]; TN: Sevier Co. GRSM, Great Smoky Mtns. Ntl. Pk, ATBI Plot: Twin Creeks 83º29.94’W 35º41.10’N, 2-14 August 2000, Parker Stocks, Petersen, ex: malaise trap 1 [2: FSRC]; TENN: Cocke Co., Great Smoky Mtns. Ntl. Pk, 83º16’17”W, 35º45’33”N, 12 October 2000 W.B. Sikora coll. #WS-00-

031 [1: FSRC]; USA: TENNESSEE Sevier Co., Great Smoky Mtns. Natl. Pk. Greenbrier Area, Porter's Creek Trail, 762 m, 35.679ºN, 83.989ºW 20-VII-2003, J.S. Ashe GSMNP1A03 038 Ex. Mushrooms [1: SEMC]. **VIRGINIA:** Rhymbus ulkei, Cr. on Fungus E. Falls Church, Va. Aug. 24, 1927 E.A. Chapin [1: USNM]; Va near Plummers Id Md Sep.10 18 / HBarber Collector / ex. Elfingia megalomma [7: USNM]; Sawdust pile EFallsChurch Va 6.28-27 / EAChapin Collector [1: USNM]. **UNDETERMINED LOCATION:** L / Casey Bequest 1925 / Casey determ. ulkei [3: USNM]; Carn. Mus. Acc. 349 / J. Pakaluk Collection / Bystus ulkei (Cr.) det. J. Pakaluk [1: USNM]; America bor. Coll. Markel / Staatl. Museum für Tierkunde Dresden [5: SMTD].

Distribution (Fig. 6.136): Eastern United States. This is the only species that had detailed distributional data available prior to this study. Crotch (1873) described this species from specimens collected in Washington, DC. Blatchley (1910) later recorded it from IN. Fattig (1937) reported the species occurring in GA, and Kirk (1969, 1970) collected it in SC. Interestingly, Arnett (1975) only reported this species from DC, FL, and IN, presumably unaware of the state surveys of Fattig (1937) and Kirk (1969, 1970). Downie and Strohecker (1986) and Arnett (1996) both list the distribution of *B. ulkei* as PA, IN, DC, FL, KY, SC, TN, KS, and MO. Shockley *et al.* (2009a) added AL and AR to the known distribution of *B. ulkei*. This study newly records *B. ulkei* from IA, IL, MD, MS, OK, OH and VA. Although we have yet to examine specimens collected in WV and NC, this species undoubtedly occurs there as well.

Additional Notes: Boving and Craighead (1930) and Chu and Cutkomp (1992) illustrated the larva of this species. Crotch (1873) described *Alexia ulkei* for one of two small species found in the Ulke collection collected from Washington, DC, erroneously describing the tarsi as 5-segmented. Horn (1875) included *Alexia ulkei* in his checklist of Coleoptera of the U.S., but argued that it belonged in *Rhymbus*. LeConte and Horn (1883) disagreed and subsequently transferred *Rhymbus ulkei* to *Symbiotes*, a placement followed by Henshaw (1885). Ganglbauer argued that *A. ulkei* could not belong to *Symbiotes* because *Symbiotes* has 11-segmented antennae, while *A. ulkei* only had 10-segmented antennae. Perhaps based in part on Ganglbauer's argument, Csiki (1901) transferred *Symbiotes ulkei* back to *Rhymbus*.

In his "Conspectus of the Mycetaeinae", Csiki (1905) created *Parexysma* and designated *Exysma parvula* Gorham as the type species. Arrow (1920) pointed out the inadequacy of Csiki's definition for *Parexysma*, arguing that it unjustifiably and incorrectly makes *Alexia ulkei* congeneric with *Exysma parvula*. Instead, he implied that *Exysma parvula* and *Alexia ulkei* were in fact congeneric but should be placed under *Clemmus* Hampe, 1850, a placement never accepted. Blatchley (1910) described *Rhymbus ulkei* var. *granulatus* for a single specimen from northwestern Indiana. Strohecker (1953) synonymized *R. ulkei* under *Bystus*. Poole and Gentili (1996) elevated *Rhymbus ulkei granulatus* Blatchley to the species level as *Rhymbus granulatus* and then synonymized it under *Bystus ulkei*.

***Bystus unicolor* (Gorham)**

Bystus unicolor (Gorham) Strohecker, 1953: 22.

Rhymbus unicolor Gorham, 1898: 338.

Diagnosis: This species is endemic to St. Vincent and known only from the type series. Its uniform body coloration, with the head, pronotum and elytra light reddish brown, readily separates it from the other West Indian *Bystus* species, *B. globosus*.

Redescription: Length = 1.75 -1.95 mm. Body (Fig. 6.43) elongate oval, subhemispherical, highly convex dorsally. Dorsal surfaces uniformly reddish brown with the head often darker, almost black in some specimens. Vestiture very thick, comprised of moderately long suberect grayish setae; vestiture thicker on pronotum and head, less on the elytra. Antenna (Fig. 6.65) 10-segmented, stout, dark red-brown with apical antennomeres lighter; antennomere III subequal to IV; antennomeres IV-VII subequal in length, antennomere X conspicuously truncate apically. Pronotum with lateral margins narrow and reflexed. Pronotal sulci widely separated basally, strongly convergent apically; antebasal foveae poorly developed. Males unknown.

Etymology: Derived from the combination of the Latin “uni-,” meaning “one,” and the root “color,” based on the uniform, dark red color of this species, including legs and antennae, which are typically lighter or darker than the body in most species.

Type(s): **Lectotype (here designated):** SYN- TYPE / TYPE / Type / W. Indies. 98.237. / St. Vincent W.I. H.H. Smith [BMNH]. **Paralectotypes (here designated):** SYN- TYPE / St. Vincent. H.H. Smith. 99-37 [9: BMNH].

Distribution (Fig. 6.137): St. Vincent.

Additional Notes: The hind wing was badly damaged during dissection so no photograph has been provided. Superficially, the wing appears similar to that of *B. globosus.* Only known from the type series, and no males were available for examination so there are no illustrations of the prothoracic basitarsus or aedeagus.

Bystus vestitus **(Gorham)**

Bystus vestitus (Gorham) Strohecker, 1953: 22.

Rhymbus vestitus Gorham, 1887-99: 144.

Diagnosis: The short antennae and pronotal sulci expanded into wide depressions margined by lateral carinae readily separate this species from other similar species.

Redescription: Length = 1.75 – 2.0 mm. Body (Fig. 6.44) elongate oval, subhemispherical, less convex dorsally. Dorsal surfaces uniformly light to dark brown. Vestiture thick, comprised of long erect golden-colored setae, particularly on elytra. Antenna (Fig. 6.66) 10-segmented, relatively short, yellowish brown; antennomere III subequal to IV; antennal club not longer than preceding segments combined; antennomere X elongate, broadly rounded apically. Pronotum with pronotal sulci wide and shallow, margined laterally by conspicuous carinae; antebasal foveae poorly developed. Punctation fine on thorax and elytra. Hind wing (Fig. 6.86) weakly melanized. Males unknown.

Etymology: Derived from the combination of the Latin root "vesti-," meaning "clothing," and the past participle suffix "-tus," a reference to the dense, uniformly-colored golden pubescence found in this species.

Type(s): **Holotype:** Holo- type / Type / V. de Chiriqui, 25-4000 ft. Champion. / Rhymbus vestitus Gorh. / B.C.A, Col., VII. R. vestitus, Gorh [BMNH].

Additional Specimens Examined: **PANAMA:** Almirante, Bocas del Toro Prov., PANAMA March 22 1959 / leg. H.S. Dybas / FM(HD) # 59-262, Berlese # B-556; in dirt, wood borer sawdust etc. accumulated in split in tree / Bystus vestitus Gorham DET. 1978 H. F. Strohecker [1: FSCA]

Distribution (Fig. 6.138): Panama.

Additional Notes: No males were available for study during this project so no illustrations of the male prothoracic basitarsus or aedeagus are available.

CONCLUDING REMARKS

Although this review constitutes a significant contribution to the knowledge of the species of *Bystus*, it is not intended to be the final word on the genus. Additional species are likely to exist beyond those presented, but the information and keys provided should help aid in their discovery and contribute to their eventual description. A complicating factor contributing to the difficulty of this work is the relatively poor understanding of generic limits within the

Anamorphinae. In short, the entire subfamily Anamorphinae is in desperate need of revision. Only in the context of a full revision of the entire subfamily with the morphology of each genus carefully reviewed can the generic limits be clarified as well as the internal classification of the subfamily.

