

MORPHOLOGY AND PHYLOGENY OF THE WEEVIL SUBFAMILY  
BARIDINAE (COLEOPTERA: CURCULIONIDAE)

by

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and the graduate faculty of the University of Kansas  
in partial fulfillment of the requirements for the degree of  
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Date defended: \_\_\_\_\_ 23 June 2008 \_\_\_\_\_

The Thesis Committee for Steven R. Davis certifies  
that this is the approved Version of the following thesis:

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# **Chapter I: Morphology of Baridinae and related groups**

## **(Coleoptera: Curculionidae)**

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### **Abstract**

Even though the phylogenetic classification of Curculionoidea is still in its infant stages, knowledge of the morphology of the group also is relatively lacking. Significant morphological reviews have been done at the family level; however, little has been reviewed at the subfamily level and below (beyond description of genitalia morphology). Morphological studies within the subfamily Baridinae are limited and have mostly been restricted to the study of genitalia morphology, provided a few exceptions. This study provides a fairly comprehensive, though by no means exhaustive, review of baridine external and internal morphology to aid future studies on the group, particularly in phylogenetics.

### **Introduction**

Currently there are approximately 550 genera belonging to the subfamily Baridinae (Morimoto and Yoshihara 1996), placed into 9 tribes and 17 subtribes (Alonso-Zarazaga and Lyal 1999). Indeed the morphological diversity within Baridinae is vast (Figs. 1-96); however, baridines are quite easily differentiated from most other weevil groups by their characteristic round shape and ascended mesepimeron; however, these traditional diagnostic characters certainly are not apomorphic to baridines only, and beyond the level of subfamily, baridine identification is difficult at best. Due to the scarcity in knowledge of morphological diversity in Baridinae, the following is a review of baridine morphology. Although studies have been done examining the adult morphology of numerous weevil groups, such as those done by Morimoto (1962a, 1962b), Morimoto *et al.* (2006), and Franz (2006), none to date have treated Baridinae. With the exception of Morimoto and Yoshihara (1996), few baridine studies have illustrated structures that are beyond importance to the taxonomist (namely genitalia and some external features). Given the number of morphological characters one can sample from an organism is infinite, those of particular relevance to baridine phylogeny are the foci of this treatment. Because there have been no comprehensive studies assessing character systems for baridine weevils, those characters which are thought to be of phylogenetic significance are reviewed. The morphology of all structures covered within Baridinae is also described for taxa outside of the subfamily for comparison. Unless indicated otherwise, all morphological terms are reproduced from Morimoto *et al.* (2006), Morimoto (1962a), Morimoto and Kojima (2003), and Chaboo (2007).

## **Materials and methods**

### *Taxon sampling* (Appendix I)

Following Alonso-Zarazaga and Lyal (1999), species were sampled from each of the 9 tribes and 17 subtribes in Baridinae, with a total of 283 baridine species, representing 231 genera, included in the analysis (Table 1). A total of 29 species were sampled for the outgroup, consisting of 12 subfamilies outside of Baridinae. The final analysis included a total of 302 taxa (Appendix I). Outgroup selection was based on phylogenies produced by Marvaldi *et al.* (2002), and previous baridine classifications by Zherikhin and Egorov (1990), and Zherikhin and Gratshev (1995).

Taxa were borrowed from the following institutions:

USNM – National Museum of Natural History (United States National Museum),

Smithsonian Institution, Washington, D.C., USA.

SEMC – Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA.

CMNC – Canadian Museum of Nature, Ottawa, Canada.

IZCAS – Institute of Zoology, Chinese Academy of Sciences, Beijing, China.

CAS – California Academy of Sciences, San Francisco, California, USA.

FMNH – Field Museum of Natural History, Chicago, Illinois, USA.

### *Specimen dissection and preparation*

Body and genitalia dissection:

All dissections were performed using an Olympus SZ60 microscope. For each taxon in which multiple specimens were available, a full-body dissection was done for the male and abdominal dissection for the female (including genitalia). For taxa in which only holotype or paratypes were available (Table 2), no dissections were made and only external characters were coded. In some taxa, full-body dissections were not permitted by the borrowing institution and thus only abdominal dissections were done for those males.

For body dissections, specimens were first relaxed by soaking them in warm water for ~10-15 minutes, the duration depending on the size of the specimen. The head, pro-thorax, meso- meta-thorax complex, and abdomen were then separated. Before digesting any internal tissues, the elytra and hind wings were removed and stored in glycerin, as digesting was not required for these parts. The remaining dissected parts were digested in a weak (~10%) KOH solution for 10-15 minutes, again depending on the size of the specimen. Following digestion, all remaining internal tissues were removed and the sclerotized parts cleaned. The meso- and meta-nota were separated from the mesepimera, metepisterna, and metepimera, and subsequently separated from each other. The terga were separated from the sterna along one side, and the genitalia removed together with the 8<sup>th</sup> terga. After dissections were completed, all parts were stored in glycerin.

Mouthpart dissection:

Following dissection of the body, the head was digested further in 10% KOH for ~15-30 minutes, depending on specimen size. Under the microscope, the head was placed with the ventral side facing upwards. One pair of fine-tipped forceps was used to stabilize the rostrum while another pair was used to gently separate the postmentum of the labium from the submentum of the rostrum. The maxilla were subsequently removed in a similar fashion, separating them from the submentum at the cardo-submentum junction. The mandibles were then removed, separating them from the postcoila.

Hind wing and mouthpart preparation:

Following dissection of the hind wing from the thorax and mouthparts from the rostrum, these parts were then mounted on glass microscope slides for further examination. One hind wing from each body dissection was mounted on a slide in Euparal mounting medium. The labium, maxilla, and mandibles from the same specimen were mounted on the same slide as the hind wing, but in Canadian balsam. The slide was then placed on a slide warmer to dry the mounting mediums.

Scanning Electron Microscopy:

All SEM images were captured using a LEO 1550 FESEM. Specimens were mounted on an SEM stub using Leit-C-Plast adhesive and an isopropanol-based colloidal graphite. Whole specimens were placed on insect pins or glued to paper points, securing the pin or point on an SEM stub using Leit-C-Plast. Dissected parts

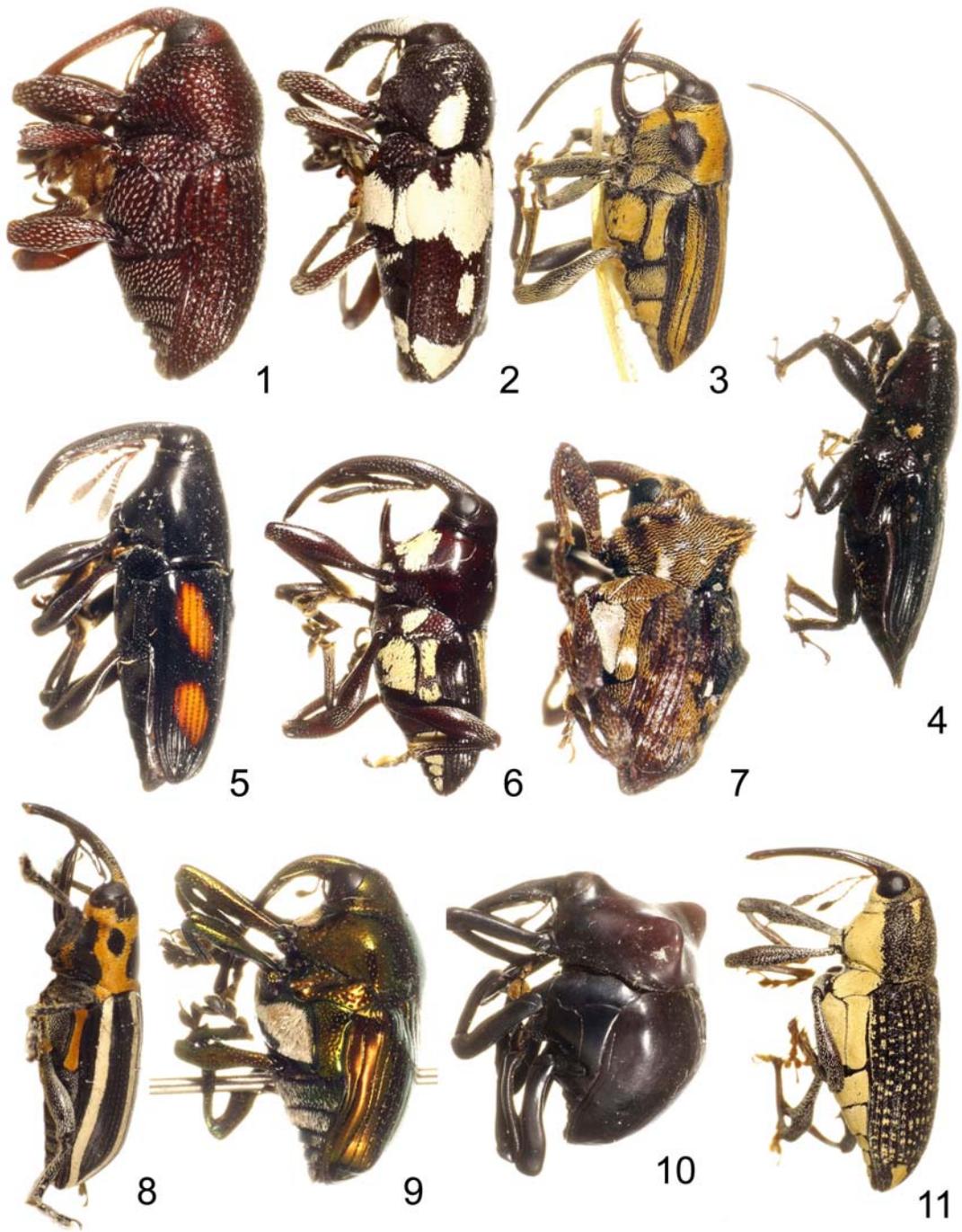
were mounted on a stub by securing them with a thin layer of colloidal graphite.

After the desired parts were mounted, coating was performed using gold.

### **Adult morphology**

#### *General appearance* (Figs. 1-42, 49-90)

Many adult baridines have a characteristic round or ball-like appearance, where all anterior, posterior, dorsal, and ventral margins are smooth and contiguous. This common body form usually is also complemented by a dark color (brown/black) and a largely glabrous derm. However, as one might expect from any large insect lineage, there are many aberrant taxa that fall beyond the stereotypic form. For instance, the body can be relatively round as viewed dorsally and laterally (Figs. 97-100); round as viewed dorsally, ball-like and strongly arcuate as viewed laterally (Figs. 101, 102); round as viewed dorsally, dorso-ventrally compressed as viewed laterally (Figs. 103, 104); elongate as viewed dorsally, relatively round as viewed laterally (Figs. 105-107). In the dorsal view, although many taxa have a round appearance formed by the pronotum and elytra, this round quality can be quite different when making comparisons, mostly due to





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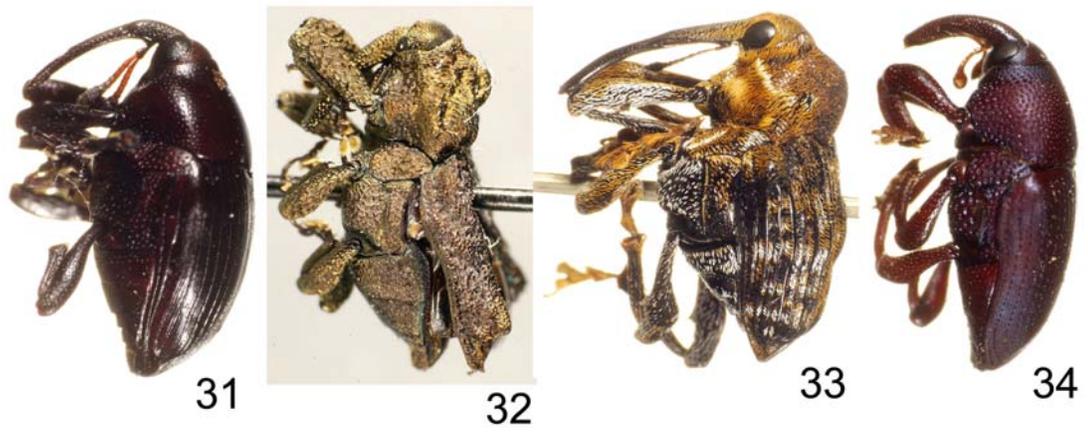
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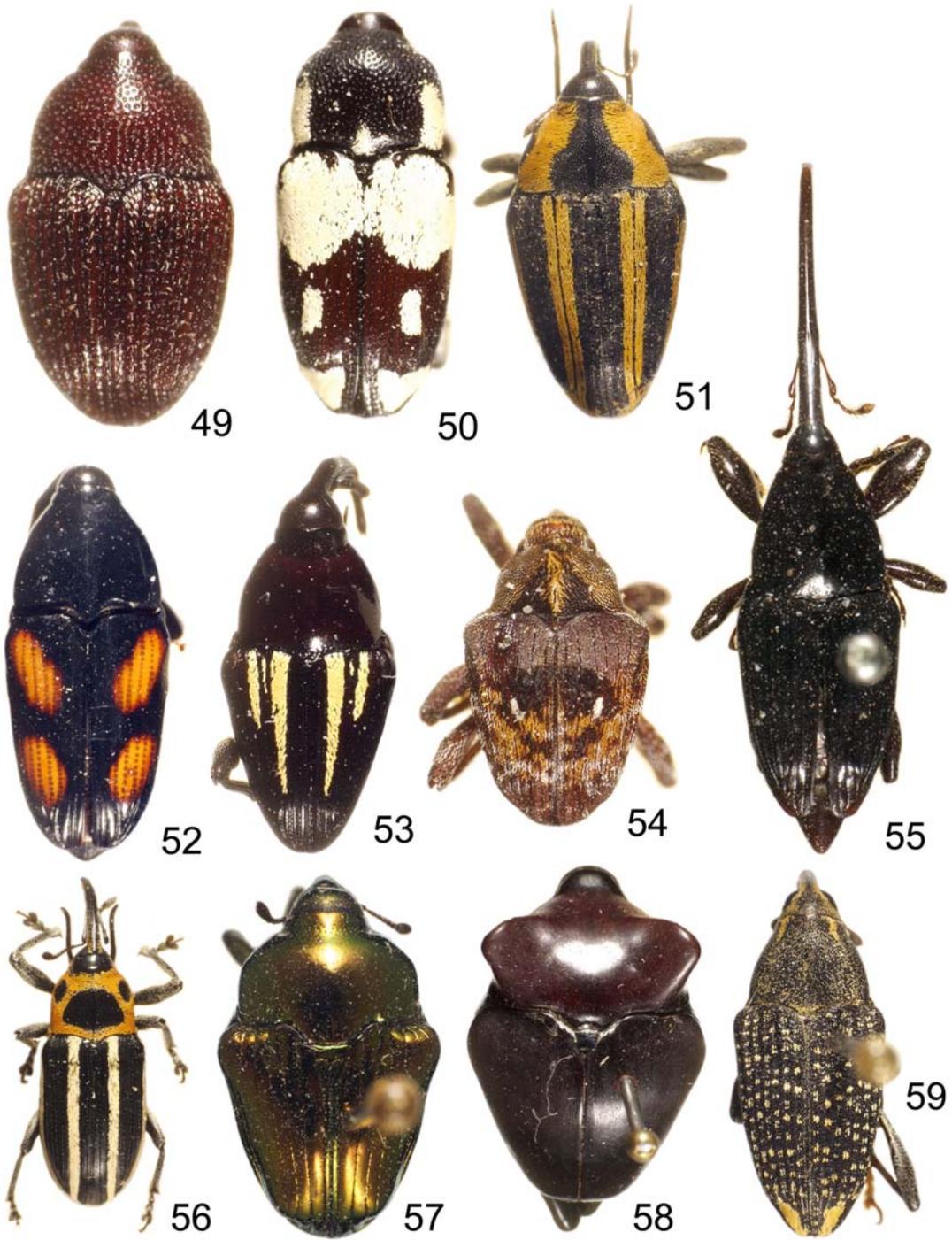
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contrasting size ratios of the posterior margin of the pronotum and anterior margins of the elytra. A round appearance is formed in the following ways: the posterior margin of the pronotum is narrower than the elytra, mostly due to wide, projecting elytral shoulders; the posterior margin of the pronotum is contiguous with the anterior margin of the elytra; the pronotum is slightly expanded laterally, thus wider than the elytra.

Many baridines are largely glabrous, in which the derm is bare dorsally, with scales usually present laterally and ventrally in each cuticular puncture. Few, though, actually appear to be entirely glabrous (Fig. 109). The majority, however, have varying degrees of vestiture on the pro-thorax, legs, abdomen, and elytra (Fig. 108).

*Scales* (Figs. 110-126, 131)

In Baridinae, variously modified scales are present on different areas of the body. Typical scales present on the thorax, elytra, and occasionally on the ventrites are ribbed, often with short, acute projections or spines along the lateral and apical margins (Figs. 113-118). These scales have varying numbers of ribs and can range from being narrow to broad and more rounded. Although scales mostly are appressed against the body, some taxa (*Plocamus*) bear ones that protrude from the pronotum and elytra and are more narrow and elongate (Fig. 110). Types of specialized scales include those present medially on the basal ventrites of some male taxa. These scales are quite distinct from surrounding ones on the ventrites, being erect and slightly elongate (Fig. 119). The apex of these scales seem to form fimbriate fringes (Fig. 120), suggesting they may function as a type of sex scale, possibly similar to those present in Lepidoptera. The tergites bear quite unusual scales, possibly owing to their involvement in fastening the wings. Those on the 7<sup>th</sup> tergite are usually fan-like with numerous long lobes projecting from the apex (Figs. 121-123). The spiculate patches, which are most developed on the 7<sup>th</sup> tergite but typically are present on most tergites in baridines, are also highly modified scales or setae, functioning in wing-locking (Figs. 125). Those scales modified for sound production, called plectra, are also present on the 7<sup>th</sup> tergite (Figs. 122, 124) and function by scrapping against a file on the inner side of the elytra. It is likely that some of the strangest scales in Baridinae are those along the ventral margin of the metepisternum-the sclerolepidia. Although observed to be modified into four general forms, baridines possess only two of these forms. One is usually trifurcate, but can have more furcations (~5) and is

more appressed against the body (Figs. 111, 112). The second form bears many fimbriate flanges along the apical margin and protrudes from the body. Further discussion on sclerolepidia is below.

#### *Head and rostrum* (Figs. 127-165)

The compound eyes in the majority of the genera are not particularly notable, as compared to those of molytines, ceutorhynchines, and conoderines which are large and anteriorly situated on the frons (Figs. 152-154). Those of baridines typically are elongate, although many genera possess sub-circular eyes, and are situated antero-ventrally (Figs. 137, 139, 149).

Between the compound eyes in some genera (*Peridinetus*, *Pteracanthus*, *Tenemotes*) is a fovea (Figs. 133, 138, 139, 149), which can be relatively large (i.e. the size of a puncture) or small (smaller than a puncture). A fovea is normally present when the junction between the rostrum and frons is flush.

The fashion of how the rostrum meets the head also differs between taxa. The junction between the rostrum and frons may be contiguous and flush (Fig. 165), form a slight depression or sulcus (Figs. 160, 161, 163), or form a strong sulcus (Figs. 156-159, 162). There is great variation with regard to rostrum form, both in length and width. The majority of baridines possess a relatively long rostrum, which is wider basally, gradually narrows apically, and is broadly curved, as viewed laterally (Figs. 156, 157). In some groups, however, this type is also present, but the rostrum is strongly curved (Figs. 158, 162). Punctuation on these types of rostra follows the

general pattern of larger punctures present basally and punctures becoming smaller apically. A similar type of rostrum, possessed by groups such as *Crotanius*, *Dactylocrepis*, and *Myctides*, is again wide basally, gradually narrowing apically, only more elongate (Figs. 159-161). A few taxa (*Myctides*) possessing this type also bear an elongate, dense patch of setae along the apical region of the rostrum (Fig. 161). A modification of this moderately long, broadly curved type of rostrum is the enlargement or inflation of the basal part (Fig. 162). This type is distinct from the more gradually narrowing type in that the basal third or half of the rostrum is markedly enlarged, and the apical remainder abruptly narrower. Another more distinctive, but less common, rostrum form is shorter and thicker/more robust (Fig. 163). The last general type of rostrum is slender, linear (or only with a slight curve), and cylindrical, but can be dorso-ventrally flattened in some taxa (Fig. 164). Punctures on this rostrum type often are subequal in size along the length of the rostrum.

**Antenna** (Figs. 166-182): The baridine antenna bears 12 articles (Morimoto *et al.* 2006). The scape often is fairly elongate when inserted at the middle of the rostrum or beyond, but can be extremely short when inserted near the base. The pedicel always is longer than any of the individual flagellar articles. The flagellum consists of 6 articles, which may be almost moniliform and bead-like (Figs. 137, 149, 169) to cylindrical with the articles flush and often compacted (Figs. 144, 146, 177, 181). In most genera, the club consists of the remaining 3 articles; however, it may also be composed of 4 articles, in which the fourth article may be small and difficult

to distinguish. The club is of 2 general forms: the first, in which the club is compact, and the first basal article is longest, with the remaining 3 articles short (Figs. 168, 178); the second, in which all of the articles are subequal in length (Figs. 135, 171, 172). When this second type is observed, the club may be only slightly longer than the first type or may be elongate (Figs. 140, 151, 179, 180). In a few genera the flagellar articles may be modified, with lateral pectinations (Fig. 143), though any modification of the antenna is rare in baridines.

### *Mouthparts*

**Labium** (Figs. 183, 186, 195-269): Although variation in the labium is seen in the length and size of the prementum, palpus, and setae on these parts, the number of palpal segments is static in Baridinae (3). The palpus is usually moderately elongate, but can be small in some taxa where the prementum is enlarged (Figs. 200, 206, 208, 233). The basal two palpal segments are large and globular to slightly elongate, while the third apical segment typically is smallest and elongate and bears a number (~5-10) of small sensilla on the apical margin (Fig. 190). Setae can be present on all three palpal segments, however the largest setae are present on the basal two. Those taxa possessing setae on the basal two segments often bear 1-2 larger setae on the first basal segment, while any other setae present on this segment are much smaller. The prementum typically is moderate in size, but can be smaller in some taxa where the palpus is elongate (Figs. 202, 210, 218, 222) and larger in others where the palpus often is shortened (Figs. 227, 234). Setae appear in 2 general

patterns on the prementum: the first is a sparse to dense bunch or patch of elongate setae along the anterio-lateral margins (Figs. 198, 203, 218); the second is a distinct transverse (although sometimes angled) row of setae near the anterior margin (Figs. 183, 201, 212, 225). Seemingly independent of the setal arrangement, there often are 1-3 larger setae positioned at the antero-lateral margins, similar to those on the first basal segment of the palpus (Figs. 234, 238, 239). The postmentum often is long, although its length, like the palpus and prementum, is proportional to the other parts. When the prementum is enlarged, the postmentum typically is shorter (Figs. 206, 208, 233, 244, 245). Likewise, when the prementum is smaller, the postmentum tends to be elongate (Figs. 205, 210, 218, 229). The labia in the outgroups (outside of Baridinae) tend to possess a much longer labial palpus, and thus also a smaller prementum and postmentum (Figs. 247, 263, 269), although a few also possess an enlarged prementum and reduced palpus (Figs. 248, 262). The labia of Conoderinae and Ceutorhynchinae all are very similar to those of baridines (Figs. 259-269), suggesting close phylogenetic relationships.

**Maxilla** (Figs. 184, 186, 189, 270-352): The shape of baridine maxillae is relatively conserved, and variation is seen in shape, relative size of the various parts, as well as number in reference to setae. The palpus always is 3-segmented and relatively long, though it may be shorted and more compact in some taxa (Figs. 285, 299, 325). Setae are found on all palpal segments, but mainly are concentrated on the basal two. The basal two palpal segments tend to be larger and slightly compact, while the third apical segment often is elongate and narrow, with numerous (5-12)

sensilla along the apical margin. This apical segments also bears elongate sensilla that are positioned laterally (Figs. 187, 189, 278, 345) and vary in number between taxa (~3-20). While setae on the basal two segments is often sparse, when setae are present, there usually are 1-2 larger setae at the apico-lateral margin (Figs. 273, 289, 296). The palpiger is relatively uniform in shape and size, although it can be slightly smaller or larger in taxa. Setae are most often present and are arranged in 3 general patterns: the first is a sparse patch of elongate setae along the antero-lateral margin (Figs. 276, 279, 286, 288, 289, 296); the second is a fairly dense scattering of setae throughout the palpiger, including along the lateral and anterior margins (Figs. 274, 277, 317, 323); the third is a distinct transverse row of setae near the anterior margin (Figs. 272, 294, 322). Also appearing independent of the setal arrangement, there often are ~1-3 large, elongate setae positioned at the antero-lateral margin of the palpiger (Figs. 289, 297, 309), similar to those on the first basal segment of the palpus but larger. Only in a few taxa do these enlarged setae appear absent (Figs. 274, 289, 299, 300, 321). The cardo and stipes are conserved in shape and size, although they may vary in length. The stipes often bears 1-3 elongate setae, though these may be absent. The lacinia and galea are separate, with the galea slightly more developed. The lacinia often possesses some elongate setae, although the majority of setae are present on the galea. Setae on the galea are seen in 3 general types: the first being massive, teeth-like setae that vary in shape and size, some elongate and rectangular (Fig. 322) and the others triangular (Figs. 272, 298, 317). This type is only found along the lateral margin of the galea and often in a dense row. The second type are

smaller setae, though still slightly enlarged, and they are found interspersed throughout types one and three, though mostly situated posterior to type 1. The third type of setae are more normal in appearance, thin and elongate, and are interspersed throughout the first and second type. This third type is the only one present along the posterior region of the galea and the anterior portion of the lacinia (Figs. 281, 304, 310, 318). Maxillae in the outgroups are very similar to those in Baridinae, especially when considering the great diversity within Baridinae. Within the bounds of taxa studied, only maxillae in Entiminae were found to distinctly differ (Fig. 326). Although certainly not particular to Baridinae, the tendons attaching to the maxillae are quite long and notably fascinating, narrow while extending throughout the length of the rostrum, then suddenly widening for attachment to the tentorium (Fig. 432).

**Mandibles** (Figs. 185, 191-194, 353-431): Mandibles in Baridinae are quite variable, although this variation is fairly easy to categorize. Mandibles, in the case of baridines, can be atomized into bearing a variable number of incisors and a molar region. The right and left mandibles are consistently different, often not only in the number of incisors but also in shape. The difference in incisor number between the left and right mandible is one, with the right mandible always bearing one more incisor than the left. When comparing the right mandible only, incisor number varies from 1-3. In regards to a mandible with 1 incisor, this quality is also variable because there distinctly are taxa with 1 incisor and a molar region (Figs. 362, 370) and then there are taxa with a fused incisor and molar region (Figs. 368, 388). Mandibles bearing 2 (Figs. 361, 366, 376) and 3 (Figs. 355, 367, 374, 384, 395) incisors and a

molar region are unambiguous. In accordance with incisor number, the mandible also forms two general shapes, which can be determined from the striations present on the incisors. The first is a more or less linear shape, where the first incisor is enlarged and straight, with any other incisors and the molar region positioned laterally (Figs. 359, 366, 376, 378, 388). The second shape is angled or curved, where the incisors and molar region all fall on a lateral or angled axis (Figs. 357, 363, 383, 391, 410). In this second type, the incisors vary in size, in which the first, second, or sometimes even third incisor may be larger than the others. A curious form that has been found in a few taxa is what appears to be the presence of a deciduous tooth on the first incisor (Fig. 399). This tooth is thought to be deciduous due to ease in detaching it from the remainder of the mandible. Another peculiarity is the presence of strong lateral lacerations on the incisors (usually the first) (Figs. 360, 366, 374, 388). These cuts can penetrate quite deep into the incisor and often can lead to detachment of the apical half of the incisor (Fig. 370). It is possible that these marks form as a result of generalized feeding, but exactly how they come to be is unknown.

In the outgroups, the mandibles tend to be quite different from the general baridine types, mainly due to shapes of the mandible and incisors (Figs. 406, 409, 411-414). Those mandibles most similar to ones in Baridinae include Ceutorhynchinae and Conoderinae. Again, although not particular to Baridinae, the tendons attaching to the mandibles are worth noting (Figs. 433, 434).

*Proventriculus and associated internal structures*

The structure of the proventriculus is quite conserved within Baridinae and in related genera outside of the subfamily (Figs. 435-450). The only observed variation is in shape, where it can range from short and round (Figs. 442, 446, 447, 450) to elongate and cylindrical (Figs. 435, 439-441, 444).

Other internal structures are illustrated in Figs. 451-459 (according to Snodgrass 1935), including the various divisions of the digestive system and the ventral nerve ganglia (Fig. 458).

#### *Pro-thorax*

The pro-thorax in baridines is usually narrow anteriorly, widening posteriorly, as viewed dorsally (Figs. 460); however, in some groups it is widest at the middle and narrower both anteriorly and posteriorly (Figs. 461). Punctures most often are round to slightly elongate (Figs. 462-464), although in some taxa the punctures become oriented in such a way as to form a pattern of longitudinal ridges, normally only present on the pro-notum (Figs. 465, 466). Along the collar there typically is a ring of punctures that varies in size and puncture-depth among genera. The punctures are small and shallow along the dorsal portion of the collar and become large towards the ventral side, sometimes terminating in two large punctures anterior to the pro-coxae (Figs. 471, 472). Some taxa possess a puncture collar that is developed, with large, deep punctures (Figs. 467, 469, 470), others possess a weakly developed puncture collar, where the punctures are nearly absent (Fig. 473), but the vast majority have a puncture collar that is intermediate between these two extremes (Fig. 468).

The pro-notum may possess various modifications of the typical form. In most genera there is a central, longitudinal smooth line which does not bear any punctures or scales (Figs. 463-465). This line may be absent in some taxa, in which case punctures and scales are evenly distributed across the dorsal surface (Figs. 462, 466). Also along this central line there may be a developed hump or crest (Figs. 474, 475). Although the pro-notum often is relatively flat and broadly convex, a more inflated and globular form may be present (Figs. 476).

The pro-sternum is typically flat and smooth (Fig. 483), often with a small depression along the anterior margin, bearing small lateral carina (Figs. 484, 485). Sometimes there may be a depression anterior to the pro-coxae or what may appear to be a highly reduced canal for the reception of the rostrum. When a canal for the reception of the rostrum is present it is always obvious and moderately deep, often with strong carina along the lateral margins. Although other related groups also possess a ventral canal (Cryptorhynchinae, Conoderinae), those present in Baridinae are restricted to the pro-sternum. The pro-coxae often are positioned relatively close (less than one diameter of a pro-coxa), although the inter-coxal distance varies from less than one to greater than one diameter of a pro-coxa. The prosternal process in baridines usually is developed, forming a quadrate process (Figs. 490, 494), a slightly concave process (similar to the quadrate process but with a slight concavity along the posterior margin) (Figs. 498, 499), or a bilobed process (or one with a central cleft) (Figs. 489, 491, 497, 500). The prosternal process may also be reduced, with a

posterior margin that is straight (or slightly curved), projecting (Fig. 493), or with a central cleft (Fig. 484, 488).

Also on the pro-sternum of many baridine taxa are a pair of horns. These horns have been observed to be associated with male-male sparring during mating competitions (Eberhard and Garcia-C. 2000). The horns themselves, although simple in structure, do not appear homologous across all of the taxa in which they appear. The horns can be cylindrical, dorso-ventrally flattened, and laterally flattened, and vary in length, from being small stubs or protrusions near the pro-coxae (Figs. 507, 508) to elongate tusks (Figs. 509, 510). Often also associated with these horns is an invagination between the pair in the middle (Fig. 501-506). This invagination often extends quite far posteriorly into the pro-thorax and can be a single invagination (Figs. 502-504, 506) or bifurcate (Fig. 501, 505). Although present in many taxa, the invagination can also be reduced to absent. The invagination can also be termed an acarinarium, as mites often are found dwelling inside.

### *Meso-thorax*

**Mesonotum** (Figs. 511, 514-577): The structure of the mesonotum in Baridinae is relatively conserved, with most variation found in the mesoscutellum, followed by the axillary cord, the mesothoracic phragma and suture, and the anterior margin of the mesonotum. The central anterior margin of the mesonotum is always developed, a characteristic of baridines and related outgroups. In Baridinae the anterior margin can form an acute angle (Figs. 518, 528) or form a subacute

protrusion (Figs. 511, 522, 579-581). In most outgroups, this margin is reduced and relatively flat (not produced) (Figs. 563-577). The antero-lateral margins can also be different in form, being either relatively linear (Figs. 521, 534, 536, 543) or concave (Figs. 514, 518, 544). The mesoscutellum is quite variable in form in Baridinae. The anterior margin often is broadly round (Figs. 587, 592, 593) to quadrate (Figs. 585, 589, 590), but can also be acute, oval, or cardiform, with a central cleft (Figs. 582, 588). Likewise, the posterior margin is just as variable, being concave (Figs. 587, 590, 593, 599), concave with an acute central projection (Figs. 583, 591, 596), convex and broadly round (Figs. 582, 584, 600), acute, oval, quadrate (Figs. 585, 588, 589, 591, 592, 595), or cardiform (Figs. 586, 598). The axillary cord is produced and can either be round and lobe-like (Figs. 527, 537, 540, 541) or more truncate and quadrate (Figs. 522, 531, 536, 539). In most outgroups it is reduced and broadly rounded. The mesothoracic phragma bears a few areas that are different among taxa. The general shape can be quadrate (Figs. 518, 531, 547), longitudinally elongate (Figs. 526, 537, 541, 542), or transversely elongate (Figs. 515, 521, 534, 543). The anterior margin may be continuous and smooth (Figs. 527, 531, 548) or may have a cleft of variable size at the longitudinal mesothoracic suture (Figs. 518, 535, 556). Punctures may be present on the entire or part of the surface of the phragma (Fig. 526, 529, 541), restricted to the anterior margin of the phragma (Figs. 515, 520, 543), or may be absent entirely.

*Elytra*

The elytra are of various shapes and length, ranging from moderately wide and short to slender and elongate. All elytra possess 10 striae along the dorsal surface, with variation seen in the punctures present along the striae and number and length of setae (Figs. 601-628). The intervals are typically flat, though may form elevated ridges in a few genera (Figs. 602, 605, 613). They also may be smooth (lack punctures), possess a single row of punctures (Figs. 614, 624, 626, 628), or possess multiple punctures not organized into rows (Figs. 612, 617, 623, 625).

The elytral suture is densely clothed with elongate setae (Fig. 629). Together with the spiculate patches on the abdomen and ventral surface of the elytra, these setae likely are also involved in a wing-locking function. Another feature of the elytral intervals of some taxa is that they appear to have small pores situated at regular intervals (Figs. 619-621).

Along the ventral surface, the elytra possess a number of particular areas where modified setae are present that function in securing the elytra to the tergites and thorax. While these areas are generally along the anterior, posterior, and outer margins, the most significant of these wing-locking patches are along the right and left anterior margins (Figs. 634, 635, 638-640, 652), the central region along the outer margin (Figs. 630, 631), and the outer apical margin (Figs. 632, 633, 636, 637, 641-651). The microtrichial patches along the anterior and outer margins consist of flattened, spade-like projections, whereas the apical patch consists of large spines that interlock with a corresponding patch of spines of the 7<sup>th</sup> tergite. Another particularly modified area is along the postero-medial margin where a file of 2 general types may

be present for involvement in acoustic communication. One type of file consists of many dense, parallel ridges (Figs. 648, 650), and the second type consists of fewer, more sparsely situated ridges.

#### *Meta-thorax*

As noted by Zherikhin and Egorov (1990) and Zherikhin and Gratshev (1995), the metepisternum and metepimeron are fused in Baridinae (Fig. 578). All baridines also possess the characteristic large, ascending mesepimera (Fig. 578).

**Metanotum** (Figs. 655-716): The thorax is a significant structure in terms of examining differences among baridine taxa. Although closely related groups to Baridinae possess a thorax similar in appearance, the baridine thorax is distinctively unique and has certain diagnostic features. The anterior margin of the prescutum bears a pair of lobes, which may be large and protrude or small, reduced, and relatively undifferentiated from the prescutum. The lobes are separated by an invagination which may be shallow or deep. The anterior margin of the scutellar groove can be relatively flat and straight in some cases, but it mostly is broadly concave (Figs. 660, 671) or more laterally compressed transforming the concavity into more of a cleft (Figs. 664, 675, 679). In all of Baridinae, there is a central longitudinal crest on the scutellar groove. In many taxa this crest is well-developed and large (Figs. 668-670, 684), while in others it is reduced (Figs. 655, 666, 677). Related groups to Baridinae do not possess this crest. In a few taxa there is a transverse, sclerotized

bridge present at the anterior end of the scutellar groove. This bridge may be well-developed (Figs. 662, 663, 669, 678), partially developed (Figs. 655, 679), or absent (Figs. 667, 670, 685). The posterior margin of the scutellar groove may be straight, concave, or convex. The antero-medial margin of the allocrista is always rounded in Baridinae, whereas it is more angular to quadrate in related outgroups (Figs. 697-716). The shape of the metascutum is variable within Baridinae. It is always rounded, varying from subcircular (Figs. 655, 675, 679), transversely elongate (Figs. 662, 663, 669, 678), or to longitudinally elongate (Figs. 658, 664, 670, 680, 681). The postero-medial margin can be convex (Figs. 655, 671, 684), relatively straight (Figs. 661, 664, 665), or concave (Figs. 662, 666, 680). In a few taxa this margin can be strongly convex and forming an angular margin (Figs. 658, 673, 679). In Ceutorhynchinae and Conoderinae, the metascutum typically is transversely elongate, and the postero-medial margin quadrate or rectangular. This feature may be similar with the few baridine taxa that also share an angular postero-medial margin; however, taking the shape of the entire metascutum into account, all of the metascutal margins in Baridinae are rounded, while those in outgroups tend to be entirely quadrate, with the exception of Oorbitidinae, which may be closely related. The metascutum may also bear small or large punctures, or punctures may be absent. The degree of development of the postnotum is closely related to the size and shape of the metascutum. In some taxa where the metascutum is subcircular or transversely elongate and its posterior margin well-defined, the postnotum usually is well-developed (Figs. 659, 669, 682, 686). When the metascutum becomes longitudinally

elongate and/or its posterior margin becomes less defined, the postnotum appears reduced to nearly absent (Figs. 661, 668, 680, 683). On the metascutellum, there can be a weak ridge or crest, here termed the metascutellar line, from the posterior end of the scutellar groove to the metascutum (Figs. 657, 659, 669, 689). In most outgroup taxa this ridge is absent. In all of Baridinae, the postero-lateral margins of the metanotum are developed and projecting, whereas taxa outside of the subfamily do not possess this feature and the lateral margins are straight (Figs. 697-716).

**Metendosternite** (Figs. 717-771): The typical form of the baridine metendosternite has a moderately short, quadrate metafurcal lamina (metafurcal stalk), which may be longitudinally or laterally elongate and always is wide (Figs. 717-719, 729-731, 740-743). Many taxa, however, have a metafurcal lamina in which the lateral margin migrates inwards towards the suture, creating an upside-down V-shaped lamina (Figs. 720-726, 736, 737). In this type, the metafurcal lamina is wide ventrally and narrows towards the metafurcal arm. The lateral arm is always well-developed in Baridinae, but sometimes reduced in outgroups (Figs. 755, 765, 767). The apex of the lateral arms may be simple (Figs. 717-719, 738-743) or bifurcate (Figs. 727, 729) in Baridinae. The anterior metafurcal tendons vary in their position, being adjacent to the longitudinal suture, approximately centered between the longitudinal suture and the base of the metafurcal arm, or closer to the metafurcal arm.

**Sclerolepidia:** Following Lyal and King (2006), there are four basic types of sclerolepidia found in weevils, two of these types are only found in Baridinae. One

type is composed of flattened, strongly appressed scales which are often trifurcate but also can be multifurcate (Figs. 772, 773, 776-780). The second type is composed of elongate, projecting scales that have fimbriate apices (Figs. 774, 775, 781-784). The specific function of sclerolepidia is unknown, but they are believed to be associated either with a secretory or sensory function.

**Wing-locking patches:** Dorsal microtrichia fields have been found in many insect groups and function as types of body-appendage arresting mechanisms through frictional forces as probabilistic fasteners (Gorb and Goodwyn 2003; Gorb *et al.* 2002; Gorb 1999; Gorb and Popov 2002). In Coleoptera, these fields are concentrated on the dorsal surface, particularly on the thorax and abdomen. As illustrated in other beetle groups, such as Tenebrionidae (Gorb 1998, 1999) and Carabidae (Baehr 1980), all baridines also possess interlocking microtrichia fields which function to fasten the elytra and hind wings to the body. While many tergites are modified with dorsal fields of spines (Figs. 785, 786) for interaction in wing fastening with corresponding areas on the ventral apical region of the elytra (Figs. 791-793), the thorax also plays a large role in this process. In Baridinae, the lateral region of the thorax just above the posterior area of the metepisternum possesses a microtrichial field for attachment to the ventral side of the elytra. This patch is composed of spade-like cuticular microprojections and is consistently found in all baridine taxa (Figs. 789, 790). The largest microtrichial field on the thorax involved in wing-fastening is located on each metascutum and is composed of similar spade-like cuticular outgrowths (Figs. 785-788). These fields interact with corresponding

fields on the inner antero-ventral side of the elytra (Figs. 794, 795) and setal spines on the hind wings (Figs. 796-799).

*Hind wings* (Figs. 800, 801, 803-845)

Following wing terminology of Zherikhin and Gratshev (1995), the baridine wing, like many other morphological features, is relatively conserved, in which mostly subtle changes are seen when comparing genera. Generally, the larger-bodied taxa retain greater sclerotization in the hind wing, and smaller taxa often show reduction in many of the veins and sclerotizations on the wing. For the most part, C, Sc, R, Cu, and A remain relatively undifferentiated among taxa. Rr is most often present and fully developed, although it may be reduced in length or even absent. The rfi is always present, but may be somewhat ambiguous in less sclerotized wings. The rc often is present, fully enclosed by the rcm, and may vary slightly in size. It may sometimes be open, though, due to discontinuities in the rcm. The sclerotized regions, particularly the rms, rsc, and msc are always present, but may also be inconspicuous in less sclerotized wings. The rm can be absent or present, but differentiating the two states may be difficult when the rm is faint. 1rs is always present, and can also be faint in many taxa, but 2rs may be present or absent. R3 is usually present as a thin, sclerotized vein (Figs. 815, 816, 821, 831), though it may lose the majority of sclerotization along its length and therefore take the form of a long, thin, white line (Figs. 800, 804, 812, 823). In a few taxa R3 is absent. The pst is always present and developed in the majority of genera, though it may become

narrower or slightly reduced in length medially (Figs. 810, 811, 825). The mst also usually is elongate and developed, but it too may be reduced in length medially (Figs. 808, 819, 825).  $Cu_1$  never reaches the wing margin, and is extended by a light sclerotization at the apical fold of  $Cu_1$ . This sclerotization may become reduced in length apically.  $1A_1$  and  $1A_2$  usually are completely absent, though when present, they typically are only defined near the wing margin (Figs. 804, 806, 815, 821). In only a few genera, the  $1A_1$  or  $1A_2$  veins are extended dorsally towards A and fused by  $a_1$ - $a_2$  (Figs. 813), though both veins are never found to extend dorsally in the same instance.  $3A$  in the majority of genera is reduced (Figs. 809, 819, 824), though it may be developed and nearly touching A (Figs. 805, 813, 815, 821, 826).  $3A$ , however, is never fused with A in Baridinae.

Since the sclerites at the base of the hind wing in Baridinae have never been demarcated, they are illustrated in Fig. 801. Terminology follows that of Kukalova-Peck and Lawrence (1993), Browne and Scholtz (1995), and Fedorenko (2002). Particularly noteworthy is that Br and BSc are fused. In this illustration, Mr is visible, but cannot be seen well in the full-wing illustrations because of its short length and small size.

### *Legs*

The pro-, meso-, and meta-femora are often bare and relatively similar in size. Sometimes one or more teeth are present near the apico-ventral surface, and the ventral surface may be sulcate for reception of the tibia. The tibiae usually are not

particularly modified and do not bear tarsal grooves along the apical surfaces, thus the apical setal comb will more or less form a complete ring around the apical margin (Figs. 850, 855, 856); however, in some taxa, such as species of *Fryella*, tarsal grooves are present for reception of the tarsi when they are folded. Variation is seen in the presence and absence of an apical tibial uncus. When an apical uncus is present, it most often arises from the inner angle and is accompanied by an adjacent tuft of elongate setae that converge with the uncus (Figs. 847, 849, 857, 858, 860). In some cases a small mucro may form from the inner carina adjacent to the uncus (Fig. 850-852). The uncus, however, does not always arise from the inner angle, and can also arise from the middle (Fig. 847, 858). In other cases the apex of the tibia may be bear, with both mucro and uncus absent. Although the uncus may be absent in some taxa, a mucro may be present at opposite sides of the tibial apex, on both inner and outer angles (Fig. 855).

The number of tarsi in baridines is 5. Tarsomeres 1 and 2 usually are cylindrical or conical (Fig. 853), although they may be dorso-ventrally flattened and expanded laterally (Fig. 854). Tarsomere 3 typically is bilobed, though the lobes may be highly reduced and appear more cylindrical. When lobes are present they vary in size between genera. When they are enlarged and expanded laterally, tarsomeres 1 and 2 usually are expanded as well. Tarsomere 4 is always reduced in size and inconspicuous. Tarsomere 5 always is cylindrical, but varies in length. Usually it is shorter when the lobes of tarsomere 3 are expanded (and often when tarsomeres 1 and 2 are expanded) and longer when the lobes are reduced in size. The ventral setal tufts

on the tarsus are as Figs. 862-864 The pre-tarsal ungues may be connate (Figs. 865, 867, 868) or divergent/free (Figs. 864, 866) and are always simple (not bearing any serrations or teeth).

#### *Tergites* (Figs. 802, 869-927)

A unique feature of Baridinae is that most taxa possess a strongly sclerotized tergum, in which the intersegmental membrane between the tergites is even sclerotized, forming a hardened shell. A few sister taxa to Baridinae also possess this strong sclerotization of the tergum. Only relatively few baridine taxa possess a weakly sclerotized abdomen, thus this feature appears to be plesiomorphic in Baridinae. There are 7 visible tergites in Baridinae (Morimoto *et al.* 2006). Each tergite is composed of 3 separate parts, the median sclerite, which is the largest, the spiracular sclerite, and the laterotergites (Fig. 802), which are small and each subdivided into many smaller sclerites. Median tergite 7 is never modified or subdivided, and its associated spiracular sclerite is always fused. Median tergite 1 is always divided in the middle, and these two separate sclerites are further subdivided into two parts. Median tergites 2-6 may also be individually separated with a median fissure in different taxa. The spiracular sclerites, as the median sclerites, may be individually fused or separated from the median sclerites. The laterotergites are always separated from the spiracular sclerites.

On the dorsal side of the tergites, as in many weevil subfamilies, spiculate patches (patches of spines) are found (Figs. 913-919). These patches are present only

on the median and spiracular sclerites, and there is variation found between taxa on which tergites they are present. Only the patches on the 7<sup>th</sup> median sclerite and lateral sclerites interact with corresponding patches on the postero-ventral and latero-ventral margins of the elytra, respectively. The other spiculate patches seem to interact with the hind wings.

Sound production, particularly by stridulation, has been described in numerous beetle groups (Kasper and Hirschberger 2005; Serrano *et al.* 2003). Such as described by Lyal and King (1996), in many genera of Baridinae, two longitudinal rows of plectra are present on the dorsal surface of the 7<sup>th</sup> tergite (Figs. 920-927). These rows are seen to be of two types, those that are composed of densely-situated plectra (Figs. 920-925) and those that are composed of sparsely-situated plectra (Fig. 926, 927). These two types of plectra correspond to the presence of two types of files on the apico-ventral surface of the elytra (Figs. 928-932). The type of plectra that form dense rows correspond to a file type that is composed of dense longitudinal ridges (Figs. 928, 930, 931). The second type of plectra, forming sparse rows, correspond to a file type that is composed of more sparse ridges (Figs. 929, 932). This type of combination of plectral rows and file is the most common among weevils, present in 13 other curculionid subfamilies (Lyal and King 1996). Although three other types of strigulating mechanisms are present within Curculionidae, only one type is found within Baridinae.

*Ventriles* (Figs. 933-980)

The ventrites (visible sternites) in Baridinae are relatively uniform, showing variation mainly in the shape of the posterior margin of ventrite 5. The posterior margin may be developed and rounded (Figs. 935, 937, 946, 948), truncate and convex, occasionally with a small central projection (Figs. 933, 945, 956, 957, 969), truncated and concave (Figs. 951, 952, 976), truncated and sinusoidal (Figs. 950, 958, 978), or truncated with a small central projection (Figs. 940, 971, 977, 979). Punctures covering the ventrites is normal, but punctures along the anterior margin of ventrite 5 may be present or absent (Figs. 978-980). In the majority of Baridinae, the posterior margin of ventrite 1 is sinusoidal, with the lateral parts convex and the central part concave. The posterior margins of ventrites 2-4 or broadly concave.