The species of *Bystus* cluster into two large species groups, based on their relative sizes, antennal structure, and development of the male prothoracic basitarsus. Larger species, designated below as belonging to the *coccinelloides* group, range in size from 2.75-4.0 mm in length and have the male prothoracic basitarsus well-developed. Further, all species in the *coccinelloides* group have their antennae 9-segmented. In contrast, the species of the *ulkei* group range in size from 1.25-2.5 mm in length, generally have a less-developed male prothoracic basitarsus, and the antennae are 10-segmented.

CHECKLIST OF VALID SPECIES OF *BYSTUS* GUÉRIN-MÉNEVILLE, 1857

B. coccinelloides species-group

- *B. apicalis* (Gerstaecker), 1858.
- *B. coccinelloides* Guérin–Méneville, 1857.
- *B. decipiens* (Gorham), 1875.
- *B. drakei* (Weise), 1903.
- *B. hemisphaericus* (Gerstaecker), 1858.
- *B. limbatus* (Gorham), 1873.
- *B. marginatus* Shockley and McHugh, new species.
- *B. pallidulus* (Gerstaecker), 1858.
- *B. piceus* (Gorham), 1887–99.

B. rhizobioides (Gorham), 1875.

B. rodmani Shockley and McHugh, new species.

B. rufus (Weise), 1903.

B. ulkei species-group

B. ashei Shockley and McHugh, new species.

B. decorator Leschen and Carlton, 1993.

B. fibulatus (Gorham), 1887-99.

B. foveatus Strohecker, 1957.

B. globosus (Gorham), 1898.

B. humeralis Shockley and McHugh, new species.

B. seminulum (Gorham), 1873.

B. ulkei (Crotch), 1873.

B. unicolor (Gorham), 1898.

B. vestitus (Gorham), 1887–99.

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Table 6.1. Distribution of Anamorphinae Across All Biogeographical Regions. Region names follow those of Pielou (1992).

	Biogeographical Regions						
Genus	**Ethiopian**	**Australasian**	**Oriental**	**Nearctic**	**Neotropical**	**Oceanian**	**Palearctic**
Aclemmysa							X
Acritosoma				X	X		
Afralexia	X						
Anagaricophilus	X		X				
Anamorphus				X	X		
Anamycetaea			X				
Asymbius			X			X	
Austroclemmus					X		
Baeochelys	X						
Bryodryas	X						
Bystodes							
Bystus				X	X		
Catapotia				X	X		
Clemmus		X		X			X
Coryphus						X	
Cyrtomychus			X				
Cysalemma	X						
Dexialia			X				X
Dialexia	X		X		X		X
Discolomopsis					X		
Endocoelus			X				
Erotendomychus		X					
Exysma					X		
Exysmodes	X						
Geoendomychus	X	X	X				
Idiophyes	X	X	X			X	X
Loeblia			X				
Malagaricophilus	X						
Micropsephodes				X	X		
Micropsephus					X		
Mychothenus	X						X
Papuella			X			X	
Pararhymbus			X				
Parasymbius			X				
Rhymbillus	X						
Rhymbomicrus				X	X		
Symbiotes				X			X

Table 6.2. Host fungi of species of *Bystus* Guérin–Méneville, 1857. Data summarized from Shockley *et al.* (2009b).

	Host Fungus			
***Bystus* spp.**	**Phylum**	**Order**	**Family**	**Species**
	Basidiomycota	Agaricales	Pleurotaceae	*Pleurotus* sp.
	Basidiomycota	Polyporales	Polyporaceae	*Favolus brasiliensis*
	Basidiomycota	Polyporales	Polyporaceae	*Favolus* sp.
	Basidiomycota	Polyporales	Polyporaceae	*Polyporus* sp.
	Basidiomycota	Polyporales	Polyporaceae	*Poria* sp.
	Ascomycota	Xylariales	Xylariaceae	*Daldinia* sp.
	Ascomycota	Xylariales	Xylariaceae	*Hypoxylon* sp.
	Ascomycota	Xylariales	Xylariaceae	*Xylaria* sp.

Table 6.3. Endosymbiotic yeasts isolated from *Bystus* Guérin–Méneville, 1857. Data summarized from Shockley *et al.* (2009b).

	Yeasts			
***Bystus* spp.**	**Phylum**	**Class**	**Species**	**BBY Voucher**[1]
B. piceus	Ascomycota	Saccharomycetes	*Candida ambrosiae*	05-8-4-012A
B. piceus	Ascomycota	Saccharomycetes	*Candida barrocoloradensis*	06-6-7-006B
B. piceus	Ascomycota	Saccharomycetes	*Candida boleticola*	06-6-2-018A
B. piceus	Ascomycota	Saccharomycetes	*Candida homilentoma*	02-7-18-025A

[1] Numbers refer to beetle vouchers in the Beetle Belly Yeasts (BBY) database (NSF BS&I Project # 0072741). Specimens deposited in the University of Georgia Collection of Arthropods (UGCA).

Table 6.4. Geographical distribution of *Bystus* species known prior to this study.

	Geographical Region														
	NA		CA + West Indies						SA						
Taxa	Mexico	USA	Belize	Costa Rica	Grenada	Guatemala	Panama	St. Vincent	Argentina	Brazil	Colombia	French Guiana	Paraguay	Peru	Venezuela
B. apicalis	+					+					+				
B. coccinelloides											+				
B. decipiens										+					
B. decorator														+	
B. drakei													+		
B. fibulatus	+														
B. foveatus															+
B. globosus					+						+				
B. hemisphaericus	+		+	+		+	+								
B. limbatus	+														
B. pallidulus			+							+					
B. piceus							+								
B. rhizobioides										+					
B. rufus									+				+		
B. seminulum												+			
B. ulkei		+													
B. unicolor								+							
B. vestitus							+								
Totals	**4**	**1**	**2**	**1**	**1**	**2**	**3**	**1**	**1**	**3**	**3**	**1**	**2**	**1**	**1**

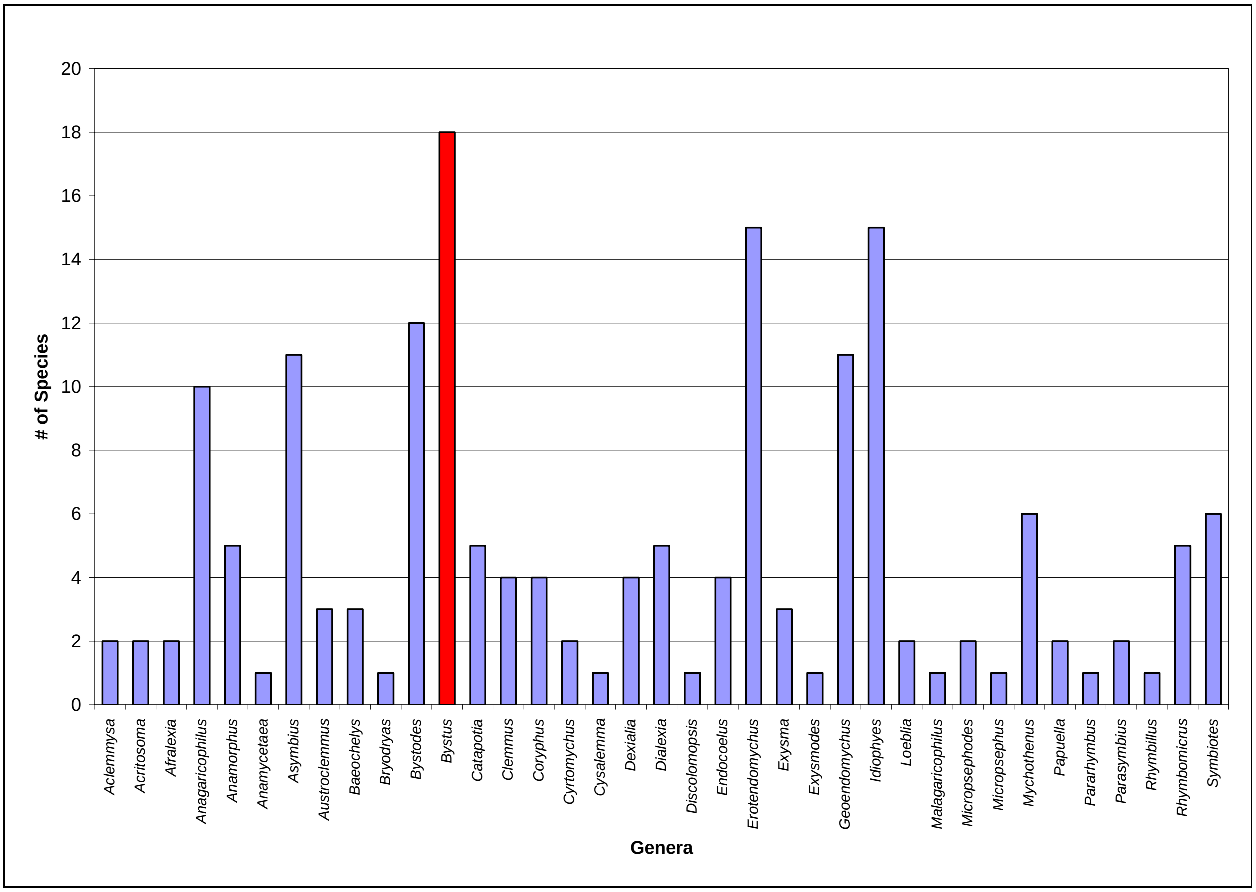


Figure 6.1. Species diversity of genera of Anamorphinae. Bars correspond to the # of described species of each genus (*Bystus* indicated in red).