*Male genitalia* (Figs. 981, 982, 985-1043)

**8<sup>th</sup> sternite:** The 8<sup>th</sup> sternite in Baridinae is divided and forms paired sclerites, their medial margins rounded and distal margins often acute (Figs. 982). They most often are fairly wide (medial-distal length long) and have a short length (anterior-posterior length short) (Figs. 993, 995, 1008, 1009, 1013). In some taxa this pair of sclerites may be enlarged and more round (Figs. 986, 989, 1001), the length becoming more equal to the width.

**9<sup>th</sup> sternite (spiculum gastrale):** The spiculum gastrale usually is approximately  $\frac{1}{2}$  to  $\frac{3}{4}$  the length of the aedeagus. It often is broadly curved and relatively narrow (Figs. 985, 990, 999, 1005), though it may be more straight (Figs. 1007, 1008, 1023) or have an angled apex (Figs. 990, 1001, 1004, 1019), and may

also be slightly wider (Figs. 1000, 1022). The apex may be subequal in width to the remainder, but more often is flattened and expanded (Figs. 990, 991, 1009, 1022).

**Aedeagus:** The median lobe may be short in length (Figs. 991, 992, 994, 1011, 1013) to long (Figs. 986, 989, 998, 1007, 1009, 1015), with lateral margins straight and parallel-sided (Figs. 986, 987, 1008, 1030), even and sinusoidal (Figs. 1001, 1020, 1022), or broadly curved (Figs. 988, 994, 999, 1012, 1019). The median lobe may also be relatively wide (usually also short in length) (Figs. 992, 996, 1000) or narrow (usually also elongate) (Figs. 986, 998, 1023, 1025). The apex may range from acutely lobed (Figs. 989, 1004, 1007), lobed with a central projection (Figs. 993, 1009, 1032), broadly curved (Figs. 985, 991, 999, 1021), or concave (Figs. 986, 992, 996, 1020). The apex may also have a wide margin, in which the median orifice is more posterior (Figs. 988, 1005, 1008, 1011), or the apical margin may be narrow, in which the median orifice is adjacent to the apex (Figs. 986, 992, 1001, 1010, 1019, 1021). Pairs of setal tufts may also be present at the apex (Figs. 987, 1014, 1023). The median orifice varies in Baridinae from being open to closed. When the median orifice is open it may be widely open, with thin lateral margins of the median lobe, as viewed dorsally (Figs. 986, 993, 996, 1002, 1021), more narrowly open, where the lateral margins of the median lobe are wider (Figs. 987, 988, 1004, 1007, 1012), or may be strictly narrow, in which the margins of the median lobe nearly fuse medially, as viewed dorsally (Figs. 989, 1022). When the lateral margins of the median lobe are completely fused, the median orifice is closed (Figs. 991, 999, 1008, 1009). Internally there often is an elongate, thin, sclerotized flagellum (Figs. 993, 1011,

1014, 1016, 1022, 1024), along with other sclerotizations (Figs. 990, 999, 1000, 1028). The median struts vary tremendously between some genera, where they may be highly reduced (Figs. 990, 998, 1014, 1024), approximately subequal in length to the median lobe (Figs. 987-989, 1002-1009), slightly longer than the median lobe (Figs. 1016, 1017, 1019, 1029), or several times longer than the median lobe (Figs. 995, 1011-1013, 1018, 1020).

**Tegmen:** The tegmen normally is complete and encircles the aedeagus, but it can be incomplete. The ventral tegminal strut typically is simple and relatively long, or highly elongate in some cases (Figs. 985, 988, 995, 1005, 1008, 1018, 1027). In some taxa it may be reduced in length to short stub (Figs. 990, 999), and rarely is it bifurcate. The dorsal (lateral) lobes are always elongate.

*Female genitalia* (Figs. 983, 984, 1044-1058)

In Baridinae, the 8<sup>th</sup> sternite of the female forms two general types: one in which the lateral basal margins (where the sternite divides) are rounded (Figs. 1045, 1047, 1048, 1056) and the second in which the lateral basal margins are angular (Figs. 1044, 1046, 1049, 1052, 1057). This basal region normally is distinctly divided (Figs. 1046, 1047, 1053), although it may become more narrowly divided (Figs. 1045, 1048) or fused (Figs. 1050, 1055, 1058). The spiculum typically is relatively short, but may be more elongate (Figs. 1045, 1048, 1058). The coxites also can be quite variable in length, often moderately short (Figs. 1044, 1054, 1057) but

also elongate in some taxa (Figs. 1046, 1048, 1055). The stylus is fairly conserved in shape, typically elongate and cylindrical.

The spermatheca possess an elongate and curved cornu, which often does not vary much in shape but may become shorter or longer and vary in curvature. The collum also does not vary much, usually forming a small lobe. More variable, however, is the size and length of the ramus, which may be absent (Figs. 1048, 1051, 1053, 1054), form a similar sized lobe as the collum (Figs. 1046, 1052, 1058), or form an elongated extension, sometimes similar in length to the cornu (Fig. 1055).

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**Appendix I:** Taxa examined.

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**Bagoinae**

*Bagous transversus*

**Cossoninae**

*Cossonus impressifrons*

**Curculioninae**

*Curculio pardalis*

**Scolytinae**

*Hylurgops planirostris*

**Orobitidinae**

*Pararobitis gibbus*

**Conoderinae**

*Arachnopus gazella*  
*Cyllophorus fausciatus*  
*Metialma straminea*  
*Balanogastris kolae*  
*Telephae oculata*  
*Cylindrocopturus adpersus*  
*Cylindrocopturus operculatus*

*Acoptus suturalis*  
*Lobotrachelus troglodytes*  
*Mecopus trilineatus*  
*Trichodocerus sp.*

**Molytinae**

*Cholus rana*  
*Conotrachelus fissunguis*

Trigonocolini:  
*Trigonocolus curvipes*

**Entiminae**

*Cyrtepistomus castanaeus*

**Derelominae**

*Derelomus basalis*

**Dryophthorinae**

*Dryophthorus americanus*

**Cryptorhynchinae**

*Cryptorhynchus lapathi*

**Ceutorhynchinae**

*Ceutorhynchus obstrictus*  
*Hypurus bertrandi*  
*Phytobius oriseomicans*  
*Mononychus vulpeculus*  
*Auleutes argentinensis*  
*Coeliodes flavicaudis*

**Baridinae**

*Acentrinops brevicollis*  
*Allomegops sp.*  
*Amercedes subulirostris*  
*Amercedes orthorrhinus*  
*Anatorcus densus*  
*Anavallius ruficornis*  
*Andiblis seriata*  
*Aniops sculpturata*  
*Aniops sp.*  
*Anopsilus oblongus*  
*Anotesiops obidosensis*

*Antesis sparsa*  
*Athesapeuta vinculata*  
*Barilepsis griseus*  
*Barilepton filiforme*  
*Barilepton quadrieolle*  
*Barinus bivittatus*  
*Barinus cribricollis*  
*Baris torquata*  
*Barycerus collaris*  
*Barymerus binaries*  
*Bondariella mimica*  
*Buchananius striatus*  
*Buchananius sulcatus*  
*Busckiella lecythidis*  
*Calandrinus grandicollis*  
*Calorida binocularis*  
*Camelodes leachii*  
*Camerones semiopacus*  
*Catapastinus caseyi*  
*Catapastus conspersus*  
*Catapastus squamirostris*  
*Catapastus albonotatus*  
*Catapastus diffusus*  
*Catapastus seriatus*  
*Catapastus signatipennis*  
*Catapastus simplex*  
*Centrinites strigicollis*  
*Centrinogyna hispidula*  
*Centrinogyna strigata*  
*Centrinopsis sp.*  
*Centrinopus alternatus*  
*Centrinopus helvinus*  
*Centrinus curvirostris*  
*Chepagra rotundicollis*  
*Clandius cephalotes*  
*Coelonertus nigrirostris*  
*Coleomerus boliviensis*  
*Coluthus cribrarius*  
*Conoproctus quadripustulatus*  
*Cosmobaris americana*  
*Craptus tibialis*  
*Crostidia tenuipes*  
*Crostis subexplanata*  
*Crotanius trivittatus*

*Cryptosternum nevermanni*  
*Cylindridia prolixa*  
*Cylindrocercus comma*  
*Cymatobaris impressifrons*  
*Cyrionyx camelus*  
*Dactylocrepis flabellitarsis*  
*Dalcesia sp.*  
*Dealina carbonarius*  
*Deipyle induta*  
*Deipyruus hirsutulus*  
*Demoda vittata*  
*Dericinus habilis*  
*Desmoglyptus arizonicus*  
*Dialomia gradata*  
*Diastethus eurthinoides*  
*Dimesus rubricatus*  
*Diorymeropsis disjuncta*  
*Diorymeropsis xanthoxyli*  
*Diorymerus lancifer*  
*Dirabius calvus*  
*Dirabius rectirostris*  
*Dissopygus metallescens*  
*Eisonyx crassipes*  
*Eisonyx opaca*  
*Elasmobaris signifer*  
*Embates chaetopus*  
*Ethelda Squamosa*  
*Eucalus vitticollis*  
*Eudialomia longula*  
*Eugeraeus sp.*  
*Eumycterus albosquamulatus*  
*Eurhinus festivus*  
*Eurhinus aeneus*  
*Eusomenes curtirostris*  
*Eutoxus sp.*  
*Fishonia brevinasus*  
*Forandia duplex*  
*Forandiopsis carinulata*  
*Fryella mutilatus*  
*Garnia sp.*  
*Geraeopsis duplocincta*  
*Geraeus lineellus*  
*Geraeus penicella*  
*Glyptobaris lecontei*

*Haplostethops ellipsoidea*  
*Hiotus inflatus*  
*Idiostethus subcalvus*  
*Idiostethus tubulatus*  
*Iops bicolor*  
*Iopsidaspis truncatula*  
*Ladustaspis crocopelmus*  
*Lampobaris cicullata*  
*Lasiobaris geminata*  
*Laurentius bruchi*  
*Lepidobaris acnisti*  
*Leptogarnia polita*  
*Leptoladustes densus*  
*Leptoschoinus fucatus*  
*Lichnus longulus*  
*Limnobaris bicincta*  
*Limnobaris calandriiformis*  
*Linogarnia suturalis*  
*Linogeraeus urbanus*  
*Linogeraeus viduatus*  
*Linomadarus vorticosus*  
*Lipancylus brevirostris*  
*Loboderes citriventris*  
*Lorena simulans*  
*Lydamis cinnamomeus*  
*Macrobaris sp.*  
*Macrorevena atromicans*  
*Madarellus laticollis*  
*Madarus bistrigellus*  
*Madopterus talpa*  
*Megabaris quadriguttata*  
*Megalobaris viridana*  
*Megavallius auritarsis*  
*Melampius basalis*  
*Microbaridia delicatula*  
*Microcholus puncticollis*  
*Microcholus striatus*  
*Microforandia uniformis*  
*Microrhinus mutilus*  
*Microstegotes sp.*  
*Microstrates cocois*  
*Microtorcus tubulatus*  
*Microzalestes basalis*  
*Montella rufipes*

*Moreobaris deplanata*  
*Myctides imberbis*  
*Nanobaris sp.*  
*Nedestes sarpedon*  
*Neplaxa illustris*  
*Nertinus suturalis*  
*Nestrada compacta*  
*Nicentridia angusticollis*  
*Nicentrus decipiens*  
*Nicentrus grossulus*  
*Odontobaris sp.*  
*Odontocorynus scutellumalbum*  
*Odontocorynus creperus*  
*Oligolochus braccatus*  
*Oligolochus ornatus*  
*Onychobaris densa*  
*Oomorphidius leavicollis*  
*Opertes sp.*  
*Opseobaris alba*  
*Optatus palmaris*  
*Orchidophilus aterrimus*  
*Orissus meigenii*  
*Orissus christophori*  
*Orthoris crotchii*  
*Ortycus cristosus*  
*Ortycus setifer*  
*Ovanus picipennis*  
*Ovanus minutus*  
*Pachybaris porosa*  
*Pachygeraeus laevirostris*  
*Pacomes distortus*  
*Pacomes subglaber*  
*Palmelampius heinrichi*  
*Palmocentrinus butia*  
*Palocopsis tecta*  
*Pantoteles tenuirostris*  
*Parafishonia setulosa*  
*Parageraeus tumidirostris*  
*Parallelosomus amplitarsis*  
*Parasaldius sp.*  
*Parasomenes curvirostris*  
*Pardisomus biplagiatus*  
*Parisoschoenus sp.*  
*Peclavia hispidicollis*

*Peclaviopsis planipectus*  
*Peridinetus cretaceus*  
*Peridinetus irroratus*  
*Phacelobarus signubaris*  
*Pistus galeatus*  
*Platyonyx ornatus*  
*Plesiobaris albilata*  
*Plocamus echidna*  
*Plocamus clavisetes*  
*Prodinus sp.*  
*Pseudobaris angusta*  
*Pseudocentrinus ochraceus*  
*Pseudogeraeus macropterus*  
*Pseudorancea spissirostris*  
*Pseudorthoris devexus*  
*Pseudosaldius conjunctus*  
*Pseudotorcus rufipes*  
*Psiona densa*  
*Pteracanthus smidtii*  
*Pycnobaris pruinosa*  
*Pycnogeraeus modestus*  
*Pycnogeraeus striatirostris*  
*Pycnonicentrus gilvivistis*  
*Pycnotheantis sp.*  
*Rancea parviclava*  
*Ranceoma uniformis*  
*Remertus marginatus*  
*Ravena sexualis*  
*Reveniopsis sp.*  
*Rhoptobaris canescens*  
*Rhytidoglymma cenescens*  
*Roalius rufipes*  
*Saldiopsis armata*  
*Saldius inaequalis*  
*Scirpicola chilensis*  
*Selasella cuneipennis*  
*Sibariops concinna*  
*Sibariops concurrens*  
*Sibariopsida docilis*  
*Sodesia sparsa*  
*Solaria curtula*  
*Solenosternus dividiuus*  
*Somenes regestus*  
*Sphenobaris quadridens*

*Spolatia gradata*  
*Starcus rugulosus*  
*Stereobaris interpunctata*  
*Stethobaris commixta*  
*Stethobaris laevimargo*  
*Stethobaroides nudiventris*  
*Stictobaris cribrata*  
*Strongylotes squamans*  
*Sunilius platyrhinus*  
*Telemus sp.*  
*Tenemotes abdominalis*  
*Tenemotes parviclava*  
*Ternova biartiita*  
*Testalthea sp.*  
*Thaliabaris inermis*  
*Thanius sp.*  
*Thestonia sparsa*  
*Tonesia sp.*  
*Torcobius sp.*  
*Torcus nigrinus*  
*Torcus variabilis*  
*Trachymeropsis palmipes*  
*Trepobaris inornata*  
*Trichobaris texana*  
*Trichodirabius longulus*  
*Ulobaris loricata*  
*Valdenus laevis*  
*Valiopsis squamipes*  
*Vallius sulcatus*  
*Xystus ater*  
*Xystus ruficollis*  
*Zalestes perpolitus*  
*Zathanus sp.*  
*Zena virgata*  
*Zygobarella xanthoxyli*  
*Zygobarella tristicula*  
*Zygobarinus coelestinus*  
*Zygobaris sp. 1*  
*Zygobaris nitens*  
*Zygobaris sp.*  
*Zygozalestes oblongus*  
"Neomadarini"

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### Figure captions

**Figs. 1-11.** Adults, lateral view. 1, *Amercedes subulirostris*; 2, *Baris torquata*; 3, *Centrinus curvirostris*; 4, *Barymerus binarius*; 5, *Conoproctus quadripustulatus*; 6, *Cylindrocercus comma*; 7, *Cyrionyx camelus*; 8, *Demoda vittata*; 9, *Diastethus eurthinoides*; 10, *Diorymerus lancifer*; 11, *Embates chaetopus*.

**Figs. 12-22.** Adults, lateral view. 12, *Eurhinus festivus*; 13, *Eurhinus festivus*; 14, *Fryella mutilatus*; 15, *Geraeus lineellus*; 16, *Lepidobaris acnisti*; 17, *Loboderes citriventris*; 18, *Madarellus laticollis*; 19, *Megabaris quadriguttata*; 20, *Microstrates cocois*; 21, *Optatus palmaris*; 22, *Pacomes subglaber*.

**Figs. 23-34.** Adults, lateral view. 23, *Palmelampus heinrichi*; 24, *Pardisomus biplagiatus*; 25, *Peridinetus suturalis*; 26, *Phacelobarus signubaris*; 27, *Pistus galeatus*; 28, *Plocamus echidna*; 29, *Pteracanthus smidtii*; 30, *Remertus marginatus*; 31, *Reveniopsis* sp.; 32, *Rhytidoglymma cenescens*; 33, *Telemus* sp.; 34, *Zygobarinus coelestinus*.

**Figs. 35-43.** Adults, lateral view. 35, *Allomegops* sp.; 36, *Cymatobaris impressifrons*; 37, *Hiotus inflatus*; 38, *Megalobaris viridana*; 39, *Ortycus setifer*; 40, *Testalthea* sp.; 41, *Tonesia* sp.; 42, *Trichobaris texana*; 43, *Arachnopus gazella*.

**Figs. 44-48.** Adults, lateral view. 44, *Balanogastris kolae*; 45, *Cyllophorus fausciatus*; 46, *Telephae oculata*; 47, *Trichodocerus* sp.; 48, *Trigonocolus curvipes*.

**Figs. 49-59.** Adults, dorsal view. 49, *Amercedes subulirostris*; 50, *Baris torquata*; 51, *Centrinus curvirostris*; 52, *Barymerus binarius*; 53, *Conoproctus quadripustulatus*; 54, *Cylindrocercus comma*; 55, *Cyrionyx camelus*; 56, *Demoda vittata*; 57, *Diastethus eurthinoides*; 58, *Diorymerus lancifer*; 59, *Embates chaetopus*.

**Figs. 60-70.** Adults, dorsal view. 60, *Eurhinus festivus*; 61, *Eurhinus festivus*; 62, *Fryella mutilatus*; 63, *Geraeus lineellus*; 64, *Lepidobaris acnisti*; 65, *Loboderes citriventris*; 66, *Madarellus laticollis*; 67, *Megabaris quadriguttata*; 68, *Microstrates cocois*; 69, *Optatus palmaris*; 70, *Pacomes subglaber*.

**Figs. 71-82.** Adults, dorsal view. 71, *Palmelampus heinrichi*; 72, *Pardisomus biplagiatus*; 73, *Peridinetus suturalis*; 74, *Phacelobarus signubaris*; 75, *Pistus galeatus*; 76, *Plocamus echidna*; 77, *Pteracanthus smidtii*; 78, *Remertus marginatus*; 79, *Reveniopsis* sp.; 80, *Rhytidoglymma cenescens*; 81, *Telemus* sp.; 82, *Zygobarinus coelestinus*.

**Figs. 83-94.** Adults, dorsal view. 83, *Allomegops* sp.; 84, *Cymatobaris impressifrons*; 85, *Hiotus inflatus*; 86, *Megalobaris viridana*; 87, *Ortycus setifer*; 88, *Testalthea* sp.; 89, *Tonesia* sp.; 90, *Trichobaris texana*; 91, *Arachnopus gazella*; 92, *Balanogastris kolae*; 93, *Cyllophorus fausciatus*; 94, *Telephae oculata*.

**Figs. 95-96.** Adults, dorsal view. 95, *Trichodocerus* sp.; 96, *Trigonocolus curvipes*.

**Figs. 97-109.** Adult morphology. 97, *Dialomia gradata* (dorsal view); 98, *Orissus christophori* (dorsal view); 99, *Orissus meigenii* (lateral view); 100, *Nertinus suturalis* (lateral view); 101, *Prodinus* sp. (dorsal view); 102, *Prodinus* sp. (lateral view); 103, *Parallelosomus amplitarsis* (lateral view); 104, *Torcus nigrinus* (lateral view); 105, *Peridinetus cretaceus* (dorsal view); 106, *Barinus bivittatus* (dorsal view); 107, *Microcholus puncticollis* (dorsal view); 108, *Catapastus squamirostris* (SEM); 109, *Stethobaris laevimargo* (SEM).

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**Figs. 118-125.** Scale morphology, SEM's. 118, *Spilobaris* sp.; 119-120, *Lophobaris* sp.; 121, *Limnobaris jucunda*; 122, *Pachybaris porosa*; 123, *Taiwanobaris* sp.; 124, *Pachybaris porosa*; 125, *Acythopeus* sp.

**Figs. 126-131.** 126, *Lixus concavus*, scale morphology. 127-131, head morphology, SEM's. 127, *Taiwanobaris* sp.; 128-131, *Anthinobaris* sp. 128, latero-ventral view; 129, lateral view; 130, enlargement of lateral view; 131, scales along margin of pronotum.

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**Figs. 142-150.** Head and rostrum. 142, *Xystus ruficollis*; 143, *Odontocorynus creperus*; 144, *Eurhinus aeneus*; 145, *Diorymerus lancifer*; 146, *Spilobaris* sp.; 147, *Lamprobaris cicullata*; 148, *Telemus* sp.; 149, *Pteracanthus smidtii*; 150, *Stereobaris interpunctata*.

**Figs. 151-161.** Head and rostrum. 151, *Conoproctus quadripustulatus*; 152, *Trichodocerus* sp.; 153, *Hypurus bertrandi*; 154, *Cyllophorus fausciatus*; 155, *Acythophanes* sp.; 156, *Centrinogyna strigata*; 157, *Dealina carbonarius*; 158,

*Fishonia brevinasus*; 159, *Crotanius trivittatus*; 160, *Dactylocrepis flabellitarsis*;  
161, *Myctides imberbis*.

**Figs. 162-174.** 162-165, head and rostrum. 162, *Zygozalestes oblongus*; 163,  
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166-174, antennae. 166, *Anavallius ruficornis*; 167-168, *Oligolochus braccatus*; 169-  
170, *Camelodes leachii*; 171, *Diorymerus lancifer*; 172, *Orthoris crotchii*; 173,  
antennae; 174, *Catapastus squamirostris*.

**Figs. 175-182.** Antennae. 175, *Idiostethus subcalvus*; 176, *Stethobaris laevimargo*;  
177, *Pertorcus* sp.; 178, *Madarus bistrigellus*; 179-180, *Cylindrocercus comma*; 181-  
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mandible (right).

**Figs. 186-194.** Mouthparts. 186-187, *Demoda vittata*. 186, ventral aspect of apex of  
rostrum, showing labium, maxilla, and mandibles; 187, enlargement of apical  
maxillary palpal lobes; 188-189, *Cylindrocercus comma*. 188, lateral aspect of apex of  
rostrum; 189, enlargement of 3<sup>rd</sup> maxillary palpal lobe; 190, *Demoda vittata*, labial  
palpus; 191-192, *Ovanus picipennis*, left and right mandibles, respectively; 193-194,  
*Zygobarella xanthoxyli*, left and right mandibles, respectively.

**Figs. 195-206.** Mouthparts - labia. 195, *Zygobaris nitens*; 196, *Centrinus curvirostris*; 197, *Anthinobaris* sp.; 198, *Ovanus picipennis*; 199, *Nertinus suturalis*; 200, *Peridinetus irroratus*; 201, *Loboderes citriventris*; 202, *Antesis sparsa*; 203, *Acentrinops brevicollis*; 204, *Garnia* sp.; 205, *Pachygeraeus laevirostris*; 206, *Eisonyx crassipes*.

**Figs. 207-220.** Mouthparts – labia. 207, *Dirabius calvus*; 208, *Eisonyx opaca*; 209, *Xystus ruficollis*; 210, *Geraeus penicella*; 211, *Microcholus puncticollis*; 212, *Linogeraeus viduatus*; 213, *Ovanus minutus*; 214, *Plocamus echidna*; 215, *Oligolochus braccatus*; 216, *Oligolochus ornatus*; 217, *Odontocorynus scutellumalbum*; 218, *Odontocorynus creperus*; 219, *Camelodes leachii*; 220, *Sibariops concinna*.

**Figs. 221-233.** Mouthparts – labia. 221, *Sibariops concurrens*; 222, *Torcus nigrinus*; 223, *Madopterus talpa*; 224, *Parallelosomus amplitarsis*; 225, *Orchidophilus aterrimus*; 226, *Embates chaetopus*; 227, *Eurhinus festivus*; 228, *Eurhinus aeneus*; 229, *Coleomerus boliviensis*; 230, *Coelonertus nigrirostris*; 231, *Baris torquata*; 232, *Lydamis cinnamomeus*; 233, *Buskiella lecythidis*.

**Figs. 234-245.** Mouthparts – labia. 234, *Rhoptobaris canescens*; 235, *Parisoschoenus* sp.; 236, *Pardisomus biplagiatus*; 237, *Pycnotheantis* sp.; 238,

*Telemus* sp.; 239, *Pteracanthus smidtii*; 240, *Megabaris quadriguttata*; 241, *Conoproctus quadripustulatus*; 242, *Eugeraeus* sp.; 243, *Lepidobaris acnisti*; 244, *Phacelobarus signubaris*; 245, *Cyrtepistomus castanaeus*.

**Figs. 246-256.** Mouthparts – labia. 246, *Derelomus basalis*; 247, *Cryptorhynchus lapathi*; 248, *Bagous transversus*; 249, *Cholus rana*; 250, *Cossonus impressifrons*; 251, *Curculio pardalis*; 252, *Hylurgops planirostris*; 253, *Barycerus collaris*; 254, *Testalthea* sp.; 255, *Rhytidoglymma cenescens*; 256, *Megalobaris viridana*.

**Figs. 257-269.** Mouthparts – labia. 257, *Barymerus binarius*; 258, *Trichodocerus* sp.; 259, *Coeliodes flavicaudis*; 260, *Mononycus vulpeculus*; 261, *Hypurus bertrandi*; 262, *Trigonocolus curvipes*; 263, *Mecopus trilineatus*; 264, *Cylindrocopturus adpersus*; 265, *Telephae oculata*; 266, *Balanogastris kolae*; 267, *Metialma straminea*; 268, *Cyllophorus fausciatus*; 269, *Arachnopus gazella*.

**Figs. 270-278.** Mouthparts - maxilla. 270, *Zygobaris nitens*; 271, *Centrinus curvirostris*; 272, *Anthinobaris* sp.; 273, *Ovanus picipennis*; 274, *Nertinus suturalis*; 275, *Peridinetus irroratus*; 276, *Antesis sparsa*; 277, *Loboderes citriventris*; 278, *Loboderes citriventris*.

**Figs. 279-288.** Mouthparts - maxilla. 279, *Antesis sparsa*; 280, *Acentrinops brevicollis*; 281, *Garnia* sp.; 282, *Pachygeraeus laevirostris*; 283, *Eisonyx crassipes*;

284, *Dirabius calvus*; 285, *Eisonyx opaca*; 286, *Xystus ruficollis*; 287, *Buchananius sulcatus* (maxilla-labium complex); 288, *Geraeus penicella*.

**Figs. 289-298.** Mouthparts - maxilla. 289, *Microcholus puncticollis*; 290, *Linogeraeus viduatus*; 291, *Ovanius minutus*; 292, *Plocamus echidna*; 293, *Plocamus clavisetes*; 294, *Oligolochus braccatus*; 295, *Oligolochus ornatus*; 296, *Odontocorynus scutellumalbum*; 297, *Odontocorynus creperus*; 298, *Camelodes leachii*.

**Figs. 299-308.** Mouthparts - maxilla. 299, *Sibariops concinna*; 300, *Sibariops concurrens*; 301, *Torcus nigrinus*; 302, *Madopterus talpa*; 303, *Parallelosomus amplitarsis*; 304, *Orchidophilus aterrimus*; 305, *Embates chaetopus*; 306, *Eurhinus festivus*; 307, *Eurhinus aeneus*; 308, *Coleomerus boliviensis*.

**Figs. 309-317.** Mouthparts - maxilla. 309, *Coelonertus nigrirostris*; 310, *Baris torquata*; 311, *Cyrionyx camelus*; 312, *Lydamis cinnamomeus*; 313, *Buskiella lecythidis*; 314, *Rhoptobaris canescens*; 315, *Plesiobaris albilata*; 316, *Parisoschoenus* sp.; 317, *Pardisomus biplagiatus*.

**Figs. 318-325.** Mouthparts - maxilla. 318, *Pycnotheantis* sp.; 319, *Telemus* sp.; 320, *Pteracanthus smidtii*; 321, *Megabaris quadriguttata*; 322, *Conoproctus quadripustulatus*; 323, *Eugeraeus* sp.; 324, *Lepidobaris acnisti*; 325, *Phacelobarus signubaris*.

**Figs. 326-335.** Mouthparts - maxilla. 326, *Cyrtepistomus castanaeus*; 327, *Derelomus basalis*; 328, *Cryptorhynchus lapathi*; 329, *Cholus rana*; 330, *Dryophthorus americanus* (Dryophthorinae); 331, *Bagous transversus*; 332, *Cossonus impressifrons*; 333, *Curculio pardalis*; 334, *Hylurgops planirostris*; 335, *Barycerus collaris*.

**Figs. 336-344.** Mouthparts - maxilla. 336, *Testalthea* sp.; 337, *Rhytidoglymma cenescens*; 338, *Megalobaris viridana*; 339, *Barymerus binarius*; 340, *Trichodocerus* sp.; 341, *Coeliodes flavicaudis*; 342, *Mononychus vulpeculus*; 343, *Hypurus bertrandi*; 344, *Trigonocolus curvipes*.

**Figs. 345-352.** Mouthparts - maxilla. 345, *Trigonocolus curvipes*; 346, *Mecopus trilineatus*; 347, *Cyllophorus fausciatus*; 348, *Cylindrocopturus adspersus*; 349, *Telephae oculata*; 350, *Balanogastris kolae*; 351, *Metialma straminea*; 352, *Arachnopus gazella*.

**Figs. 353-367.** Mouthparts - mandibles. 353, *Zygobaris nitens*; 354, *Centrinus curvirostris*; 355, *Anthinobaris* sp.; 356, *Ovanus picipennis*; 357, *Peridinetus irroratus*; 358, *Loboderes citriventris*; 359, *Antesis sparsa*; 360, *Acentrinops brevicollis*; 361, *Garnia* sp.; 362, *Pachygeraeus laevirostris*; 363, *Eisonyx crassipes*;

364, *Dirabius calvus*; 365, *Eisonyx opaca*; 366, *Xystus ruficollis*; 367, *Buchananius sulcatus*.

**Figs. 368-384.** Mouthparts - mandibles. 368, *Geraeus penicella*; 369, *Microcholus puncticollis*; 370, *Linogeraeus viduatus*; 371, *Ovanius minutus*; 372, *Plocamus echidna*; 373, *Plocamus calvisetes*; 374, *Oligolochus braccatus*; 375, *Oligolochus ornatus*; 376, *Odontocorynus scutellumalbum*; 377, *Odontocorynus creperus*; 378, *Camelodes leachii*; 379, *Sibariops concinna*; 380, *Torcus nigrinus*; 381, *Sibariops concurrens*; 382, *Madopterus talpa*; 383, *Parallelosomus amplitarsis*; 384, *Orchidophilus aterrimus*.

**Figs. 385-400.** Mouthparts - mandibles. 385, *Embates chaetopus*; 386, *Eurhinus festivus*; 387, *Eurhinus aeneus*; 388, *Coleomerus boliviensis*; 389, *Coelonertus nigrirostris*; 390, *Baris torquata*; 391, *Cyrionyx camelus*; 392, *Lydamis cinnamomeus*; 393, *Busckiella lecythidis*; 394, *Rhoptobaris canescens*; 395, *Plesiobaris albilata*; 396, *Parisoschoenus* sp.; 397, *Pardisomus biplagiatus*; 398, *Pycnotheantis* sp.; 399, *Telemus* sp.; 400, *Pteracanthus smidtii*.

**Figs. 401-415.** Mouthparts - mandibles. 401, *Megabaris quadriguttata*; 402, *Conoproctus quadripustulatus*; 403, *Eugeraeus* sp.; 404, *Lepidobaris acnisti*; 405, *Phacelobarus signubaris*; 406, *Cyrtepestomus castanaeus*; 407, *Derelomus basalis*; 408, *Cryptorhynchus lapathi*; 409, *Dryophthorus americanus*; 410, *Bagous*

*transversus*; 411, *Cholus rana*; 412, *Cossonus impressifrons*; 413, *Curculio pardalis*; 414, *Hylurgops planirostris*; 415, *Barycerus collaris*.

**Figs. 416-431.** Mouthparts - mandibles. 416, *Testalthea* sp.; 417, *Rhytidoglymma cenescens*; 418, *Megalobaris viridana*; 419, *Barymerus binarius*; 420, *Trichodocerus* sp.; 421, *Coeliodes flavicaudis*; 422, *Mononychus vulpeculus*; 423, *Mecopus trilineatus*; 424, *Hypurus bertrandi*; 425, *Trigonocolus curvipes*; 426, *Cylindrocopturus adpersus*; 427, *Telephae oculata*; 428, *Balanogastris kolae*; 429, *Metialma straminea*; 430, *Cyllophorus fausciatus*; 431, *Arachnopus gazella*.

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**Figs. 460-467.** SEM images of Pronotum. 460, *Taiwanobaris* sp.; 461, *Centrinogyna strigata*; 462, *Catapastus squamirostris*; 463, *Trichodirabius longulus*; 464, *Pycnogeraeus modestus*; 465, *Centrinogyna strigata*; 466, *Pertorcus* sp.; 467, *Odontocorynus creperus*.

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*Optatus palmaris*; 525, *Peridinetus cretaceus*; 526, *Strongylotes squamans*; 527, *Nertinus suturalis*; 528, *Peridinetus irroratus*; 529, *Leptoschoinus fucatus*; 530, *Barilepton filiforme*; 531, *Garnia* sp.; 532, *Eisonyx crassipes*; 533, *Dirabius calvus*; 534, *Xystus ruficollis*; 535, *Parasomenes curvirostris*; 536, *Plocamus echidna*; 537, *Odontocorynus creperus*.

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**Figs. 601-611.** Elytra. 601, *Demoda vittata*; 602, *Orissus christophori*; 603, *Garnia* sp.; 604, *Madopteris talpa*; 605, *Telemus* sp.; 606, *Anthinobaris* sp.; 607, *Catapastus signatipennis*; 608, *Centrinopus alternatus*; 609-611, *Anthinobaris* sp.

**Figs. 612-618.** Elytra, SEM's. 612, *Catapastus signatipennis*; 613-614, *Anthinobaris* sp.; 615-616, *Anthinobaris* sp.; 617-618, *Lophobaris* sp.

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**Figs. 627-632.** Elytra. 627-628, *Baris* sp.; 629, *Zygobaris* sp., elytral suture; 630, *Diorymeropsis disjuncta*, ventral view; 631, *Diorymeropsis disjuncta*, lateral margin (ventral view); 632, *Pertorcus* sp., elytral apex (ventral view).

**Figs. 633-640.** Elytra. 633, *Pertorcus* sp.; 634-635, *Acythopeus* sp.; 636-637, *Stethobaris commixta*; 638-640, *Stethobaris laevimargo*.

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**Figs. 655-672.** Metanota (dorsal view). 655, *Centrinus curvirostris*; 656, *Tenemotes abdominalis*; 657, *Demoda vittata*; 658, *Acythophanes* sp.; 659, *Pycnogeraeus modestus*; 660, *Stethobaroides nudiventris*; 661, *Pycnogeraeus ochraceus*; 662,

*Orissus christophori*; 663, *Orissus meigenii*; 664, *Pantoteles tenvirostris*; 665,  
*Optatus palmaris*; 666, *Strongylotes squamans*; 667, *Nertinus suturalis*; 668,  
*Peridinetus irroratus*; 669, *Leptoschoinus fucatus*; 670, *Barilepton filiforme*; 671,  
*Garnia* sp.; 672, *Eisonyx crassipes*.

**Figs. 673-690.** Metanota (dorsal view). 673, *Dirabius calvus*; 674, *Xystus ruficollis*;  
675, *Parasomenes curvirostris*; 676, *Plocamus echidna*; 677, *Odontocorynus*  
*creperus*; 678, *Camelodes leachii*; 679, *Pseudotorcus rufipes*; 680, *Madopteris talpa*;  
681, *Lipancylus brevirostris*; 682, *Eurhinus aeneus*; 683, *Diorymerus lancifer*; 684,  
*Spilobaris* sp.; 685, *Acythopeus* sp.; 686, *Zena* sp.; 687, *Orthoris crotchii*; 688,  
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**Figs. 691-708.** Metanota (dorsal view). 691, *Solenosternus dividius*; 692, *Telemus*  
sp.; 693, *Pteracanthus smidtii*; 694, *Stereobaris interpunctata*; 695, *Conoproctus*  
*quadripustulatus*; 696, *Athesapeuta vinculata*; 697, *Cyrtepistomus castanaeus*; 698,  
*Derelomus basalis*; 699, *Cryptorhynchus lapathi*; 700, *Dryophthorus americanus*;  
701, *Bagous transversus*; 702, *Cossonus impressifrons*; 703, *Curculio pardalis*; 704,  
*Hylurgops planirostris*; 705, *Trichodocerus* sp.; 706, *Coeliodes flavicaudis*; 707,  
*Mononychus vulpeculus*; 708, *Hypurus bertrandi*.

**Figs. 709-716.** Metanota (dorsal view). 709, *Trigonocolus curvipes*; 710, *Mecopus*  
*trilineatus*; 711, *Cylindrocopterus adspersus*; 712, *Telephae oculata*; 713,

*Balanogastris kolae*; 714, *Metialma straminea*; 715, *Cyllophorus fausciatus*; 716, *Pararobitis gibbus*.

**Figs. 717-734.** Metendosternite, posterior view. 717, *Centrinus curvirostris*; 718, *Pycnogeræus modestus*; 719, *Stethobaroides nudiventris*; 720-721, *Orissus christophori*; 721, dorsal view; 722, *Pantoteles tenvirostris*; 723, *Optatus palmaris*; 724, *Peridinetus cretaceus*; 725, *Nertinus suturalis*; 726, *Peridinetus irroratus*; 727, *Leptoschoinus fucatus*; 728, *Garnia* sp.; 729, *Dirabius calvus*; 730, *Parasomenes curvirostris*; 731, *Plocamus echidna*; 732, *Odontocorynus creperus*; 733, *Calandrinus grandicollis*; 734, *Camelodes leachii*.

**Figs. 735-752.** Metendosternite, posterior view. 735, *Pseudotorcus rufipes*; 736, *Madopteris talpa*; 737, *Lipancylus brevirostris*; 738, *Eurhinus aeneus*; 739, *Diorymerus lancifer*; 740, *Spilobaris* sp.; 741, *Acythopeus* sp.; 742, *Zena* sp.; 743, *Orthoris crotchii*; 744, *Pseudogeræus macropterus*; 745, *Anavallius ruficornis*; 746, *Solenosternus dividius*; 747, *Pardisomus biplagiatus*; 748, *Telemus* sp.; 749, *Pteracanthus smidtii*; 750, *Stereobaris interpunctata*; 751, *Athesapeuta vinculata*; 752, *Cyrtepistomus castanaeus*.

**Figs. 753-771.** Metendosternite, posterior view. 753, *Derelomus basalis*; 754, *Cryptorhynchus lapathi*; 755, *Dryophthorus americanus*; 756, *Bagous transversus*; 757, *Cholus rana*; 758, *Cossonus impressifrons*; 759, *Curculio pardalis*; 760,

*Hylurgops planirostris*; 761, *Trichodocerus* sp.; 762, *Coeliodes flavicaudis*; 763, *Mononychus vulpeculus*; 764, *Hypurus bertrandi*; 765, *Trigonocolus curvipes*; 766, *Mecopus trilineatus*; 767, *Cylindrocopterus adspersus*; 768, *Balanogastris kolae*; 769, *Metialma straminea*; 770, *Cyllophorus fausciatus*; 771, *Parorobitis gibbus*.

**Figs. 772-779.** Sclerolepidia. 772-773, *Megavallius auritarsis*; 774-775, *Pteracanthus smidtii* (dorso-lateral view); 776-777, *Amercedes subulirostris*; 778, *Zygobarella zanthoxyli*; 779, *Pseudocentrinus ochraceus* (dorsal view).

**Figs. 780-787.** 780-784, sclerolepidia. 780, *Pseudocentrinus ochraceus* (dorsal view); 781-784, *Lydamis cinnamomeus*. 781-782, lateral view; 783-784, dorsal view. 785-787, thoracic wing-locking patches. 785-787, *Anthinobaris* sp.

**Figs. 788-795.** 788-790, thoracic wing-locking patches. 788, *Anthinobaris* sp., metascutum; 789-790, *Anthinobaris* sp. (lateral view). 791-795, elytra (ventral view). 791-792, *Amercedes orthorrhinus*; 793, *Acythophanes* sp., elytral apex; 794-795, *Lixus concavus* (Lixinae). 794, medial humeral margin; 795, lateral humeral margin.

**Figs. 796-799.** Hind wings, SEM's. 130-133, *Anthinobaris* sp.

**Figs. 800-802.** 800, *Optatus palmaris*, hind wing venation: C=Costa; Sc=Subcosta; Rr=radial recurrent vein; R=Radius; r-m=radiomedia; rms=radiomedial

sclerotization; rcm=margin of radial cell; rc=radial cell; rfi=radial fissure; 2rs, 1rs=radial sclerites; R3=3<sup>rd</sup> radial; rsc=radial sclerotization; pst=postradial stripe; mst=medial stripe; Cu<sub>1</sub>=1<sup>st</sup> Cubital; af=apical fold of Cu<sub>1</sub>; msc=medial sclerotization; 1A<sub>1</sub>, 1A<sub>2</sub>=1<sup>st</sup> Anal branches; Cu=Cubital; A=Anal; ac=anal cell; 3A=3<sup>rd</sup> Anal. 801, hind wing, basal sclerites: Mr=medial recurrent vein; 1Ax, 2Ax, 3Ax=Axillary sclerites; BCu=cubital basivenale; Bm=medial basivenale; Br+BSc=radial basivenale + subcostal basivenale. 802, tergites: SS=spiracular sclerite; MS=median sclerite; lt=laterotergite.

**Figs. 803-814.** Hind wings. 803, *Centrinus curvirostris*; 804, *Optatus palmaris*; 805, *Eutoxus* sp.; 806, *Parasaldius* sp.; 807, *Buchananius sulcatus*; 808, *Haplostethops ellipsoidea*; 809, *Linogeraeus viduatus*; 810, *Plocamus echidna*; 811, *Plocamus clavisetes*; 812, *Odontocorynus scutellumalbum*; 813, *Lipancylus brevirostris*; 814, *Orchidophilus aterrimus*.

**Figs. 815-826.** Hind wings. 815, *Embates chaetopus*; 816, *Diorymerus lancifer*; 817, *Cyrionyx camelus*; 818, *Solaria curtula*; 819, *Palmelampus heinrichi*; 820, *Pycnotheantis* sp.; 821, *Telemus* sp.; 822, *Megabaris quadriguttata*; 823, *Zygobaris* sp.; 824, *Trachymeropsis palmipes*; 825, *Cyrtepistomus castanaeus*; 826, *Cryptorhynchus lapathi*.

**Figs. 827-840.** Hind wings. 827, *Dryophthorus americanus*; 828, *Bagous transversus*; 829, *Cholus rana*; 830, *Cossonus impressifrons*; 831, *Curculio pardalis*; 832, *Hylurgops planirostris*; 833, *Testalthea* sp.; 834, *Pacomes distortus*; 835, *Trichodocerus* sp.; 836, *Coeliodes flavicaudis*; 837, *Mononychus vulpeculus*; 838, *Hypurus bertrandi*; 839, *Trigonocolus curvipes*; 840, *Mecopus trilineatus*.

**Figs. 841-845.** Hind wings. 841, *Cylindrocopturus adpersus*; 842, *Telephae oculata*; 843, *Balanogastris kolae*; 844, *Metialma straminea*; 845, *Cyllophorus fausciatus*.

**Figs. 846-856.** Legs. 846, *Dirabius calvus*; 847, *Peridinetus cretaceus*; 848-849, *Peridinetus cretaceus*. 848, femoral tooth; 849, apex of tibia, showing uncus and setal comb; 850, *Peridinetus irroratus*; 851, *Eurhinus aeneus*; 852, *Zena* sp.; 853, *Camelodes leachii*, tarsus; 854, *Nertinus suturalis*, tarsus; 855, *Catapastus squamirostris* (SEM); 856, *Baris* sp. (SEM).

**Figs. 857-868.** Legs. 857-860, tibial unci. 857, *Pertorcus* sp.; 858, *Madarus bistrigellus*; 859, *Cylindrocercus comma*; 860, *Demoda vittata*. 861-868, tarsi and pre-tarsal ungues. 861-862, *Baris* sp.; 863, *Demoda vittata*; 864, *Centrinopus helvinus*; 865, *Zygobarella zanthoxyli*; 866, *Baris* sp.; 867-868, *Zygobarella zanthoxyli* (lateral views).

**Figs. 869-877.** Tergites. 869, *Centrinus curvirostris*; 870, *Tenemotes abdominalis*; 871, *Demoda vittata*; 872, *Pycnogeraeus striatirostris*; 873, *Orissus christophori*; 874, *Nertinus suturalis*; 875, *Peridinetus irroratus*; 876, *Leptoschoinus fucatus*; 877, *Barilepton filiforme*.

**Figs. 878-886.** Tergites. 878, *Garnia* sp.; 879, *Eisonyx crassipes*; 880, *Dirabius calvus*; 881, *Xystus ruficollis*; 882, *Parasomenes curvirostris*; 883, *Plocamus echidna*; 884, *Odontocorynus creperus*; 885, *Calandrinus grandicollis*; 886, *Camelodes leachii*.

**Figs. 887-895.** Tergites. 887, *Pseudotorcus rufipes*; 888, *Lipancylus brevirostris*; 889, *Eurhinus aeneus*; 890, *Diorymerus lancifer*; 891, *Limnobaris* sp.; 892, *Anthinobaris* sp.; 893, *Anthinobaris* sp.; 894, *Orthoris crotchii*; 895, *Orthoris crotchii*.

**Figs. 896-904.** Tergites. 896, *Lamprobaris cicullata*; 897, *Pseudogeraeus macropterus*; 898, *Anavallius ruficornis*; 899, *Solenosternus dividius*; 900, *Conoproctus quadripustulatus*; 901, *Athesapeuta vinculata*; 902, *Cyrtepistomus castaneus*; 903, *Bagous transversus*; 904, *Cossonus impressifrons*.

**Figs. 905-912.** Tergites. 905, *Hylurgops planirostris*; 906, *Mononychus vulpeculus*; 907, *Trigonocolus curvipes*; 908, *Mecopus trilineatus*; 909, *Telephae oculata*; 910, *Balanogastris kolae*; 911, *Cyllophorus fausciatus*; 912, *Parorobitis gibbus*.

**Figs. 913-923.** Tergites. 913, *Diastethus eurthinoides*; 914, *Cylindridia prolixa*; 915, *Zygobarella tristicula*; 916, *Pertorcus* sp.; 917-918, *Acythopeus* sp.; 919, *Athesapeuta* sp., enlargement of spiculate patches; 920-921, *Amercedes subulirostris*, 7<sup>th</sup> tergite and associated plectra; 922-923, *Deipyryrus hirsutululus*, 7<sup>th</sup> tergite and associated plectra.

**Figs. 924-932.** 924-927, tergites. 924, *Pycnogeræus modestus*, 7<sup>th</sup> tergite; 925, *Pycnogeræus ochraceus*, plectra on 7<sup>th</sup> tergite; 926-927, *Diastethus eurthinoides*, 7<sup>th</sup> tergite and associated plectra. 928-932, files on ventral apex of elytra. 928, *Zygocharis nitens*; 929, *Idiostethus subcalvus*; 930, *Diastethus eurthinoides*; 931, *Pachybaris porosa*; 932, *Pseudorthoris devexus*.

**Figs. 933-948.** Ventrites. 933, *Centrinus curvirostris*; 934, *Pycnogeræus striatirostris*; 935, *Orissus christophori*; 936, *Nertinus suturalis*; 937, *Peridinetus irroratus*; 938, *Barilepton filiforme*; 939, *Garnia* sp.; 940, *Eisonyx crassipes*; 941, *Dirabius calvus*; 942, *Xystus ruficollis*; 943, *Parasomenes curvirostris*; 944, *Plocamus echidna*; 945, *Odontocorynus creperus*; 946, *Calandrinus grandicollis*; 947, *Camelodes leachii*; 948, *Pseudotorcus rufipes*.

**Figs. 949-964.** Ventrites. 949, *Lipancylus brevirostris*; 950, *Eurhinus aeneus*; 951, *Limnobaris* sp.; 952, *Anthinobaris* sp.; 953, *Anthinobaris* sp.; 954, *Orthoris crotchii*; 955, *Lamprobaris cicullata*; 956, *Pseudogeraeus macropterus*; 957, *Anavallius ruficornis*; 958, *Conoproctus quadripustulatus*; 959, *Athesapeuta vinculata*; 960, *Cyrtepistomus castanaeus*; 961, *Cossonus impressifrons*; 962, *Hylurgops planirostris*; 963, *Mononychus vulpeculus*; 964, *Balanogastris kolae*.