6.2

6.3

Figures 6.2-6.3. *Bystus* feeding and natural history. **6.2)** *Bystus* adults feeding on the spore field of a wood-rotting basidiomycete fungus (photo courtesy of H.E. Fierro-López); **6.3)** *Bystus piceus* adult with shed pupal exuviae hanging from lower surface of decaying log (photo courtesy of J.V. McHugh).

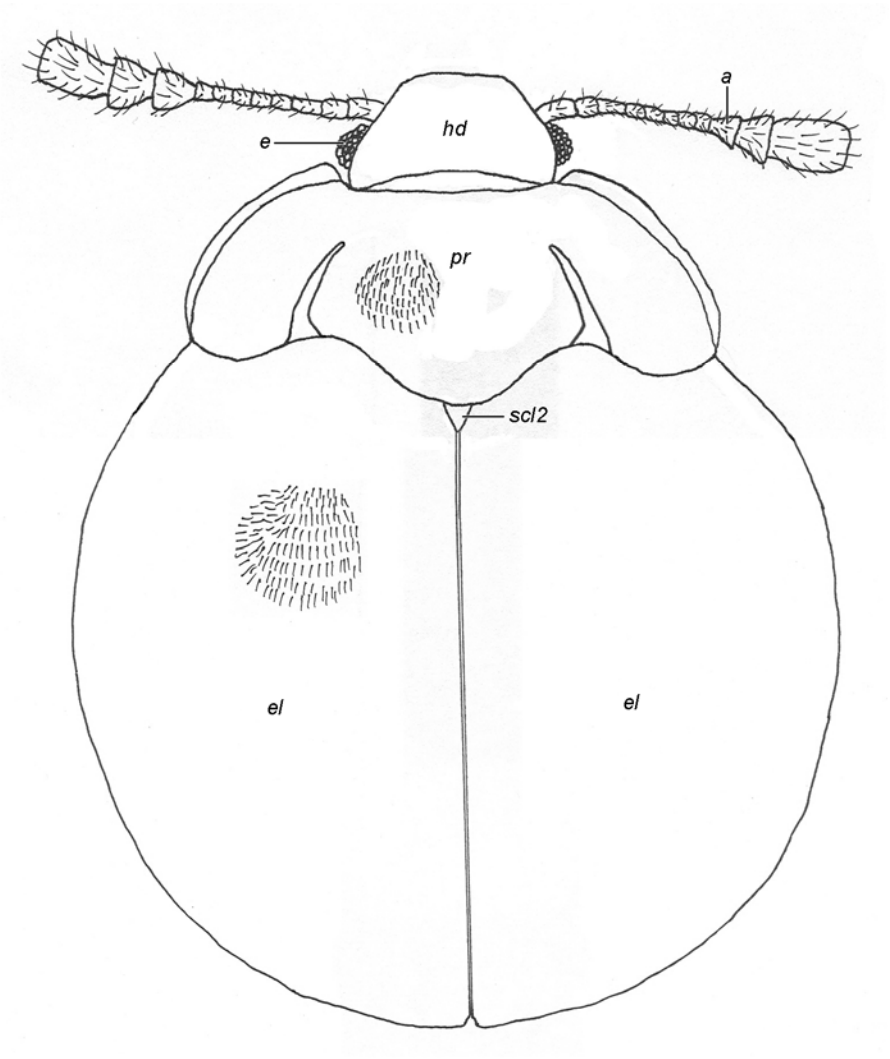


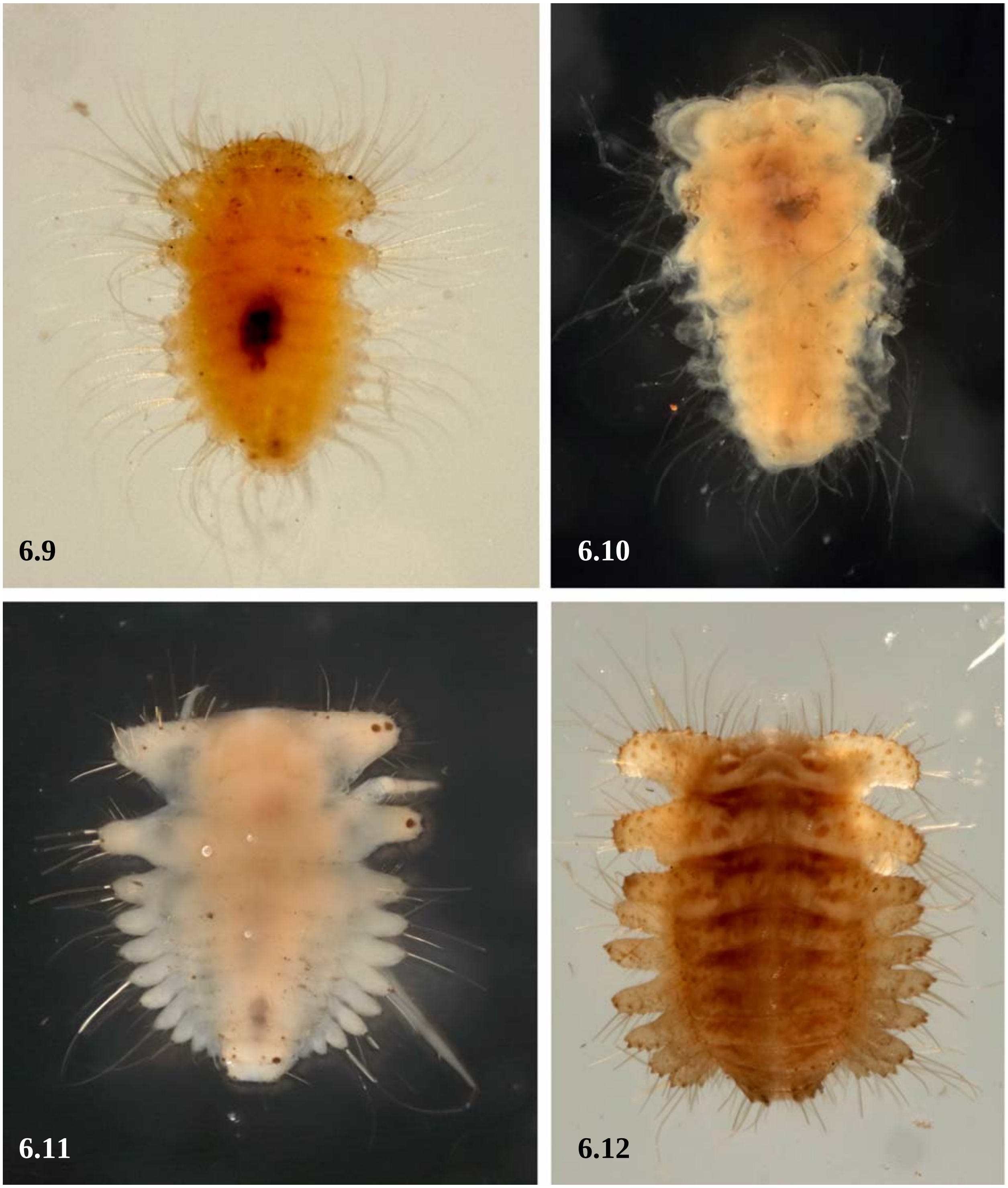
Figure 6.4. *Bystus* spp. dorsal habitus. a = antenna; e = compound eye; el = elytron; hd = head; pr = pronotum; scl2 = scutellum.

Figures 6.5-6.6. Pupae of *Bystus decorator* Leschen and Carlton. **6.5)** Ventral habitus, last larval exuvium removed; **6.6)** Dorsal habitus, last larval exuvium intact.