**Figs. 965-966.** Ventrites. 965, *Cyllphorus fausciatus*; 966, *Parorobitis gibbus*.

**Figs. 967-975.** Ventrites (SEM's). 967, *Idiostethus tubulatus*; 968, *Cylindridia prolixa*; 969, *Pertorcus* sp.; 970, *Pertorcus* sp.; 971, *Acythopeus* sp.; 972, *Stethobaris commixta*; 973, *Stethobaris laevimargo*; 974, *Pycnogeraeus striatirostris*; 975, *Pachybaris porosa*.

**Figs. 976-980.** Ventrites (SEM's). 976, *Acythophanes* sp.; 977, *Spilobaris* sp.; 978, *Spilobaris* sp.; 979, *Acythopeus* sp.; 980, *Pycnogeraeus modestus*.

**Figs. 981-984.** Terminalia. 981-982, *Anthinobaris* sp., male genitalia. 981, aedeagus; 982, spiculum gastrale; 983-984, *Peridinetus cretaceus*, female genitalia. 983, 8<sup>th</sup> sternite; 984, spermatheca.

**Figs. 985-993.** Male genitalia: aedeagus and 9<sup>th</sup> sternite (dorsal view). 985, *Centrinus curvirostris*; 986, *Demoda vittata*; 987, *Acythophanes* sp.; 988, *Pycnogeraeus modestus*; 989, *Stethobaroides nudiventris*; 990, *Pycnogeraeus ochraceus*; 991, *Orissus christophori*; 992, *Orissus meigenii*; 993, *Pantoteles tenvirostris*.

**Figs. 994-1004.** Male genitalia: aedeagus and 9<sup>th</sup> sternite (dorsal view). 994, *Peridinetus cretaceus*; 995, *Nertinus suturalis*; 996, *Peridinetus irroratus*; 997, *Leptoschoinus fucatus*; 998, *Barilepton filiforme*; 999, *Garnia* sp.; 1000, *Eisonyx crassipes*; 1001, *Dirabius calvus*; 1002, *Xystus ruficollis*; 1003, *Plocamus echidna*; 1004, *Odontocorynus creperus*.

**Figs. 1005-1012.** Male genitalia: aedeagus and 9<sup>th</sup> sternite (dorsal view). 1005, *Calandrinus grandicollis*; 1006, *Camelodes leachii*; 1007, *Pseudotorcus rufipes*; 1008, *Madopterus talpa*; 1009, *Lipancylus brevirostris*; 1010, *Diorymerus lancifer*; 1011, *Eurhinus aeneus*; 1012, *Acythopeus* sp.

**Figs. 1013-1021.** Male genitalia: aedeagus and 9<sup>th</sup> sternite (dorsal view). 1013, *Spilobaris* sp.; 1014, *Anthinobaris* sp.; 1015, *Orthoris crotchii*; 1016, *Lamprobaris cicullata*; 1017, *Pseudogeraeus macropterus*; 1018, *Solenosternus dividiuus*; 1019, *Anavallius ruficornis*; 1020, *Pardisomus biplagiatus*; 1021, *Pteracanthus smidtii*.

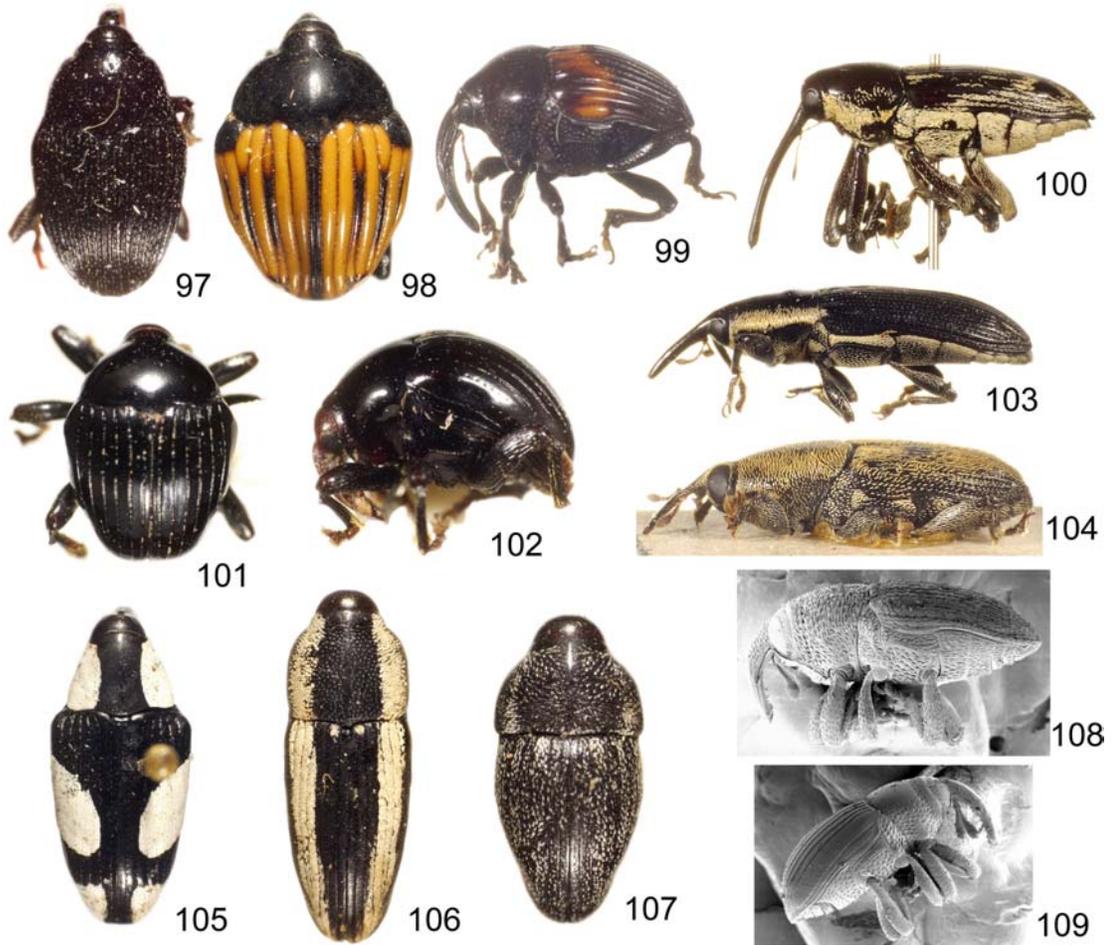
**Figs. 1022-1030.** Male genitalia: aedeagus and 9<sup>th</sup> sternite (dorsal view). 1022, *Stereobaris interpunctata*; 1023, *Conoproctus quadripustulatus*; 1024, *Athesapeuta vinculata*; 1025, *Derelomus basalis*; 1026, *Cryptorhynchus lapathi*; 1027, *Dryophthorus americanus*; 1028, *Cholus rana*; 1029, *Cossonus impressifrons*; 1030, *Curculio pardalis*.

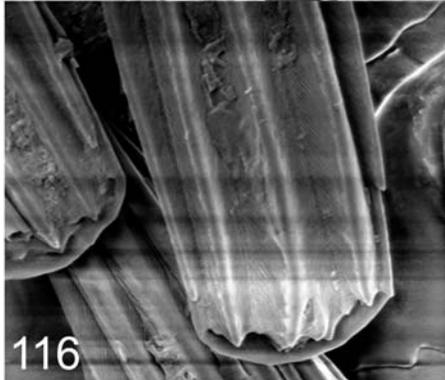
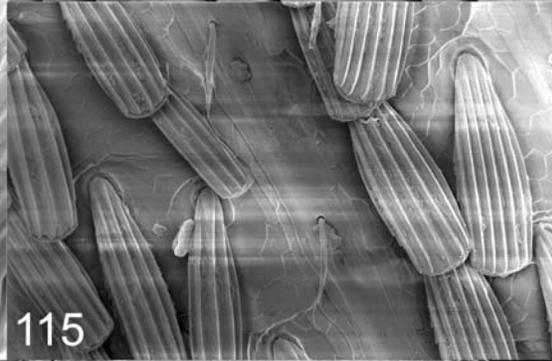
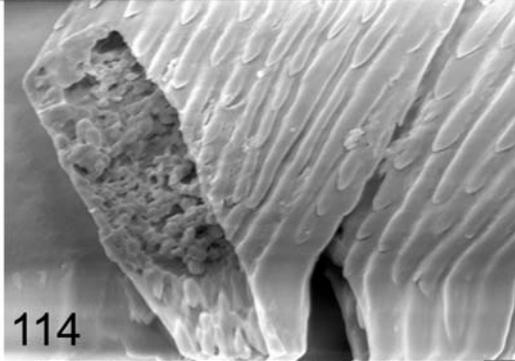
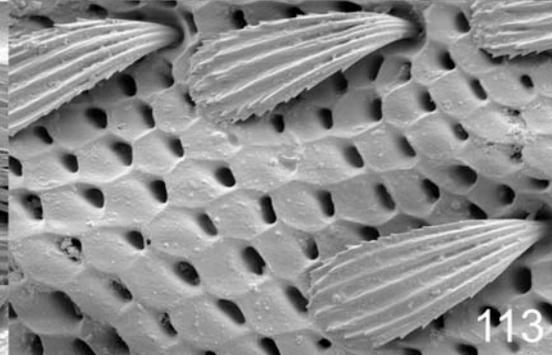
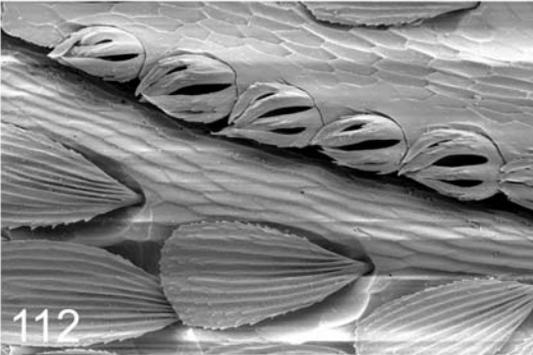
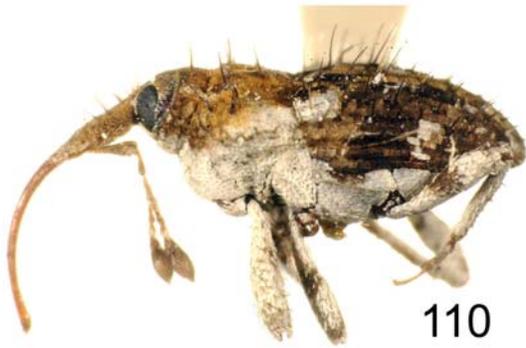
**Figs. 1031-1040.** Male genitalia: aedeagus and 9<sup>th</sup> sternite (dorsal view). 1031, *Hylurgops planirostris*; 1032, *Trichodocerus* sp.; 1033, *Coeliodes flavicaudis*; 1034, *Trigonocolus curvipes*; 1035, *Mononychus vulpeculus*; 1036, *Hypurus bertrandi*; 1037, *Mecopus trilineatus*; 1038, *Cylindrocopturus adpersus*; 1039, *Telephae oculata*; 1040, *Balanogastris kolae*.

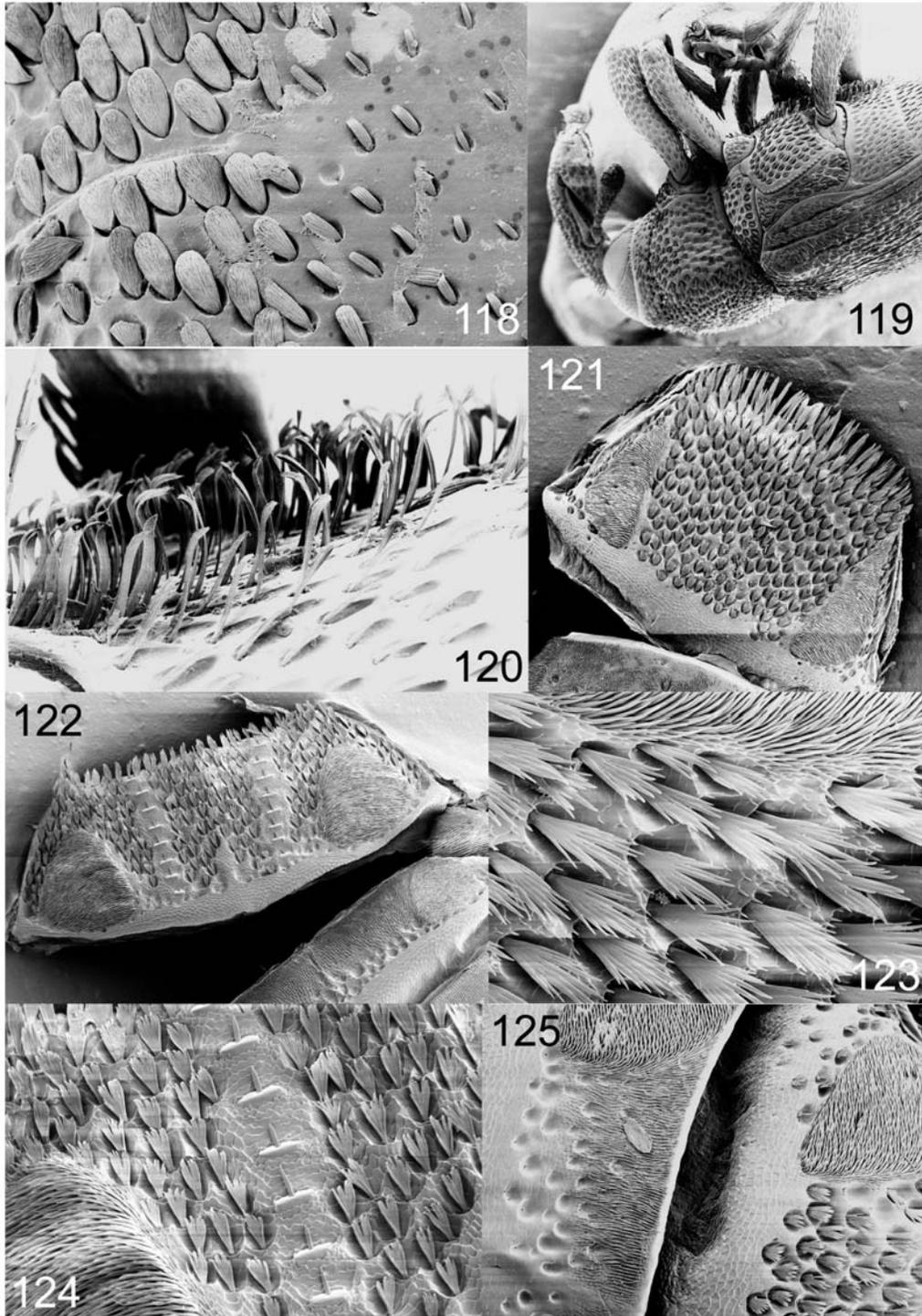
**Figs. 1041-1043.** Male genitalia: aedeagus and 9<sup>th</sup> sternite (dorsal view). 1041, *Metialma straminea*; 1042, *Cyllophorus fausciatus*; 1043, *Parorobitis gibbus*.

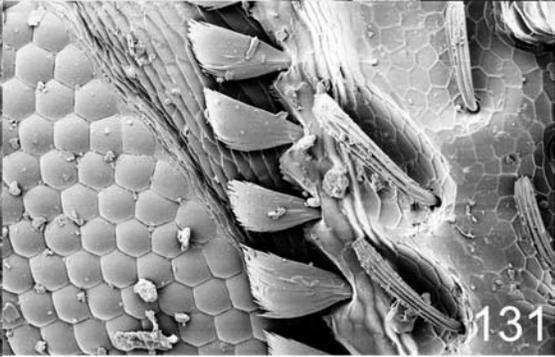
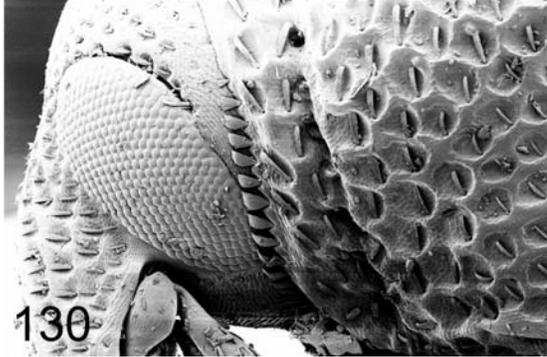
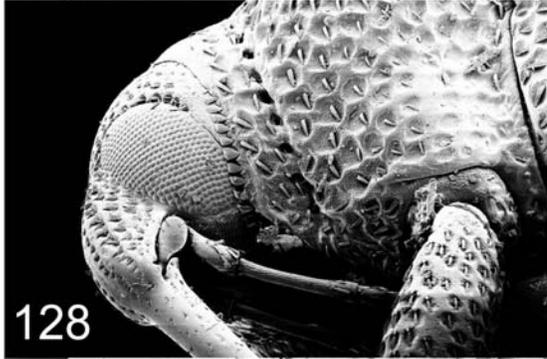
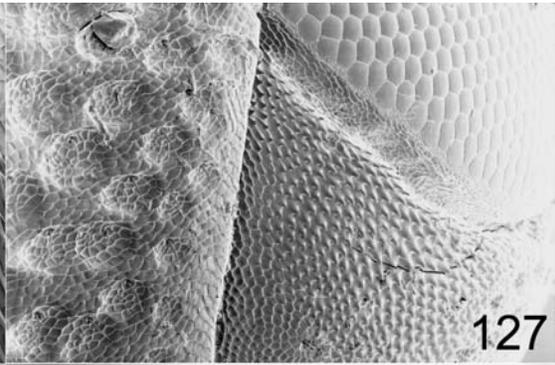
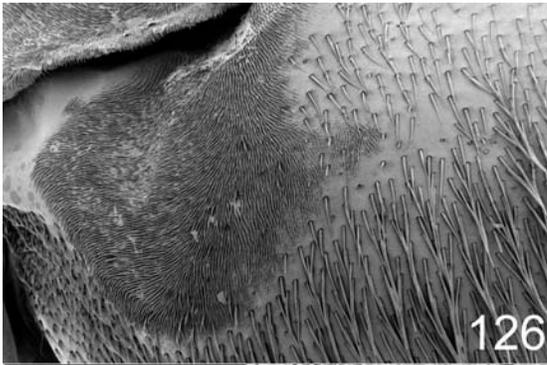
**Figs. 1044-1051.** female genitalia: 8<sup>th</sup> sternite and spermatheca. 1044, *Diastethus eurthinoides*; 1045, *Tenemotes abdominalis*; 1046, *Anthinobaris* sp.; 1047, *Pycnogeræus striatirostris*; 1048, *Nertinus suturalis*; 1049, *Peridinetus cretaceus*; 1050, *Parasomenes curvirostris*; 1051, *Strongylotes squamans*.

**Figs. 1052-1058.** female genitalia: 8<sup>th</sup> sternite and spermatheca. 1052, *Limnobaris* sp.; 1053, *Zena* sp.; 1054, *Anthinobaris* sp.; 1055, *Orthoris crotchii*; 1056, *Telemus* sp.; 1057, *Athesapeuta vinculata*; 1058, *Cyrtepistomus castanaeus*.

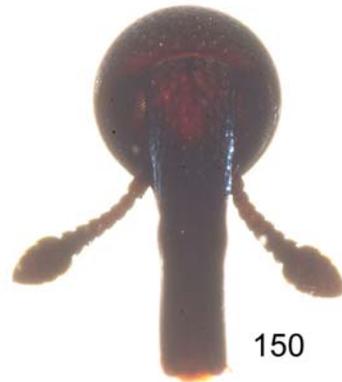




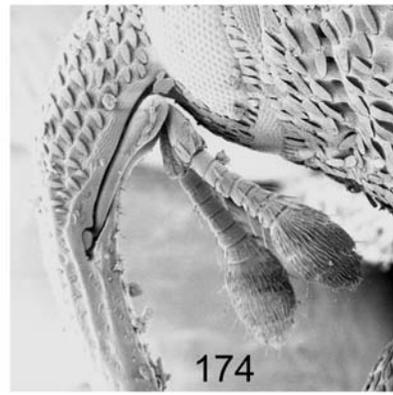
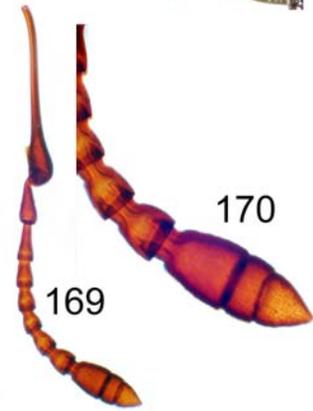
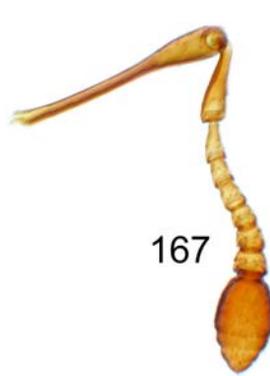
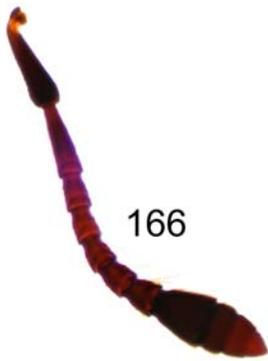


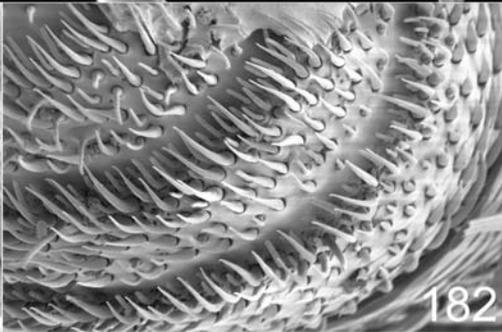
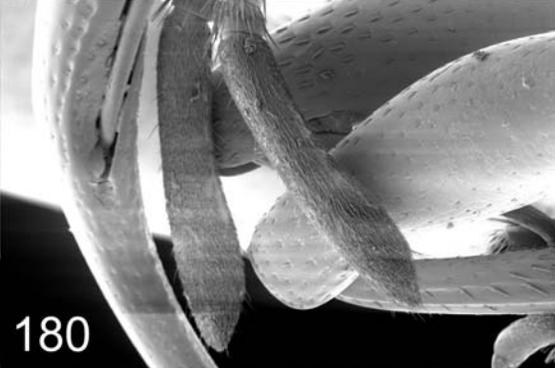
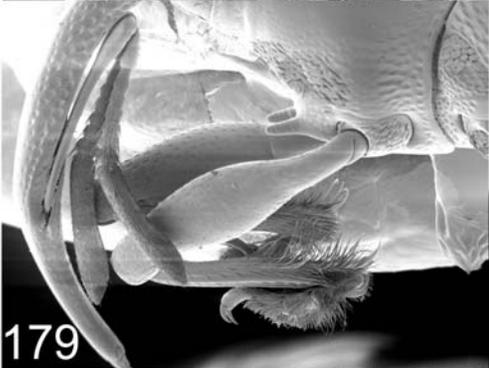
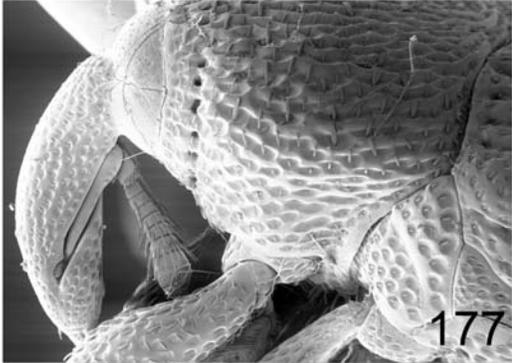
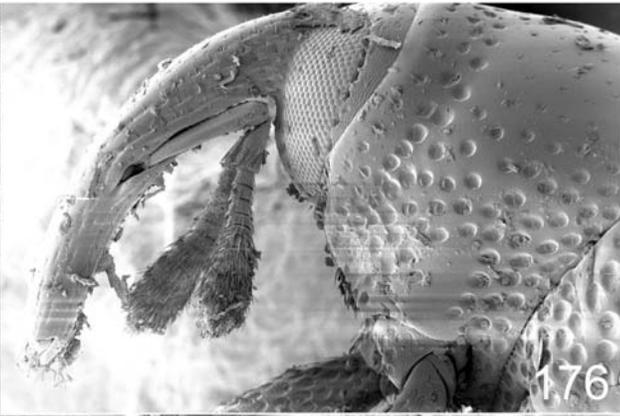


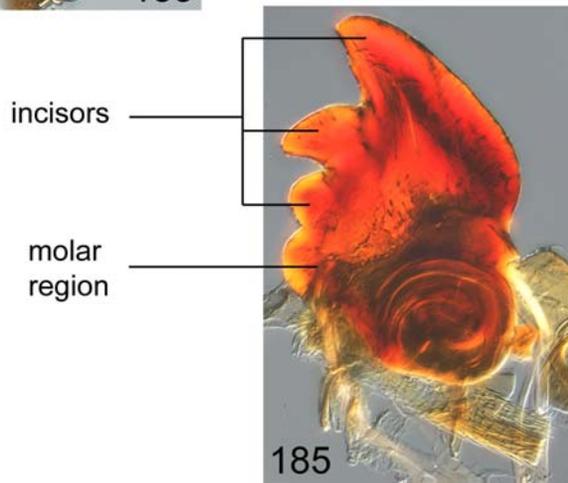
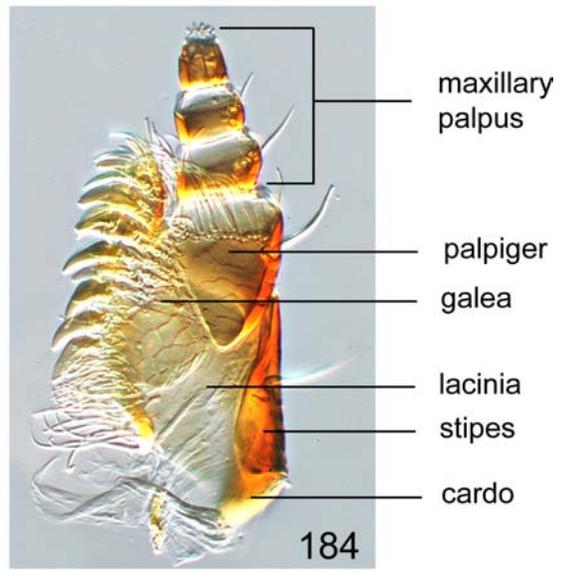
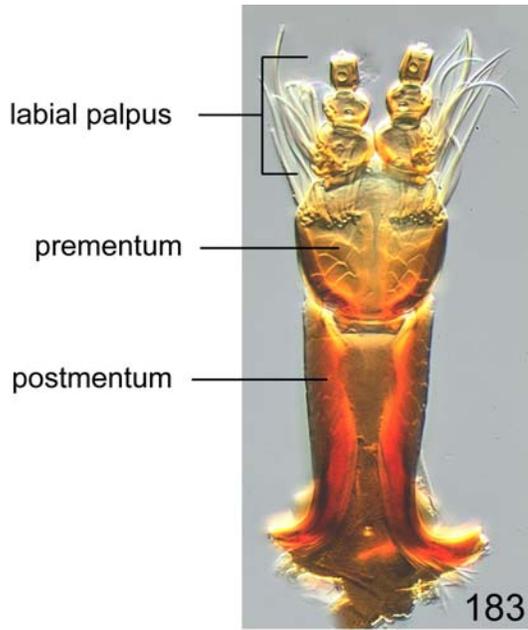


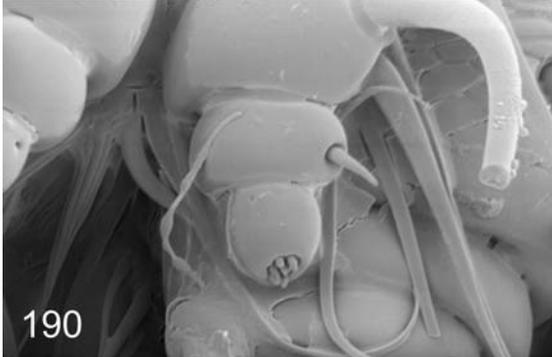
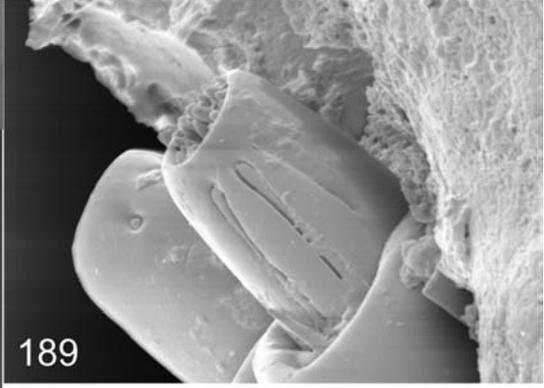
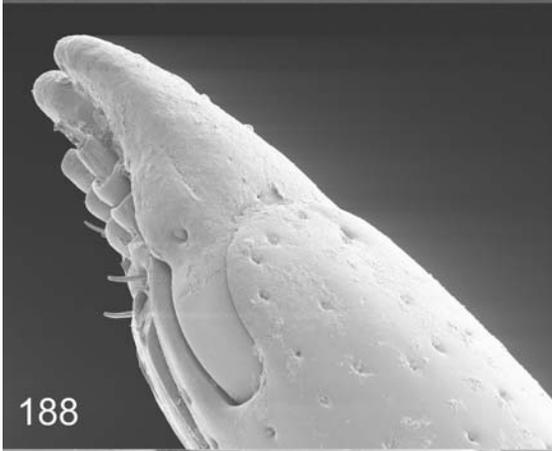
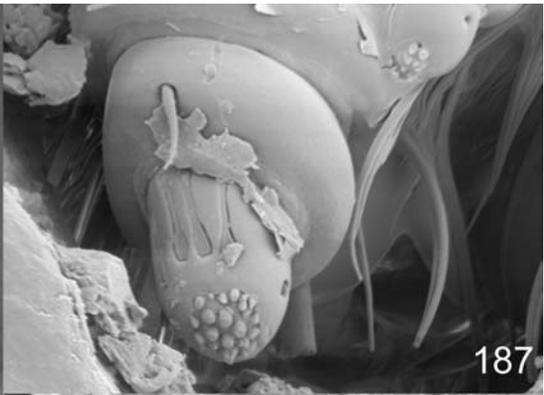
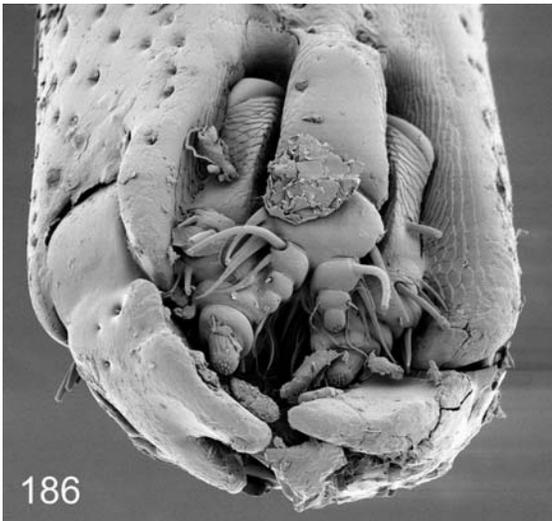