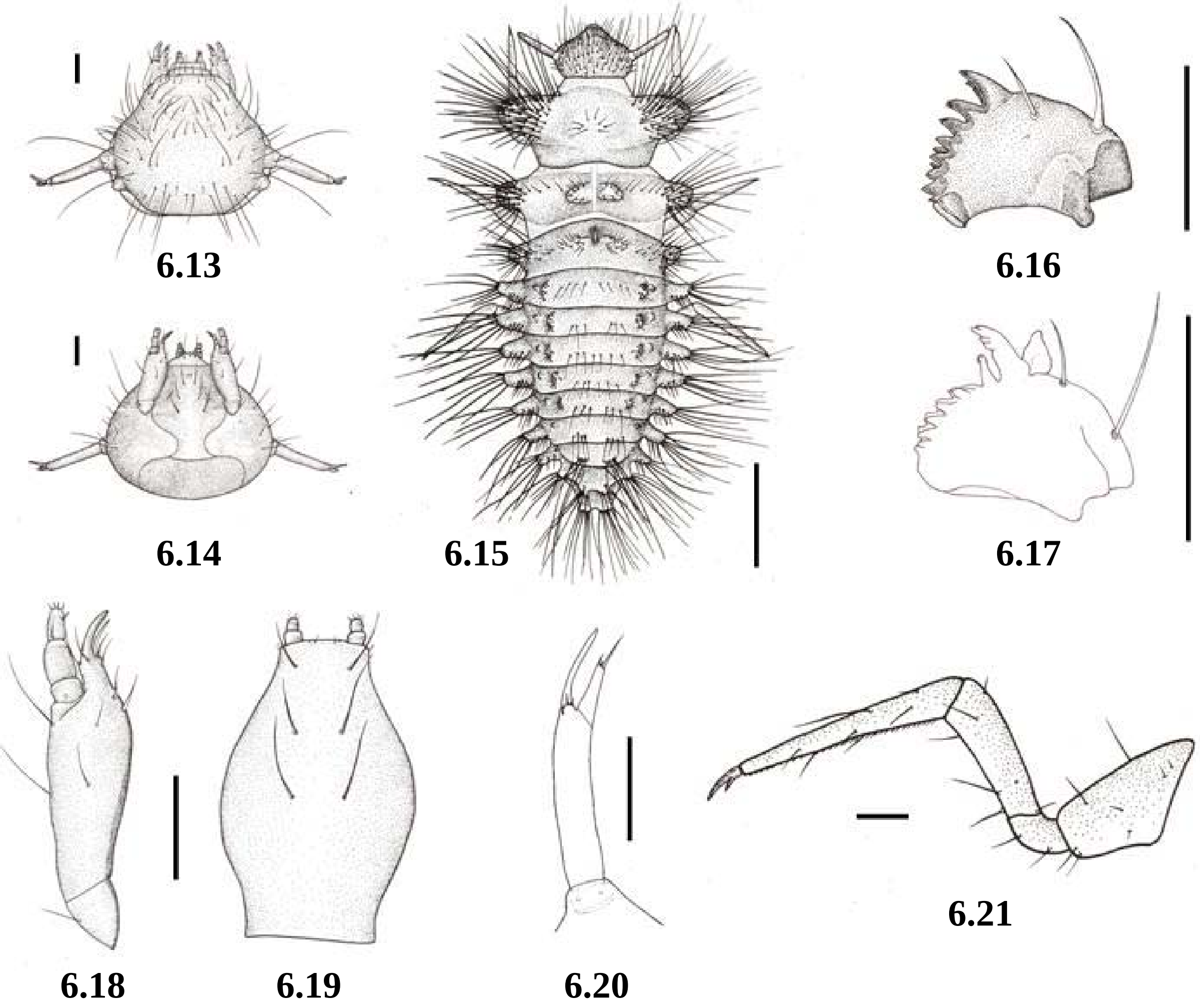
6.7

6.8

Figures 6.7-6.8. Pupa of *Bystus decorator* (setae and last larval exuvium removed). **6.7)** Ventral view (left); **6.8)** Dorsal view (right). Length = 2.2 mm. Modified with permission from Leschen and Carlton (1993).

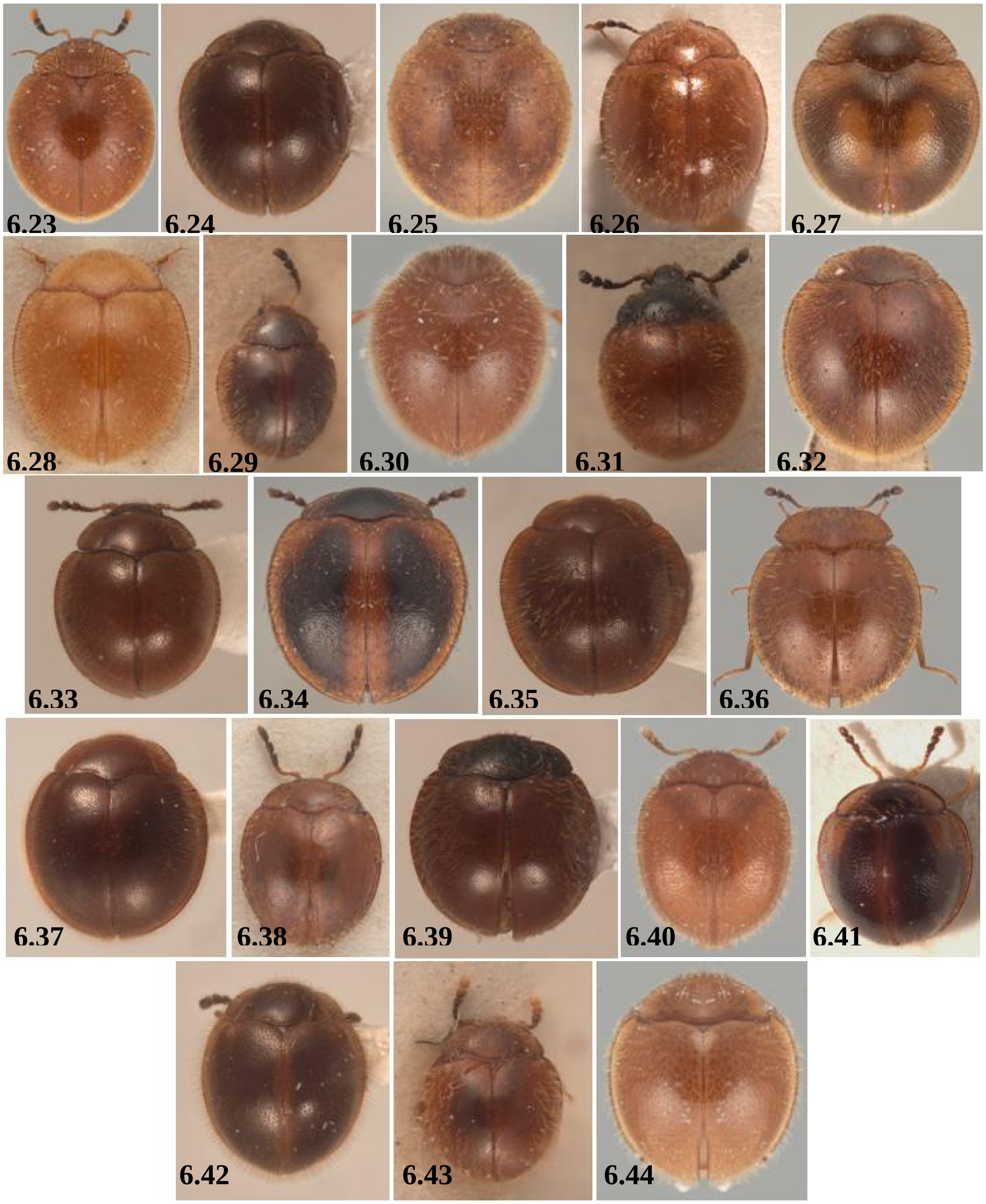


Figures 6.9-6.12. *Bystus* larvae. **6.9)** 1st instar larva of *Bystus decorator*; **6.10)** 2nd instar larva of *Bystus ulkei*; **6.11)** 3rd instar larva of *Bystus hemisphaericus*; **6.12)** 4th instar larva of *Bystus hemisphaericus*.

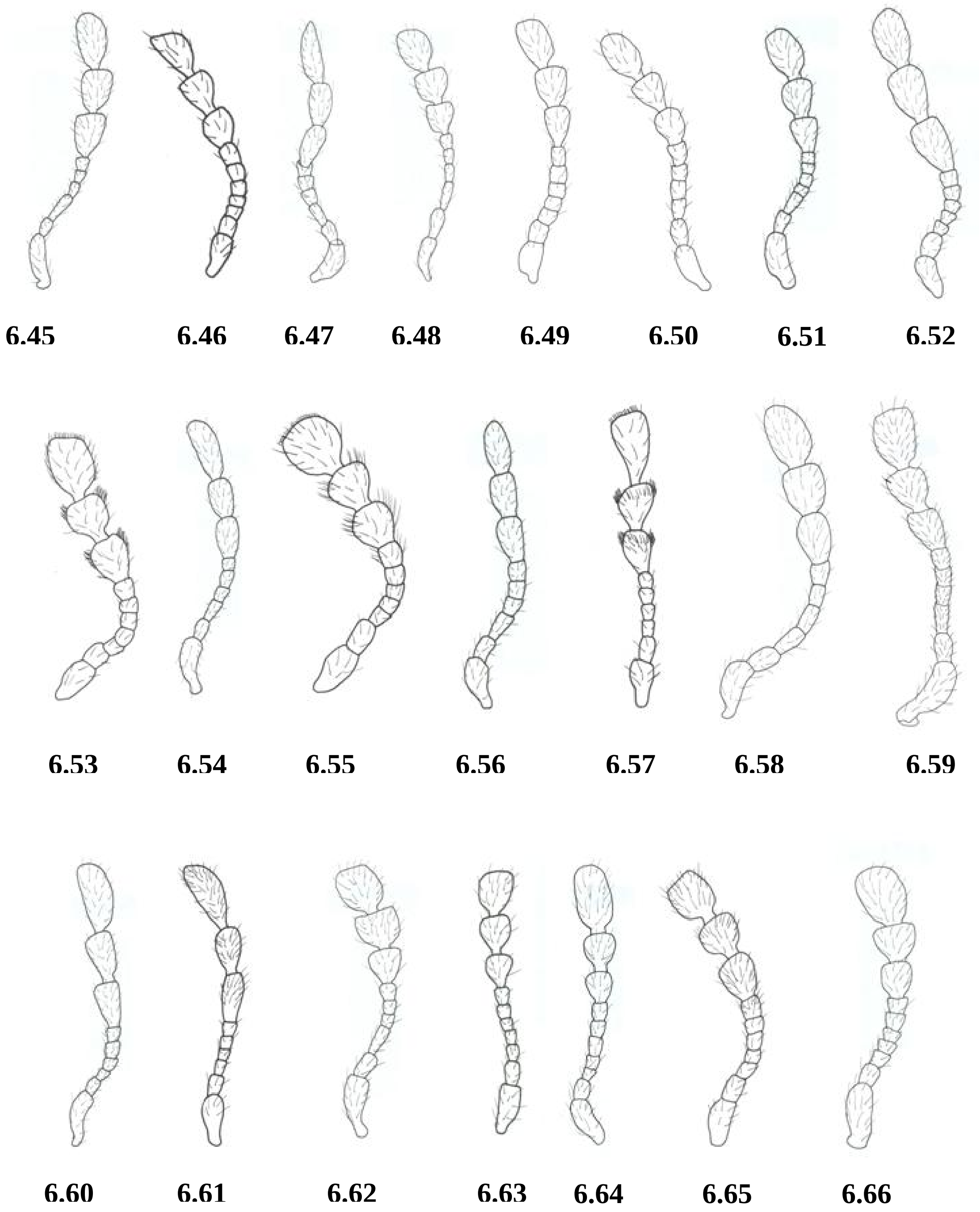


Figures 6.13-6.21. *Bystus* larvae. **6.13)** *B. pallidulus* head capsule, dorsal; **6.14)** *B. pallidulus* head capsule, ventral; **6.15)** *B. pallidulus* dorsal habitus; **6.16)** *B. pallidulus* mandible, dorsal; **6.17)** *B. decorator* mandible, dorsal; **6.18)** *B. pallidulus* maxilla, dorsal; **6.19)** *B. pallidulus* labium, ventral; **6.20)** B. decorator antenna, dorsal; **6.21)** *B. pallidulus* leg, anterior. Scale bars for 6.13-6.14, 6.16-6.21 = 0.1 mm. Scale bar for 6.15 = 1 mm. Modified with permission from Costa *et al.* (1988)[6.13-6.16, 6.18-6.19, 6.21] and Leschen and Carlton (1993)[6.17, 6.20].

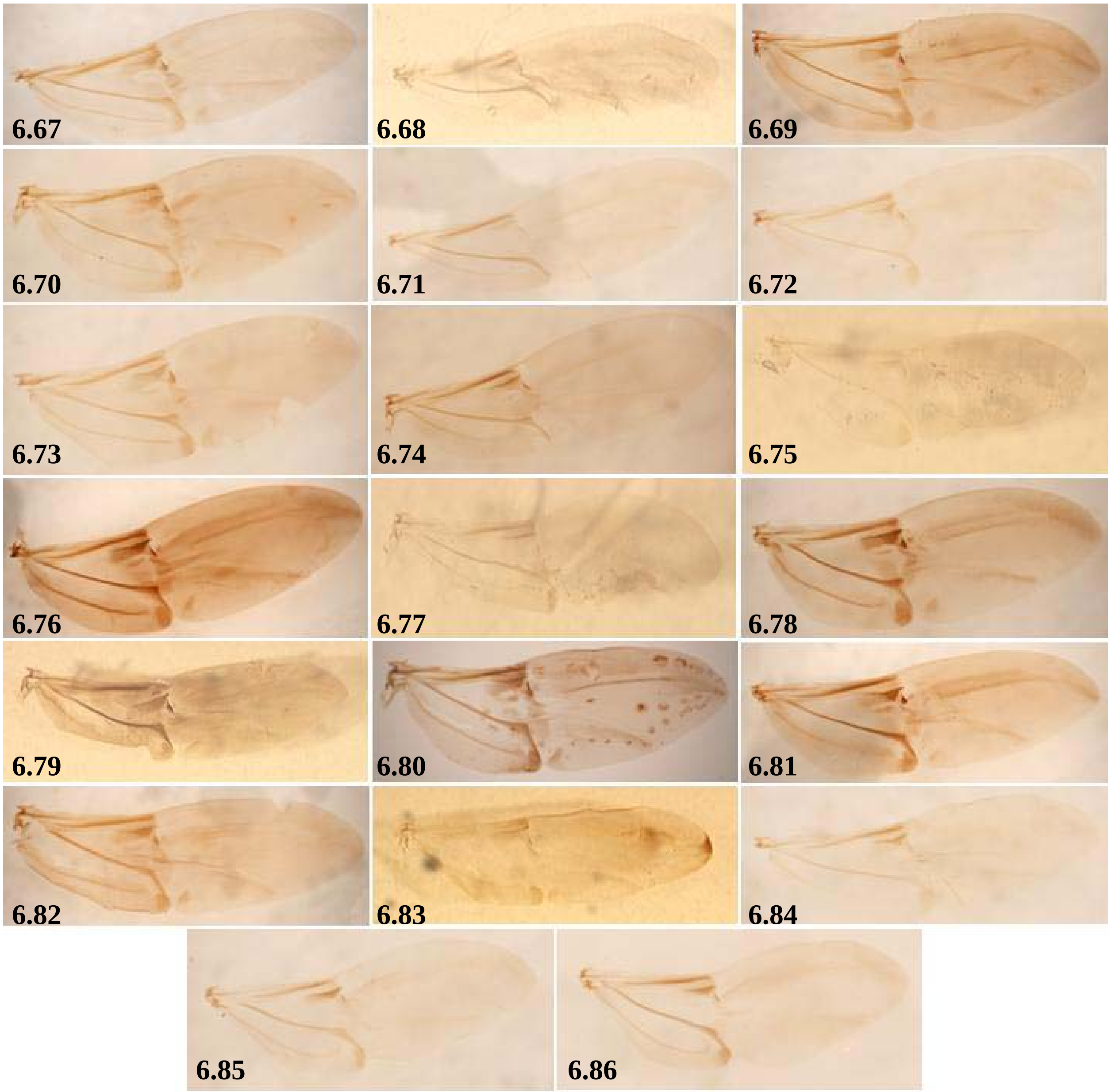
Figure 6.22. Egg of *Bystus decorator* Leschen and Carlton. Scale bar = 0.1 mm.