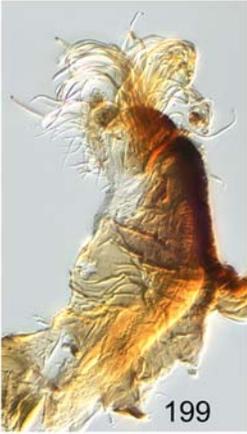












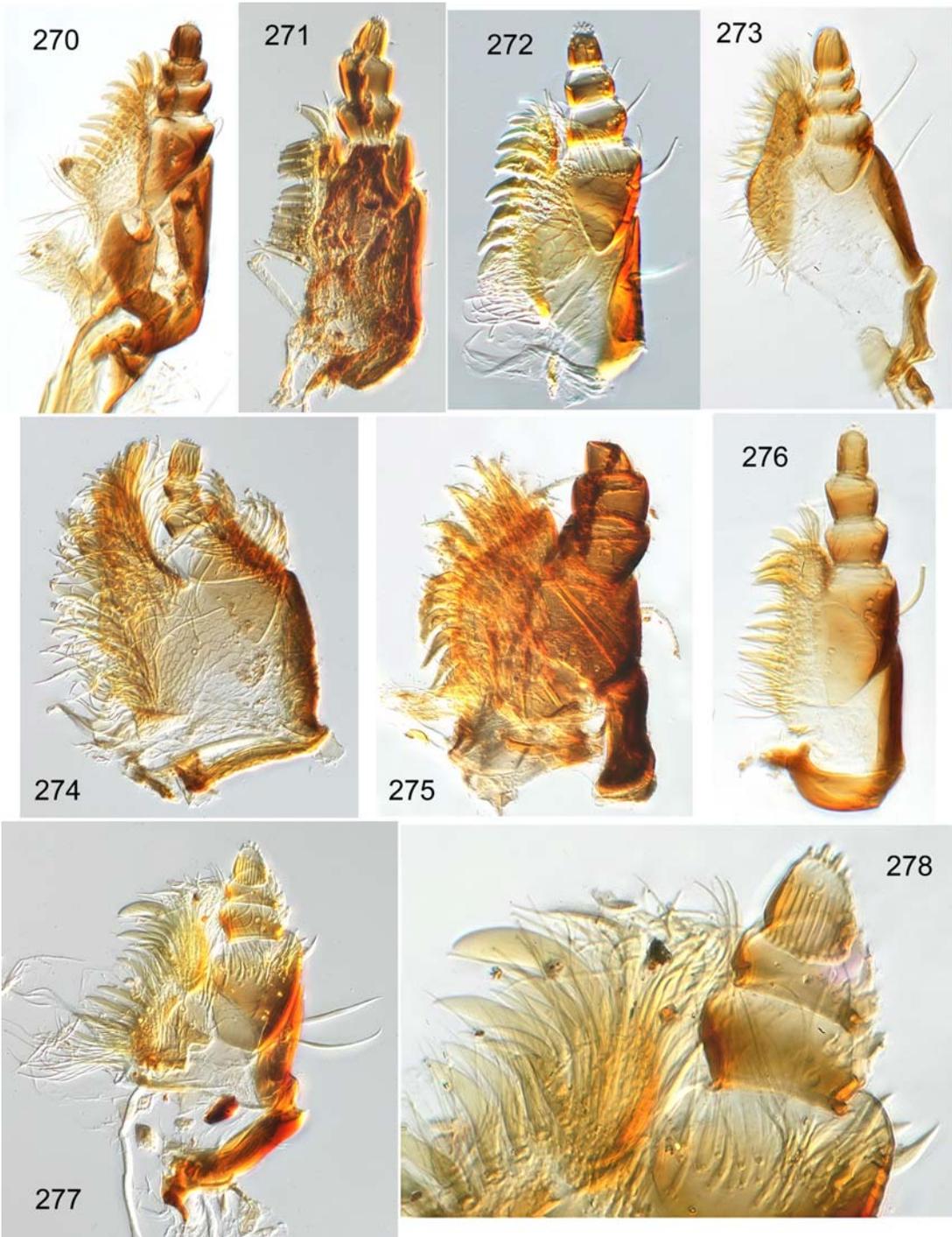




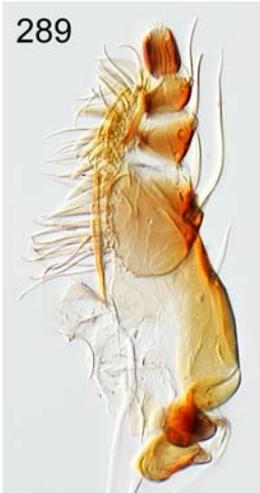


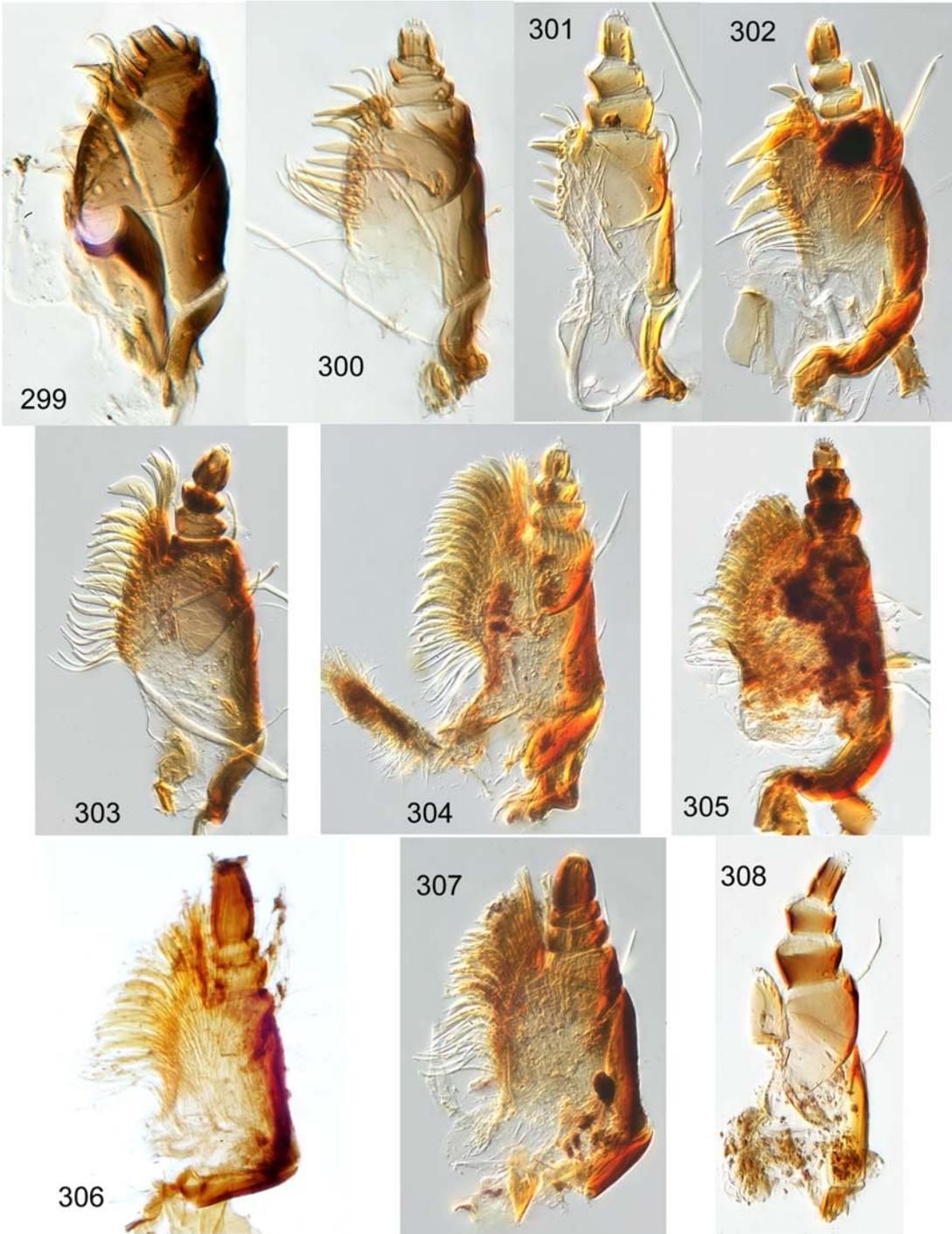






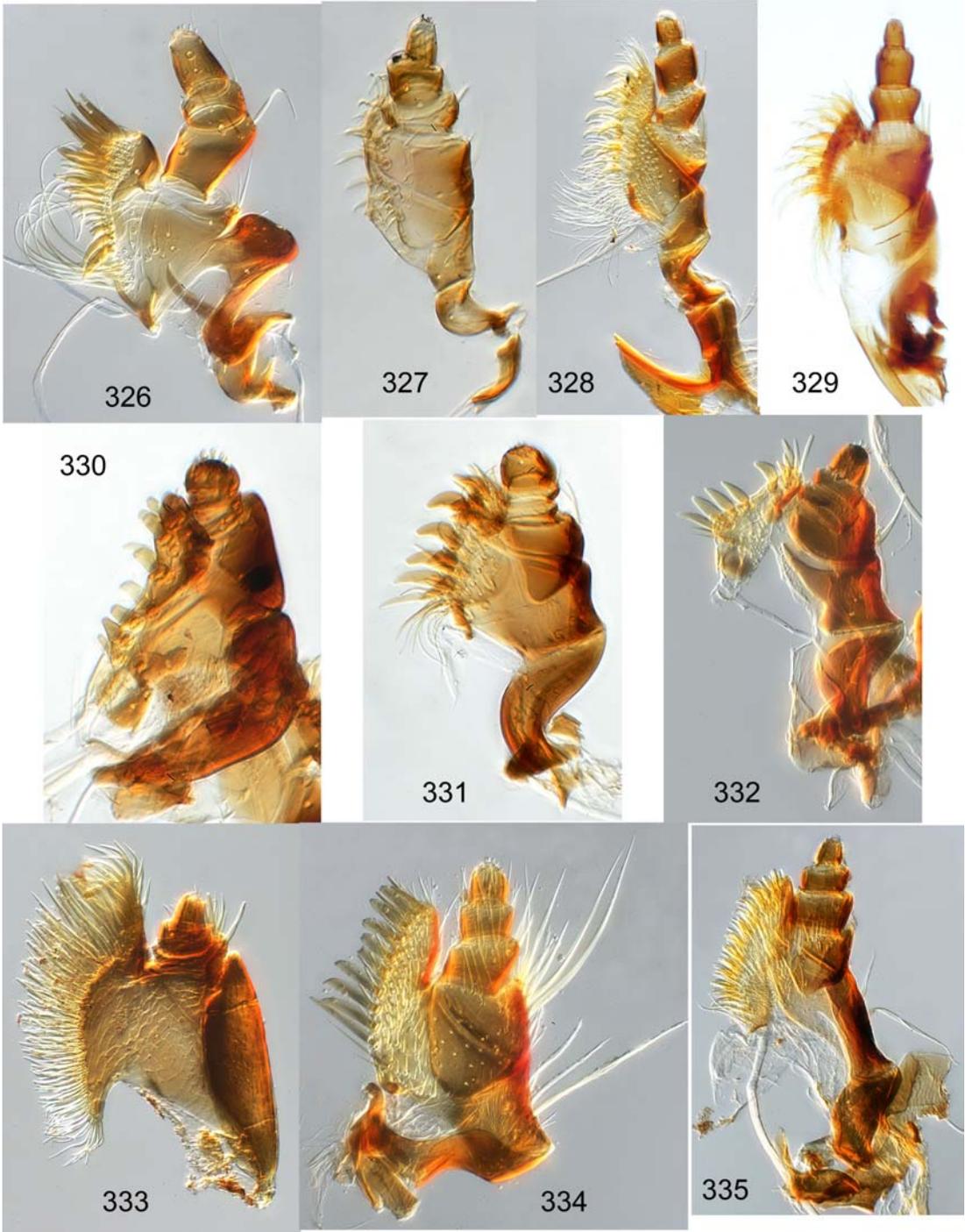






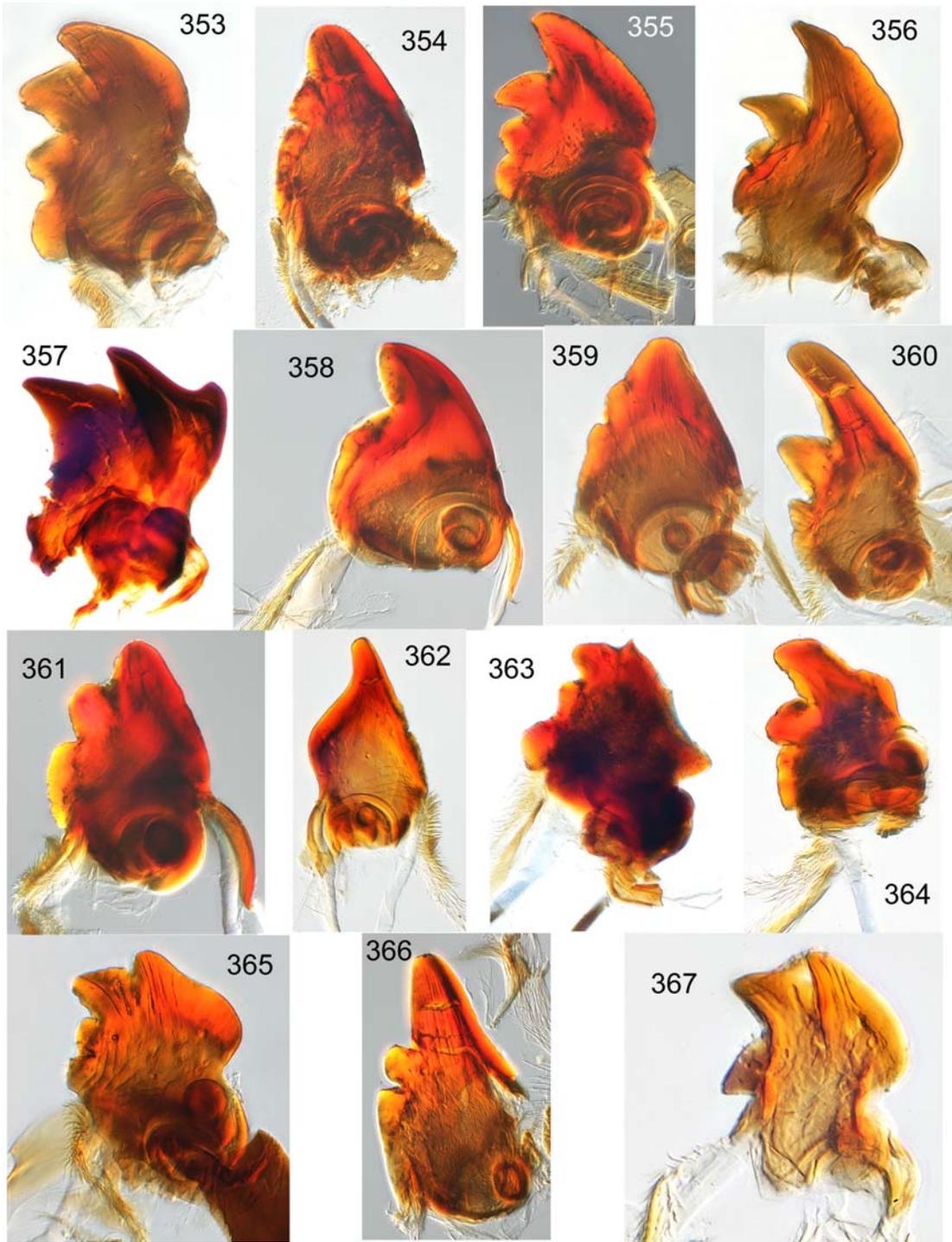


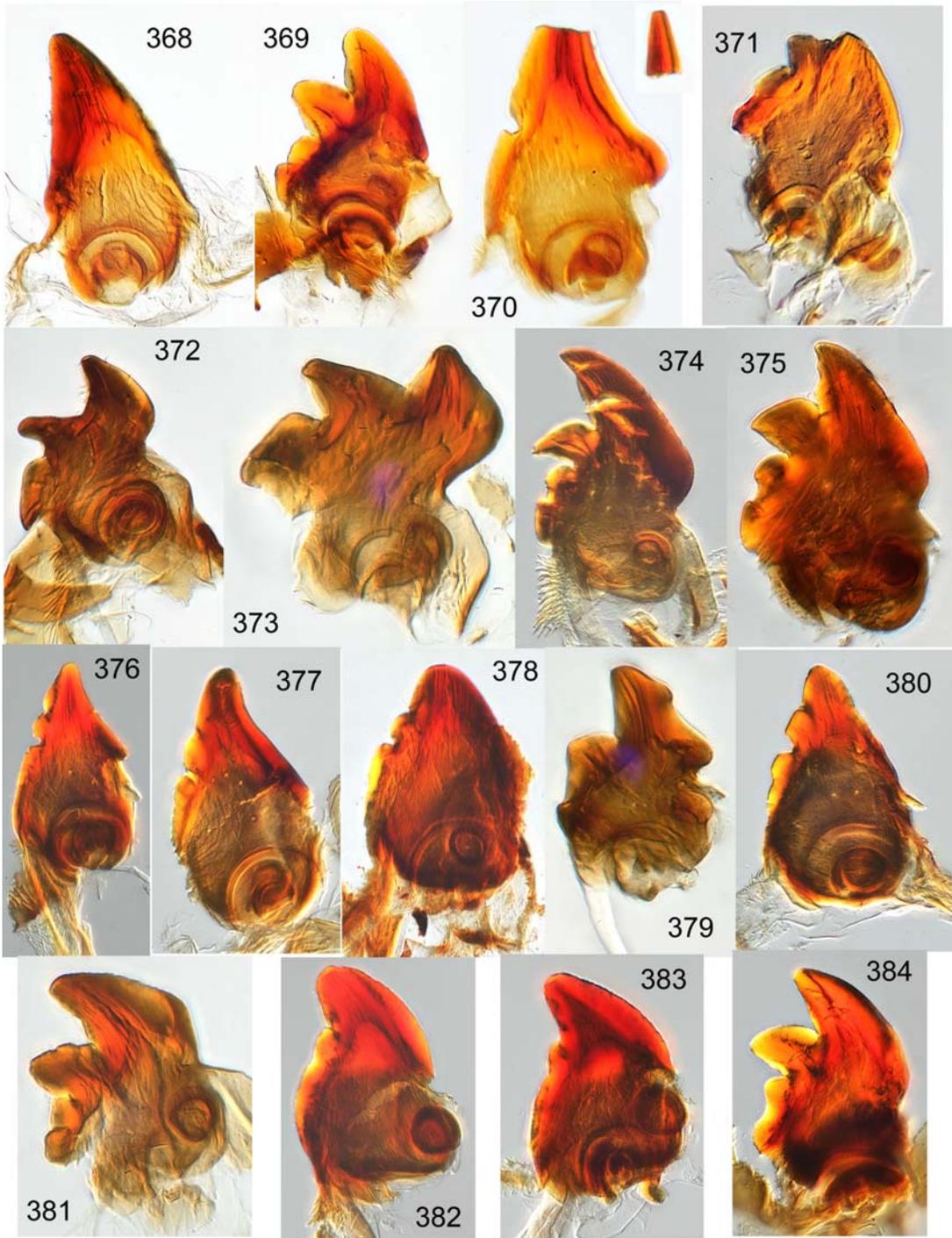


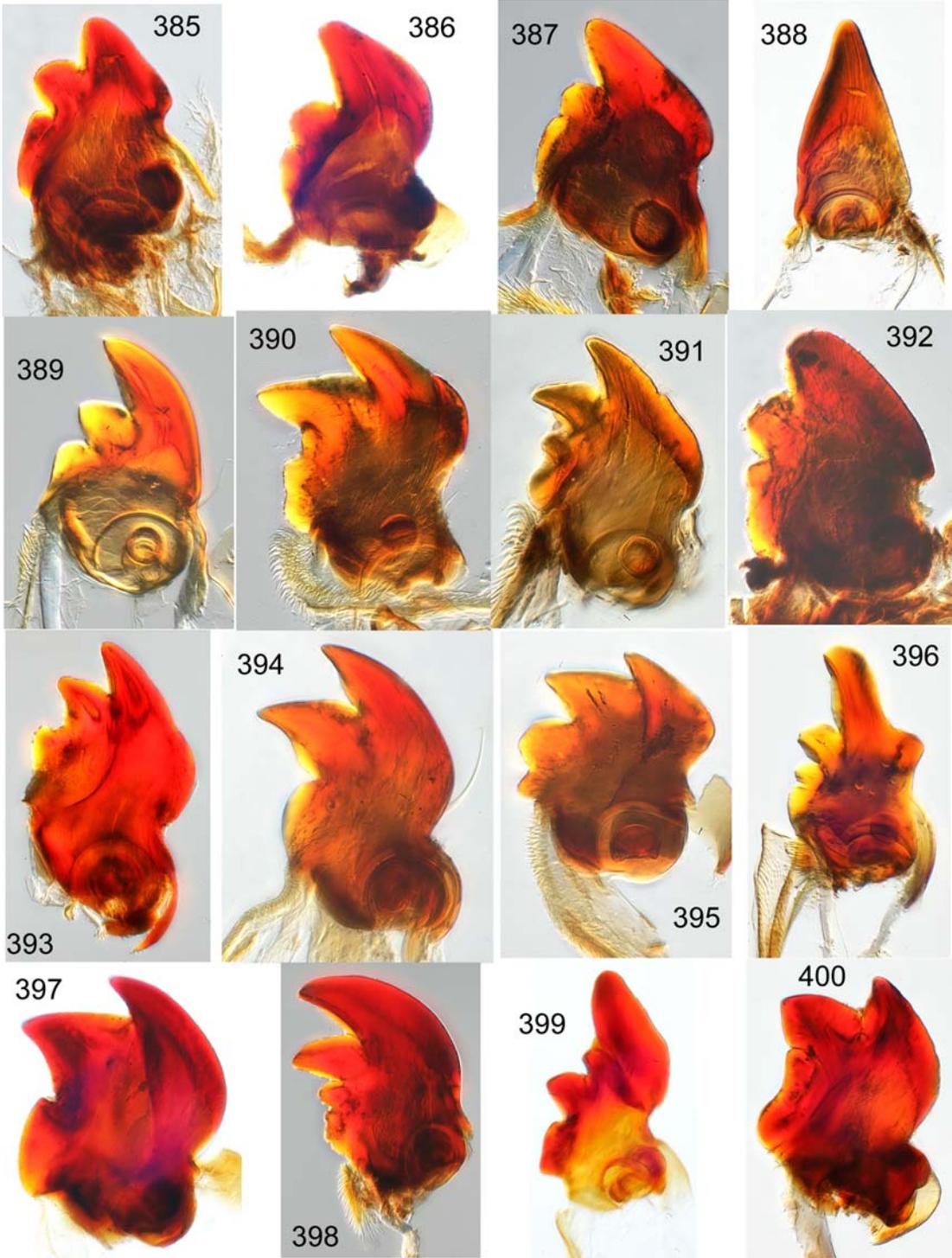


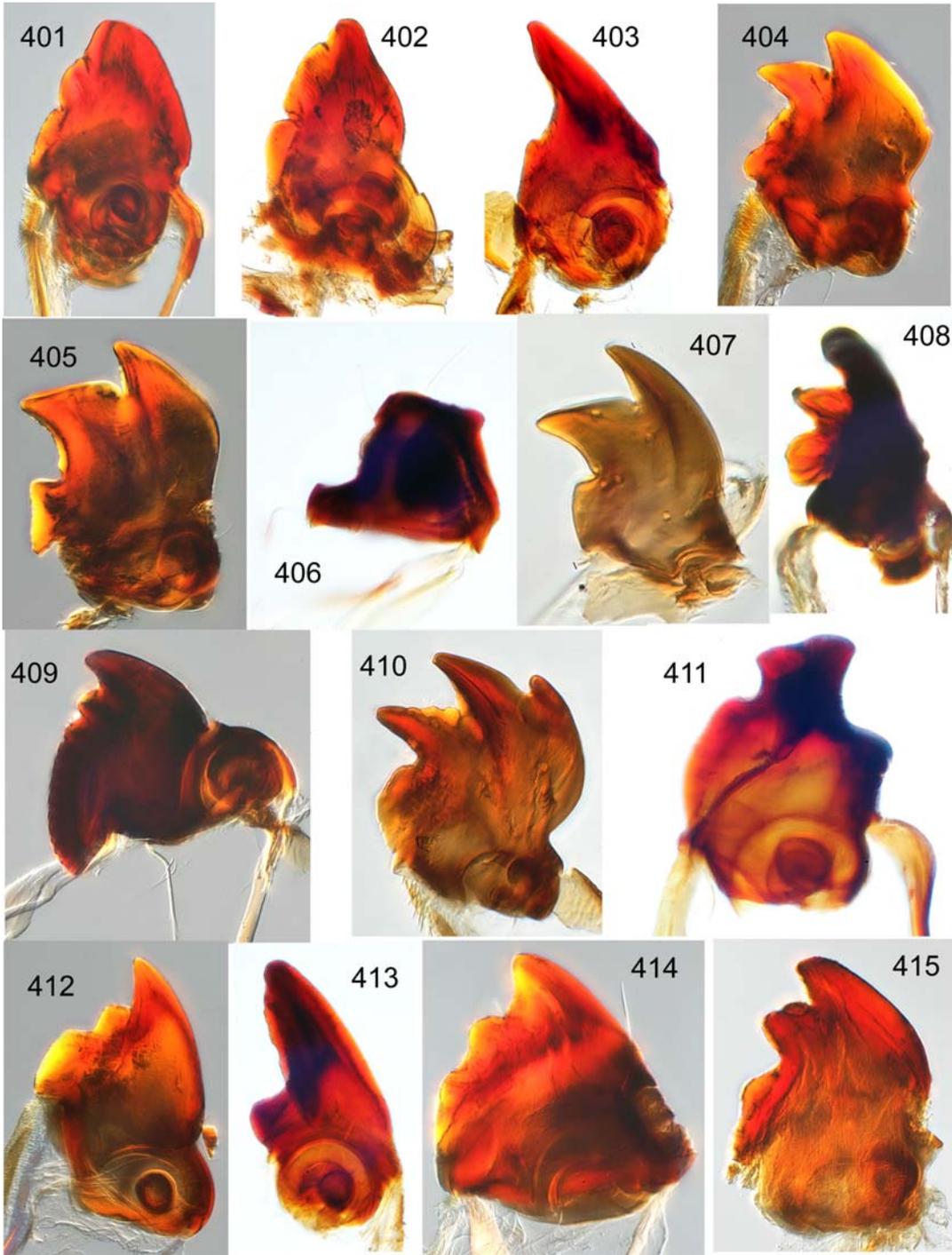


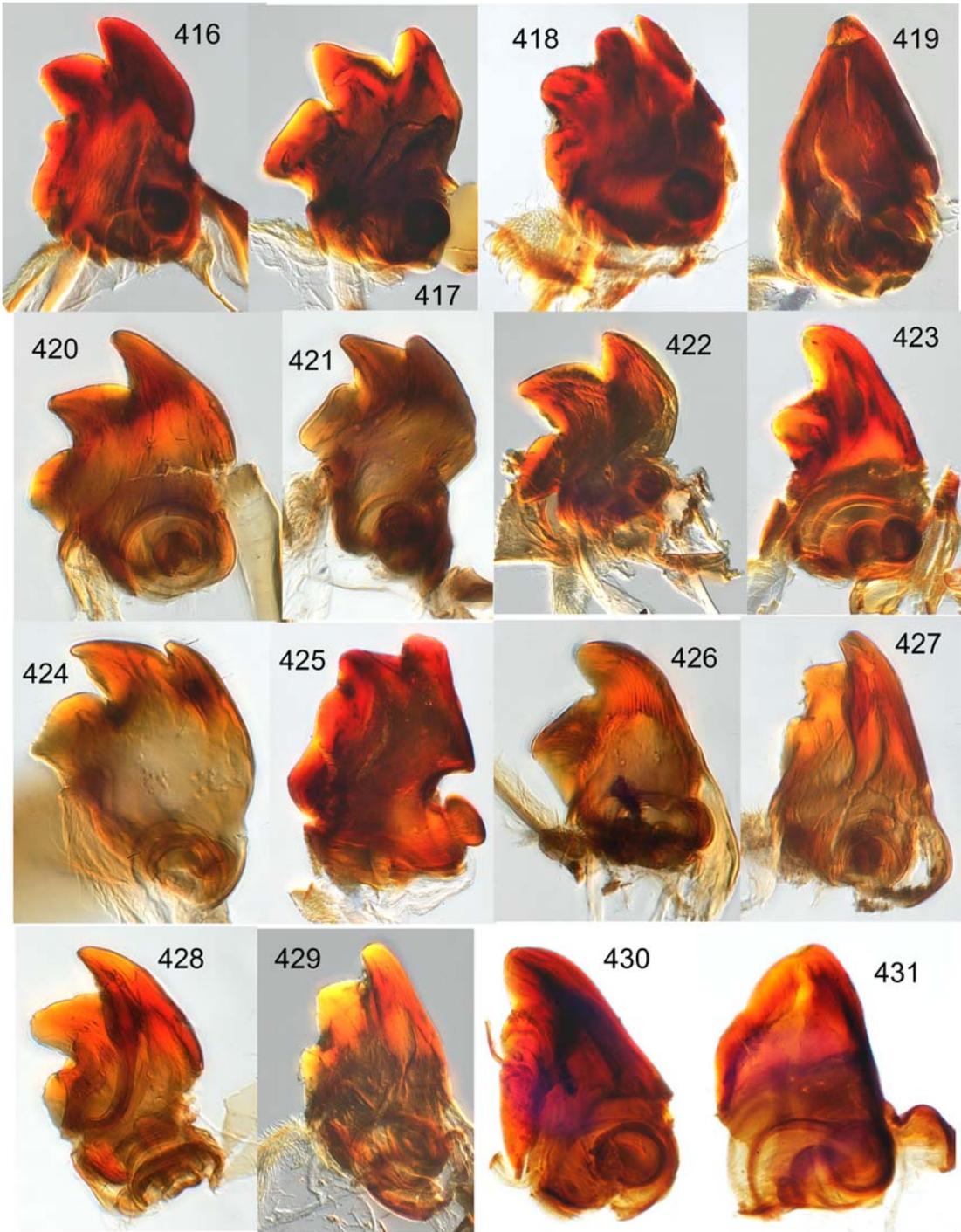


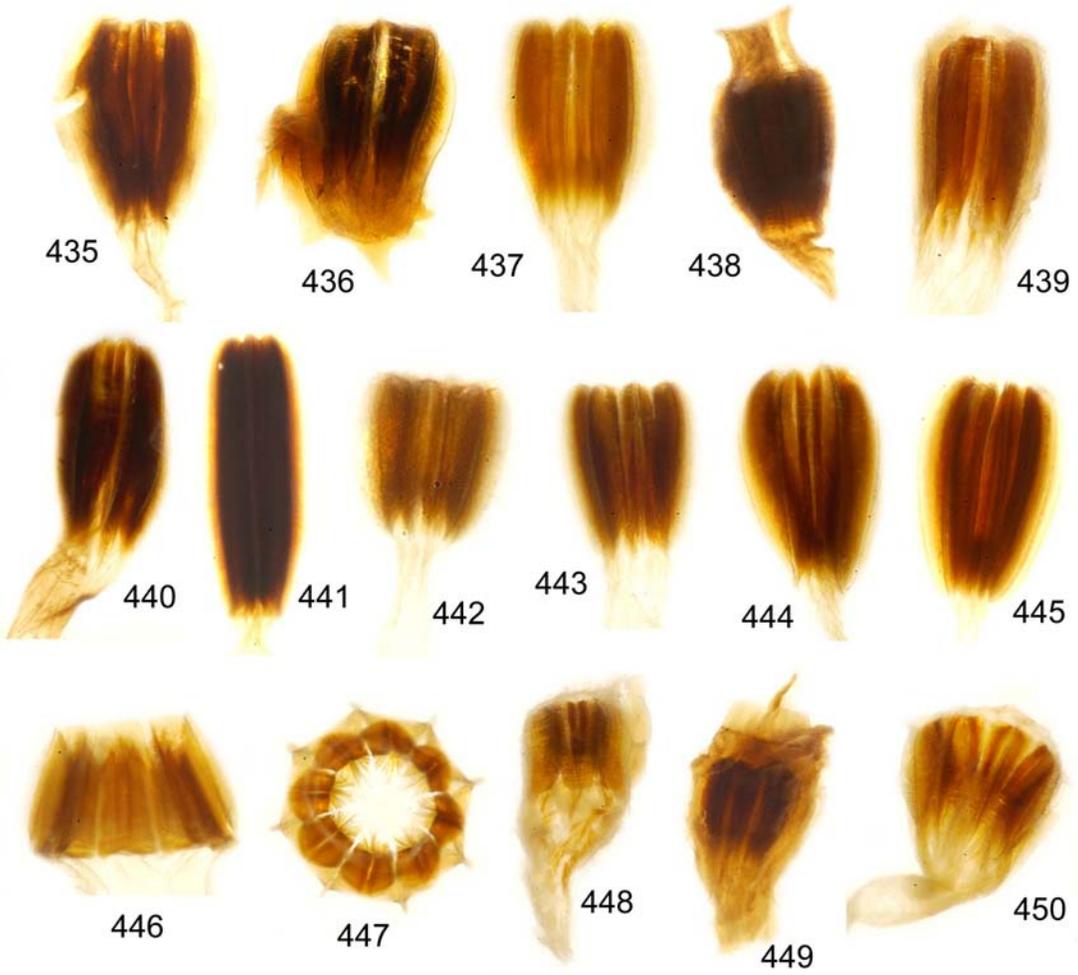
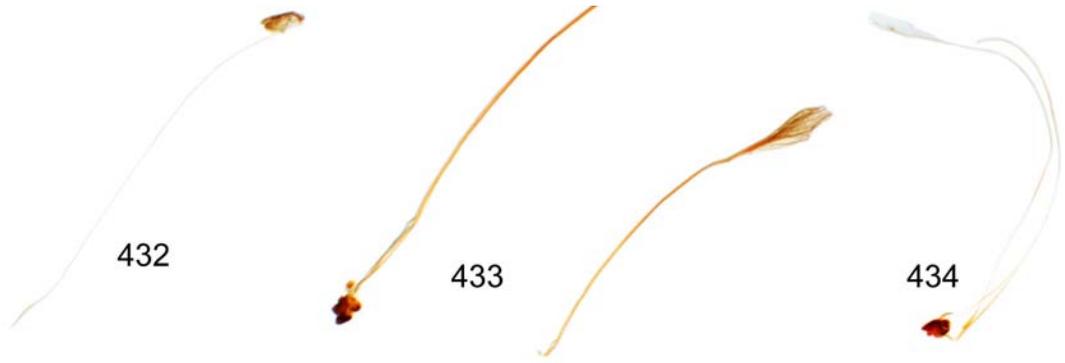


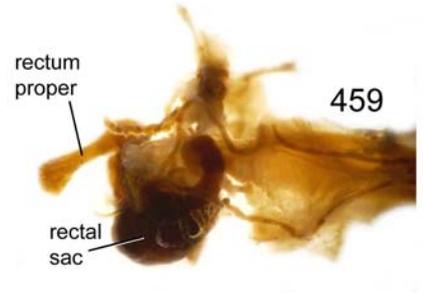
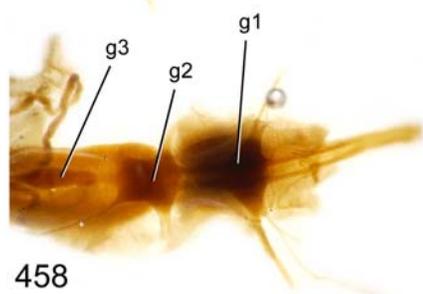
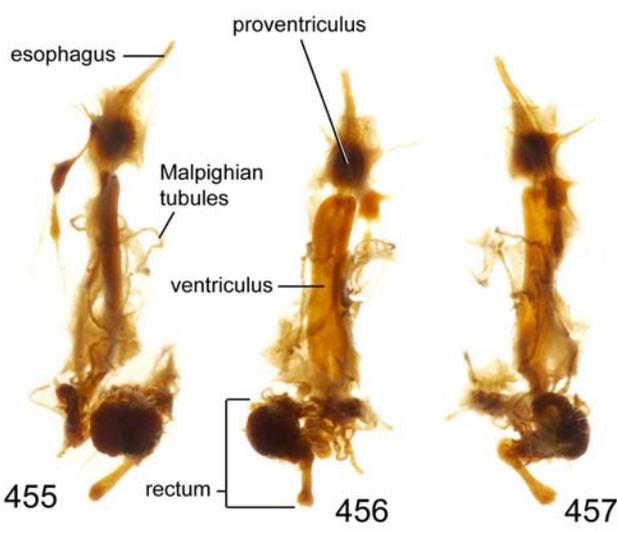
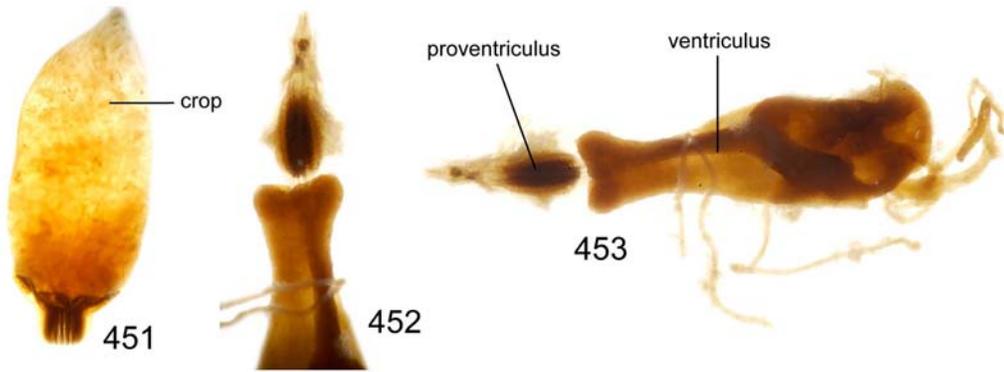


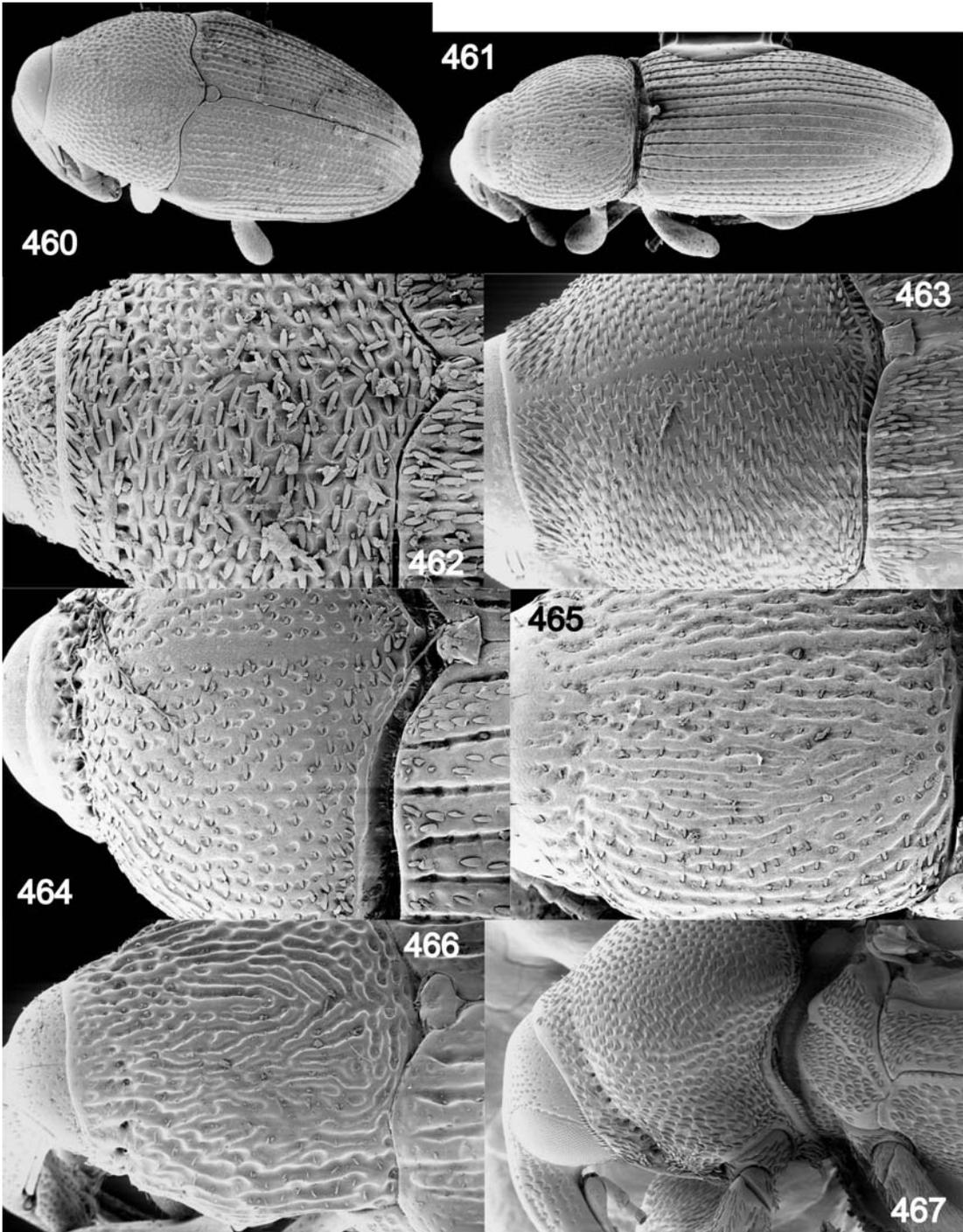


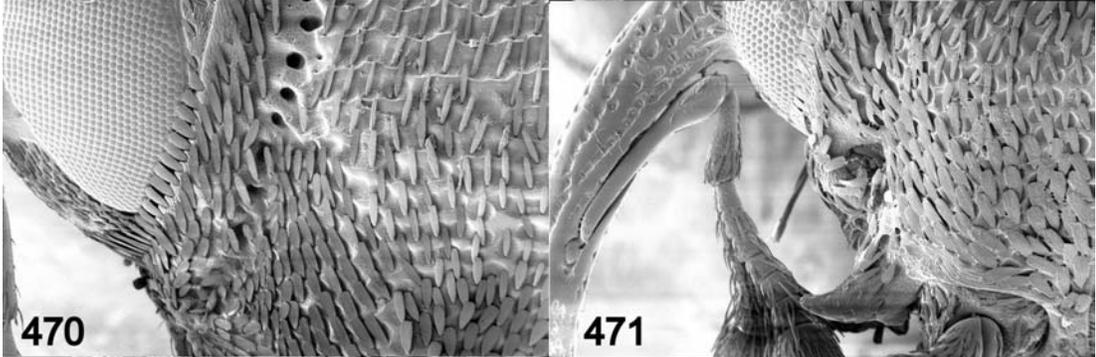


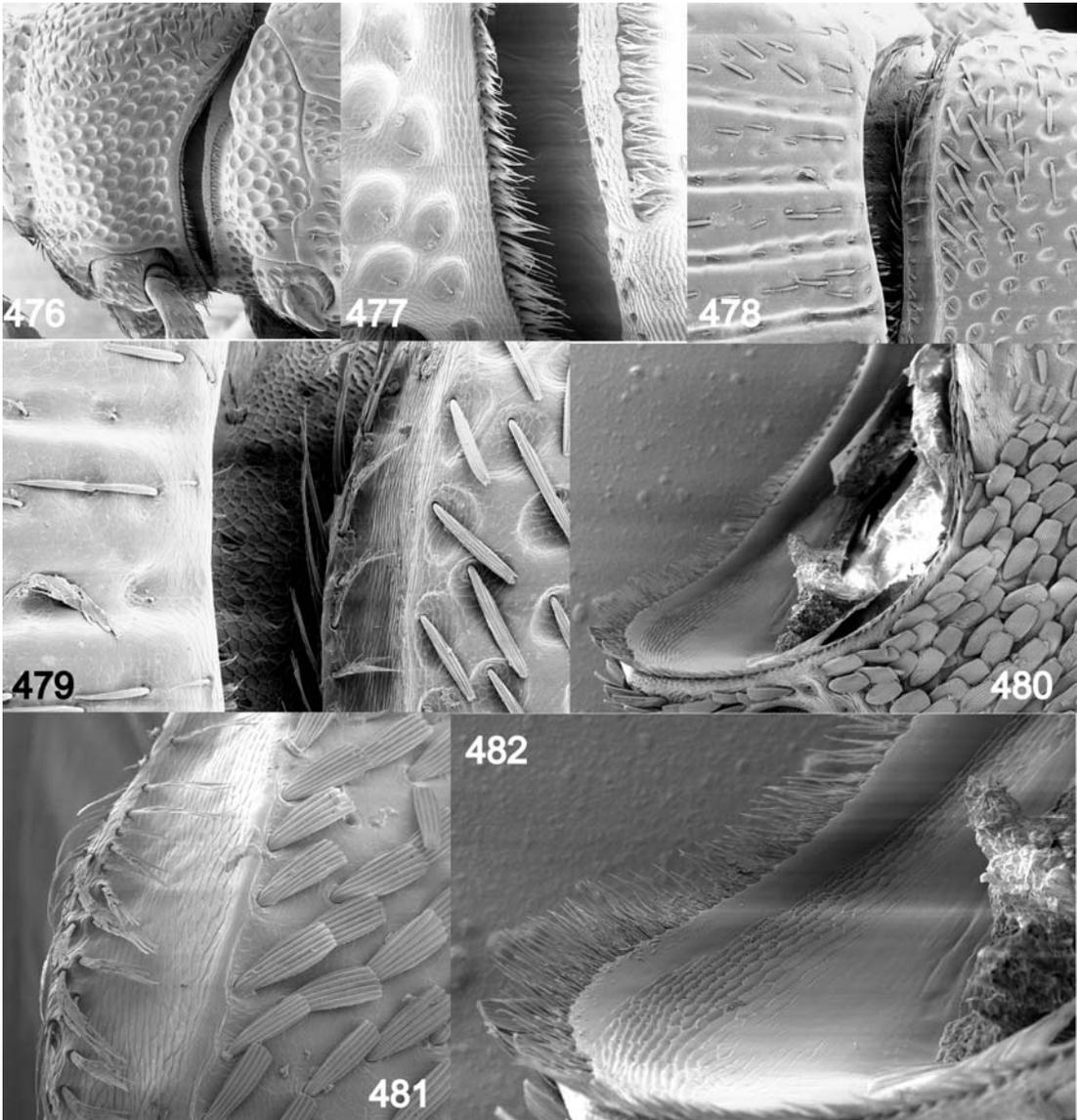






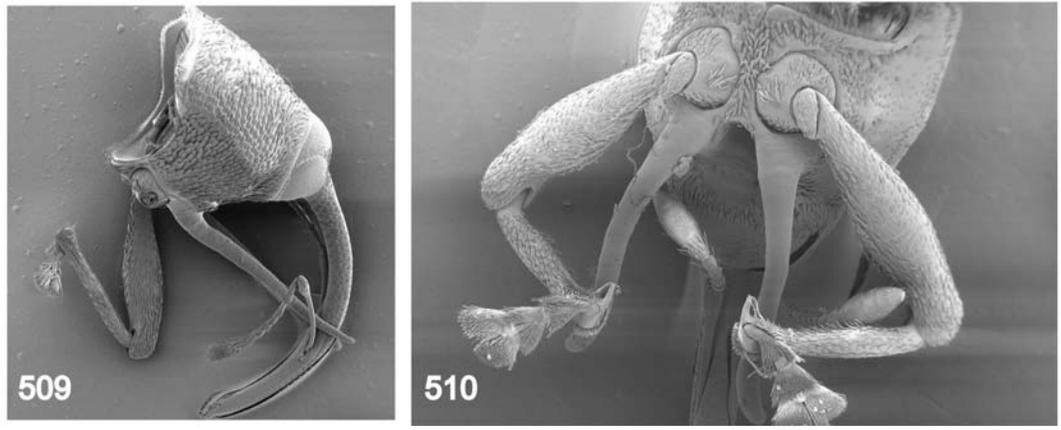
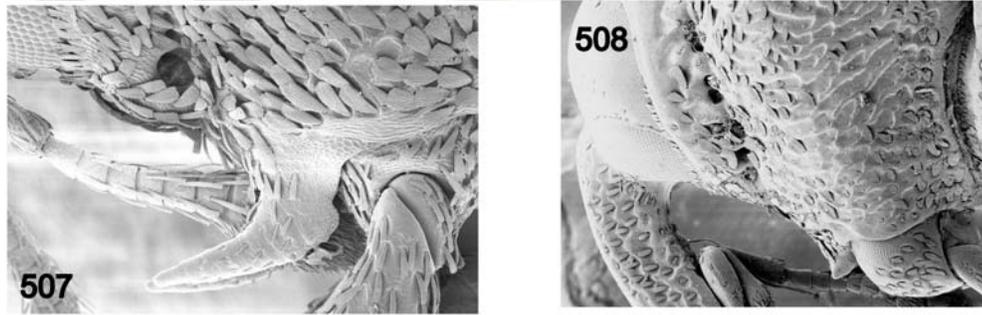
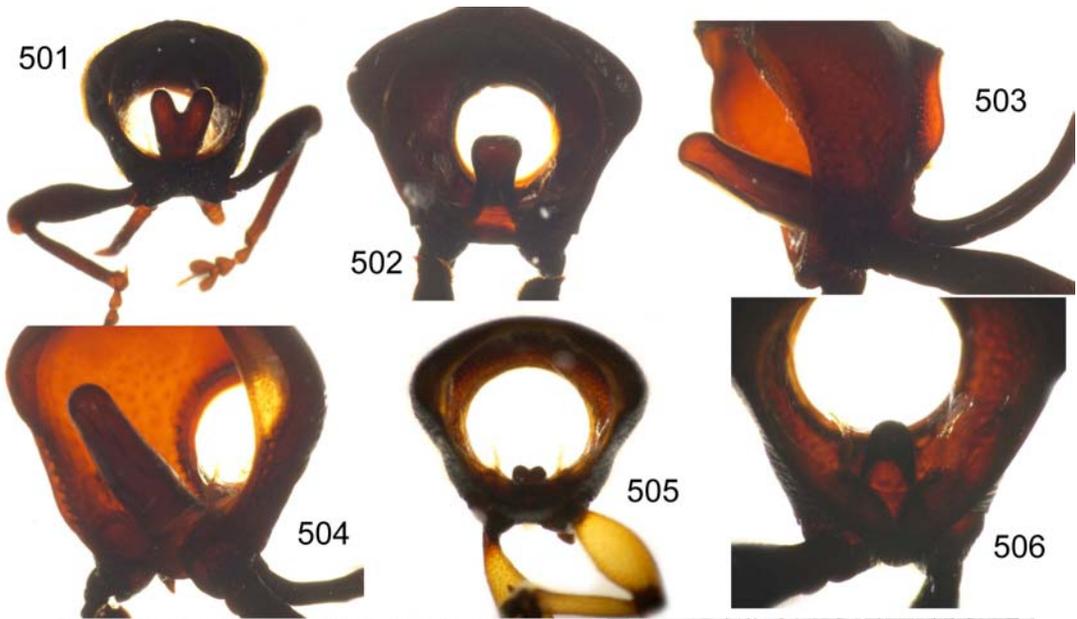


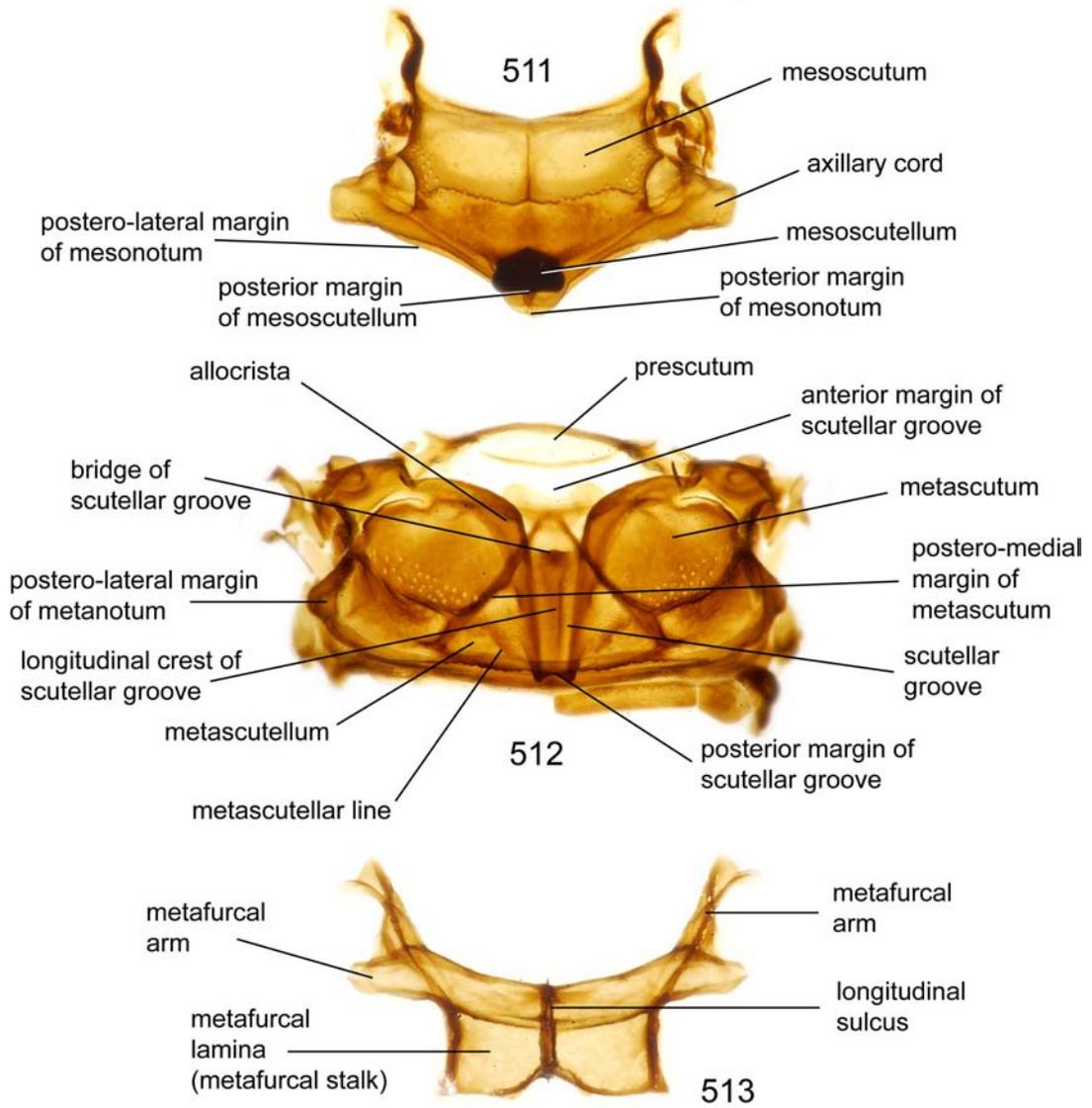


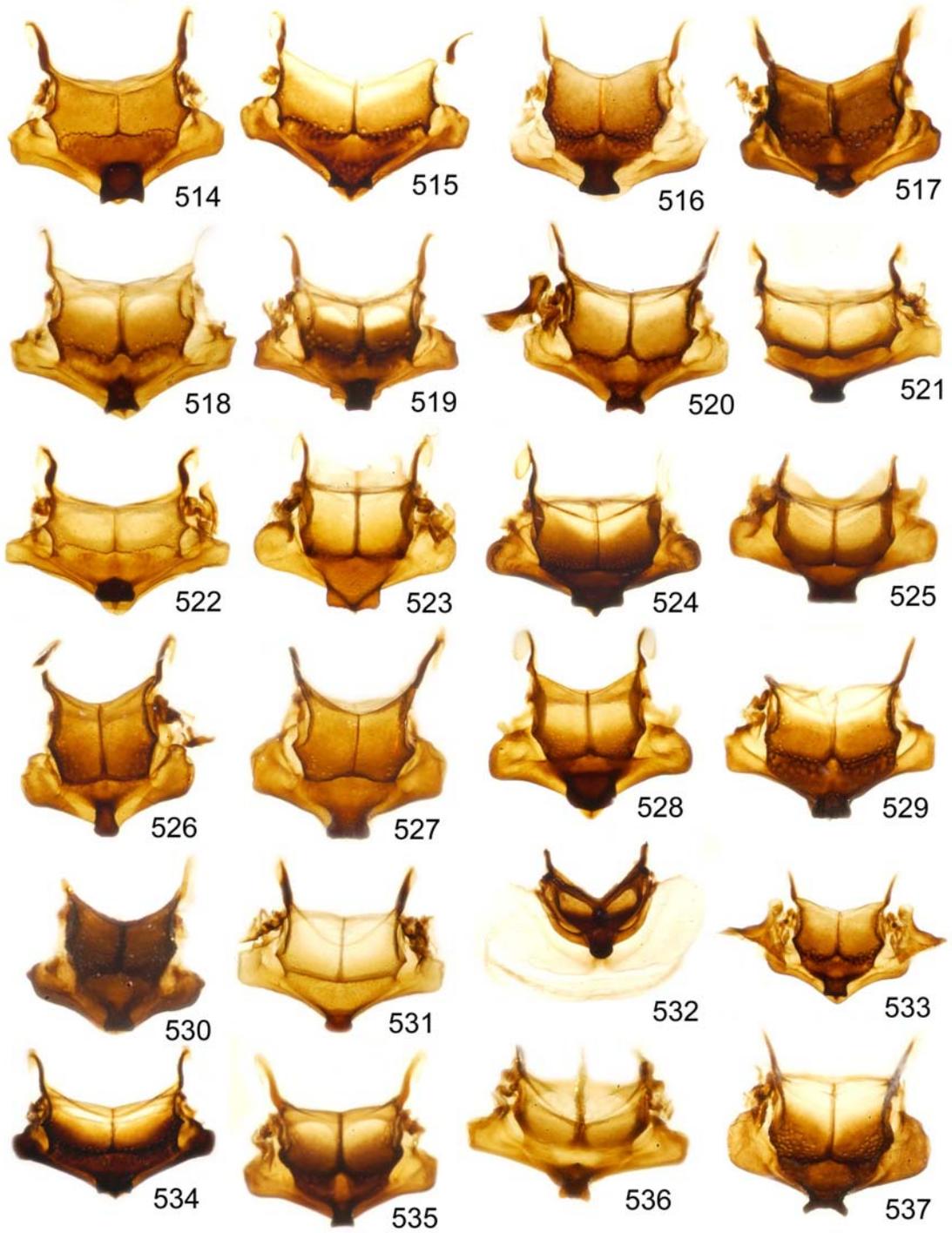




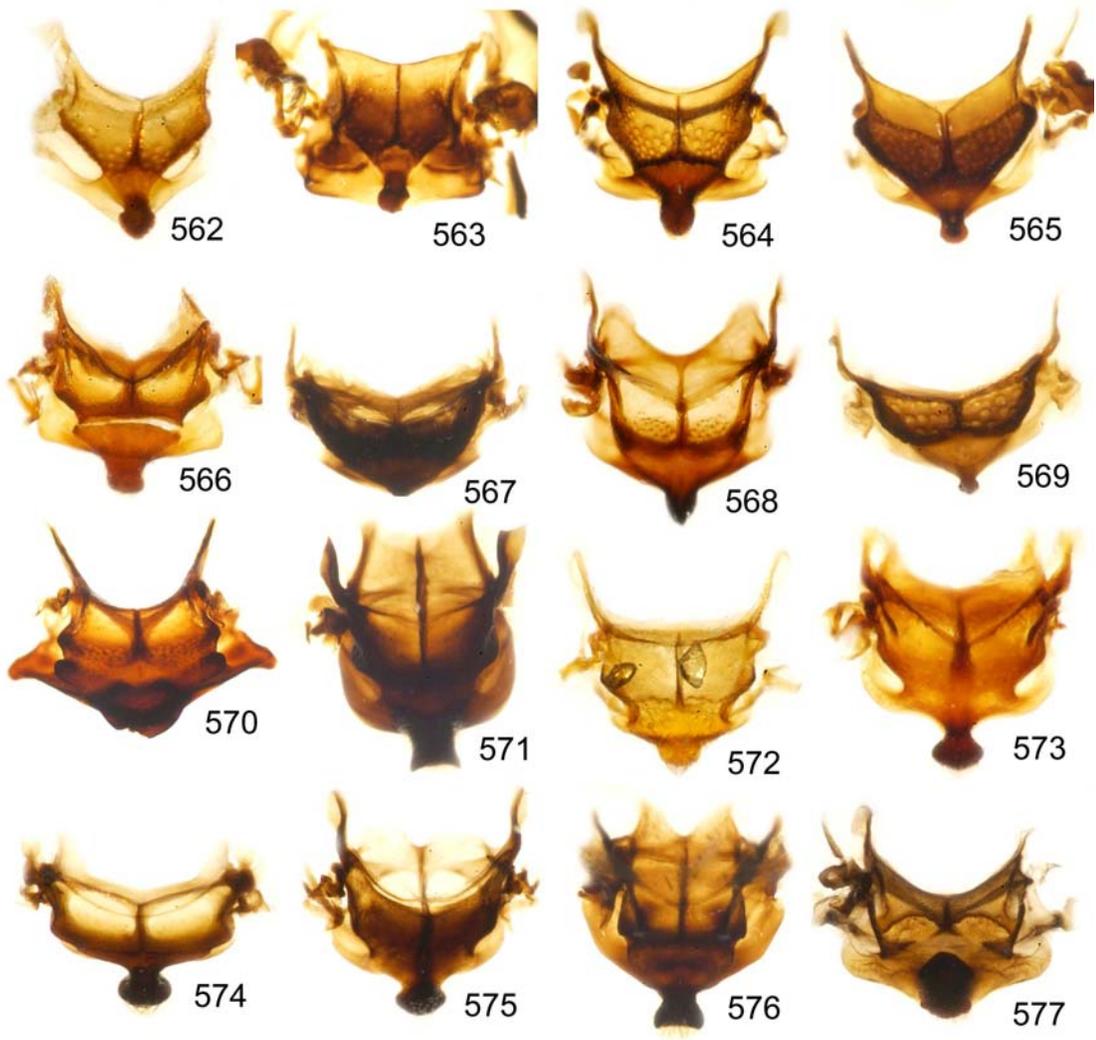


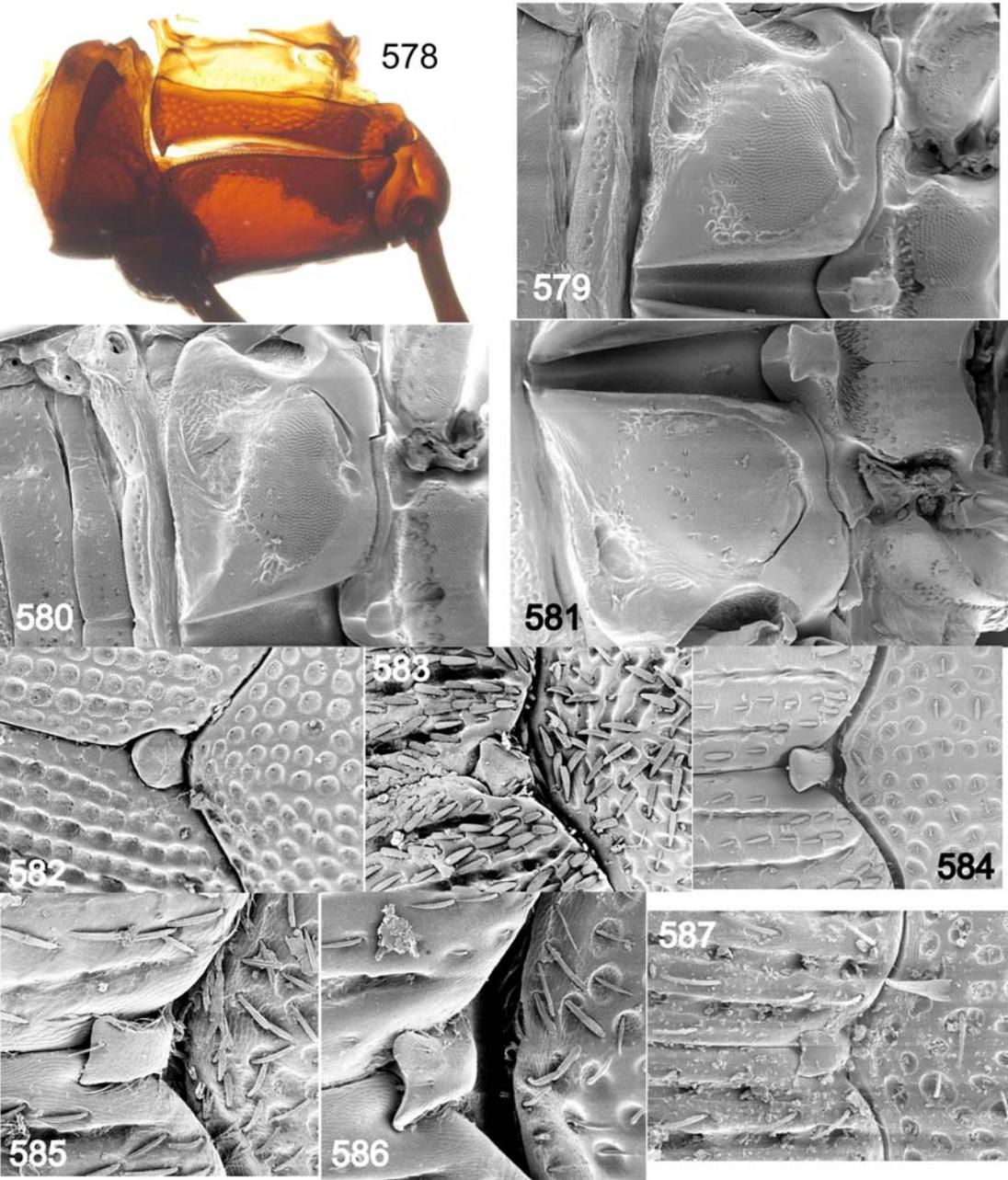


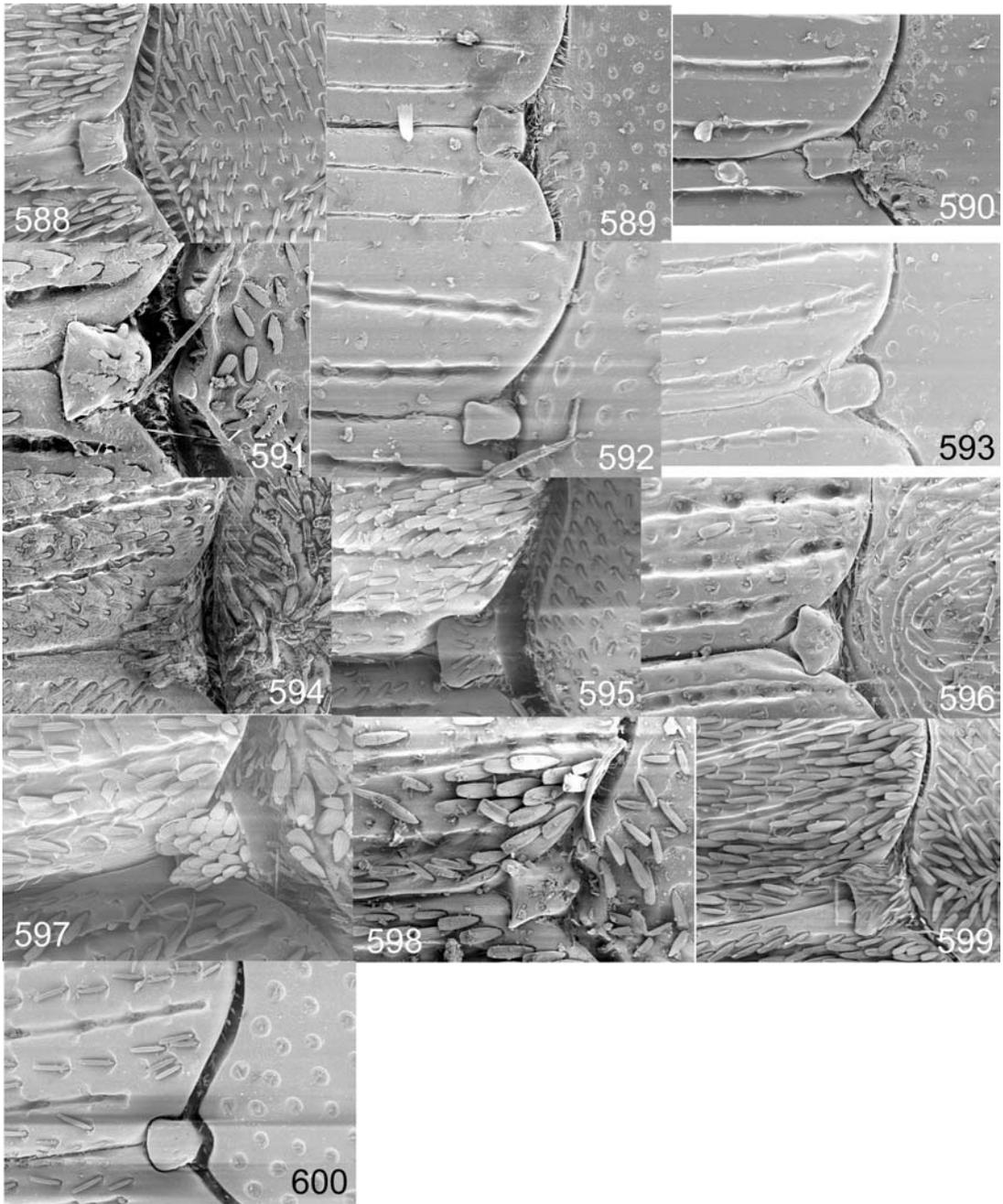


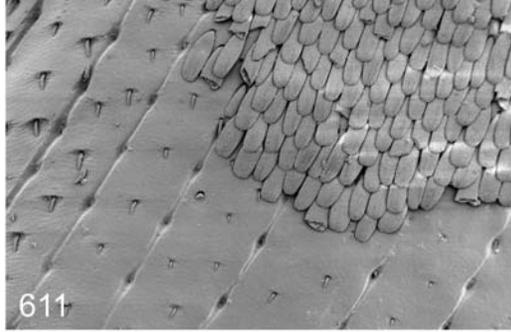
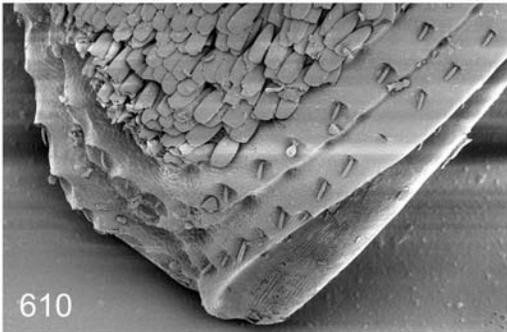
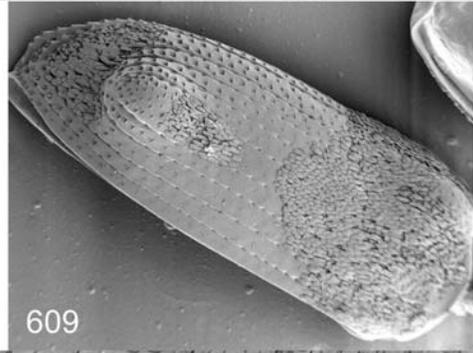
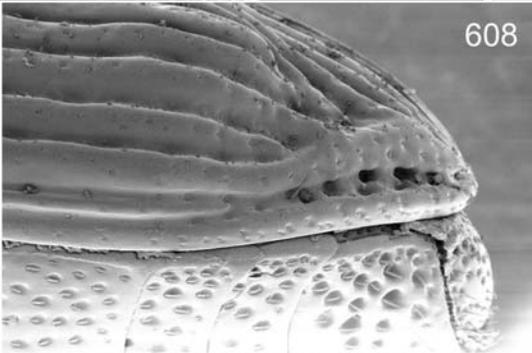
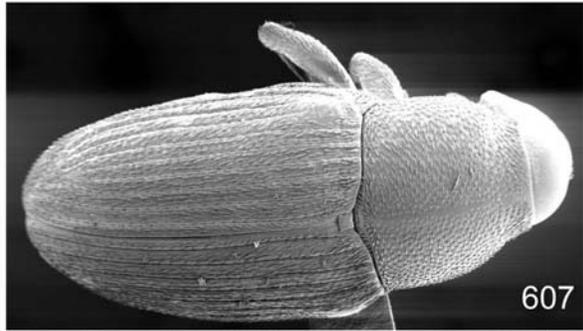
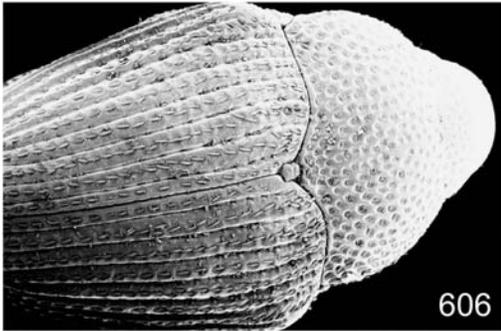
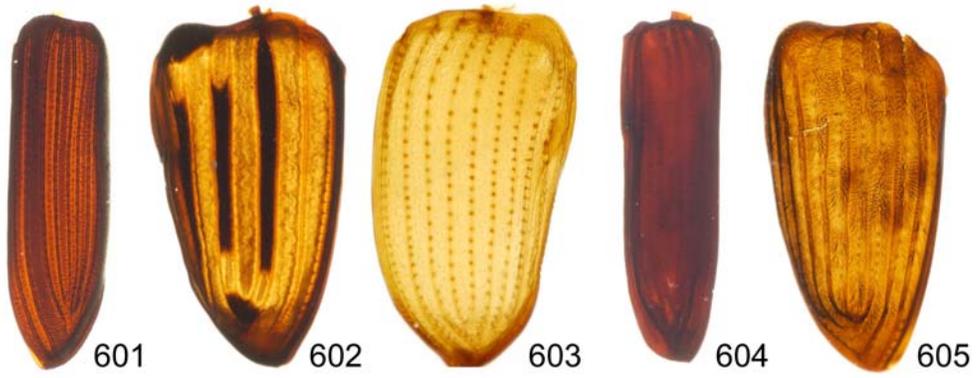


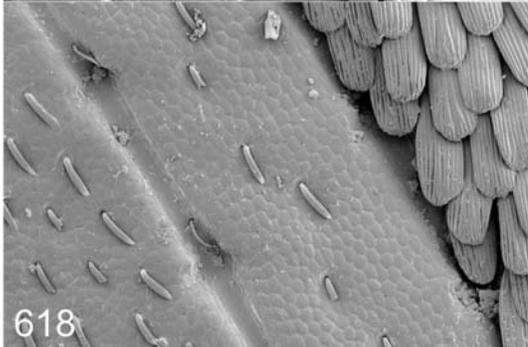
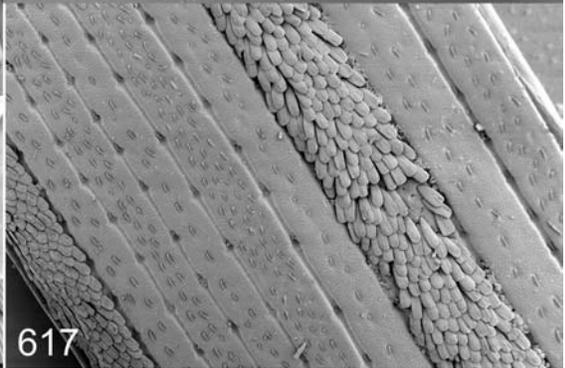
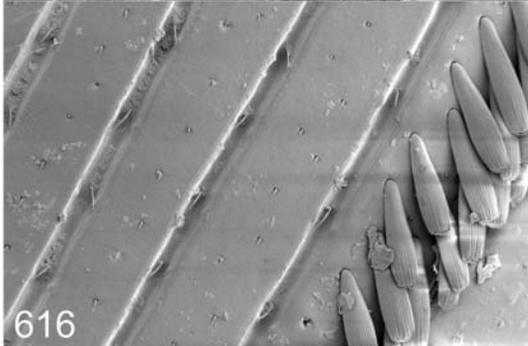
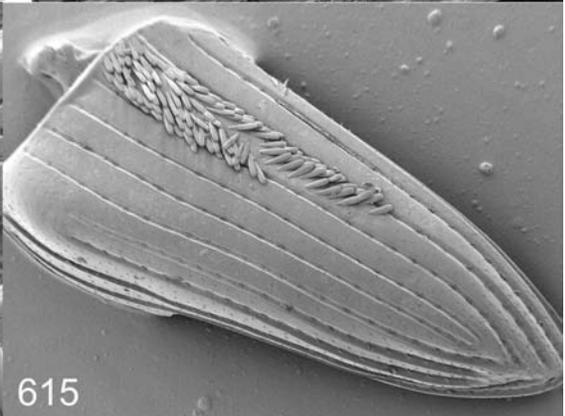
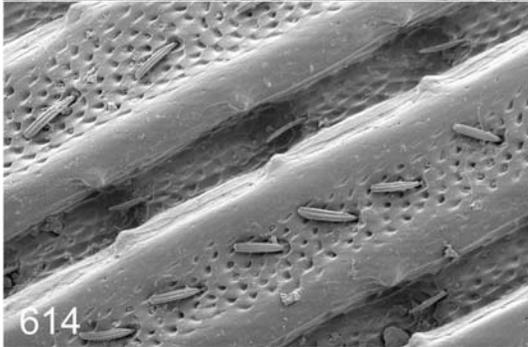
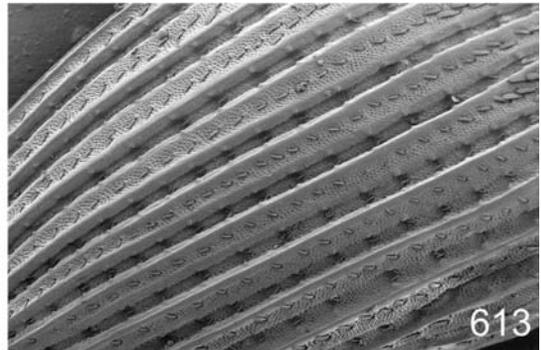
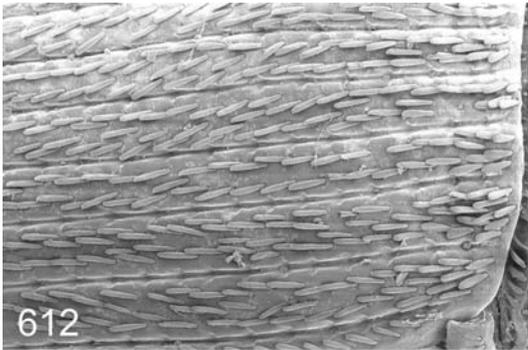


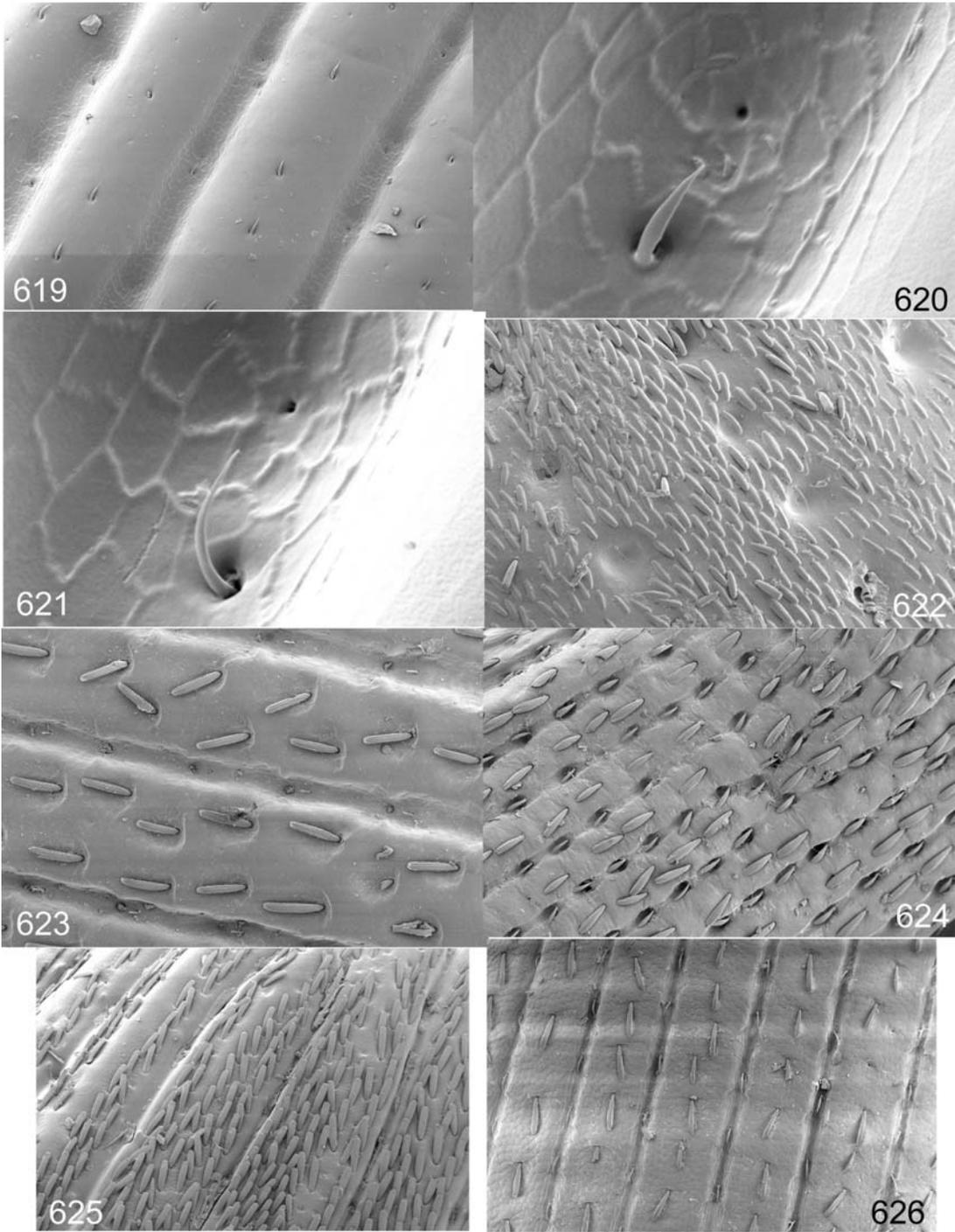


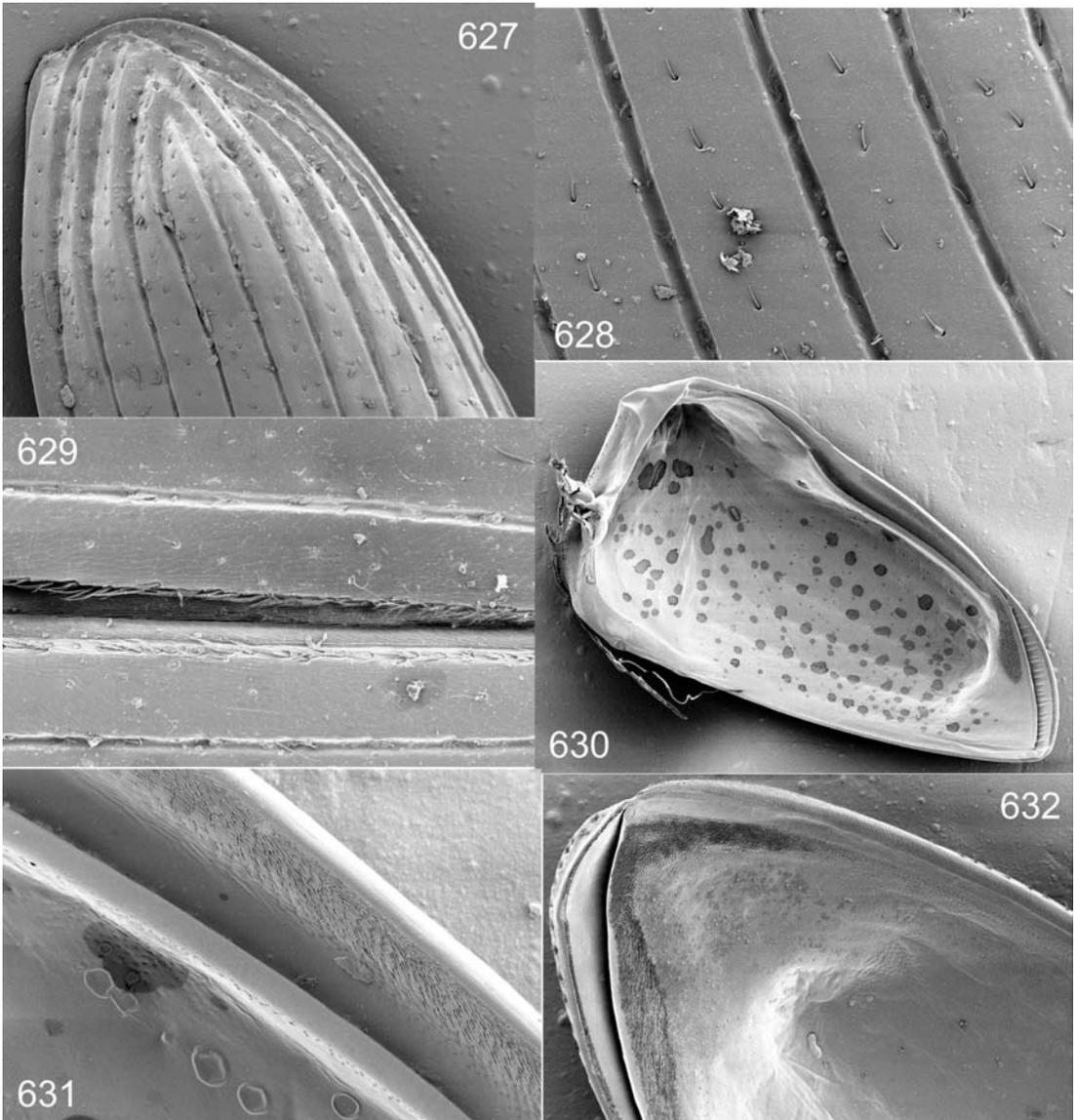


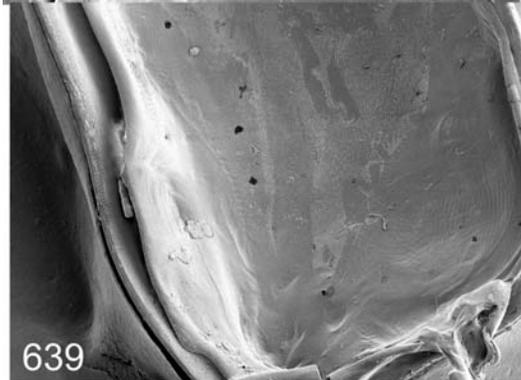
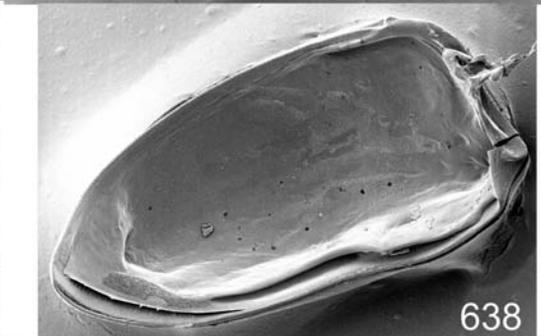
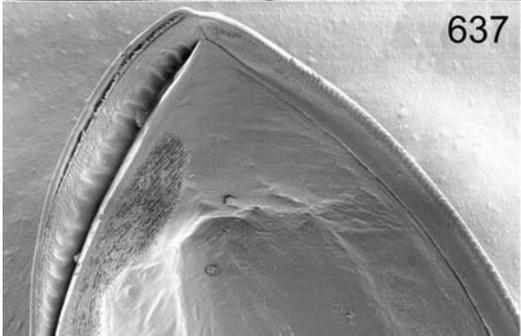
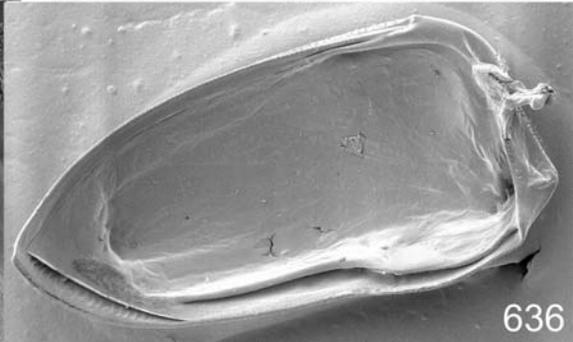
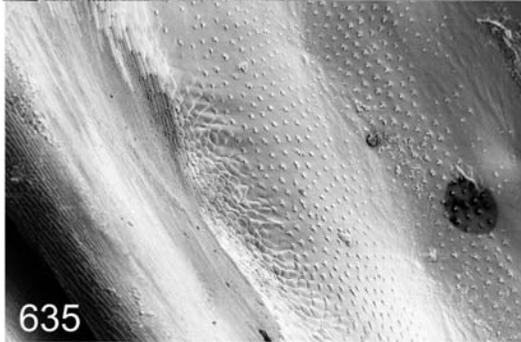
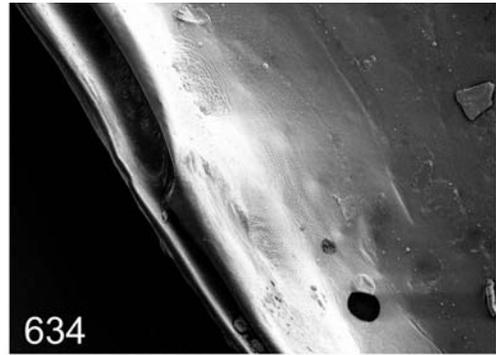


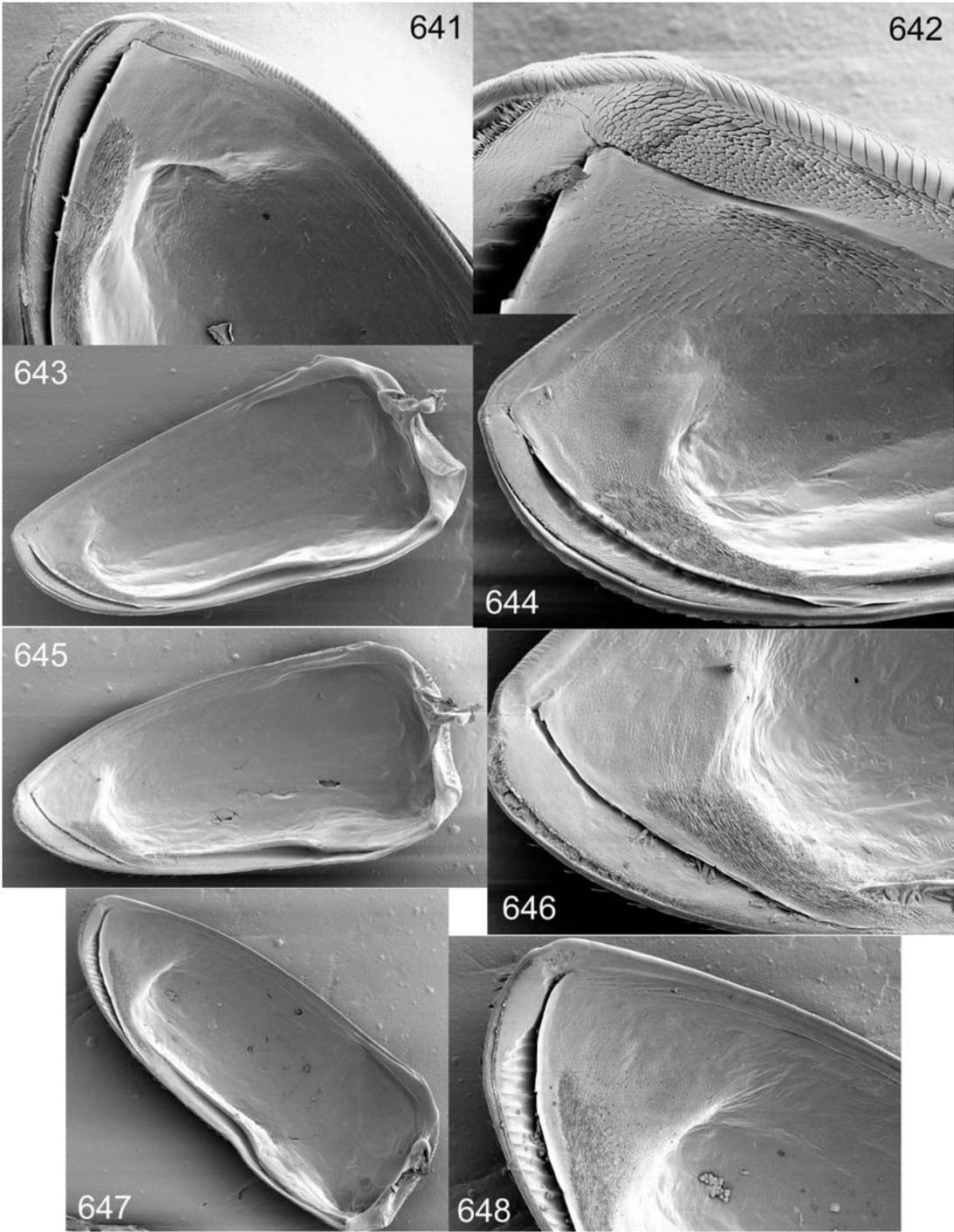


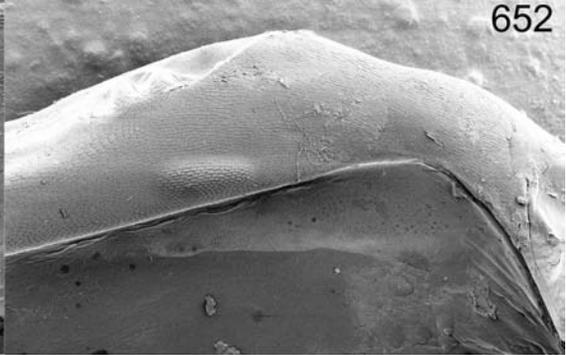
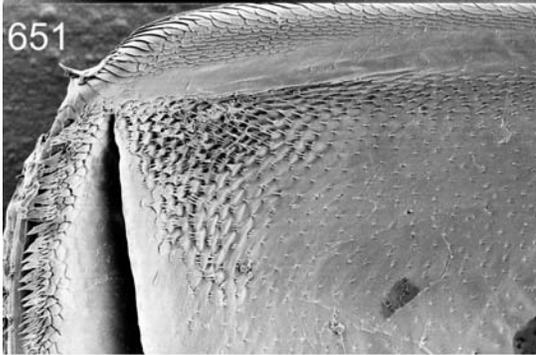
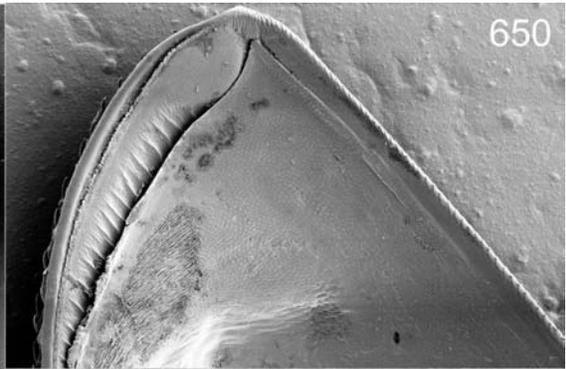
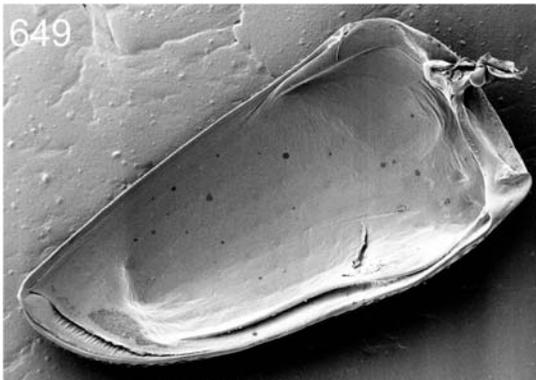


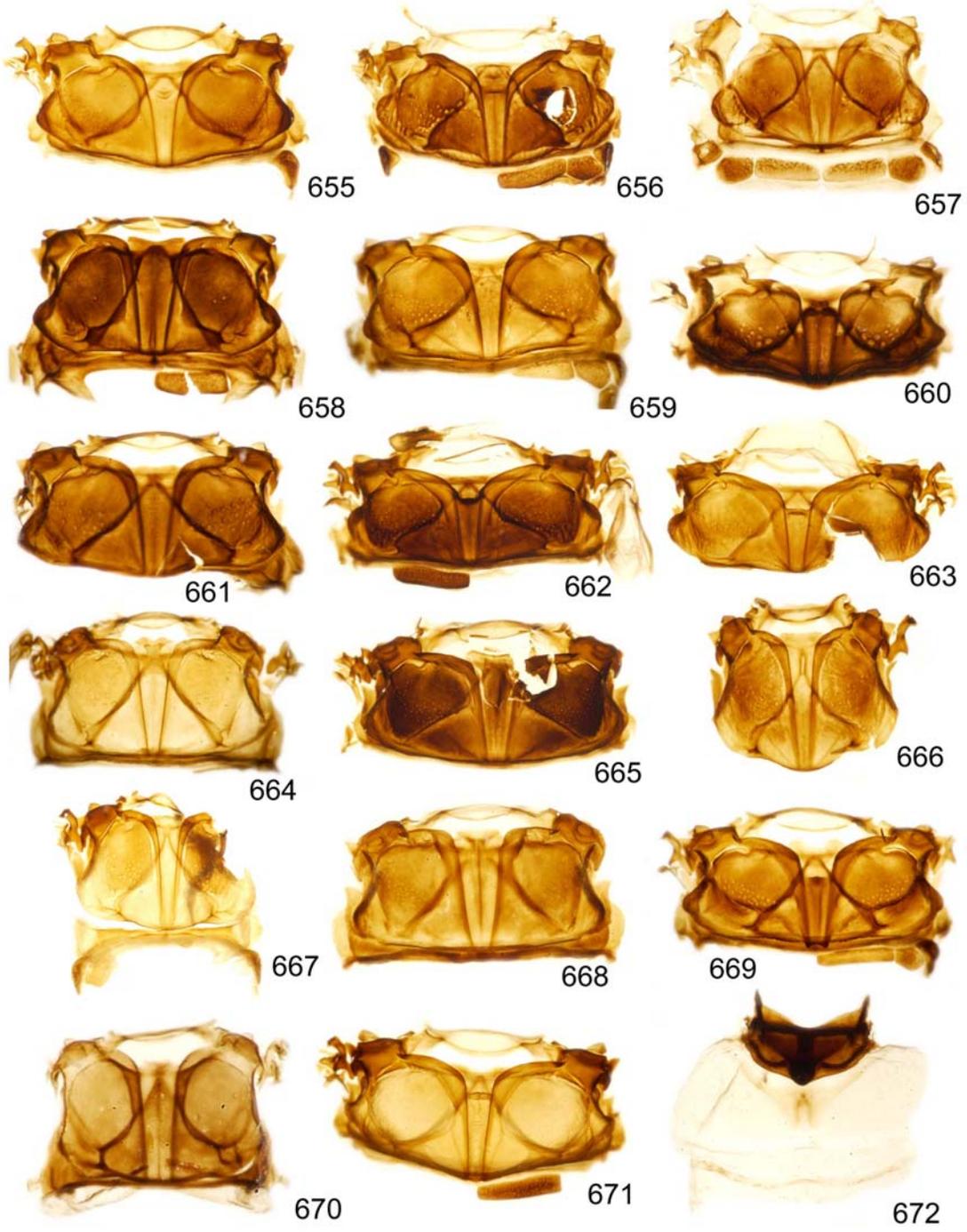


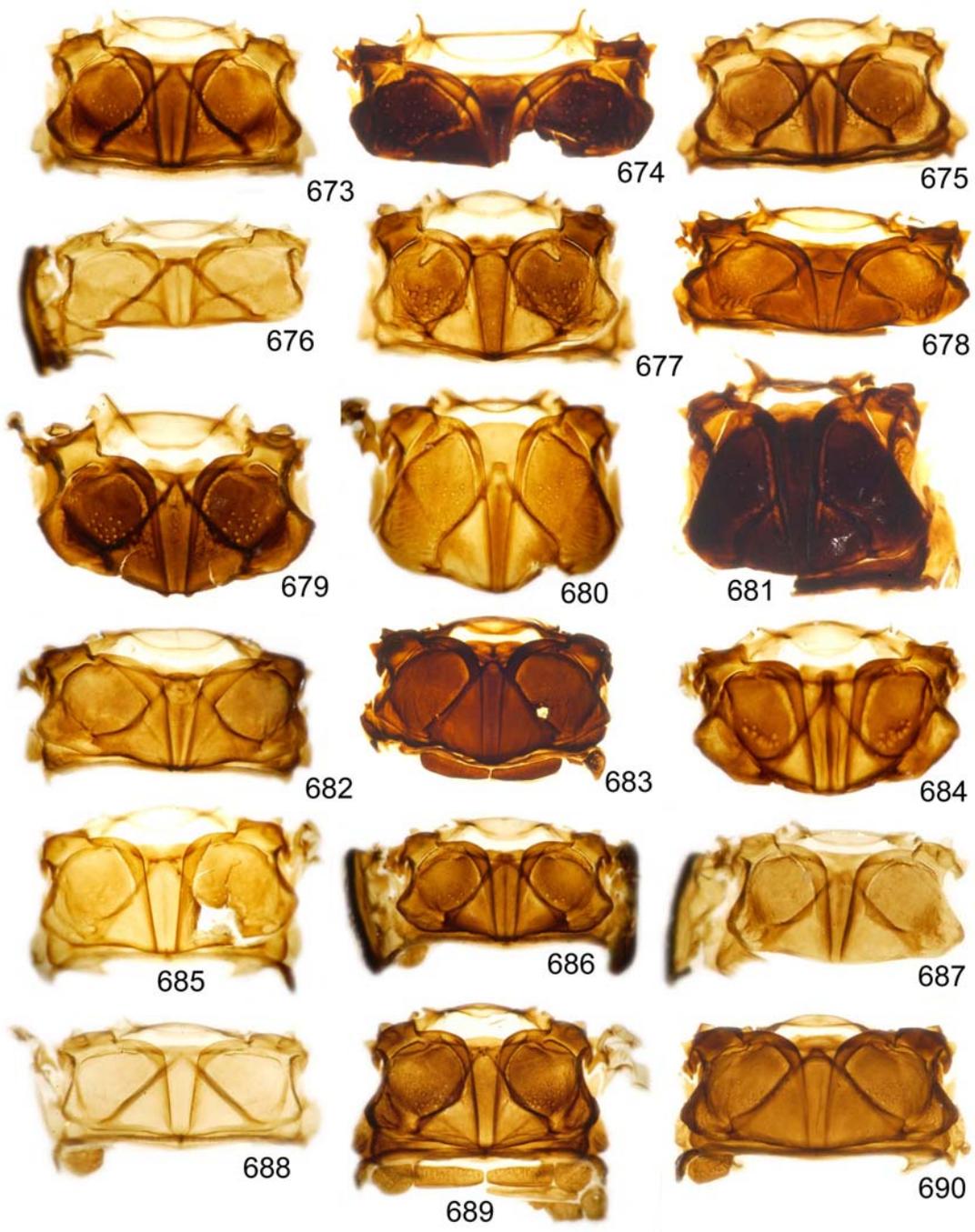


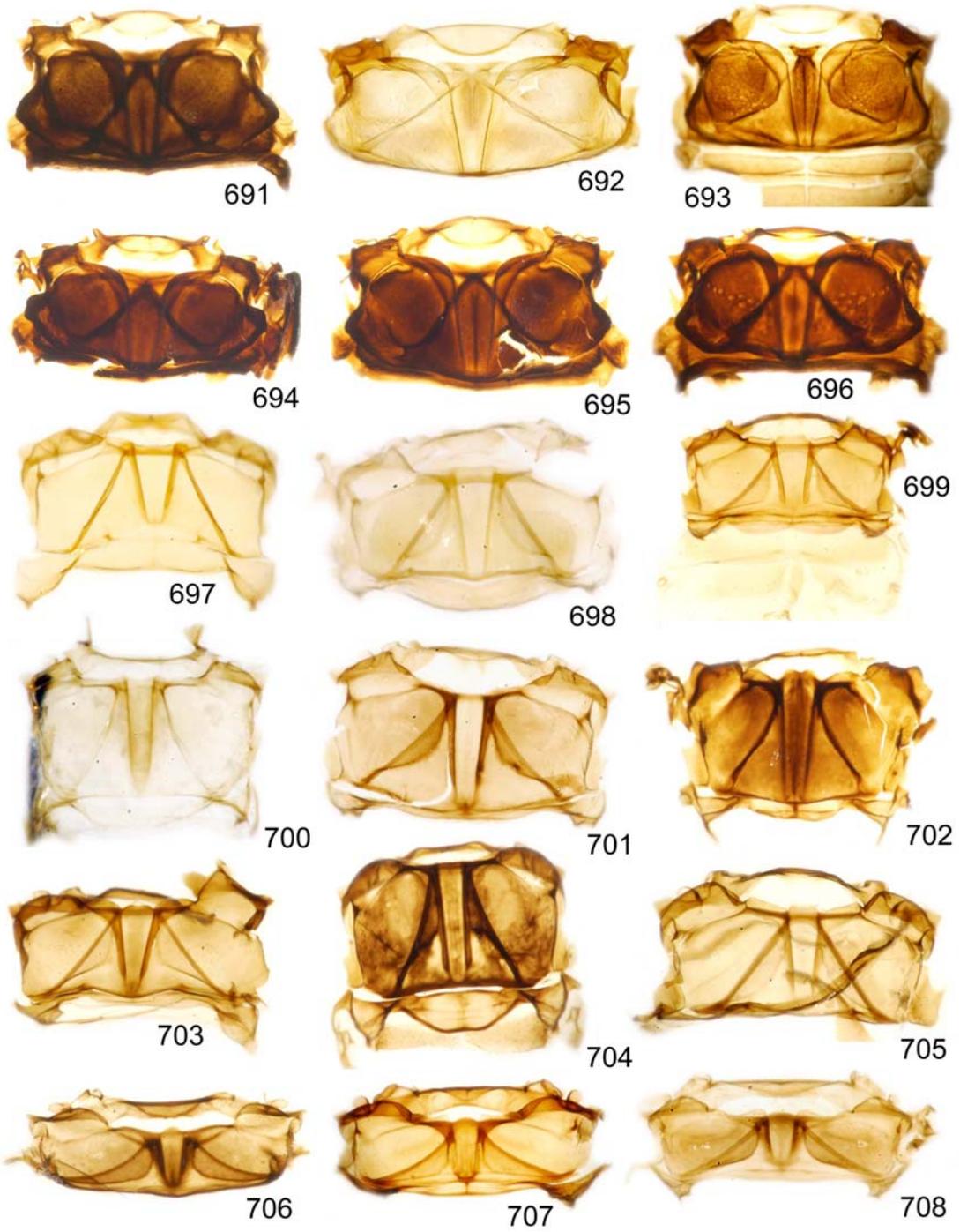














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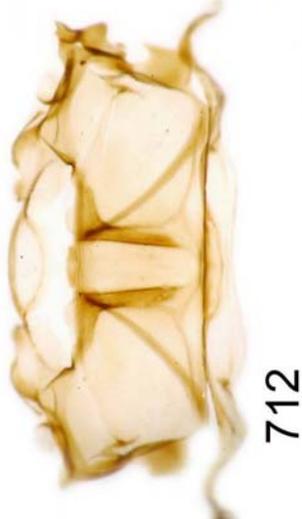
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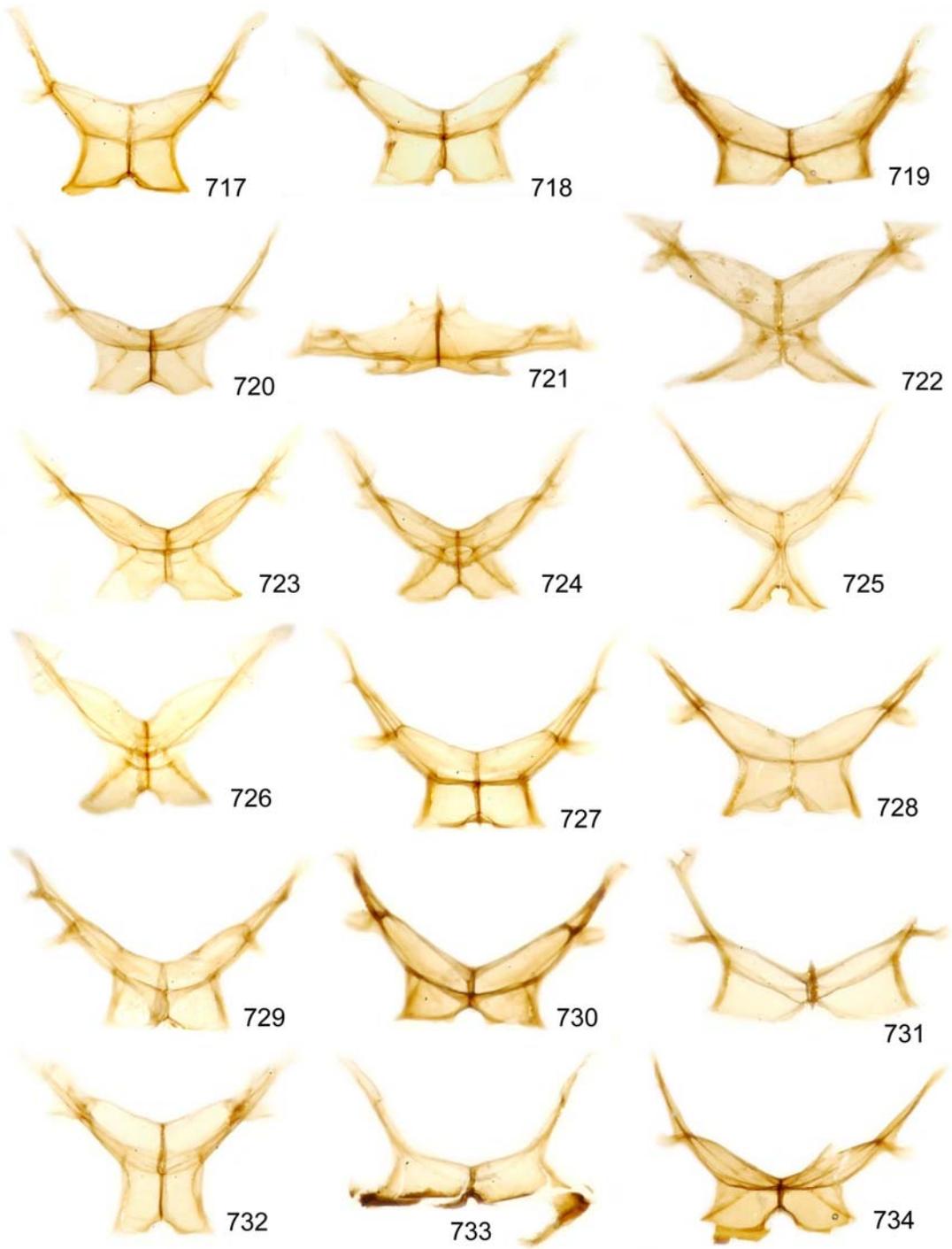
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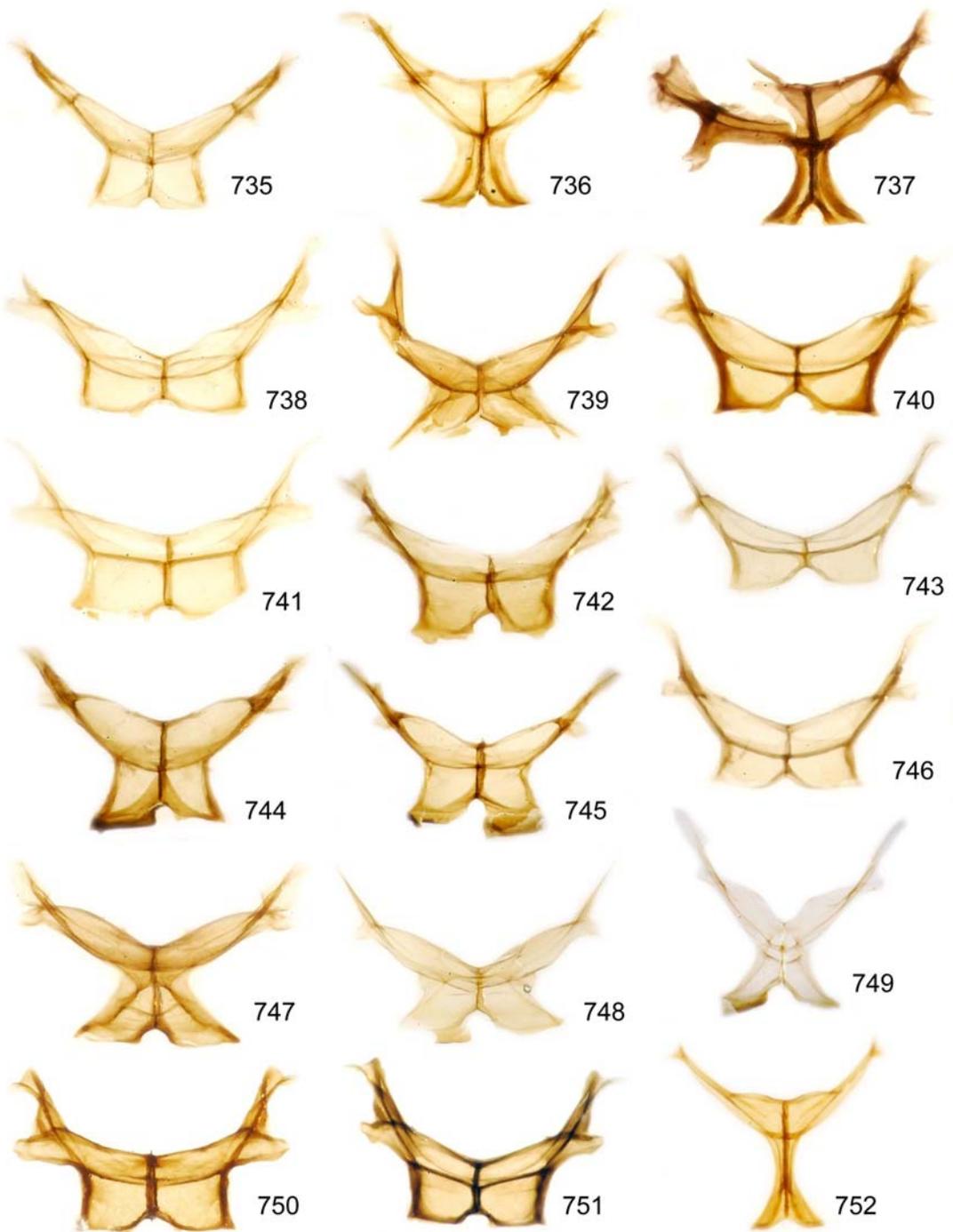