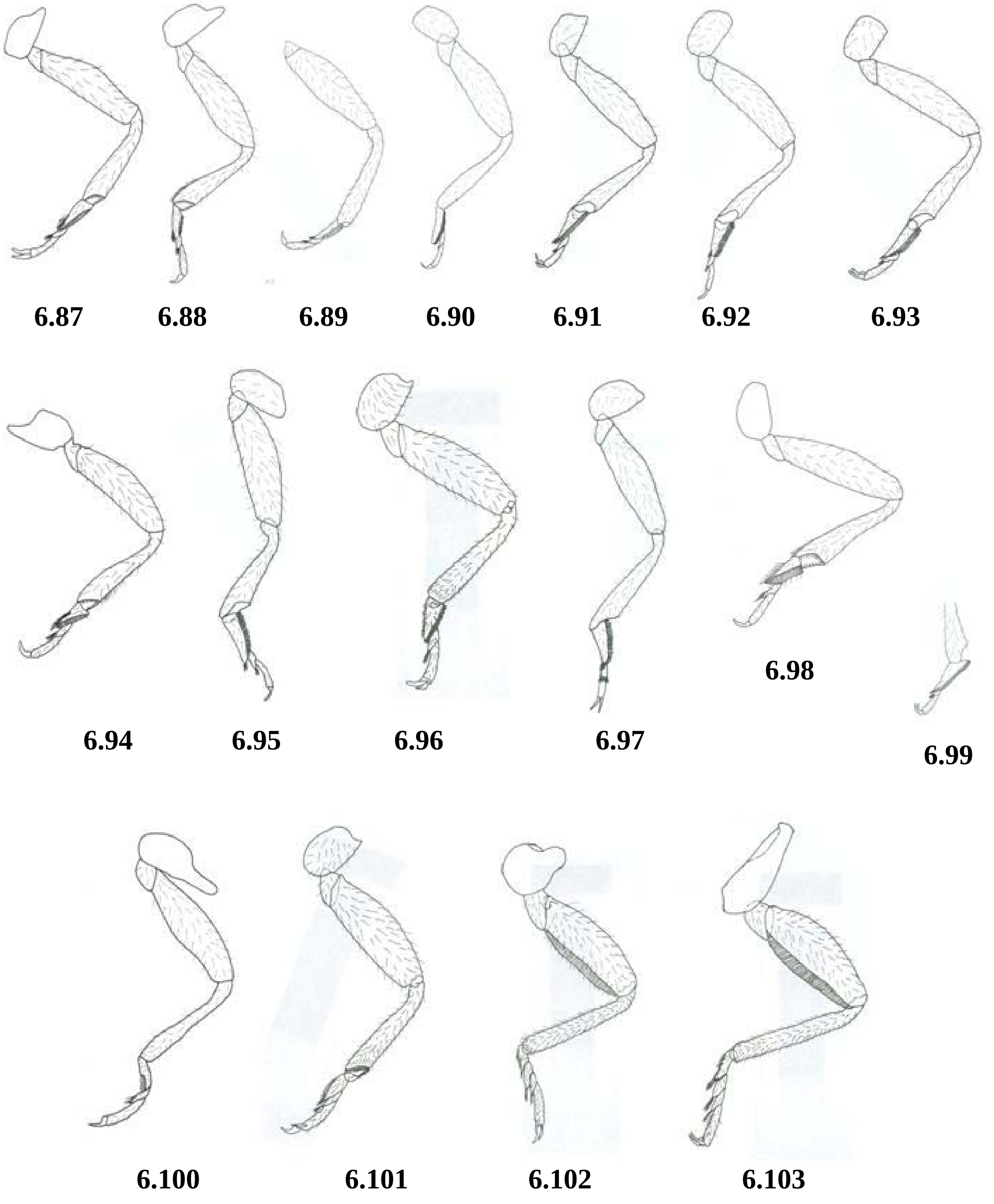
Figures 6.23-6.44. *Bystus* species. **6.23)** *B. apicalis* (Gerstaecker); **6.24)** *B. ashei* Shockley and McHugh, **new species**; **6.25)** *B. coccinelloides* (Guérin–Méneville); **6.26)** *B. decipiens* (Gorham); **6.27)** *B. decorator* Leschen and Carlton; **6.28)** *B. drakei* (Weise); **6.29)** *B. fibulatus* (Gorham); **6.30)** *B. foveatus* Strohecker; **6.31)** *B. globosus* (Gorham); **6.32)** *B. hemisphaericus* (Gerstaecker); **6.33)** *B. humeralis* Shockley and McHugh, **new species**; **6.34)** *B. limbatus* (Gorham); **6.35)** *B. marginatus* Shockley and McHugh, **new species**; **6.36)** *B. pallidulus* (Gerstaecker); **6.37)** *B. piceus* (Gorham); **6.38)** *B. rhizobioides* (Gorham); **6.39)** *B. rodmani* Shockley and McHugh, **new species**; **6.40)** *B. rufus* (Weise); **6.41)** *B. seminulum* (Gorham); **6.42)** *B. ulkei* (Crotch); **6.43)** *B. unicolor* (Gorham); **6.44)** *B. vestitus* (Gorham).



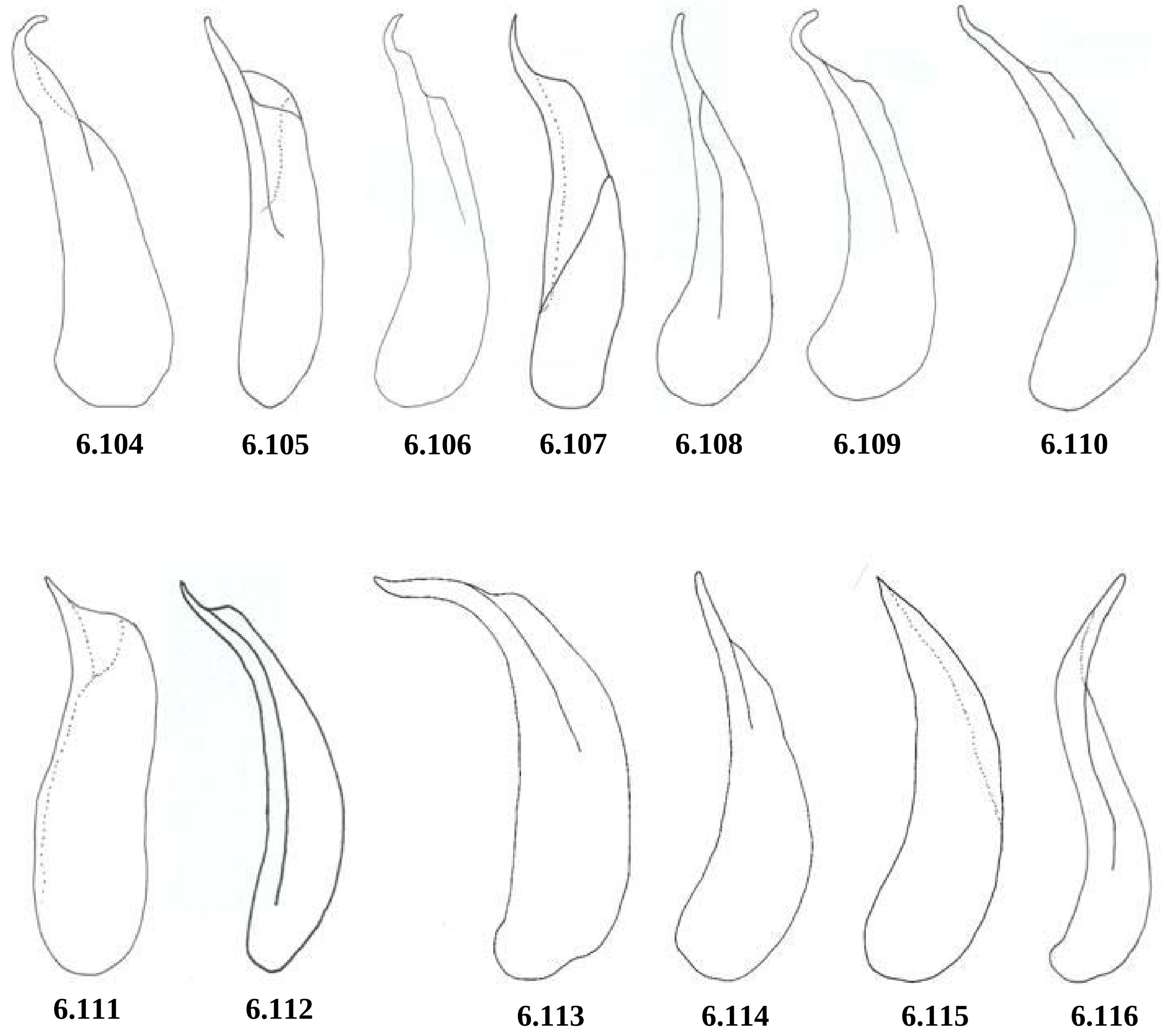
Figures 6.45-6.66. *Bystus* antennae. **6.45)** *B. apicalis* (Gerstaecker); **6.46)** *B. ashei* Shockley and McHugh, **new species**; **6.47)** *B. coccinelloides* (Guérin–Méneville); **6.48)** *B. decipiens* (Gorham); **6.49)** *B. decorator* Leschen and Carlton; **6.50)** *B. drakei* (Weise); **6.51)** *B. fibulatus* (Gorham); **6.52)** *B. foveatus* Strohecker; **6.53)** *B. globosus* (Gorham); **6.54)** *B. hemisphaericus* (Gerstaecker); **6.55)** *B. humeralis* Shockley and McHugh, **new species**; **6.56)** *B. limbatus* (Gorham); **6.57)** *B. marginatus* Shockley and McHugh, **new species**; **6.58)** *B. pallidulus* (Gerstaecker); **6.59)** *B. piceus* (Gorham); **6.60)** *B. rhizobioides* (Gorham); **6.61)** *B. rodmani* Shockley and McHugh, **new species**; **6.62)** *B. rufus* (Weise); **6.63)** *B. seminulum* (Gorham); **6.64)** *B. ulkei* (Crotch); **6.65)** *B. unicolor* (Gorham); **6.66)** *B. vestitus* (Gorham).