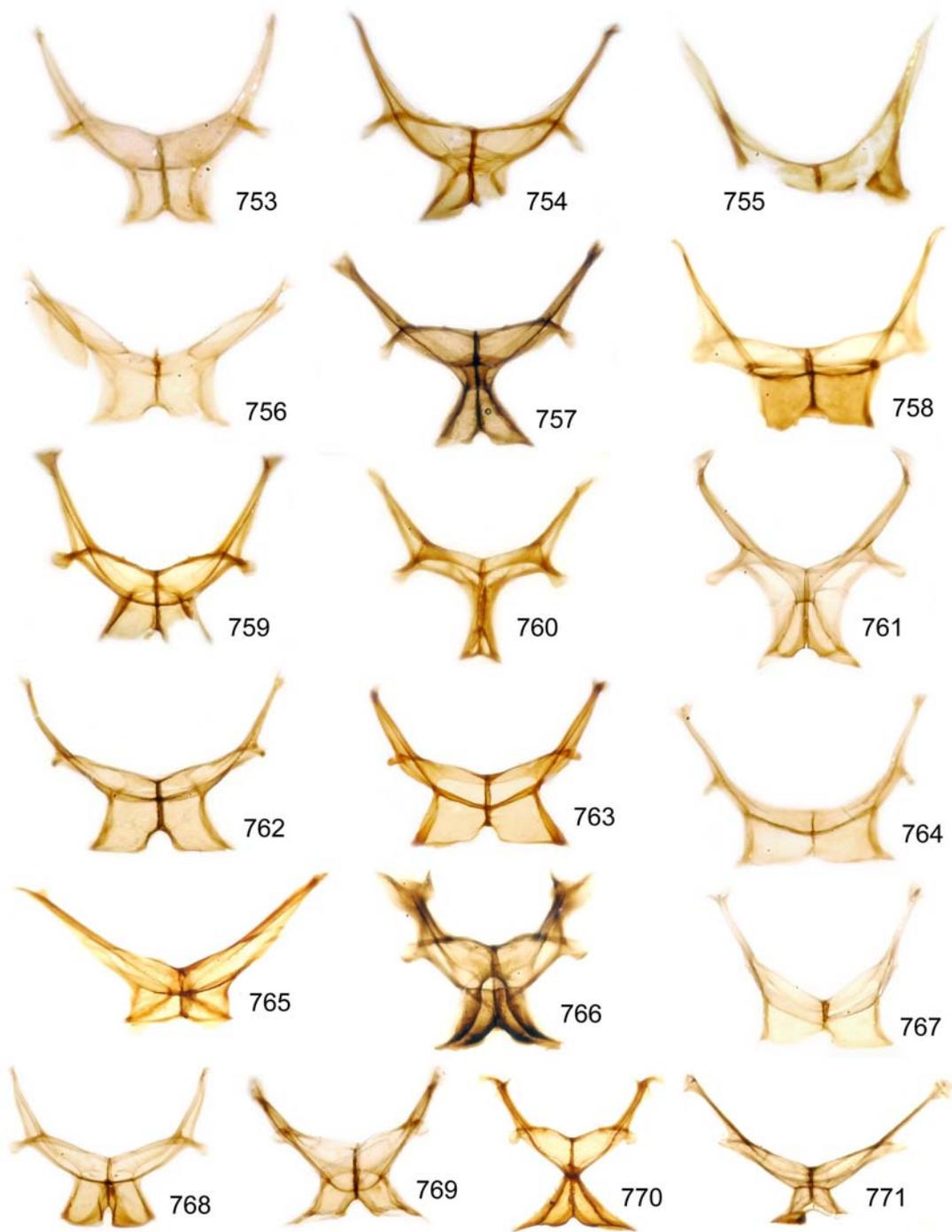
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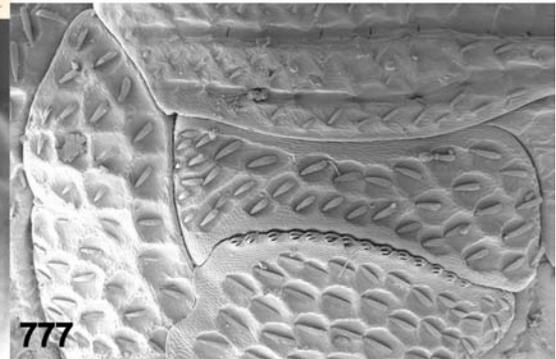
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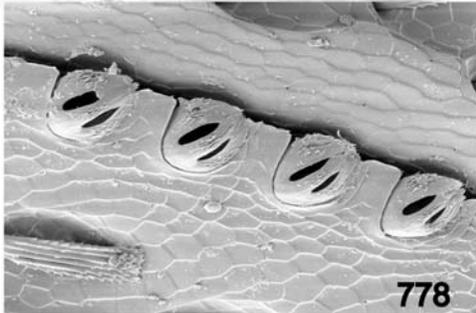
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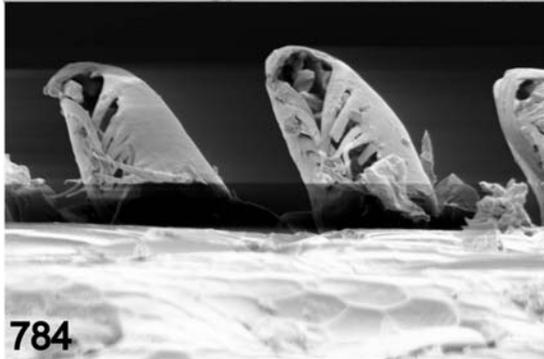
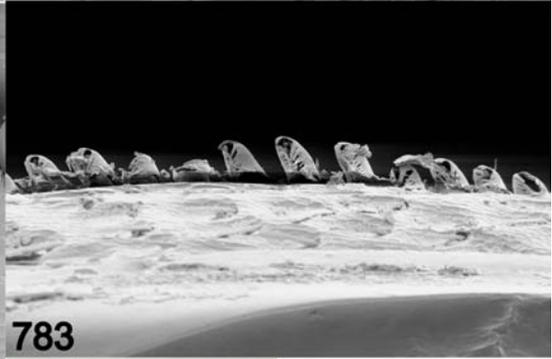
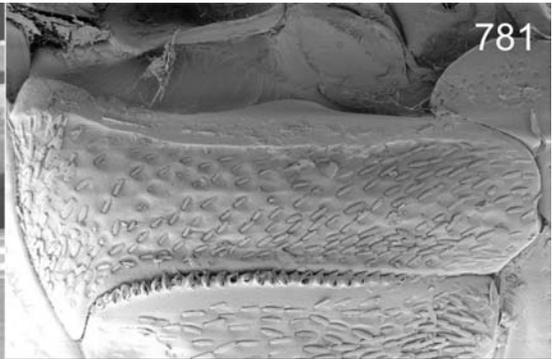
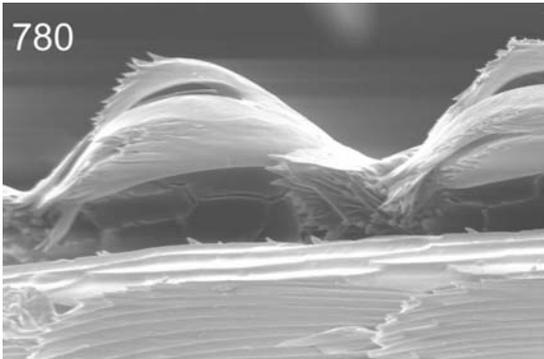
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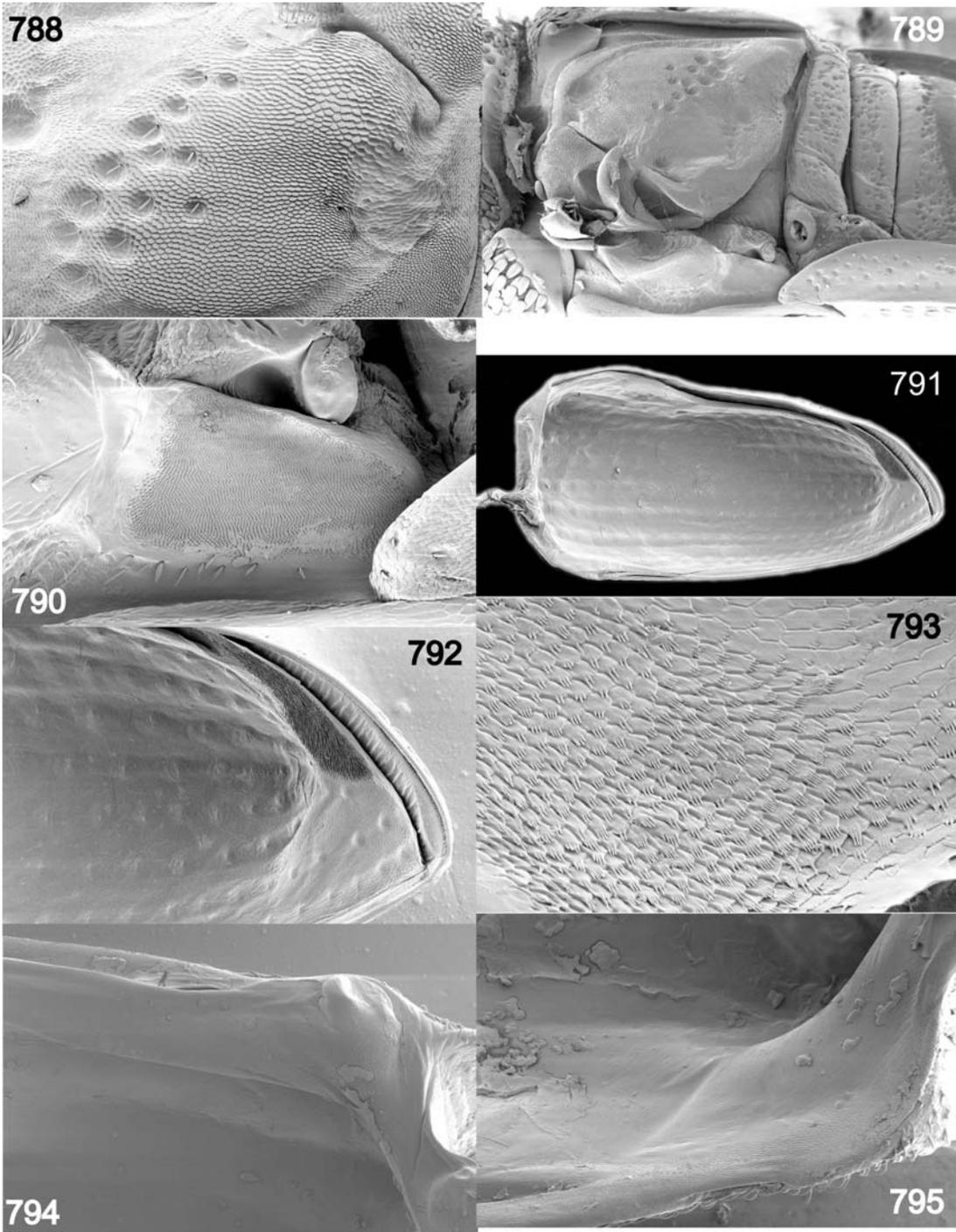


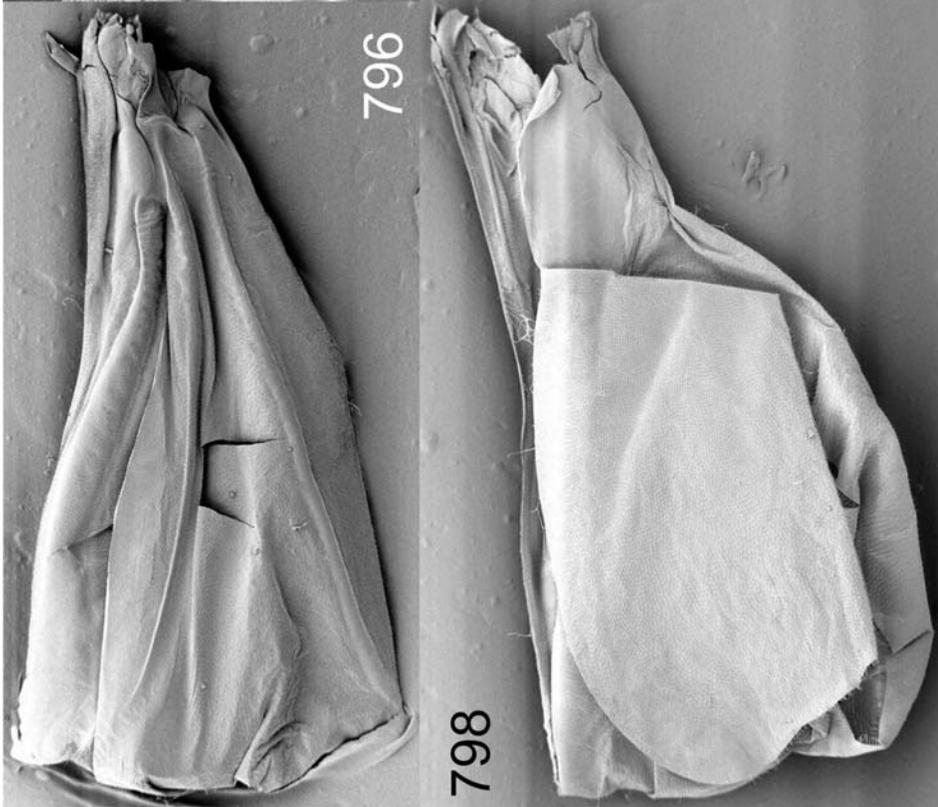
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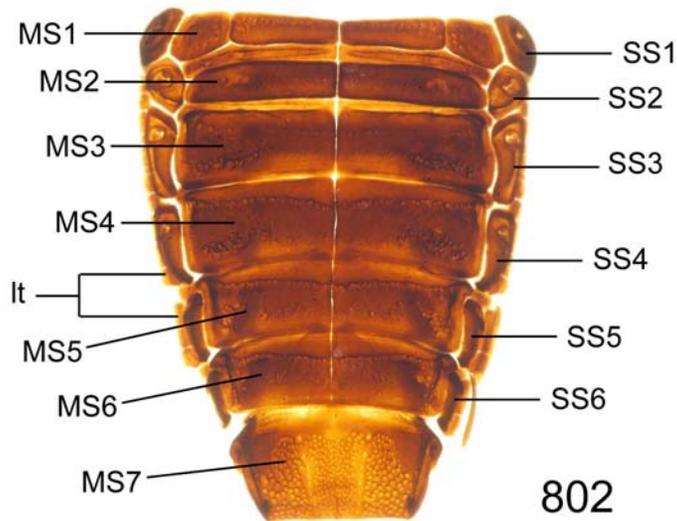
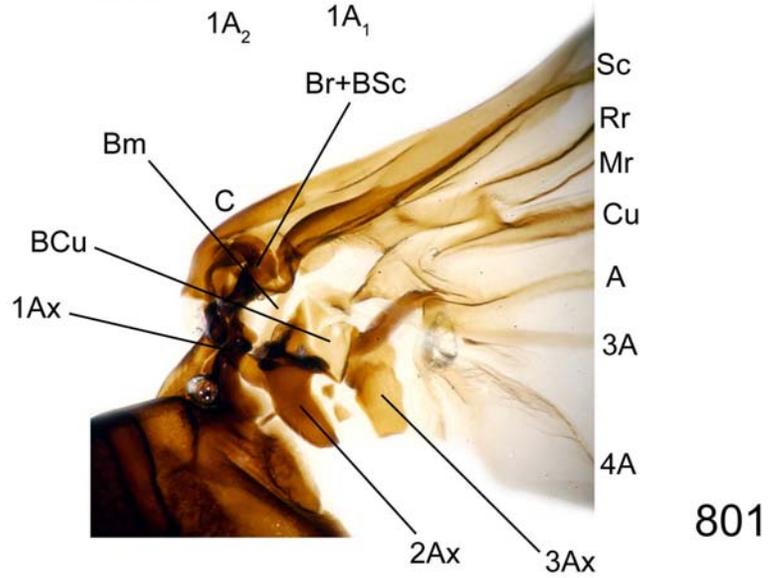
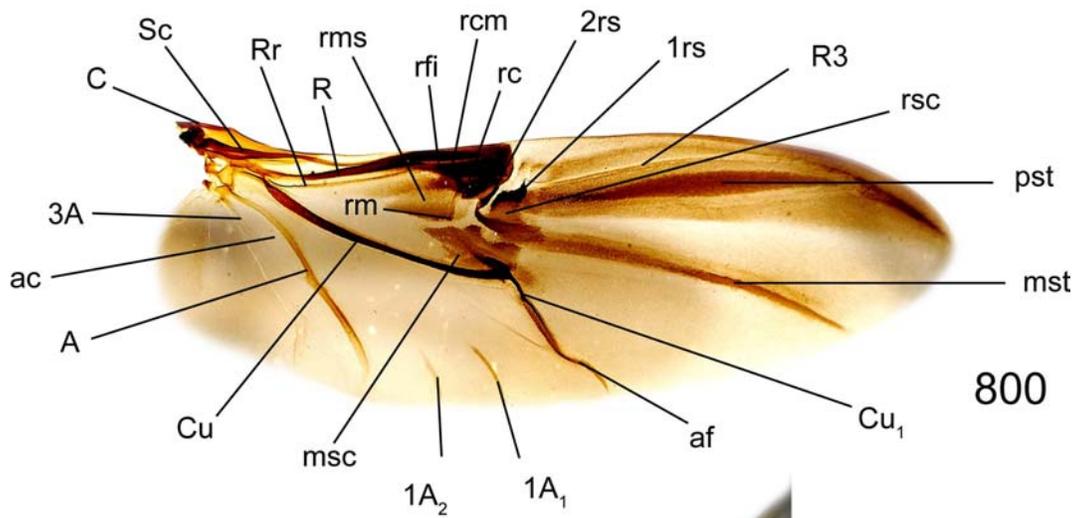


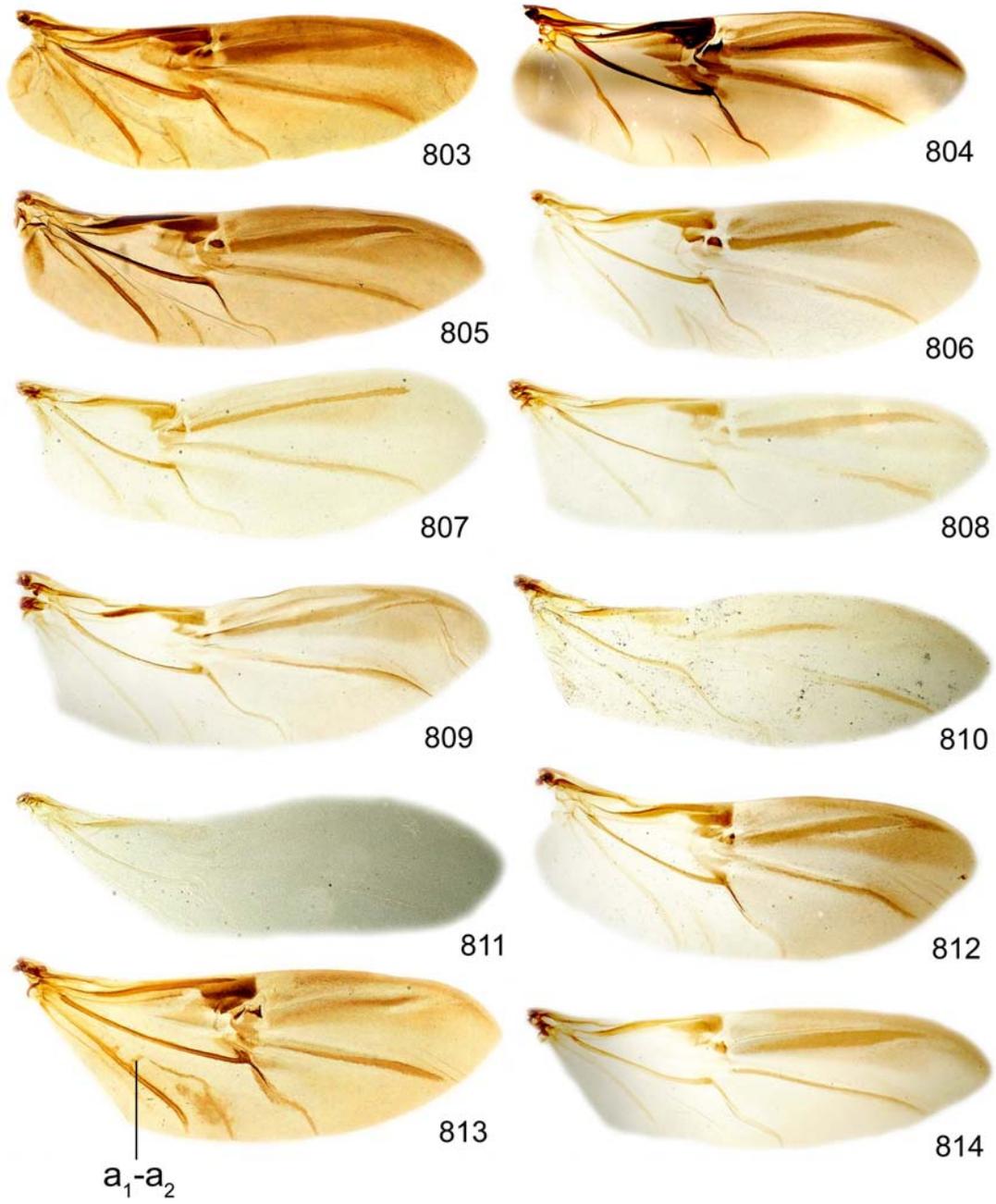
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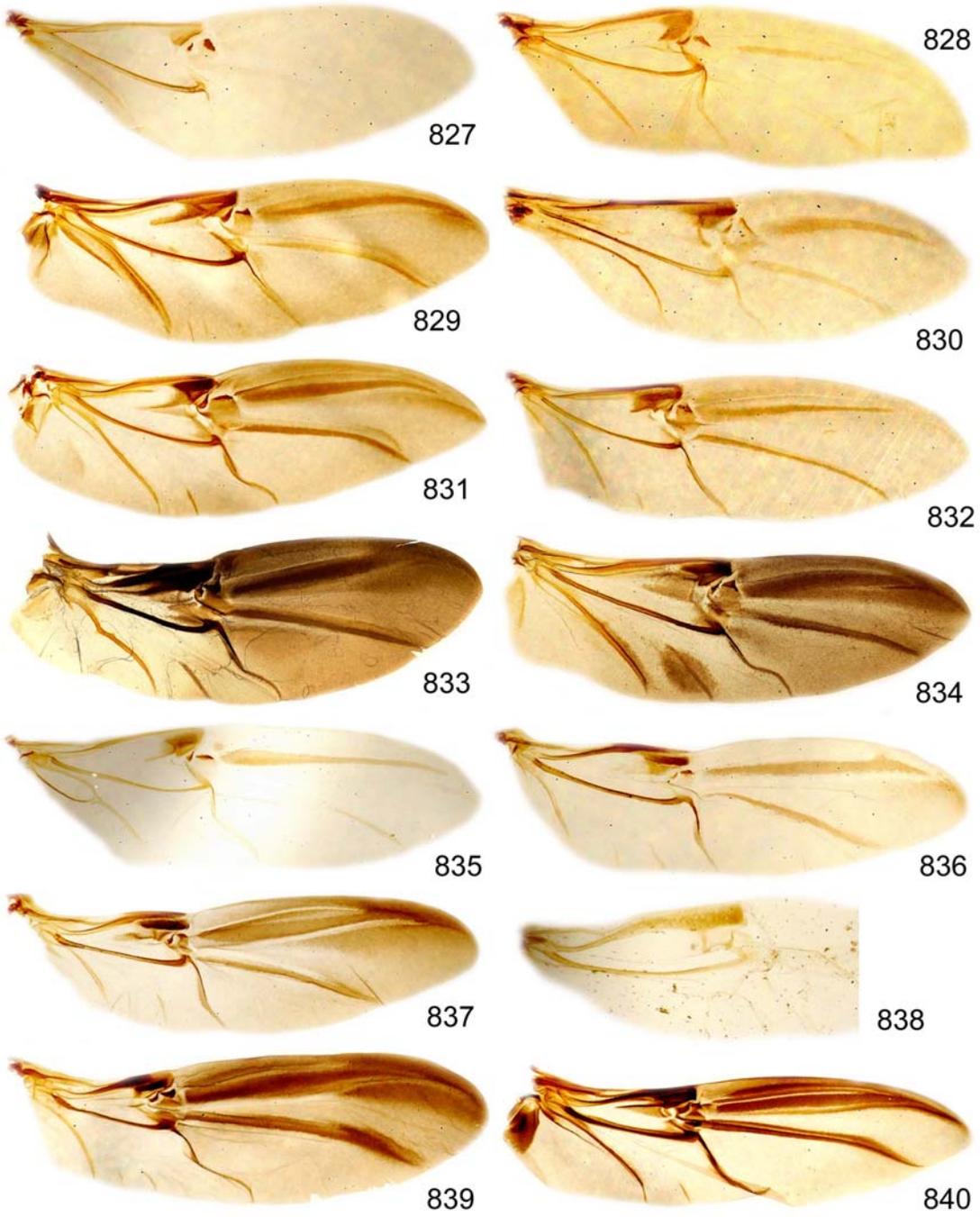
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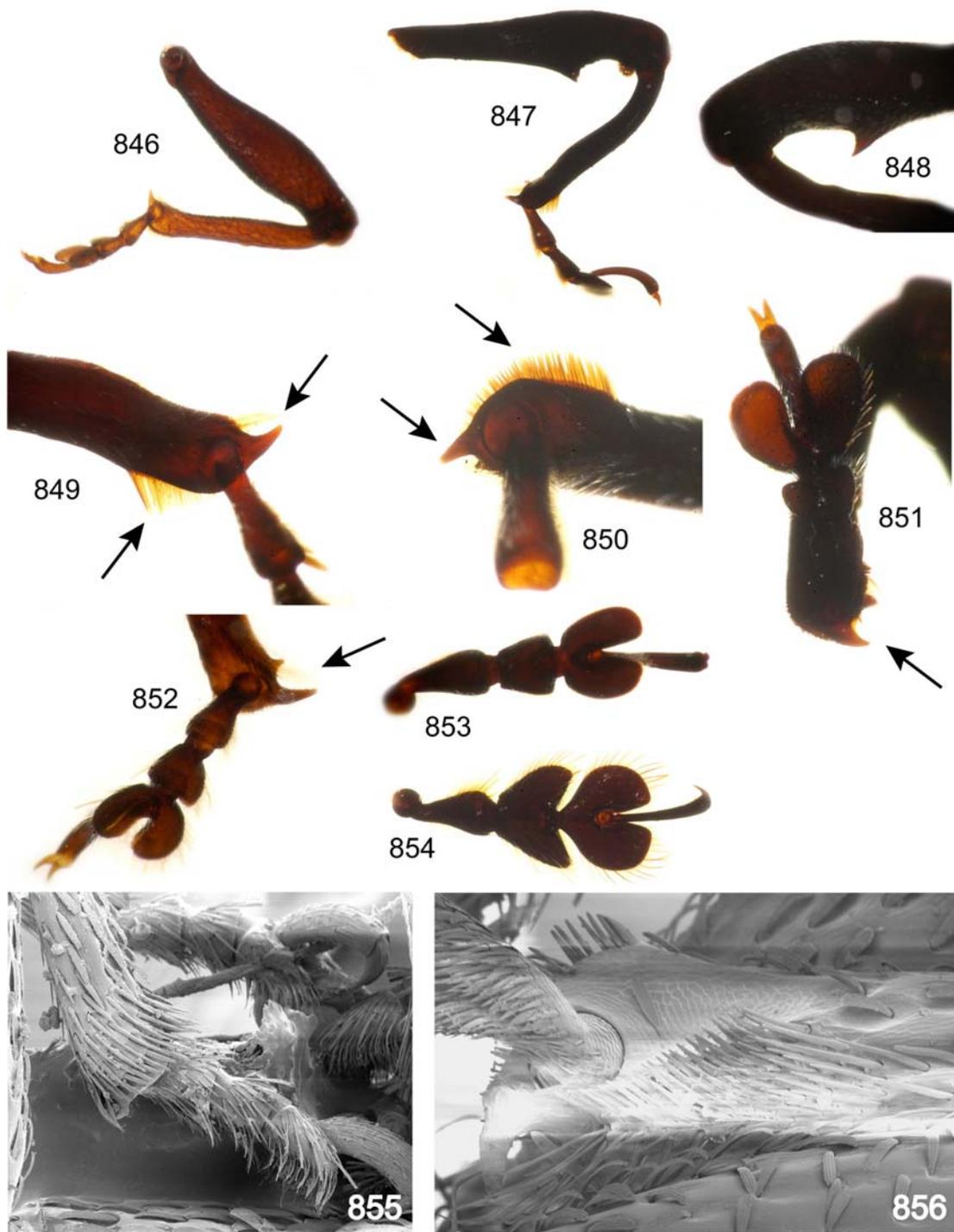
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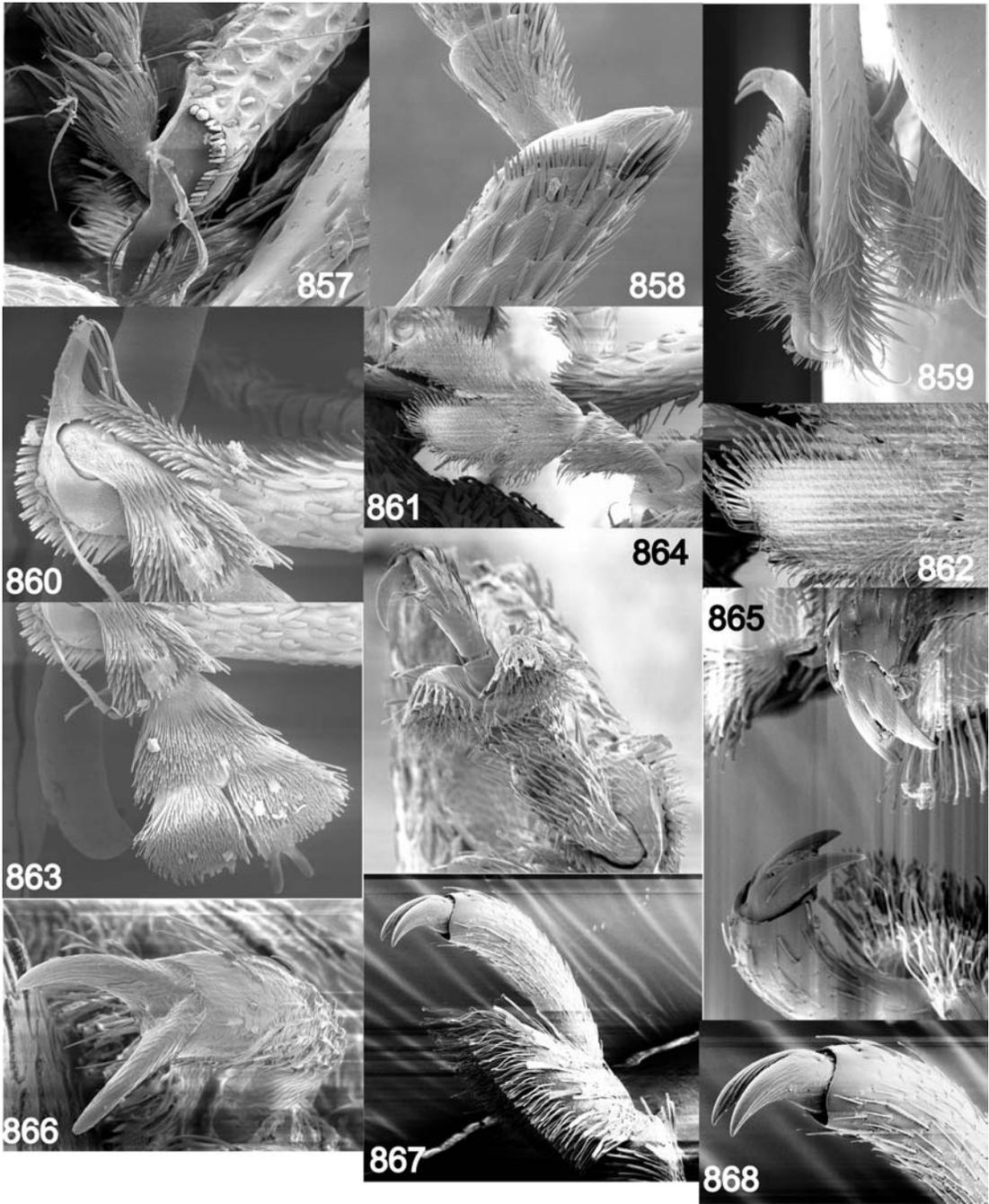
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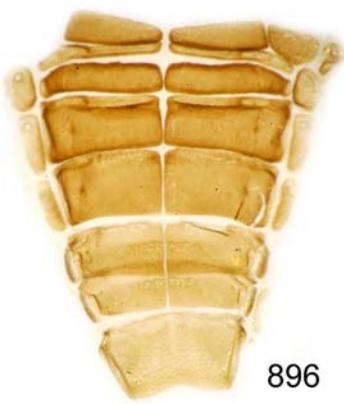
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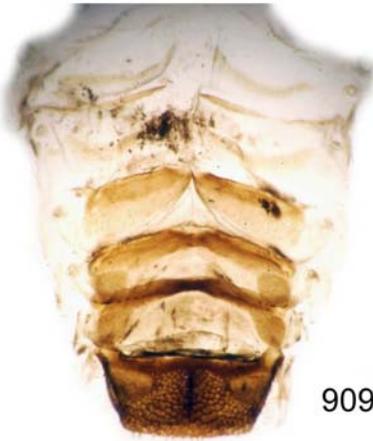
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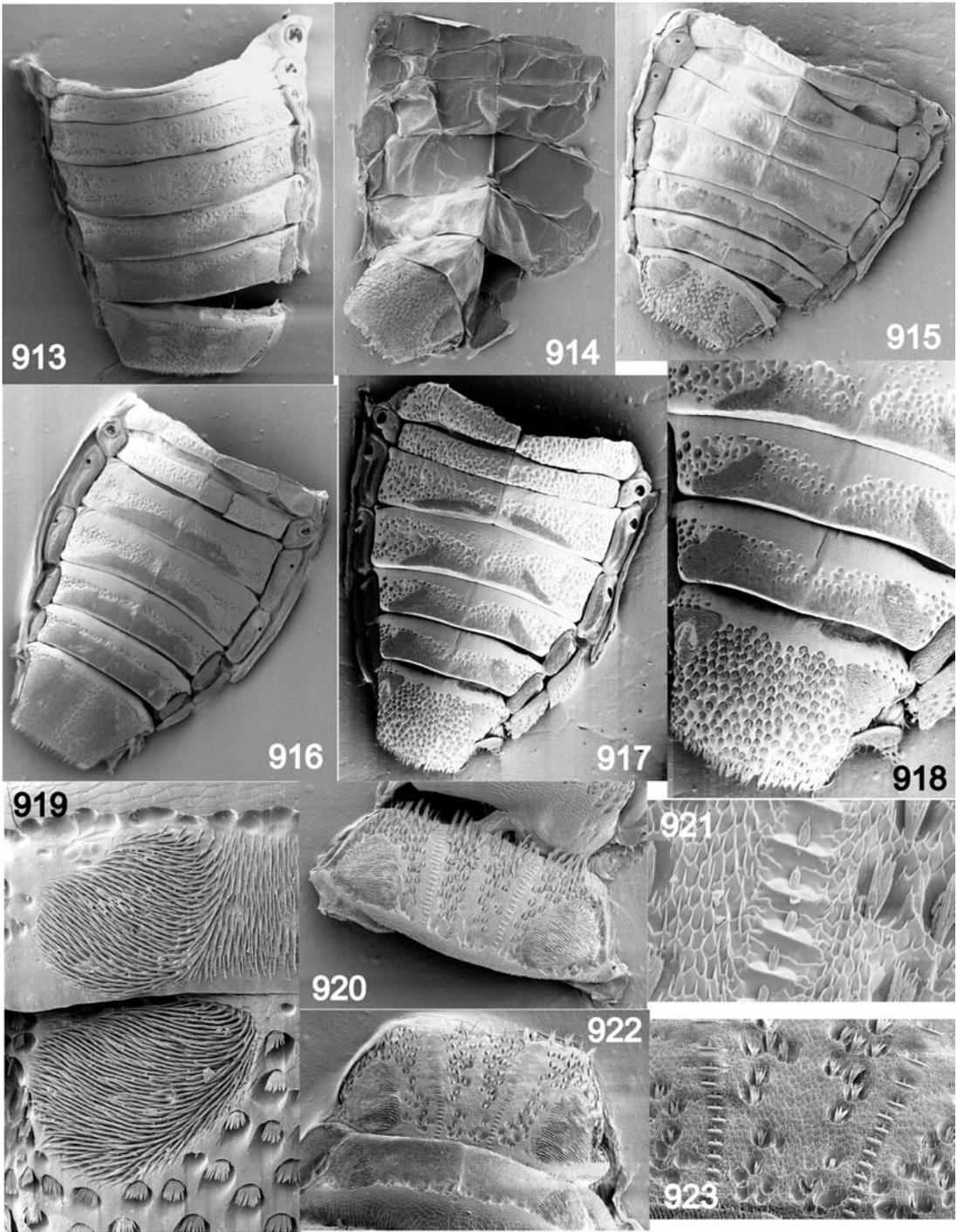
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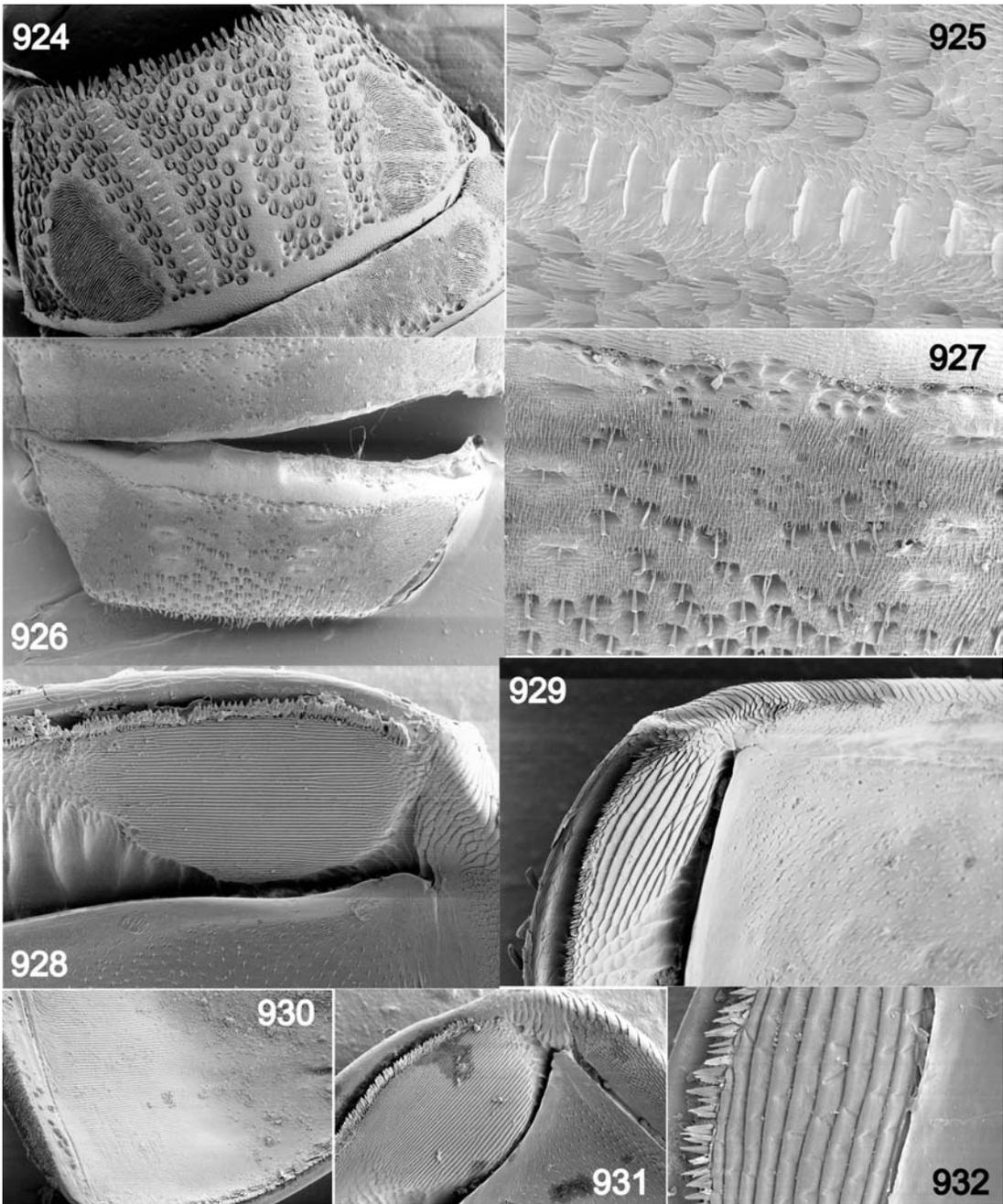


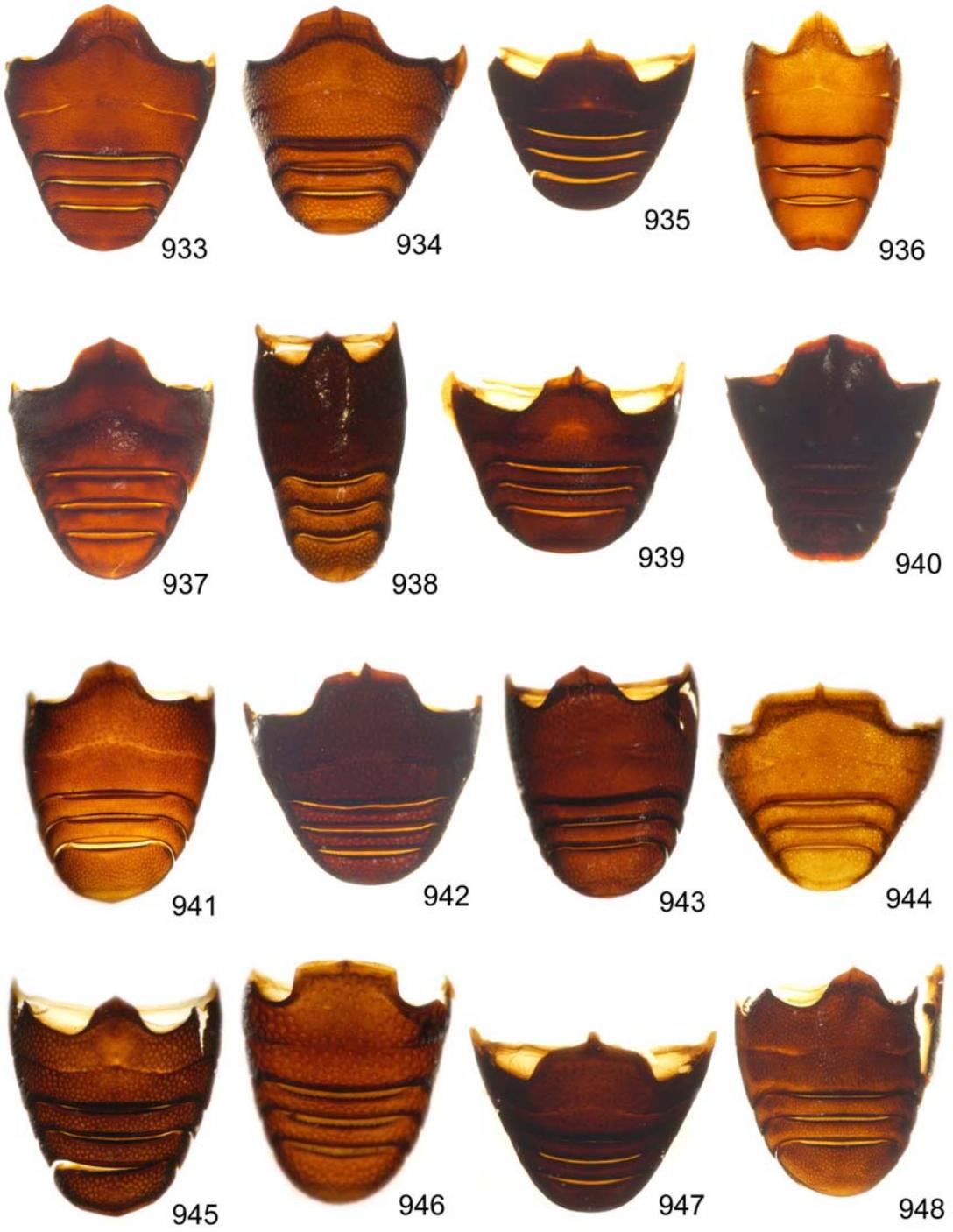
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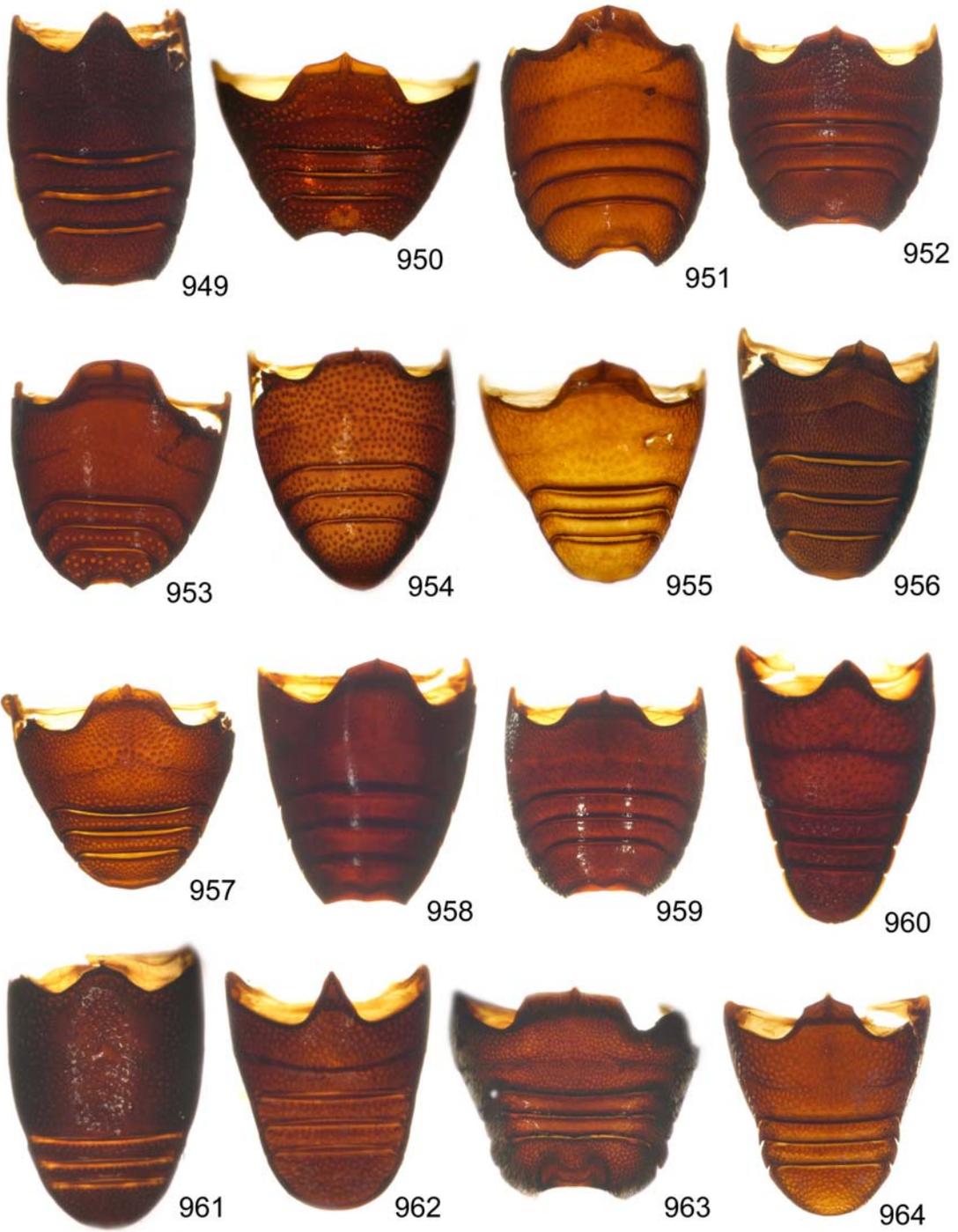


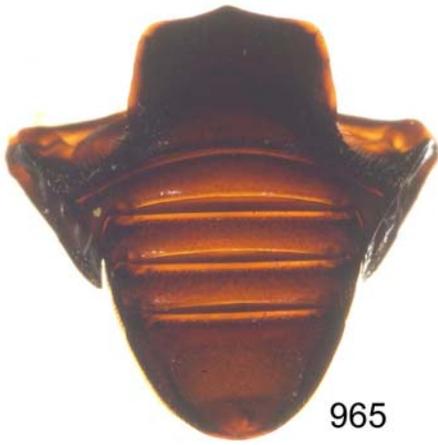
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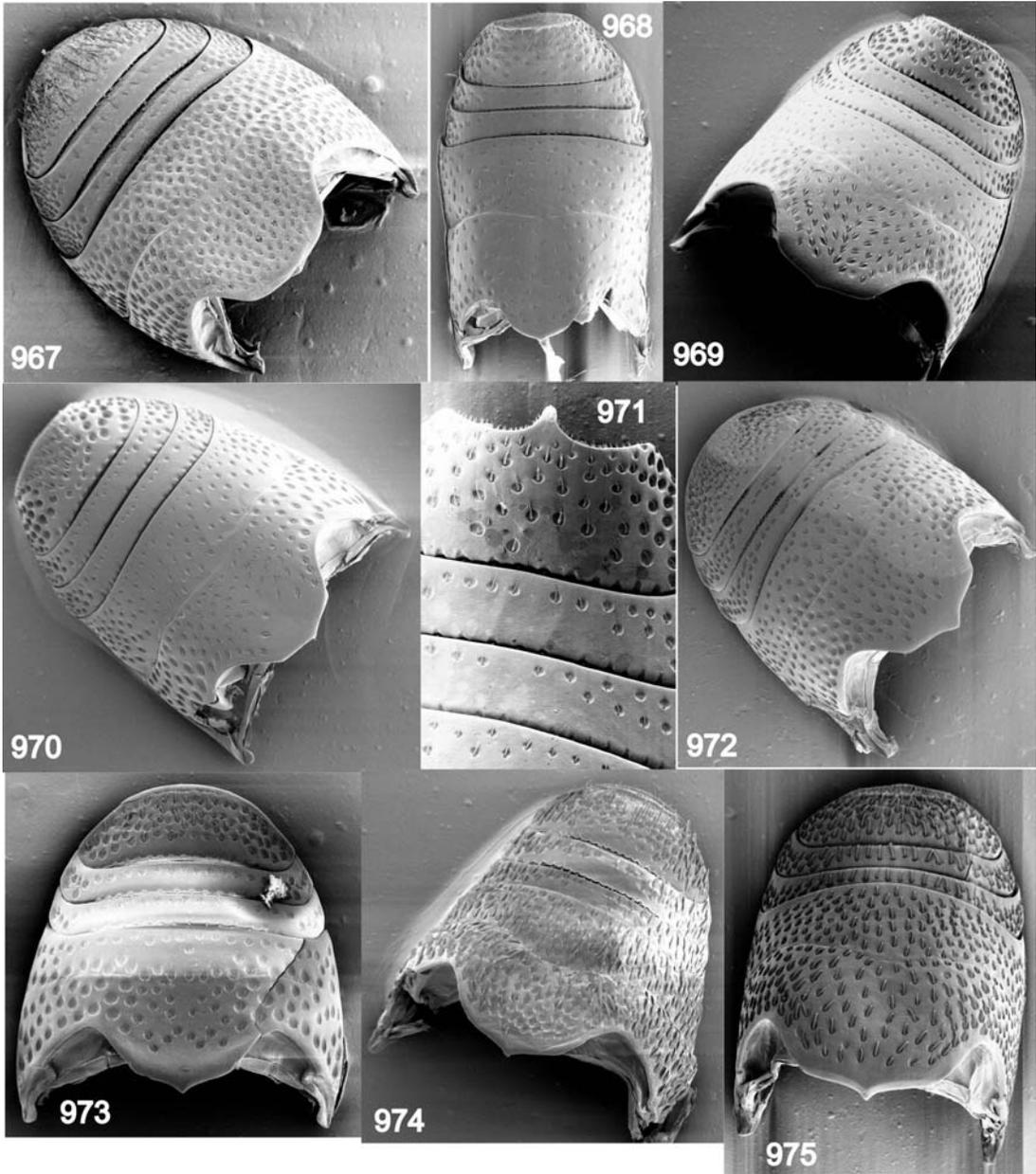


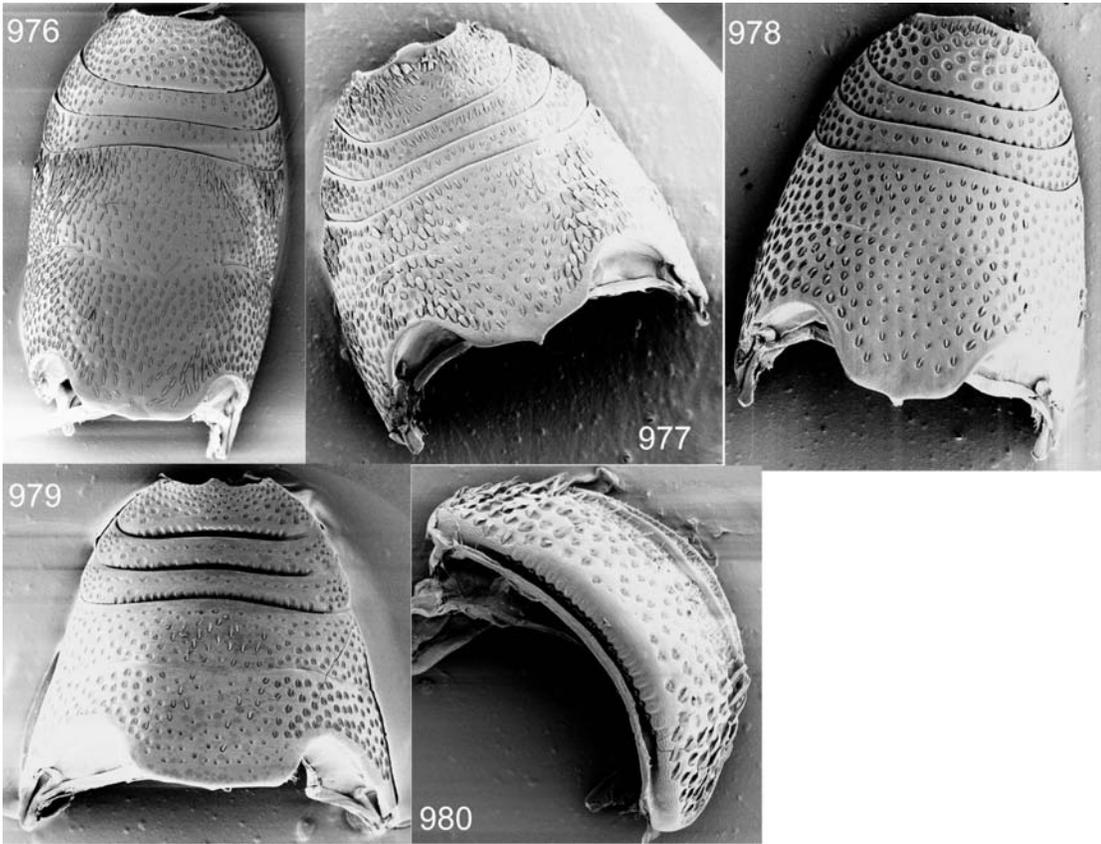


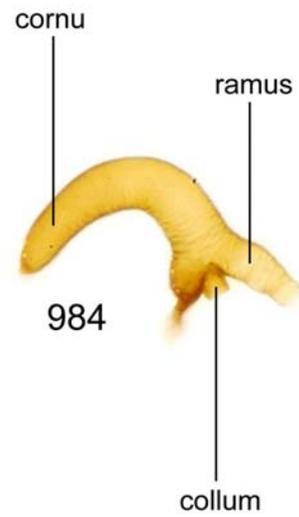
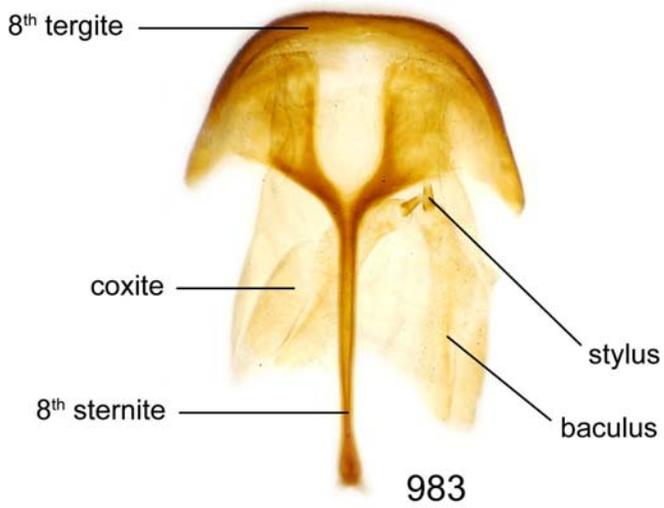
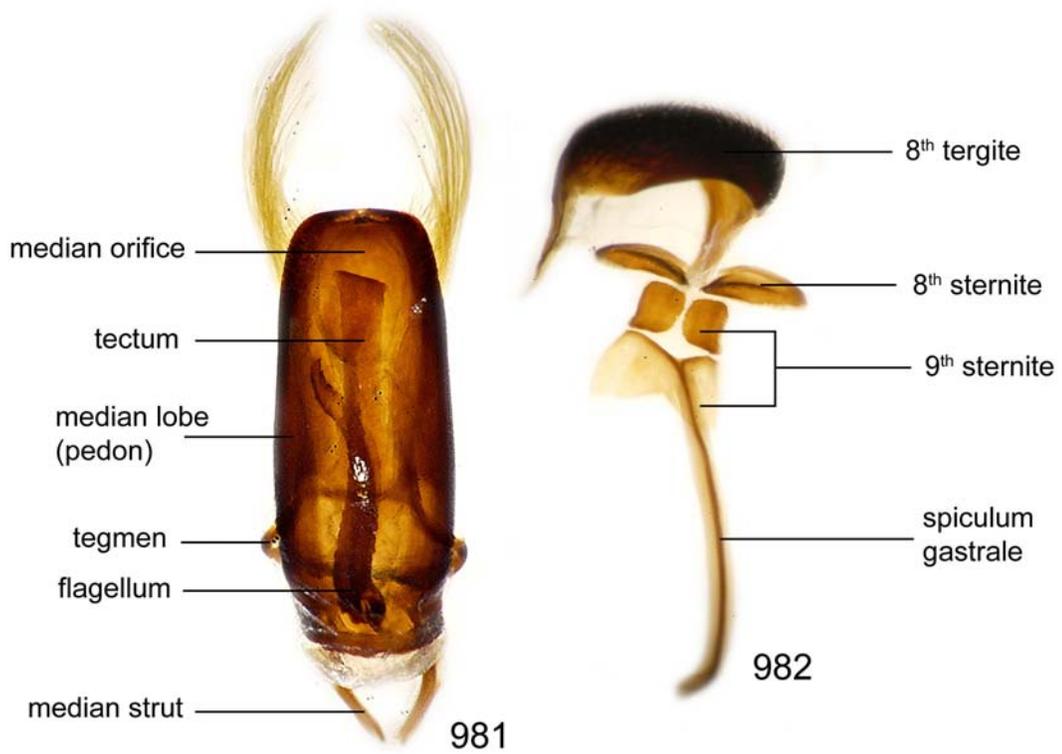
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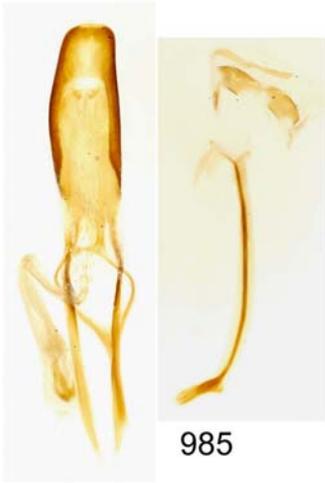


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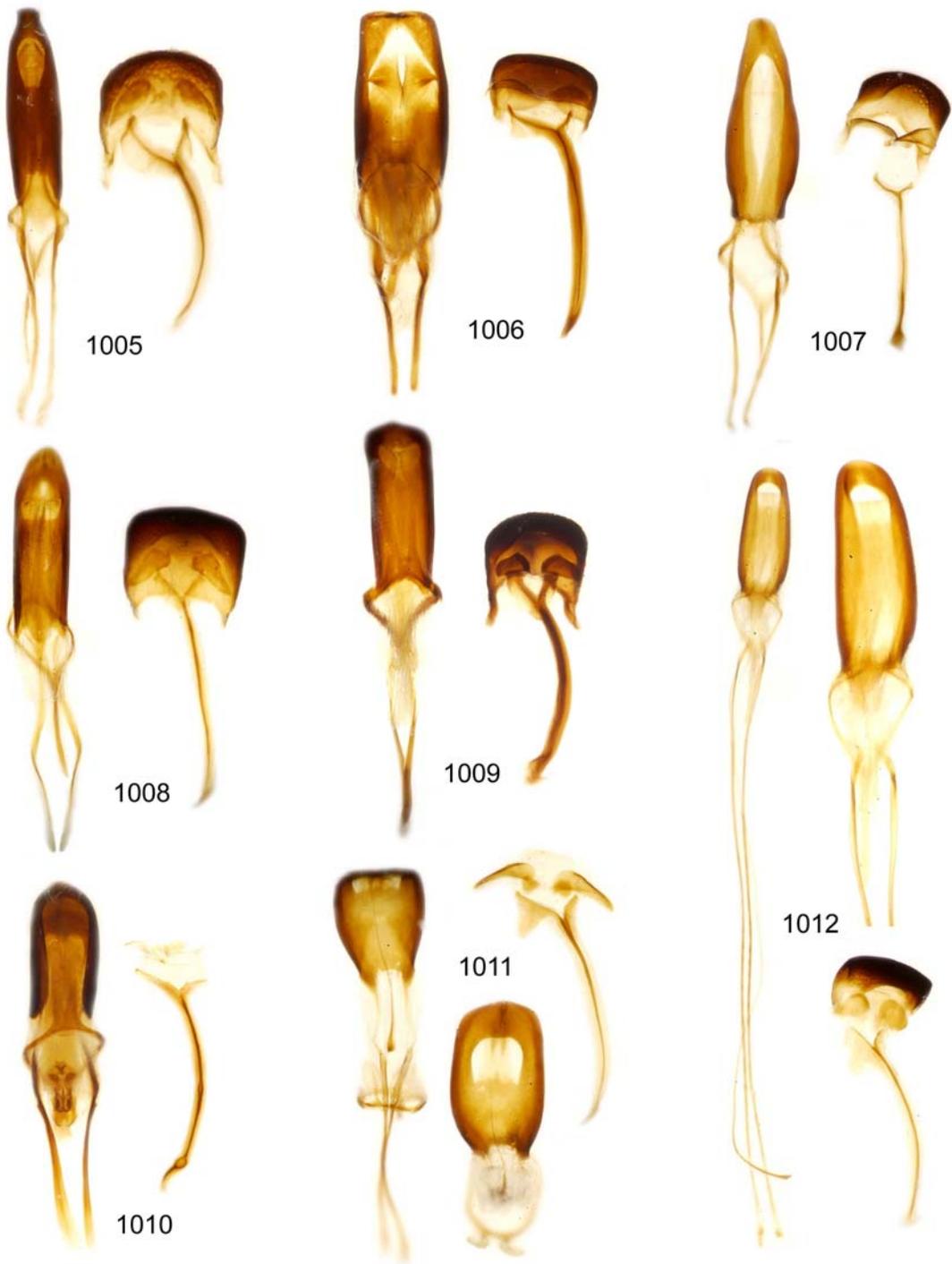


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## **Chapter II: Delimiting baridine evolution (Coleoptera: Curculionidae)**

### **Abstract**

Since the erection of the weevil subfamily Baridinae by Schoenherr in 1836, no phylogenetic hypothesis has been derived for this extraordinarily diverse group. This study provides the first phylogenetic results of Baridinae, including 301 taxa and 113 morphological characters. Despite fairly well-resolved results, indicating paraphyly of nearly all of the currently recognized intrasubfamily divisions, no change to the current classification is made. Even though groupings are proposed based on the final results, it is believed that more rigorous analyses need to be made prior to a re-evaluation of the current classification.

### **Introduction**

Currently there are approximately 550 genera belonging to the subfamily Baridinae (Morimoto and Yoshihara 1996), placed into 9 tribes and 17 subtribes (Alonso-Zarazaga and Lyal 1999). Although cosmopolitan in distribution, the greatest diversity of baridine weevils lies in the New World, particularly the Neotropics (Prena 2001). Indeed the morphological diversity within Baridinae is vast, but the number of natural groups, particularly at the generic level, is believed to be highly over-split and remains to be assessed. The major researchers to develop

baridine classification include Lacordaire (1863, 1866), Champion (1907), Hustache (1938), Casey (1892, 1920, 1922), Zherikhin and Gratshev (1995), and to somewhat a lesser extent, Pascoe (1889), Voss (1958), and LeConte and Horn (1978).

The subfamily was first erected by Schoenherr in 1836. Until the present, Baridinae has changed in both name and rank several times. Casey (1922) divided Barinae into 14 tribes in his treatment of the Brazilian fauna, Ambatini, Pantotelini, Cyrionichini, Optatini, Diorymerini, Coleomerini, Coelonertini, Centrinini, Limnobarini, Sonnetiini, Madarini, Eurhinini, Barini, Madopterini. This classification was quite dubious, owing to artificial groupings that were based on few characters of little importance when examined alone, such as inter-coxal distance and body shape. Casey, himself, admits that the limits between many of the tribes are indistinguishable, most likely due to his coarse examination of taxa and utilization of few characters.

Hustache's 1938 treatment divided Barinae (now Baridinae) into 7 tribes (Table 1).

**Table 1.** Classification of Barinae according to Hustache (1938).

Tribe	Subtribe
<b>Ambatini</b> Lacordaire	
<b>Peridinetini</b> Lacordaire	
<b>Pantotelini</b> Lacordaire	<b>Pantotelina</b> Lacordaire <b>Cyrionychina</b> Casey
<b>Optatini</b> Champion	
<b>Barini</b> LeConte	<b>Diorymerina</b> Jekel

	<b>Coleomerina</b> Casey
	<b>Coelonertina</b> Casey
	<b>Eurhinina</b> Lacordaire
	<b>Barina</b> LeConte
<b>Centrinini</b> Lacordaire	<b>Centrinina</b> Lacordaire
	<b>Madopterina</b> Lacordaire
	<b>Apostasimerina</b> Schoenherr
<b>Madarini</b> Jekel	<b>Lyteriida</b> Hustache
	<b>Leptoschoina</b> Lacordaire
	<b>Eutoxina</b> Champion
	<b>Madarina</b> Jekel
	<b>Barymerina</b> Lacordaire

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LeConte and Horn regarded Baridinae as a tribe within Curculionidae, Barini, and divided the tribe into 2 groups, Barides and Centrini, based on the North American fauna. Zherikhin and Egorov (1990) recognized Baridinae as containing 5 tribes, Baridini, Trigonocolini, Zygopini, Ceutorhynchini, and Oorbitini. This division was based on the presence of a longitudinal crest on the scutellar groove of the metanotum, a transverse carina along the hind margin of the pronotum, a strongly curved submarginal fold along the latero-ventral margin of the elytron, and the fusion of the metepimeron and the metepisternum. In a slightly later publication, Zherikhin and Gratshev (1995) proposed a similar classification as did Zherikhin and Egorov, but recognized Baridinae as a family, Barididae, and divided it into 4 subfamilies, Baridinae, Ceutorhynchinae, Trigonocolinae, and Zygopinae. They also proposed Brachyceridae as the possible sister-group to Barididae. This classification was based

largely on the examination of hind-wing characters, as well as prior hypotheses put forward by Zherikhin and Egorov. Although many of the hind-wing synapomorphies, proposed by Zherikhin and Gratshev, for Barididae are fairly precise, such as the cu-a crossvein always absent and 4A strongly reduced, most of them are not accurate as a result of poor taxon sampling, such as the absence of r-m in Baridinae (which can actually be present in a few genera). Oberprieler *et al.* (2007) follow the classification proposed by Zherikhin and Gratshev (1995), while also noting that this classification also brings together groups that share other features, such as the ascending metepisternum. They also mention, however, that none of the characters used by Zherikhin and Gratshev, nor by any previous authors who have proposed classifications of baridine weevils, have been tested in a phylogenetic analysis.

The current, most widely-accepted classification of Baridinae is based on Alonso-Zarazaga and Lyal (1999). It largely follows the classification system of Hustache (1938), and divides a total of 546 genera into 9 tribes (including 17 *incertae sedis* genera; Table 2).

**Table 2.** Current classification of Baridinae (*sensu* Alonso-Zarazaga and Lyal 1999).

Tribe	Subtribe
<b>Ambatini</b> Lacordaire	
<b>Anopsilini</b> Bondar	
<b>Baridini</b> Schoenherr	<b>Baridina</b> Schoenherr <b>Coelonertina</b> Casey <b>Coleomerina</b> Casey <b>Diorymerina</b> Jekel <b>Eurhinina</b> Lacordaire

<b>Madarini</b> Jekel	<b>Madarina</b> Jekel <b>Barymerina</b> Lacordaire <b>Eutoxina</b> Champion <b>Leptoschoinina</b> Lacordaire <b>Tonesiina</b> Alonso-Zarazaga & Lyal
<b>Madopterini</b> Lacordaire	<b>Apostasimerina</b> Lacordaire <b>Madopterina</b> Lacordaire <b>Thaliabaridina</b> Bondar <b>Torcina</b> Bondar <b>Zygobaridina</b> Pierce
<b>Nertinini</b> Voss <b>Optatini</b> Champion <b>Pantotelini</b> Lacordaire	<b>Cyrionychina</b> Casey <b>Pantotelina</b> Lacordaire
<b>Peridinetini</b> Lacordaire.	

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Despite the large size of the subfamily, the majority of genera are placed within Madopterini, Baridini, and Madarini, in succession.

Baridines are quite easily differentiated from most other weevil groups by their characteristic round shape and ascended mesepimeron; however, these traditional diagnostic characters certainly are not apomorphic to baridines only, and beyond the level of subfamily, baridine identification is difficult at best. Also, because there have been no phylogenetic studies completed to date for baridines, different classifications are being used simultaneously (Alonso-Zarazaga and Lyal 1999; Zherikhin and Egorov 1990; Zherikhin and Gratshev 1995; Oberprieler *et al.* 2007). Because there have been few comprehensive studies assessing character systems for baridine weevils, it is uncertain which classification depicts the evolution

of this group best. Although the baridines undoubtedly form a cohesive group, the delimitations of this group also remain uncertain. Due to the lack of phylogenetic structure in the subfamily, it seems of dire importance to begin the task of searching for diagnostic characters, testing these characters in a phylogenetic analysis, and ultimately working towards defining a framework for the taxa that compose a monophyletic Baridinae.

## **Materials and methods**

### *Taxon sampling* (Appendix I)

Following Alonso-Zarazaga and Lyal (1999), species were sampled from each of the 9 tribes and 17 subtribes in Baridinae, with a total of 283 baridine species, representing 231 genera, included in the analysis (Table 1). A total of 29 species were sampled for the outgroup, consisting of 12 subfamilies outside of Baridinae. Due to ambiguity in hypothesized sister-groups to Baridinae, a range of outgroups were included in attempt to produce a stronger inference (Nixon and Carpenter 1993). The final analysis included a total of 301 taxa (Appendix I). Outgroup selection was based on phylogenies produced by Marvaldi *et al.* (2002), and previous baridine classifications by Zherikhin and Egorov (1990), and Zherikhin and Gratshev (1995).

Taxa were borrowed from the following institutions:

USNM – National Museum of Natural History (United States National Museum),  
Smithsonian Institution, Washington, D.C., USA.

SEMC – Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA.

CMNC – Canadian Museum of Nature, Ottawa, Canada.

IZCAS – Institute of Zoology, Chinese Academy of Sciences, Beijing, China.

CAS – California Academy of Sciences, San Francisco, California, USA.

FMNH – Field Museum of Natural History, Chicago, Illinois, USA.

### *Specimen dissection and preparation*

Body and genitalia dissection:

All dissections were performed using an Olympus SZ60 microscope. For each taxon in which multiple specimens were available, a full-body dissection was done for the male and abdominal dissection for the female (including genitalia). For taxa in which only holotype or paratypes were available (Table 2), no dissections were made and only external characters were coded. In some taxa, full-body dissections were not permitted by the borrowing institution and thus only abdominal dissections were done for those males.

For body dissections, specimens were first relaxed by soaking them in warm water for ~10-15 minutes, the duration depending on the size of the specimen. The head, pro-thorax, meso- meta-thorax complex, and abdomen were then separated. Before digesting any internal tissues, the elytra and hind wings were removed and stored in glycerin, as digesting was not required for these parts. The remaining dissected parts were digested in a weak (~10%) KOH solution for 10-15 minutes,

again depending on the size of the specimen. Following digestion, all remaining internal tissues were removed and the sclerotized parts cleaned. The meso- and meta-nota were separated from the mesepimera, metepisterna, and metepimera, and subsequently separated from each other. The terga were separated from the sterna along one side, and the genitalia removed together with the 8<sup>th</sup> terga. After dissections were completed, all parts were stored in glycerin.

#### Mouthpart dissection:

Following dissection of the body, the head was digested further in 10% KOH for ~15-30 minutes, depending on specimen size. Under the microscope, the head was placed with the ventral side facing upwards. One pair of fine-tipped forceps was used to stabilize the rostrum while another pair was used to gently separate the postmentum of the labium from the submentum of the rostrum. The maxilla were subsequently removed in a similar fashion, separating them from the submentum at the cardo-submentum junction. The mandibles were then removed, separating them from the postcoila.

#### Hind wing and mouthpart preparation:

Following dissection of the hind wing from the thorax and mouthparts from the rostrum, these parts were then mounted on glass microscope slides for further examination. One hind wing from each body dissection was mounted on a slide in Euparal mounting medium. The labium, maxilla, and mandibles from the same

specimen were mounted on the same slide as the hind wing, but in Canadian balsam. The slide was then placed on a slide warmer to dry the mounting mediums.

#### Scanning Electron Microscopy:

All SEM images were captured using a LEO 1550 FESEM. Specimens were mounted on an SEM stub using Leit-C-Plast adhesive and an isopropanol-based colloidal graphite. Whole specimens were placed on insect pins or glued to paper points, securing the pin or point on an SEM stub using Leit-C-Plast. Dissected parts were mounted on a stub by securing them with a thin layer of colloidal graphite. After the desired parts were mounted, coating was performed using gold.

### **Character discussion**

#### *General appearance:*

#### **0. Adult body shape, dorsal view:**

elongate, cylindrical - length  $> 2x$  width (0); round, spherical - length  $2x$  width (or less) (1)

The body of the adult ranges from a general round, subcircular shape, as viewed dorsally (Fig. 2), to more elongate (Fig. 1).

#### **1. adult body shape, lateral view:**

round (0); dorso-ventrally compressed (1)

In the lateral view, adult body shape can be wide or round (Figs. 3, 4) or dorso-ventrally compressed (Fig. 5). This character is independent of body shape in the dorsal view.

**2. body, overall shape:**

spherical, round (0); not spherical (1)

In the lateral view, adult body shape may appear globose (Fig. 9). This shape is an extreme case of the round state in char. 1, where the dorsal surface, including the pronotum, become highly convex and angled.

**3. pronotum-body size ratio:**

pronotum narrower than abdomen (shoulders of elytra wide) (0); pronotum flush with abdomen, smooth, round (1); pronotum wider than abdomen (2)

In the dorsal view, the relationship between pronotum size and abdomen (elytra) size is observed in 3 conditions: the pronotum may be narrower than the elytra (Fig. 6), it may be wider than the elytra (Fig. 8), or it may be flush with the elytra, in which the lateral margins of the pronotum and elytra are smooth (Fig. 7).

**4. adult body vestiture:**

with few scales (glabrous) (0); with scales (many, hairy) (1)

This character is quite labile in its states. Although there tends to be a rather continuous range of scale-coverage on baridine adults, from few scales to a thick

covering, many taxa may also be relatively glabrous on most of their derm, while dense scale patches may exist in only a few specific locations. Entirely glabrous baridine species are relatively rare, and so in terms of this study, glabrous is interpreted as possessing few scales or minute scales that may be present in each puncture on the derm.

*Rostrum:*

**5. rostrum, base - head-rostrum junction:**

smooth, rostrum flush with outline of head in lateral view (0); a groove/bump separating rostrum from head (1)

The junction at which the rostrum intersects the head is often produced into a small cleft, in which the margins of the head and rostrum abruptly meet (Fig. 10), but it may be smooth and flush when the dorsal margin of the rostrum connects to the head at a higher position (Fig. 11). In some cases it is difficult to distinguish these two states, because this junction may be slightly concave, alluding to a reduced groove, but is smooth.

**6. rostrum, setae along ventral margin (males only):**

absent (0); present (1)

Elongate setae along the apico-ventral margin of the rostrum are only present in a few taxa in Baridinae, and they are only present in males (Fig. 13).

**7. rostrum, shape, lateral view:**

enlarged basally (0); width sub-equal along entire length (1); wide basally, gradually narrowing apically (2)

While most taxa possess a rostrum that is wide basally and gradually narrows apically (Fig. 11), some have a rostrum that is expanded or enlarged basally, abruptly narrowing later, or entirely cylindrical and subequal (Fig. 12).

**8. rostrum, shape, lateral view:**

robust, short (0); narrow, long (1)

This character can be particularly ambiguous given the large amount of variation in rostrum lengths and widths. In general, a short rostrum is much shorter than the longitudinal length of the pronotum, usually  $\frac{3}{4}$ - $\frac{1}{2}$  the length of the pronotum. Long generally applies to a rostrum which is equal in length to or longer than the pronotum.

**9. rostrum, curvature:**

straight (0); broadly curved (1); strongly curved (2)

Characterizing the curvature of the rostrum can be quite difficult. No ambiguity is faced when the rostrum is straight or sublinear. The point at which the rostrum changes from being broadly curved to strongly curved usually is not obscure. Most genera possess a rostrum which is broadly curved. Rostra which are strongly

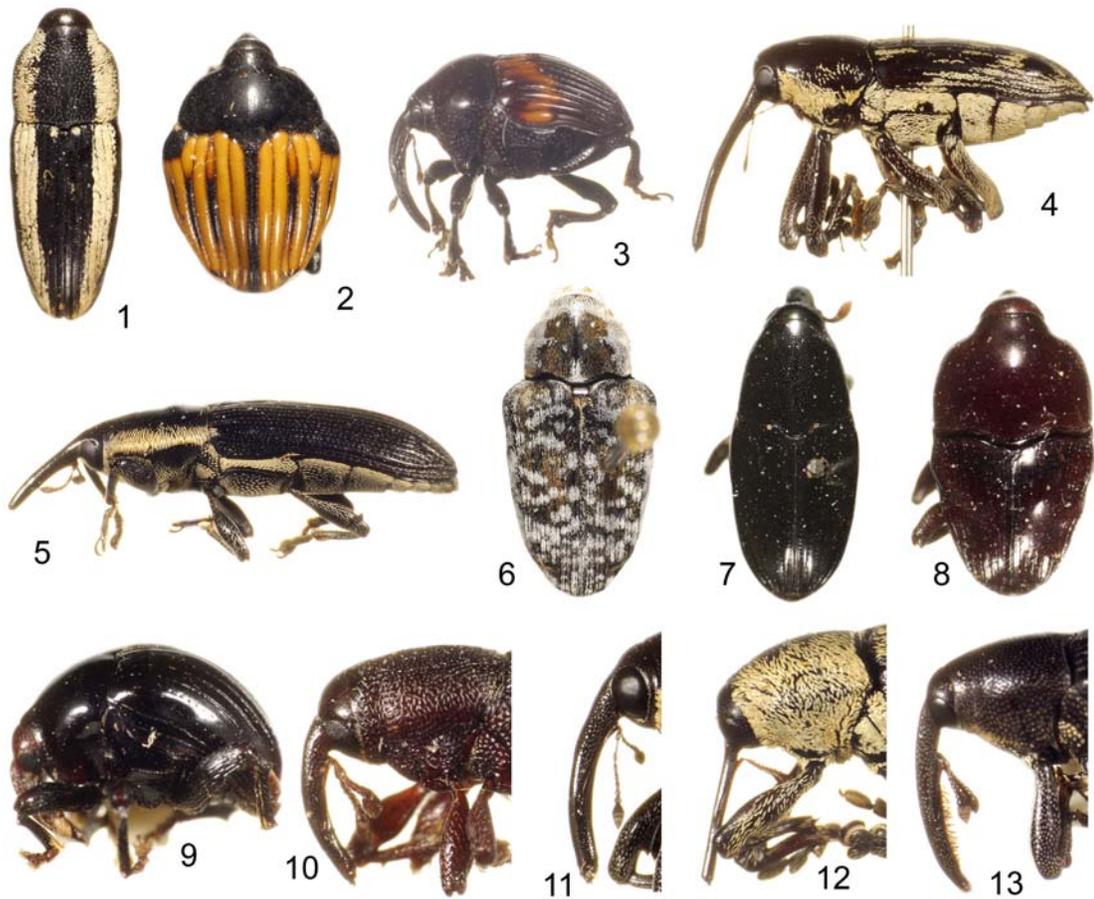
curved often are not elongate or greater in length than that of the pronotum, and the apex of the rostrum nearly is recurved underneath the prosternum in habitus.

*Antenna:*

**10. antenna, insertion:**

along basal half (0); along apical half (1); at middle (2)

Antennal insertion along the basal or apical half is not difficult to distinguish; however, insertion along the middle usually allows for a small error range. Thus, antennae which may be inserted slightly or immediately before or after the middle are also characterized as being inserted at the middle.



**11. antenna, number of funicular articles:**

6 (0); 7 (1); 3 (2)

The number of funicular articles in Baridinae is always 6, while outgroups possess varying numbers.

**12. antenna, number of club articles:**

4 (0); 3 (1)

The number of club articles in Baridinae varies between 3 (Figs. 16, 17) and 4 (Figs. 14, 15), as do the outgroups.

**13. antenna, club:**

round, globous, compact (0); elongate (1); normal (2); club absent, moniliform articles (3)

All baridines possess an antennal club. The shape of the club can be summarized into 3 forms: all of the articles may be short and compact (Figs. 14-17); the articles may be elongate, an extreme state of the length of the articles; somewhere in between these two states is the typical form of the baridine club, in which the articles typically are not compacted but are slightly longer. Only select outgroups may not possess a club.

**14. antenna, funicle-club complex:**

distinctly separate (club large, funicle narrower) (0); uniform (club + funicle similar in width) (1); uniform (club + funicle similar in width), more compact (2)

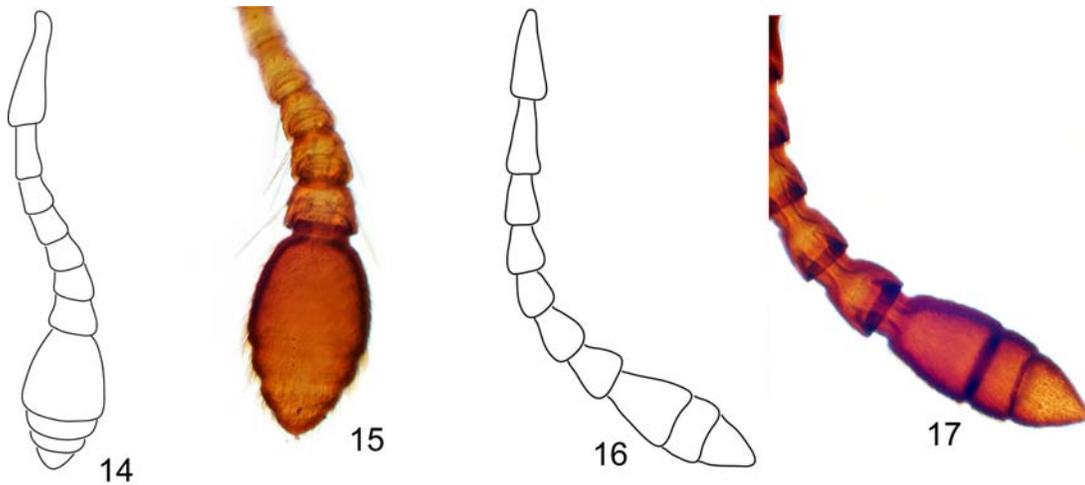
Associated with the club condition, though not dependent, is the shape form by the association of the funicle and club. Often when the club articles are short and compact, though not always, the funicular articles may also be compact and relatively wide, approximately similar in width to the club and forming a smooth lateral margin where at the funicle-club junction (Fig. 14). This condition may be slightly reduced, where the articles are more loosely compact and do not form a smooth margin upon

intersection with the club (Fig. 16). The funicular articles may also be somewhat moniliform, elongate (not compact), and narrow, in which the club often is notably larger than the funicle.

**15. antenna, length of club segments:**

short (0); long (1)

This character often highly correlates with char. 13, though it is useful in distinguishing clubs with short or long articles. A compact club always is composed of short articles (Fig. 14), and an elongate club always is composed of long articles; however, the club of intermediate size may be composed of short or long articles.



**16. antenna, scape:**

close to but not reaching anterior margin of compound eye (0); surpassing anterior margin of compound eye (1); distant from anterior margin of compound eye (2); touching eye (3)

Baridinae always possess a scape which does not surpass the anterior margin of the eye. Variation is observed in how distant or close it is situated from the eye. When distant from the eye, it always reaches within the basal half of the rostrum and is never further. The scape typically is falls close to the eye but not touching it, and in some taxa it actually meets the surface of the compound eye's anterior margin.

*Mouthparts:*

**17. mandibles, dentition:**

monodentate (molar region fused with primary incisor) (0); "monodentate", with a small tooth near apex of larger tooth (1); bidentate, with 2 large, apical teeth, and a molar region (2); tridentate, with 3 large, apical teeth, and a molar region (3); bidentate without distinct molar region (4); tridentate without distinct molar region (5); monodentate without distinct molar region (6)

The mandibles in Baridinae are divided into an incisor region and a molar region. Mandibles may display two forms of monodentation, one in which the mandible possesses a distinct molar region (Fig. 18-22), and the other which may have the molar region fused with the incisor (Fig. 23) and the dentation lost. Mandibles may also bear two incisors (Fig. 21) or three incisors (Figs. 18-20, 22).

Only outgroups have mandibles which may lose the molar region or may possess mandibles in which molar and incisor regions are indistinct.

**18. mandibles, incisor size:**

primary incisor largest (0); secondary incisor largest (1); teeth subequal (2)

Regarding incisor size, the primary incisor may be largest in both forms of monodontate mandibles (Fig. 23) or in bidentate (Fig. 21) or tridentate mandibles (Figs. 18, 22). In bidentate or tridentate mandibles, the secondary incisor may be largest (Fig. 20), or the teeth may be subequal in size (Fig. 19). The relative size of the incisors may be subject to error in some cases.

**19. mandible, shape:**

linear (0); curved (1)

This character indicates direction and orientation of the primary incisor. The primary incisor may be oriented linearly in mono-, bi-, or tridentate mandibles (Figs. 22, 23). The primary incisor is always linear in monodontate mandibles, but may be curved in bi- or tridentate mandibles (Figs. 18-21).

**20. maxilla, palpiger - setae along central region:**

absent (0); present, many arranged in a bunch (1); present, many arranged in a horizontal line (2); present, few restricted to outer corner (3)

The orientation of setae on the palpiger may be in a distinct, transverse line (Figs. 24, 25), a dense, random grouping throughout the palpiger (Fig. 26), or a sparse, small grouping largely restricted to the antero-lateral margin (Figs. 27, 28).

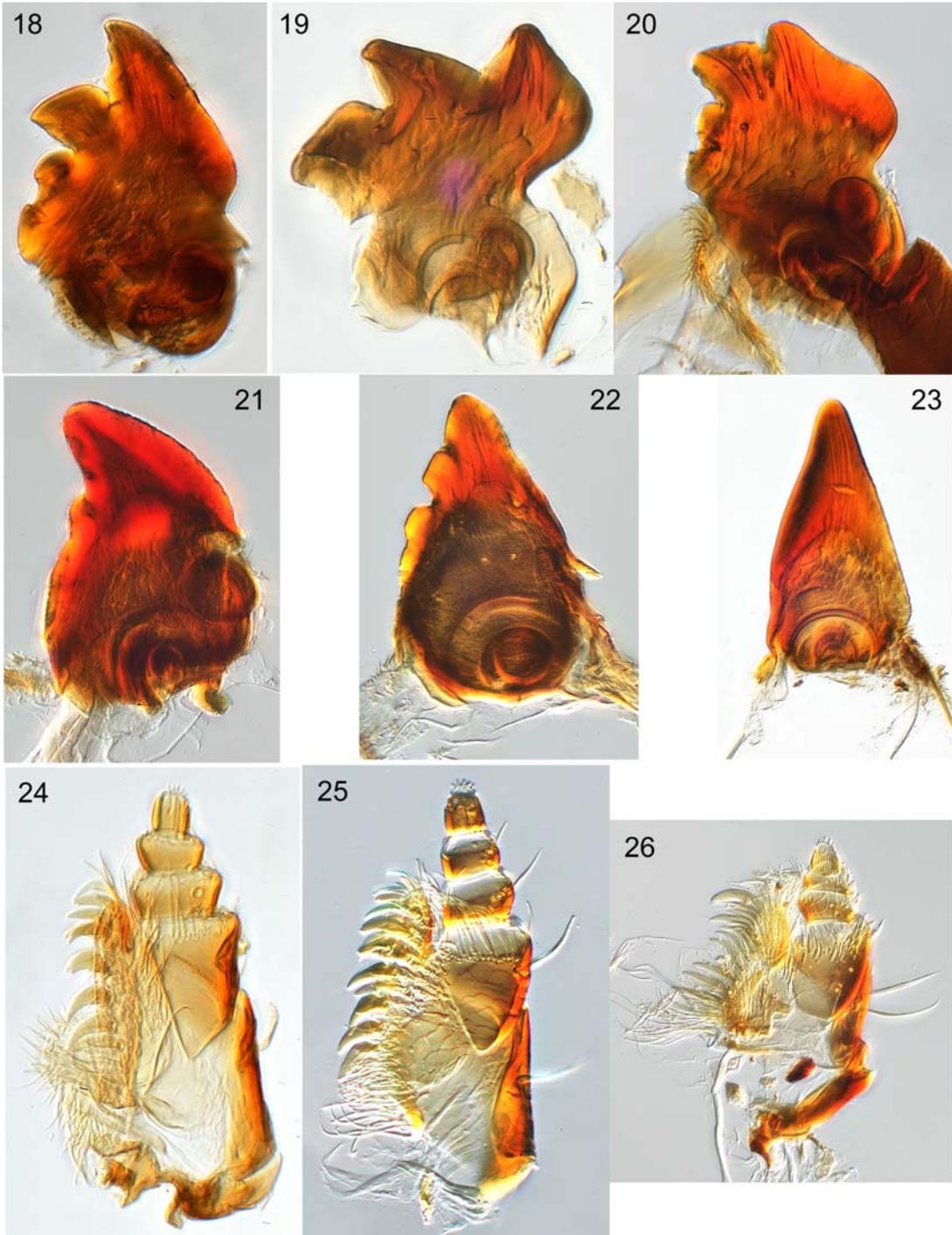
**21. labium, prementum - setae near distal margin:**

setae arranged in a bunch (0); setae arranged in a horizontal line (1); absent (2)

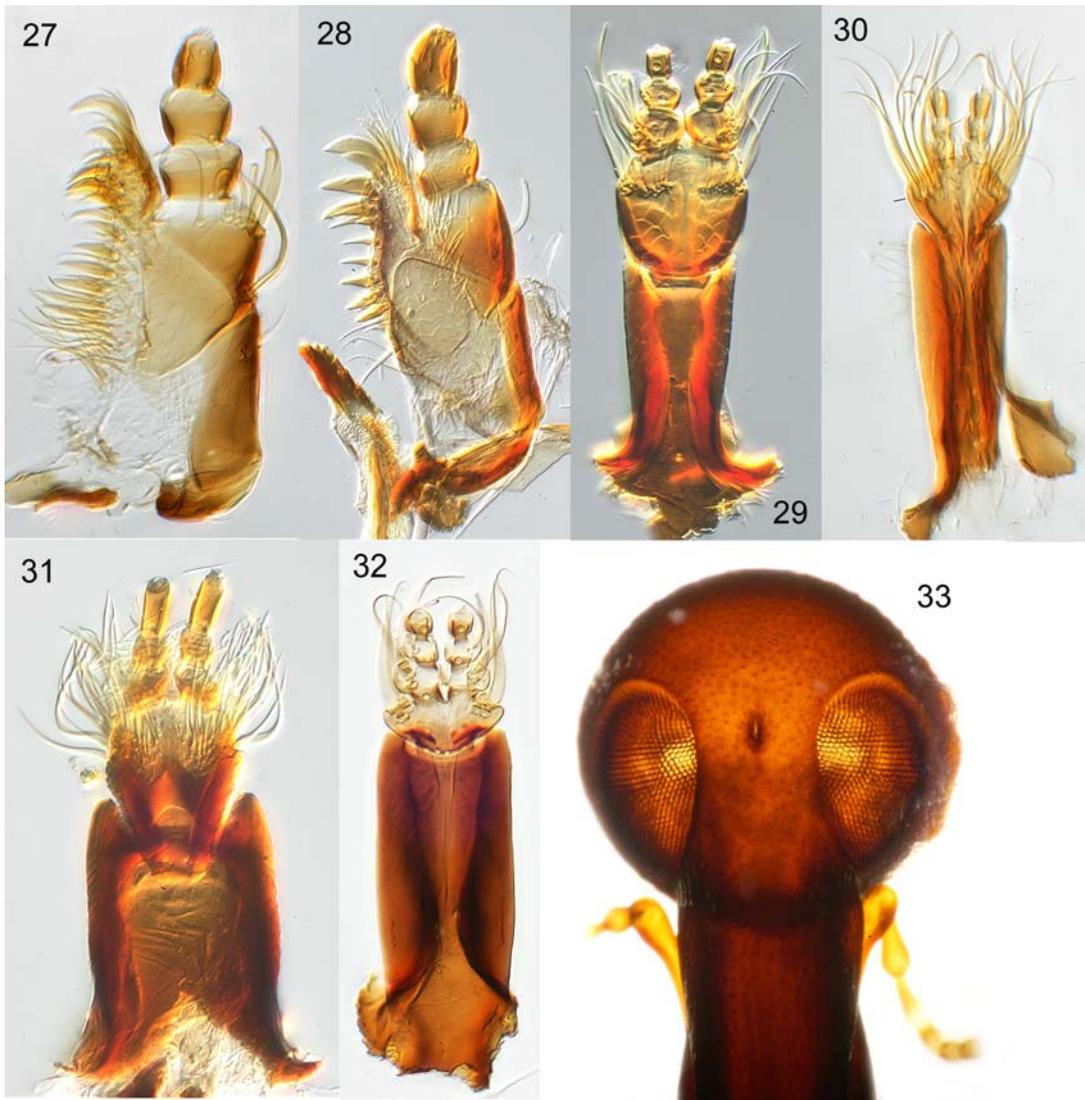
Similar to the maxilla, setal orientation may be in a distinct, transverse line (Fig. 29, 30) or randomly scattered, forming no specific orientation (Fig. 31, 32).

**22. labium:**

palps short, base large (0); palps long, base small (1); palps highly reduced, base large (2); palps highly reduced, base normal (3)



Although there is much variation in palpal length, baridines generally possess a fairly short labial palpus (in relation to the size of the postmentum), however many genera also possess shortened palpal segments, which may or may not be accompanied by an enlargement of the postmentum, or slightly elongate palpal segments, which may or may not be accompanied by a reduction of the postmentum.



*Head:*

**23. head, rostrum - foramen between eyes on frons:**

present (0); absent (1)

In most baridines, the frons is relatively smooth (except for the punctures), but some taxa possess a small hole/foramen at the center of the frons (Fig. 33).

**24. compound eyes:**

elongate, along antero-ventral surface (0); round, large, along anterior surface (1); teardrop-like, large, along anterior surface (2); round, bulging, along antero-ventral surface (3); round, along antero-ventral surface (4)

The majority of baridines have an elongate compound eye. In many outgroups, and in a few baridines, the eye may be round or sub-circular. Also in the outgroups, the eyes may be teardrop-shaped (Conoderinae) or round and bulging from the head (Ceutorhynchinae).

*Prothorax:*

**25. prothorax:**

normal, proportional to abdomen (0); enlarged (1)

The prothorax may be proportional in size to the abdomen (and elytra), often smaller than the abdomen (Figs. 6, 7), or it may be enlarged (Fig. 8).

**26. thorax, pronotum - puncture collar near anterior margin:**

absent (0); present, with small punctures (1); present, with large punctures (2)

Along the collar, particularly in baridines, there is a row of punctures. The punctures may be enlarged and deep (Figs. 34, 35) or small and reduced in size and depth (Fig. 36). In a restricted number of baridines, but mostly in the outgroup, this puncture collar is often absent.

**27. thorax, prosternal horns in males:**

present, long, with invagination simple (0); absent (1); present, with invagination bifurcate (2); present, long, with invagination reduced/absent (3); present, horns very reduced, invagination reduced/absent (4); present, horns fused (with invagination simple) (5)

Often associated with the prosternal horns in males (Fig. 37) is a deep invagination between the horns (Fig. 38). This invagination may be simple (Fig. 39), bifurcate (Fig. 40), or may be reduced in size to absent (Figs. 43, 45). The size of the horns also varies, from short (Fig. 42) to long (Figs. 41, 44), as does their structure.