Figures 6.67-6.86. *Bystus* wings. **6.67)** *B. apicalis* (Gerstaecker); **6.68)** *B. ashei* Shockley and McHugh, **new species**; **6.69)** *B. coccinelloides* (Guérin–Méneville); **6.70)** *B. decipiens* (Gorham); **6.71)** *B. decorator* Leschen and Carlton; **6.72)** *B. drakei* (Weise); **6.73)** *B. fibulatus* (Gorham); **6.74)** *B. foveatus* Strohecker; **6.75)** *B. globosus* (Gorham); **6.76)** *B. hemisphaericus* (Gerstaecker); **6.77)** *B. humeralis* Shockley and McHugh, **new species**; **6.78)** *B. limbatus* (Gorham); **6.79)** *B. marginatus* Shockley and McHugh, **new species**; **6.80)** *B. pallidulus* (Gerstaecker); **6.81)** *B. piceus* (Gorham); **6.82)** *B. rhizobioides* (Gorham); **6.83)** *B. rodmani* Shockley and McHugh, **new species**; **6.84)** *B. rufus* (Weise); **6.85)** *B. ulkei* (Crotch); **6.86)** *B. vestitus* (Gorham).



Figures 6.87-6.86. *Bystus* legs. **6.87-6.100)** Male prothoracic legs. **6.87)** *B. apicalis* (Gerstaecker); **6.88)** *B. ashei* Shockley and McHugh, **new species**; **6.89)** *B. coccinelloides* (Guérin–Méneville); **6.90)** *B. decorator* Leschen and Carlton; **6.91)** *B. fibulatus* (Gorham); **6.92)** *B. hemisphaericus* (Gerstaecker); **6.93)** *B. limbatus* (Gorham); **6.94)** *B. marginatus* Shockley and McHugh, **new species**; **6.95)** *B. pallidulus* (Gerstaecker); **6.96)** *B. piceus* (Gorham); **6.97)** *B. rhizobioides* (Gorham); **6.98)** *B. rodmani* Shockley and McHugh, **new species**; **6.99)** *B. drakei* (Weise) basitarsus; **6.100)** *B. ulkei* (Crotch); **6.101)** *B. piceus* female prothoracic leg; **6.102)** *B. piceus* mesothoracic leg; **6.103)** *B. piceus* metathoracic leg.



Figures 6.104-6.116. *Bystus* aedeagus. **6.104)** *B. apicalis* (Gerstaecker); **6.105)** *B. ashei* Shockley and McHugh, **new species**; **6.106)** *B. coccinelloides* (Guérin–Méneville); **6.107)** *B. decorator* Leschen and Carlton; **6.108)** *B. drakei* (Weise); **6.109)** *B. hemisphaericus* (Gerstaecker); **6.110)** *B. limbatus* (Gorham); **6.111)** *B. marginatus* Shockley and McHugh, **new species**; **6.112)** *B. pallidulus* (Gerstaecker); **6.113)** *B. piceus* (Gorham); **6.114)** *B. rhizobioides* (Gorham); **6.115)** *B. rodmani* Shockley and McHugh, **new species**; **6.116)** *B. ulkei* (Crotch).

Figure 6.117. Distribution of *B. apicalis* (Gerstaecker).

Figure 6.118. Distribution of *B. ashei* Shockley and McHugh, new species.

Figure 6.119. Distribution of *B. coccinelloides* Guérin–Méneville.

Figure 6.120. Distribution of *B. decipiens* (Gorham).

Figure 6.121. Distribution of *B. decorator* Leschen and Carlton.

Figure 6.122. Distribution of *B. drakei* (Weise).

Figure 6.123. Distribution of *B. fibulatus* (Gorham).

Figure 6.124. Distribution of *B. foveatus* Strohecker.

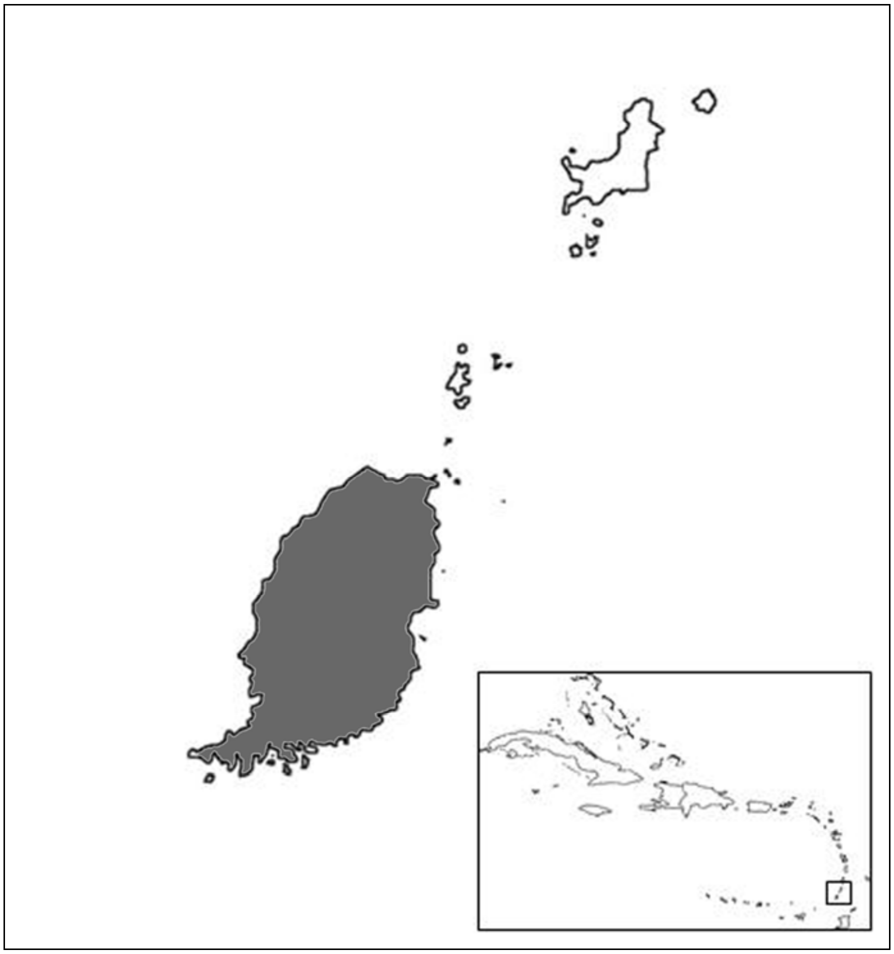


Figure 6.125. Distribution of *B. globosus* (Gorham).

Figure 6.126. Distribution of *B. hemisphaericus* (Gerstaecker).

Figure 6.127. Distribution of *B. humeralis* Shockley and McHugh, new species.

Figure 6.128. Distribution of *B. limbatus* (Guérin in Gorham).

Figure 6.129. Distribution of *B. marginatus* Shockley and McHugh, new species.

Figure 6.130. Distribution of *B. pallidulus* (Gerstaecker).

Figure 6.131. Distribution of *B. piceus* (Gorham).

Figure 6.132. Distribution of *B. rhizobioides* (Gorham).

Figure 6.133. Distribution of *B. rodmani* Shockley and McHugh, new species.

Figure 6.134. Distribution of *B. rufus* (Weise).

Figure 6.135. Distribution of *B. seminulum* (Gorham).

Figure 6.136. Distribution of *B. ulkei* (Crotch).

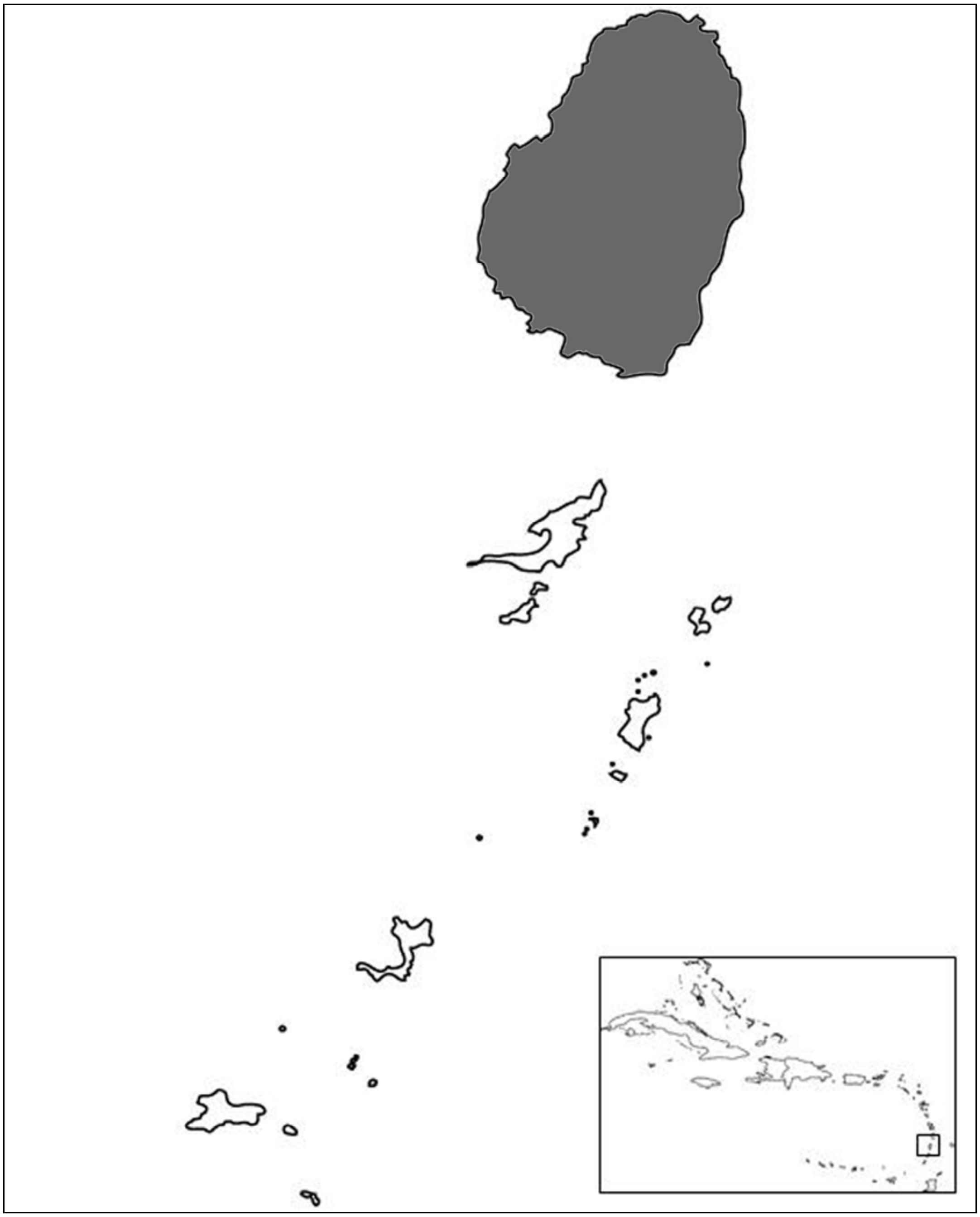


Figure 6.137. Distribution of *B. unicolor* (Gorham).

Figure 6.138. Distribution of *B. vestitus* (Gorham).

CHAPTER 7

SUMMARY AND CONCLUSIONS

Historically, references pertaining to Endomychidae have been scattered widely across the scientific literature, spanning 250+ years, and at least 15 different languages. Most previous work on the group, while outstanding in its own right, was regionally-specific, grossly out-of-date and in some cases almost entirely inaccessible. Thus, a fresh start was necessary to bring all of this information together, making it accessible for this project, but for future workers as well. Of course, this effort required many hours of cataloguing, translating, compiling and updating, beyond that spent producing the research products presented within.

The taxonomic checklist presented in Chapter 2 represents the first attempt to update the list of taxonomic names for the entire world fauna of the family since 1953. Of the 2,955 nominal taxa currently classified within Endomychidae, only 65% were valid. In other words, 35% of the names associated with endomychid taxa were discovered to be invalid synonyms or homonyms. In addition to its value as a taxonomic resource, extensive distributional data were also included for all valid nominal taxa. This checklist will help identify gaps in distribution that represent undersampled regions, help taxonomists generate regionally specific checklists for their respective countries, and clarify the previous nomenclatural issues within Endomychidae.

In the process of generating the checklist for all the endomychid species of the world, it became apparent that a vast literature existed, documenting the biological and ecological information for the family, albeit rarely in any coordinated manner that would make it easy to retrieve for subsequent workers. To provide a companion resource to the taxonomic checklist, Chapter 3 presented an exhaustive review of the natural history of Endomychidae, including discussions of food preference (mycophagy, phytophagy, predation, necrophagy and myxomycophagy), natural enemies (predators, parasitoids, parasites and pathogens), non-lethal symbioses (endosymbionts, phoretics), and other habits and behaviors exhibited by species of Endomychidae. Likewise, tables compiling fungus host records for endomychids, yeast gut endosymbionts, endomychid inquilines of social insects and other animals, and endomychid stored product pests were provided that will greatly enhance the study of the biology and natural history of this group. It was my sincere hope that the checklist and the natural history review would collectively provide future workers with access to the vast amount of published information pertaining to the family in just two references.

The molecular phylogenetic analysis did not recover a monophyletic Endomychidae. Instead, the subfamily Anamorphinae was consistently recovered outside of Endomychidae, variably placed as the sister to either Coccinellidae by itself or to a clade comprising Coccinellidae+Corylophidae. While this finding supports those of previous molecular studies, it conflicts with morphological studies which have consistently recovered a monophyletic Endomychidae. In the absence of a total evidence analysis that combines molecular and morphological character sets, we are unwilling to formally elevate Anamorphinae to the family level because we were unable to clearly resolve its relationships to the remaining CS families. The placement of the subfamilies of Mycetaeinae and Eupsilobiinae within Endomychidae was supported only by the parsimony analysis. Maximum likelihood and Bayesian analyses place it near the base but outside of Endomychidae. The clades consistently recovered within Endomychidae in all three analyses cluster into two groups—the “PML” clade (Pleganophorinae, Leiestinae and Merophysiinae) and the “SEEL” clade (Stenotarsinae, Endomychinae, Epipocinae and Lycoperdininae). Of these seven subfamilies, five were consistently recovered as monophyletic. Stenotarsinae and Endomychinae were found to be paraphyletic/polyphyletic with respect to each other in all three analyses.

In preparation for the taxonomic review of *Bystus* Guerin-Meneville in Chapter 6, it was discovered early on that many of the descriptions of the morphology of *Bystus* were wholly inadequate or grossly inaccurate. Therefore, a detailed morphological study was conducted on an exemplar species, *Bystus piceus* (Gorham). During this study, a variety of interesting anatomical modifications from the general endomychid and anamorphine body plan were discovered and discussed in light of other studies across Coleoptera. In addition to providing thorough descriptions (with accompanying figures and illustrations) of the external anatomy of *Bystus piceus*, discussion and descriptions are included for some of the major organ systems and internal anatomical structures, the first such study conducted on any endomychid. In addition to its utility as a common reference for the taxonomic review in Chapter 6, the study presented in Chapter 5 serves as an important anatomical reference for all of Endomychidae, making it finally possible to homologize both internal and external structures across Endomychidae. Although focused-topic morphological studies like this one are becoming increasingly rare in the literature, they are critical for homologizing structures and for resolving some of the ontological problems that have arisen from inconsistency in terminology being applied during revisionary and comparative morphological studies.

The final research chapter consisted of a review of the genus *Bystus,* following up on the discoveries made in Chapter 5. All 18 of the previously known species were redescribed and figured, and 4 new species were described. Lectotypes and paralectotypes were designated for the following species: *B. apicalis, B. decipiens, B. drakei, B. fibulatus, B. globosus, B.*

hemisphaericus, B. pallidulus, B. piceus, B. rhizobioides, B. seminulum and *B. vestitus*. Keys to the adults and known larvae of *Bystus* were provided. There is a brief discussion of anamorphine biogeography, as well as more specific information pertaining to the distribution of species of *Bystus*. All known biological and taxonomic information for the genus has also been provided or referenced.

The research presented within represents a significant advancement in the study of endomychids and attempts to resolve many of the problems within the family that have arisen over the years. While it is not intended to be the final word on Endomychidae, it should serve as a valuable resource to future workers.