**28. thorax, pronotum - longitudinal smooth line along middle of pronotum:**

absent, punctures scattered evenly throughout pronotal surface (0); present (1)

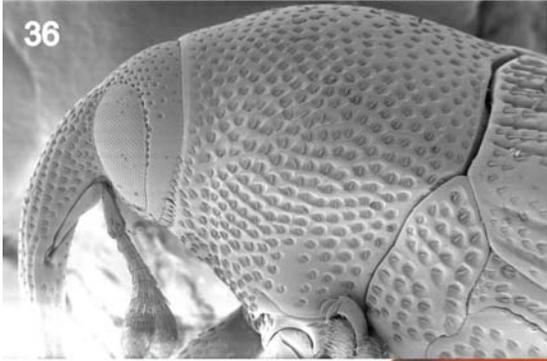
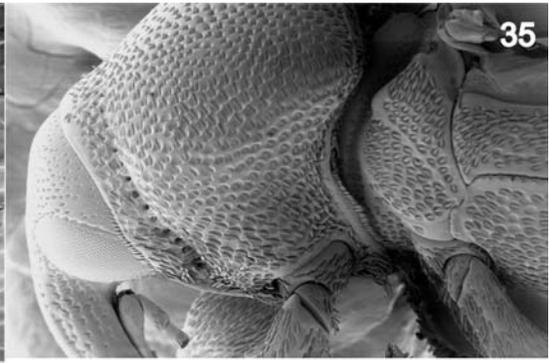
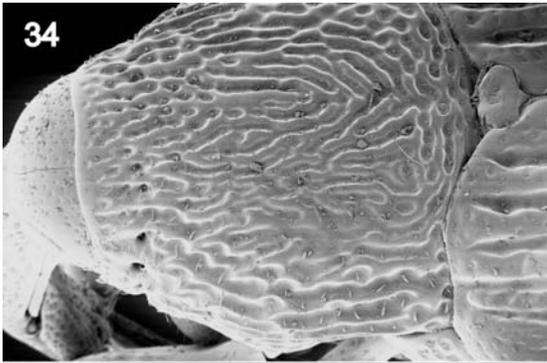
The majority of baridines possess a longitudinal smooth line along the middle of the pronotum which is absent of punctures. This line may be present (Fig. 47) or absent (Fig. 46).

**29. thorax, pronotum - mid-dorsal hump:**

absent (0); present (1)

The pronotum may have a produced swelling (Fig. 48), although it often is not present.

**30. thorax, pronotum - vestiture (scales):**



absent (0); present, only along outer margins, with middle bare (1); present, evenly distributed along surface (2)

The vestiture on the pronotum may be such that scales are evenly distributed along the surface or are restricted to the lateral margins.

**31. thorax, pronotum – sculpturing:**

round punctures (0); elongate ridges (1)

Punctures on the pronotum usually are round or elliptical (Fig. 36), though sometimes they form irregular, longitudinal ridges (Fig. 34).

**32. thorax, pronotum - shape of posterior margin:**

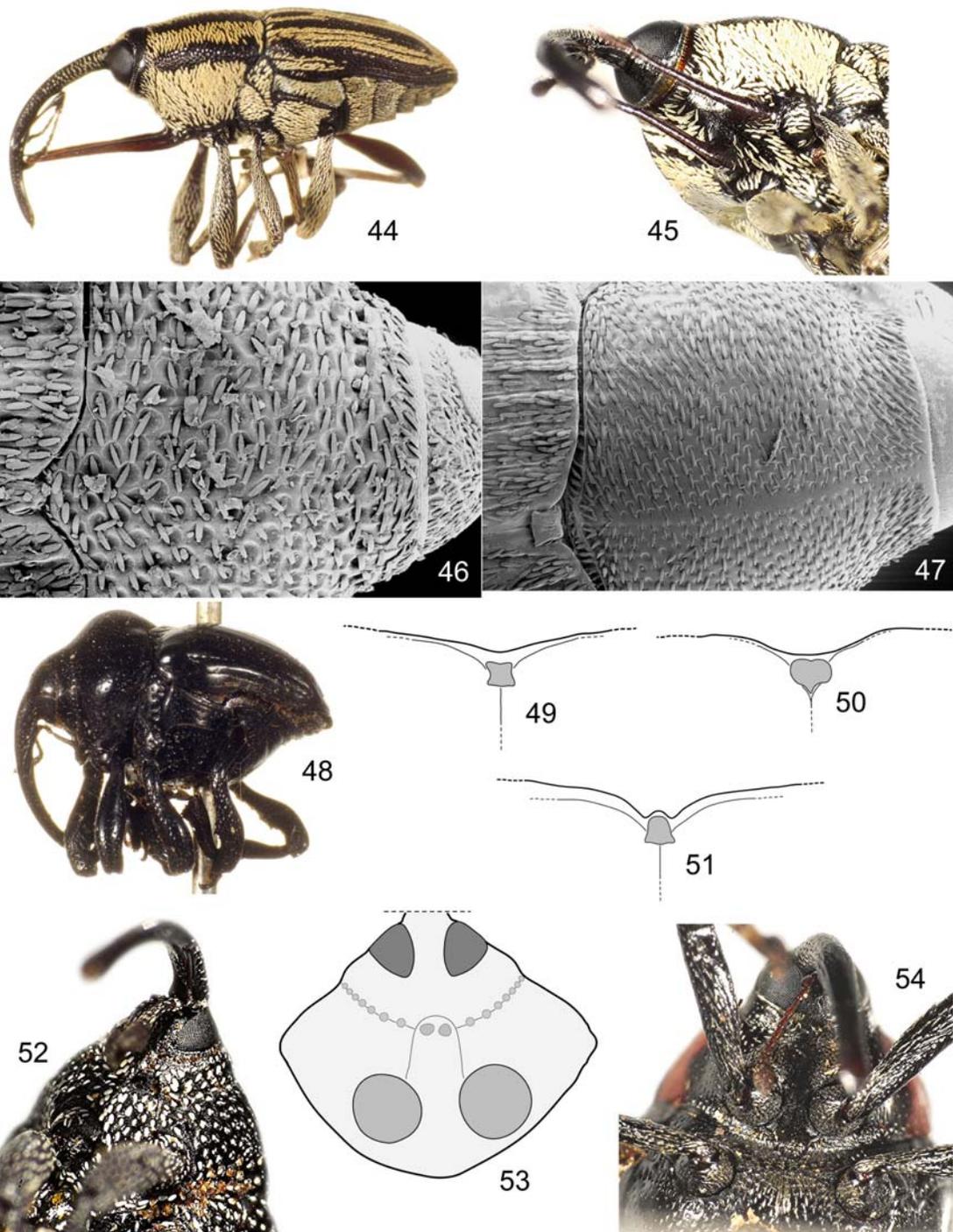
broadly round, convex (no protrusion at middle) (0); convex protrusion at middle (1); convex protrusion at middle - protrusion with concavity (2)

The posterior margin of the pronotum typically has a convex protrusion (Fig. 50) which may have a small concavity in the center (Fig. 51). Many outgroup taxa, including a few baridines, possess a fairly straight posterior margin (Fig. 49).

**33. thorax, prosternum - ventral canal for reception of rostrum:**

present (0); absent (1); only shallow depression (2)

The prosternum may possess a clearly-defined ventral canal or it may be absent. Sometimes, however, there is a shallow depression on the prosternum which may be indicative of a highly reduced canal.



34. thorax, prosternum - ventral depression along collar:

present (0); absent (1)

This depression is present in most taxa and is accompanied by small, lateral carina (Figs. 52, 53).

**35. thorax, prosternum - holes along side of ventral collar depression:**

present (0); absent (1)

When a puncture collar is present, the ventral-most pair of punctures may be particularly enlarged and deep.

**36. thorax, mesosternal process:**

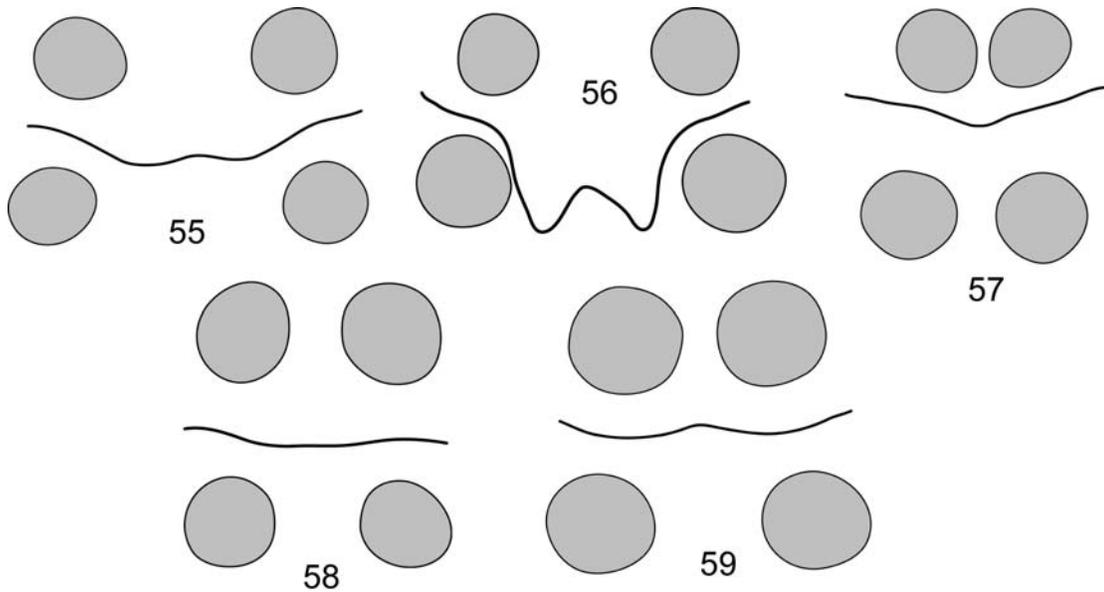
reduced (0); developed, quadrate, posterior margin straight (1); developed, V-shaped (2); developed, posterior margin with slight concavity (3); with small notch, quadrate (4); pointed (5); reduced (6)

The mesosternal process (Fig. 54) may be produced to quadrate with the posterior margin straight or concave (Figs. 55, 59), V-shaped (Fig. 56), with a small, median notch, pointed (Fig. 57), or reduced and relatively straight (Fig. 58).

*Coxae:*

**37. pro-coxae, inter-coxal distance:**

pro-coxae separated by < 1x diameter of coxa (0); pro-coxae separated by ~1x diameter of coxa (1); pro-coxae separated by >1x diameter of coxa (2); pro-coxae touching (3)



**38. meso-coxae, inter-coxal distance:**

pro-coxae separated by  $<1x$  diameter of coxa (0); pro-coxae separated by  $\sim 1x$  diameter of coxa (1); pro-coxae separated by  $>1x$  diameter of coxa (2)

**39. meta-coxae, inter-coxal distance:**

pro-coxae separated by  $\sim 1x$  diameter of coxa (0); pro-coxae separated by  $>1x$  diameter of coxa (1); pro-coxae separated by  $<1x$  diameter of coxa (2)

*Thorax:*

**40. thorax, mesosternal concavity for reception of rostrum:**

absent (0); present (1)

When a ventral canal is present in baridines, it is only present on the prosternum and never reaches the mesosternum. Only outgroup taxa have this character present.

**41. thorax, mesepimeron:**

not ascended (not visible from dorsad) (0); ascended (visible from dorsad) (1)

**42. thorax, sclerolepidia:**

absent (0); present (1); present, reduced/very small (2)

When sclerolepidia are present, they may be relatively large and noticeable or highly reduced (this latter state usually occurs when the derm is largely glabrous).

**43. thorax, sclerolepidia – shape:**

flat, small (0); projecting, large (1); absent (2); feather-like, hair-like (3); multifurcate, stringy (4)

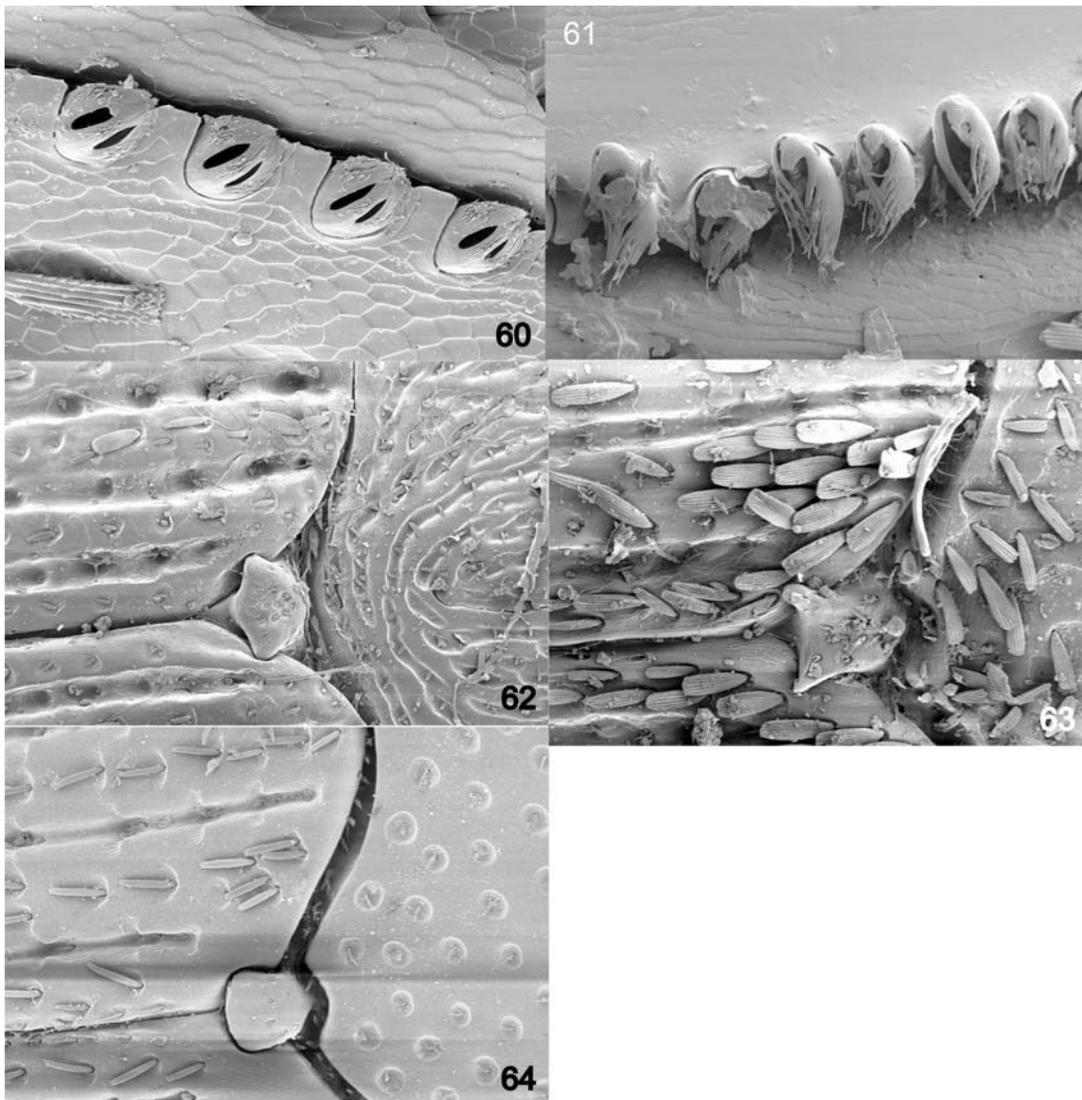
Only baridines possess the sclerolepidia of states 0 (Fig. 60) and 1 (Fig. 61), and the outgroups have different types (Lyal *et al.* 2006).

*Mesonotum:*

**44. mesonotum, scutellum - shape of posterior margin:**

round (0); heart-shaped, with a cleft at middle (1); concave (2); acute (3); quadrate (4); concave with central projection (5); round with central projection (6)

The anterior and posterior margins of the mesoscutellum form many shapes and are difficult to homologize. In general, the posterior margin may be broadly round (Fig. 64), broadly round with a central projection (Fig. 62), with a cleft in the middle, concave (Fig. 63), acute,



quadrate, or concave with a central projection. Although these states are discrete, the difference between two states may often be subtle.

**45. mesonotum, scutellum - shape of anterior margin:**

acute (0); broadly round (1); quadrate (2); heart-shaped (3); concave (4)

The anterior margin of the mesoscutellum, similar to the posterior margin, may form many shapes. The variation in shape of the anterior margin, however, appears less than that of the posterior margin, although the same subtly appears sometimes between states. In general, the anterior margin may be broadly round, acute, quadrate, cardiform or with a cleft in the middle, or concave.

**46. mesonotum – posterior margin:**

acute, with broadly concave margins (0); rounded, projecting, with abruptly concave margins (1); flat, no protrusion (2); quadrate protrusion (3)

Baridinae only possess states 0 and 1, where the posterior margin is triangular, having concave antero-lateral margins. States 2 and 3 occur in the outgroups, where the posterior margin may not be produced at all and is relatively flat and truncated, or it may form a quadrate protrusion. In Baridinae, when the antero-lateral margins of the mesonotum are broadly concave, the posterior margin forms an acute apex (Figs. 65, 66). When the antero-lateral margins are more deeply concave, the posterior margin forms a more projecting apex.

**47. mesonotum – punctures:**

only along anterior margin of notal process (0); throughout notal process (1); absent (2)

In Baridinae, the mesonotum usually bears punctures on the mesothoracic phragma. These punctures may either be scattered along the phragma or restricted to the posterior margin of the phragma.

**48. mesonotum - posterior margin of mesothoracic phragma:**

with small notch/V-shape at longitudinal suture (0); no notch at longitudinal suture (1); no notch, with 2 concavities (2)

Along the posterior margin of the mesothoracic phragma, a notch or small invagination may be present at the posterior apex of the longitudinal suture (Fig. 65). Alternatively, this notch may be absent, where the posterior margin of the phragma is smooth and continuous (Fig. 66).

*Metanotum:*

**49. prescutum - ventral margin:**

middle concavity shallow, not reaching ventral margin (0); middle concavity deep, reaching ventral margin (1); shallow and triangular (2); no concavity, lobes absent (3)

The pair of lobes on the anterior margin of the prescutum may have a shallow concavity (Fig. 67) or a deep concavity that reaches the anterior margin of the prescutum (Fig. 68). In some cases this pair of lobes may be absent.

**50. metanotum, scutellar groove - transverse bridge:**

absent (0); present, reduced (1); present, developed (2)

The transverse bridge near the anterior margin of the scutellar groove that may occasionally be present appears to only occur in Baridinae. It may be fully developed (Figs. 69, 70, 73), reduced (Fig. 71, 74), or absent (Fig. 72).

**51. metanotum, scutellar groove - longitudinal crest:**

absent (0); present, reduced (1); present, developed (2); absent, with many bumps/ridges (3)

The longitudinal crest along the middle of the scutellar groove also appears to be apomorphic to baridines, though it becomes lost several times. When present, it may be developed and enlarged (Figs. 69, 72) or reduced and small (Figs. 70, 71). When absent, the scutellar groove may bear small ridges along the midline or be smooth.

**52. metanotum, scutellar groove - lobe at anterior end:**

round, convex, smooth (0); with concavity at middle (1); with quadrate protrusion (2); straight (3); pointed (4)

The lobe at the anterior end of the scutellar groove may be simple and broadly convex, relatively straight (Fig. 73), or bilobed (Fig. 69). Only in the outgroups is it found to be pointed.

**53. metanotum, scutellar groove - posterior margin:**

straight (0); concave (1); convex (2)

The posterior margin of the scutellar groove will often be concave when it protrudes from the metascutellum (Fig. 69), straight when it is relatively flush with the posterior margin of the metascutellum (Fig. 73), or convex when it ends before the posterior margin of the metascutellum (Fig. 72).

**54. metanotum, postnotum - lateral margin:**

with acute, projecting lobe (0); without lobe, margin broadly rounded (1)

The lateral margins of the postnotum always bear a projecting lobe in Baridinae (Figs. 69-74), and this lobe is absent in most outgroups, leaving the lateral margin straight.

**55. metanotum, metascutellum - line reaching from metascutum to alacrista:**

absent (0); present (1)

In many baridine taxa, a slight, angled ridge or line may be present on the metascutellum (Fig. 69) or may be absent (Fig. 72).

**56. metanotum, metascutum - postero-medial margin:**

straight, shallowly concave (0); concave (1); convex (2); quadrate (3)

In Baridinae, the postero-medial margin of the metascutum may be relatively straight (Fig. 72), concave (Fig. 73), or convex (Figs. 69, 70). A characteristic of many outgroup taxa is a quadrate shape of this margin.

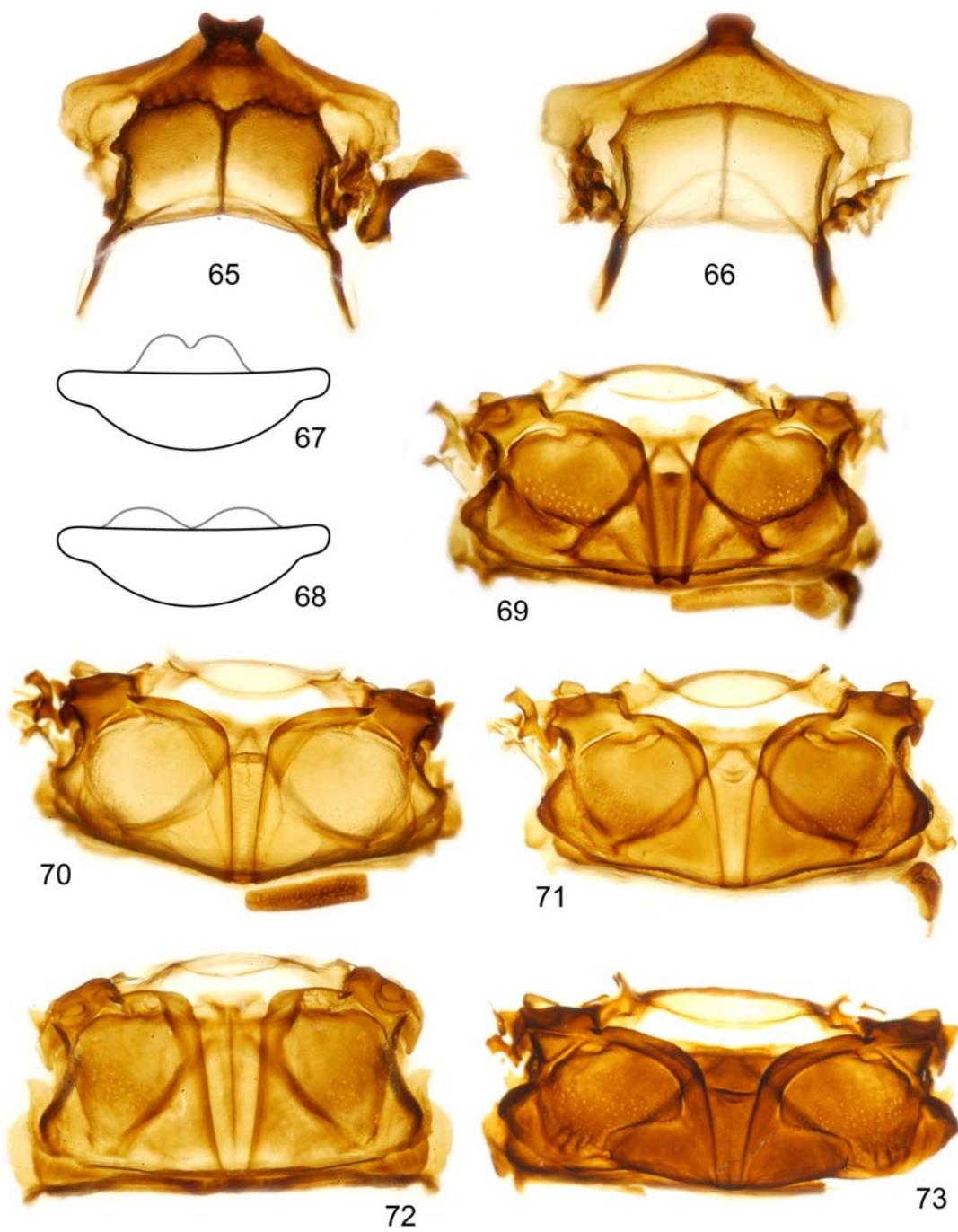
**57. metanotum, metascutum - posterior margin:**

with definite margin separating it from postnotum (0); with indefinite margin;  
merging with postnotum (1)

In Baridinae, the metascutum may be well-defined, with a distinct posterior margin separating it from the postnotum and/or the metascutum is widely separate from the postnotum (Fig. 69). Alternatively, the metascutum may have an indistinct margin, in which the metascutum appears more elongate and/or the posterior margin of the metascutum is narrowly separated from the postnotum (Figs. 70-74).

**58. metanotum, metascutum – punctures:**

large (0); small (1); none (2)



The metascutum may bear large punctures, small punctures, or may be absent of punctures.

**59. metanotum, metascutum – shape:**

transversely elongate (0); round (1); longitudinally elongate (2)

The shape of the metascutum is moderately correlated with body shape (width and length), though is not entirely indicative. The metascutum may be transversely elongate (Figs. 69, 73), round to subcircular (Figs. 70, 71), or longitudinally elongate (Figs. 72, 74). The difference between round and elongate sometimes is not completely objective.

*Metendosternite:*

**60. metendosternite - longitudinal suture:**

long (0); short (1)

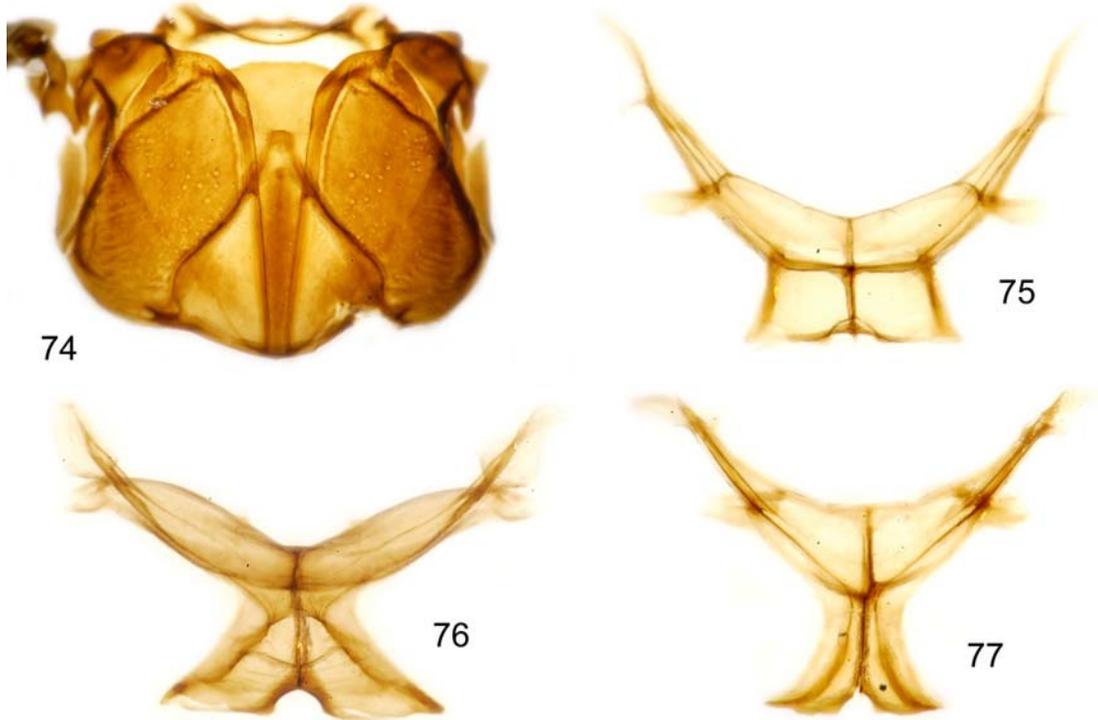
A long longitudinal suture (Figs. 75, 77) is often indicative of a quadrate metendosternite shape, though not always, and the same for a short longitudinal suture (Fig. 76) and longitudinally elongate metendosternite.

**61. metendosternite - metafurcal arm:**

bifurcate (0); monofurcate (1)

**62. metendosternite - metafurcal lamina:**

longitudinally elongate (0); quadrate (1); transversely elongate (2)



The metafurcal lamina may be longitudinally elongate (Figs. 76, 77), relatively quadrate or square (Fig. 75), or transversely elongate.

**63. metendosternite - anterior metafurcal tendons:**

closer to longitudinal suture (0); closer to metafurcal arm (1); in middle (2)

**64. metendosternite, shape:**

quadrate (transversely or longitudinally quadrate) (0); longitudinally elongate, metafurcal lamina elongate & curved (1)

Although similar to the shape of the metafurcal lamina, the general shape of the metendosternite is divided into those taxa bearing a metendosternite with quadrate angles along the margins of the metafurcal lamina (this includes lamina which are square and longitudinally or transversely quadrate) (Fig. 75) and those taxa in which the lateral margin of the lamina becomes constricted along the middle and concave (Figs. 76, 77).

**65. metendosternite, lateral arm:**

normal, produced (0); reduced, small (1)

Most Baridinae possess a large, produced lateral arm (Figs. 75-77), though a few, including many outgroup taxa, bear a small and reduced lateral arm.

*Legs:*

**66. thorax, legs - Pre-tarsal ungues (claws):**

connate, parallel (0); separate, diverging (1); only 1 claw present (2); separate, with 2 large central teeth (3); separate, widely diverging (4)

Most baridines possess connate (Figs. 80, 81) or separate/diverging (Fig. 82) pre-tarsal ungues, though a few have widely diverging ungues with nearly 180° separating them or have only a single ungue. Only outgroup taxa (Conoderinae, Ceutorhynchinae) have ungues which bear central teeth.

**67. thorax, legs - mid femoral spine on all legs:**

present, one spine present (0); absent (1); present, two or more spines present (2)

**68. thorax, legs - ventral surface of femora with depression for reception of tibia:**

present (0); absent (1)

Many baridines possess a variably-defined depression along the ventral surface of the femora. The depression ranges from being quite shallow and reduced (depression restricted to basal third of femur) to relatively deep and extending most of the length of the femur. This variation, however, is grouped into a single state, present. When the femur is completely cylindrical then the depression is absent.

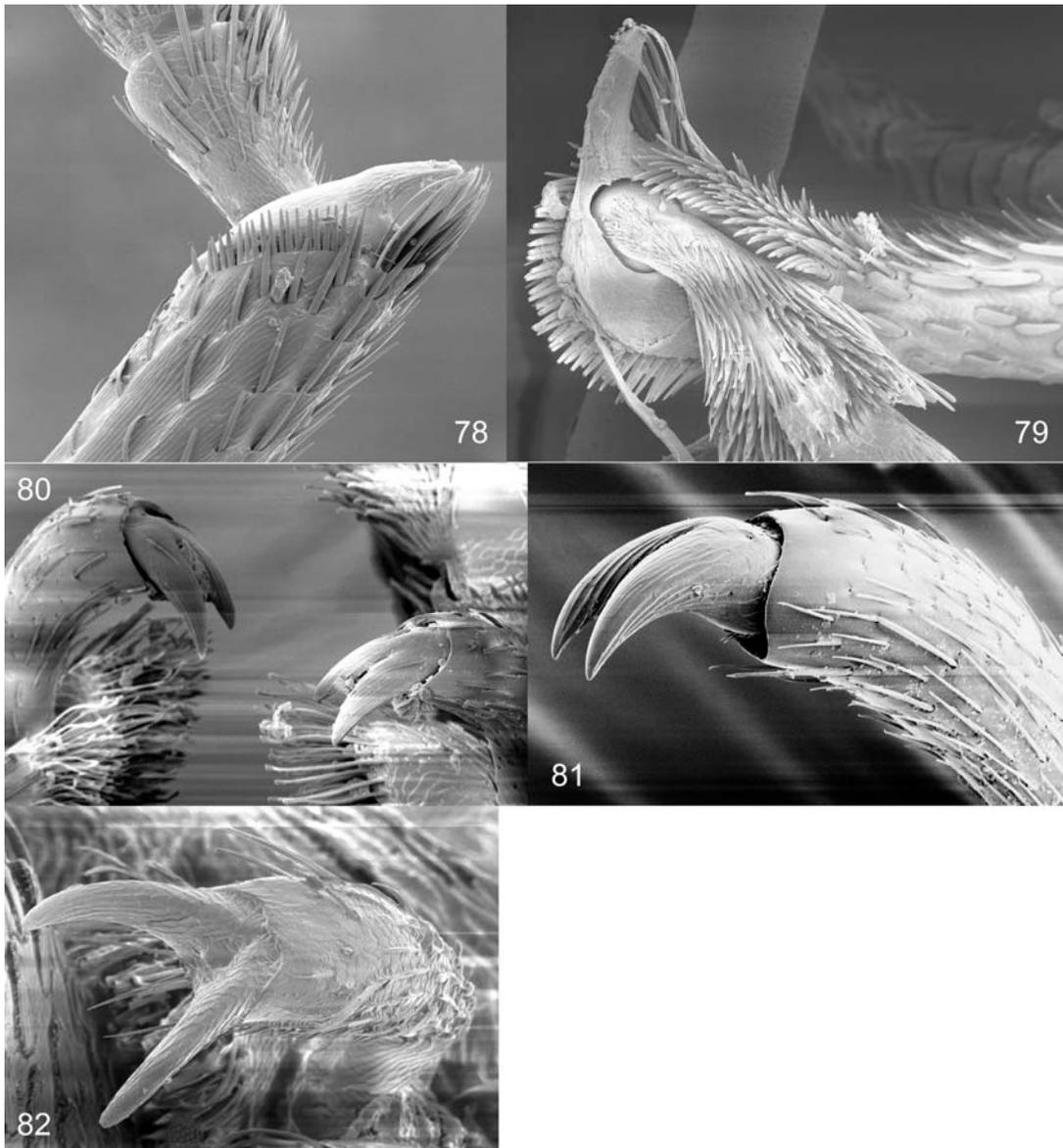
**69. thorax, legs - apical tibial spines:**

with 2 apical teeth, diverging on opposite corners (0); 1 large uncus at other corner (1); with 1 apical spine and 1 setal spine converging at one corner (2); with 2 apical spines, 1 large uncus in middle and smaller on corner (3); with no spines (4); with many spines (5); with 1 large uncus at middle (6)

Most baridines possess one large uncus at the outer apical angle (along with an adjacent tuft of elongate setae that are convergent with the uncus) (Figs. 78, 79). In some taxa the tibia may have two apical teeth of approximate size (the mucro on the inner apical angle and the uncus at the outer apical angle), the uncus on the inner apical angle (a shift in position from the typical outer apical angle), the uncus at the middle of the apex and the mucro at the outer apical angle, or no apical teeth at all.

Outgroups possess tibiae with several apical spines or the uncus at the middle of the apex and the mucro absent.

**70. tarsus, bilobed 3rd tarsomere:**



small, reduced (5th tarsomere usually elongate) (0); enlarged (5th tarsomere usually normal size) (1); normal size (2)

When the third tarsomere is small, the fifth tarsomere usually also is elongate, and when it is enlarged or expanded, the fifth tarsomere usually is shortened. It often is difficult to distinguish the intermediate (normal) sized third tarsomere from the two extreme states.

*Hind wings* (Figs. 83-86):

**71. wing, venation - R3:**

absent (0); present with dark vein (1); present with white strip (2); wing reduced or absent (3)

**72. wing, venation – 2rs:**

absent (0); present (1); wing reduced or absent (2)

**73. wing, venation - mst:**

developed (0); reduced (1); wing reduced or absent (2); absent (3)

**74. wing, venation - rm:**

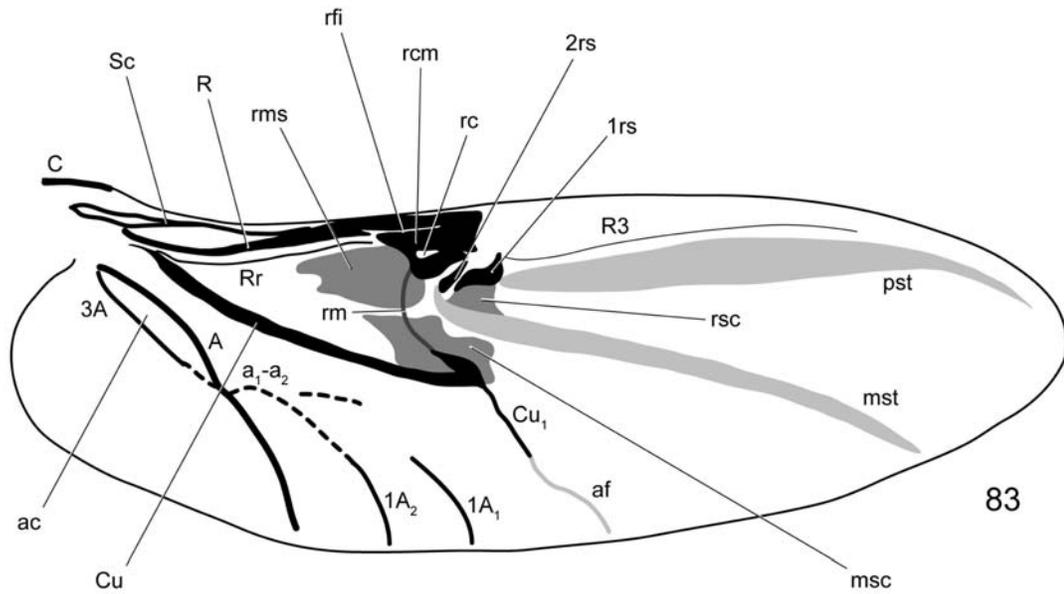
absent (0); present (1); wing reduced or absent (2)

**75. wing, venation - 1A<sub>1</sub>:**

absent (0); present (1); wing reduced or absent (2)

**76. wing, venation - 1A<sub>2</sub>:**

absent (0); present (1); wing reduced or absent (2)



**77. wing, venation - 1A:**

absent (0); present (1); wing reduced or absent (2)

**78. wing, venation - 3A:**

absent (0); present, reduced (1); present, nearly connected with 4A (2); wing reduced or absent (3)

**79. wing, venation - Rr:**

absent (0); present (1); wing reduced or absent (2)

*Elytra:*

**80. thorax, elytra - Intervals:**

with more than 1 row of punctures (0); 1 row of punctures (1); no punctures (2); ridges present (3)

The elytral intervals typically are either flattened, in which case they may be smooth, bear punctures, or have developed ridges absent of punctures. Puncture orientation may be categorized as forming a single row (Fig. 88) or not forming defined rows but with a dense scattering (Fig. 87).

**81. thorax, elytra - Hump (at apical area where many striae converge):**

absent (0); present, small (1); present, large (2)

The size of the posterior elytral hump is difficult to characterize. In general, it may be absent, present and small, or present and large.

**82. thorax, elytra - position over abdomen:**

covering abdomen completely (pygidium not visible) (0); pygidium partially or completely visible (1)

**83. elytra, apical margin – shape:**

elytra forming acute apex (0); elytra forming rounded apex (thereby exposing pygidium) (1)

The apices of the elytra may form congruent edges, in which the lateral margins of both elytra join (or nearly meet) at their acute apices. This condition often is associated with complete enclosure of the pygidium by the elytra, though not always. The other condition, which often is associated with exposure of the pygidium, is when the apices of the elytra are produced into lobes and are rounded.

*Abdomen, ventrites:*

**84. abdomen, ventrites - Lateral margins of ventrite 2:**

arched (0); straight (1)

In Baridinae, the lateral margins are always arched. Only outgroups may possess straight lateral margins.

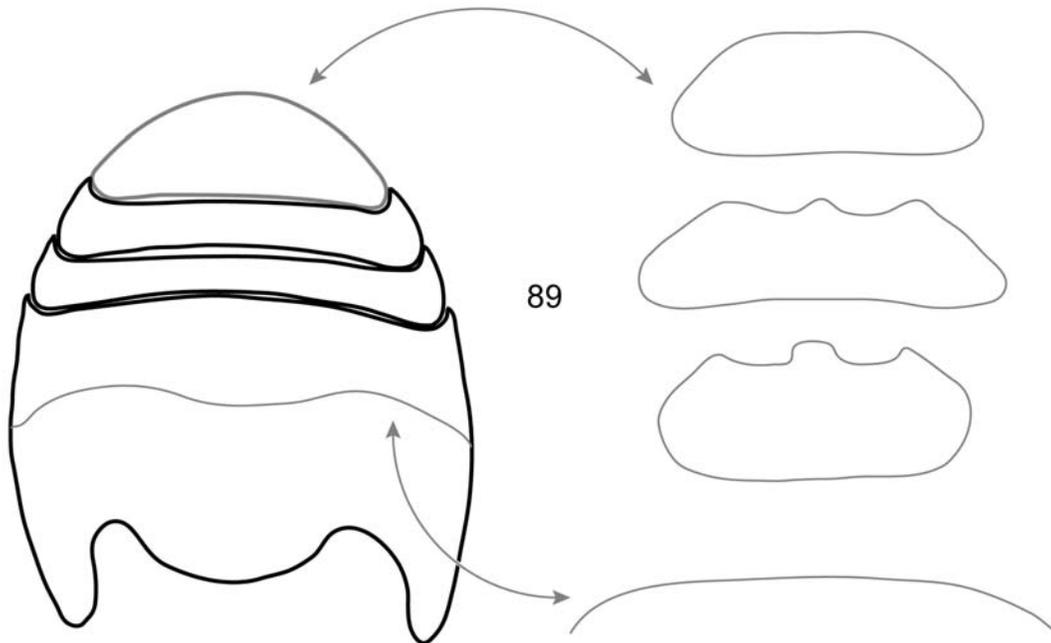
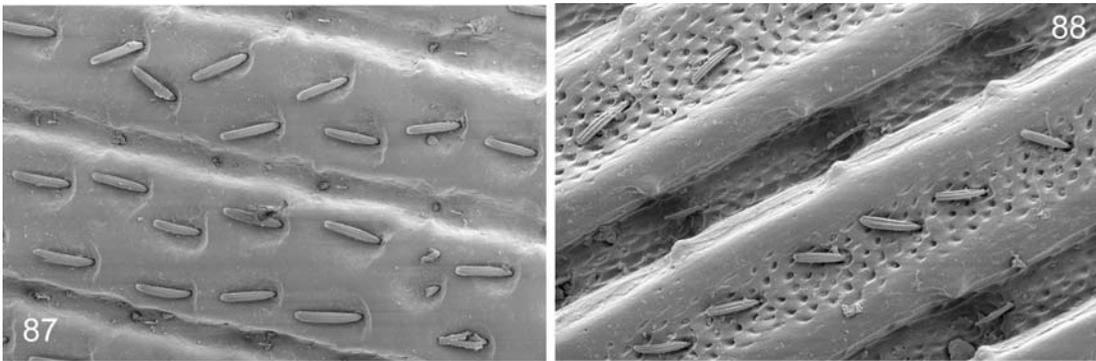
**85. abdomen, ventrites - Posterior margin of ventrite 1:**

linear (0); sinusoidal (1); broadly round (2)

Most baridines possess a sinusoidal posterior margin of ventrite 1 (Fig. 89), though this margin may sometimes be straight or broadly curved.

**86. abdomen, ventrites - Posterior margin of ventrite 5:**

rounded (0); truncate, broadly curved (convex) (1); truncate, sinusoidal (2); truncate, concave (3); truncate, sinusoidal with central projection (4); quadrate (5)



The posterior margin of ventrite 5 may be variously shaped. It may be rounded (Fig. 89), truncate but still convex, truncate and sinusoidal which may sometimes have a central projection or knob, truncate and concave, or quadrate.

**87. abdomen, ventrites - Punctures along anterior margin of ventrite 5:**

absent, margins smooth (0); present (1)

Although punctures usually are present on the ventrites, they particularly may be present along the anterior margin of ventrite 5, or they may be absent, in which this margin is smooth.

*Abdomen, tergites:*

**88. abdomen, tergites - Sclerotization of tergites:**

lightly sclerotized, almost membranous (0); heavily sclerotized (1)

When the tergites are strongly sclerotized they maintain a rigid convexity (Figs. 90, 95-97). When the tergites are weakly sclerotized they collapse and become shriveled *post mortem* (Fig. 98).

**89. abdomen, tergites - central spiculate patches of central tergites (Figs. 90-92):**

absent (0); on tergites 2-6 (1); on tergites 3-6 (2); on tergites 4-6 (3); on tergites 5-6 (4); 6 (5); 1-6 (6)

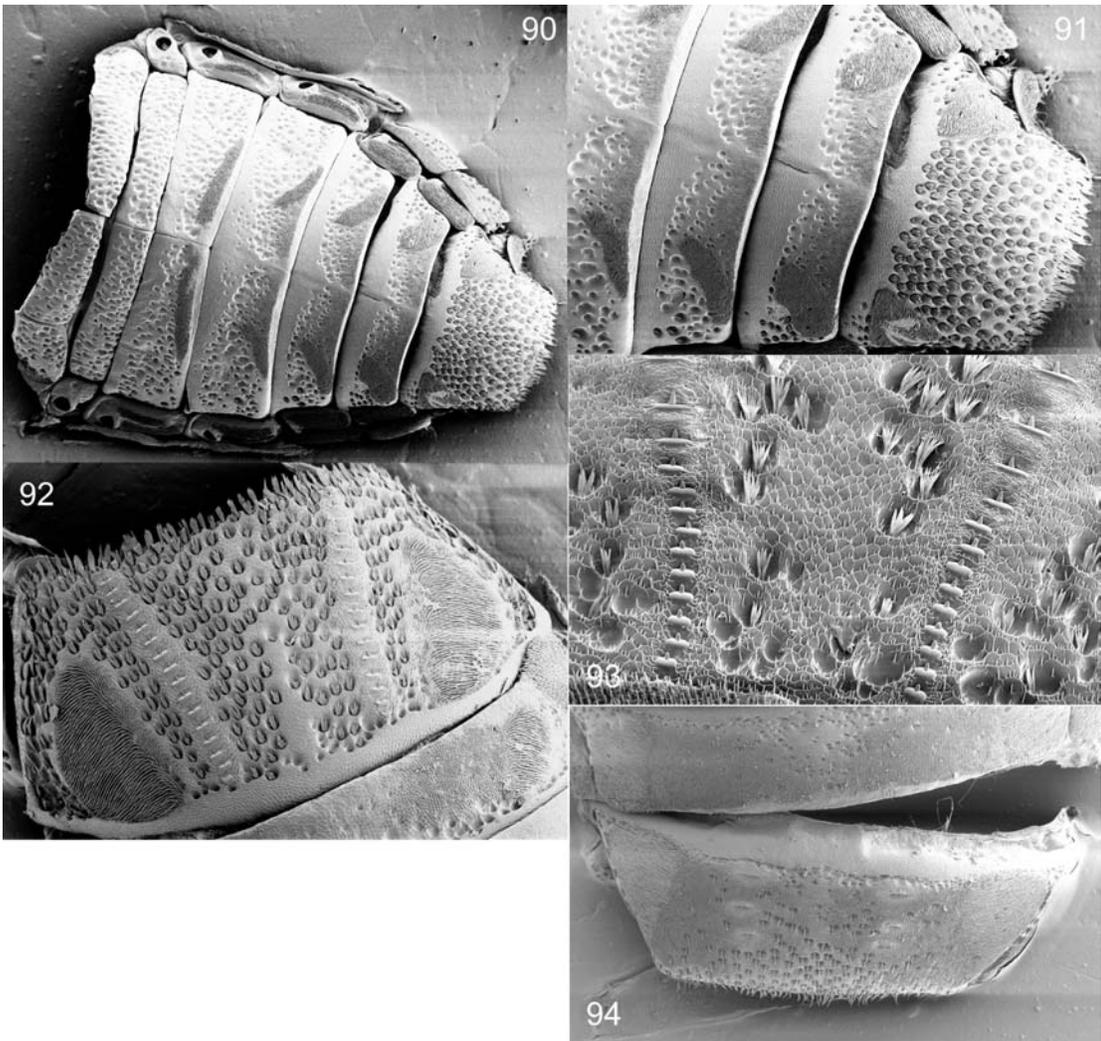
See Chapter V for baridine spiculate patch morphology.

**90. abdomen, pygidium (tergite 7) - Plectral tubercles:**

present, sparse (0); absent (1); present, dense (2)

When plectra are present on tergite 7 (of males and females) they may form dense rows (Figs. 92-93) or more sparse rows (Fig. 94). These different plectral densities correspond to morphologically distinct file types on the inner apical margin of the elytra. The males were used for character coding, as females almost always exhibit reduced plectral development.

**91. abdomen, pygidium (tergite 7) - with longitudinal median line/crest:**



absent (0); present (1)

When a longitudinal median line is present on tergite 7, it may extend the full length of the tergite or be restricted to the anterior half.

**92. abdomen, central tergite 1:**

fused (0); separated (1)

**93. abdomen, central tergite 2:**

fused (0); separated (1)

**94. abdomen, central tergite 3:**

fused (0); separated (1)

**95. abdomen, central tergite 4:**

fused (0); separated (1)

**96. abdomen, central tergite 5:**

fused (0); separated (1)

**97. abdomen, central tergite 6:**

fused (0); separated (1)

**98. abdomen, lateral tergite 1:**

fused (0); separated (1)

**99. abdomen, lateral tergite 2:**

fused (0); separated (1)

**100. abdomen, lateral tergite 3:**

fused (0); separated (1)

**101. abdomen, lateral tergite 4:**

fused (0); separated (1)

**102. abdomen, lateral tergite 5:**

fused (0); separated (1)

**103. abdomen, lateral tergite 6:**

fused (0); separated (1)

**104. abdomen, tergites - lateral spiculate patches of central tergites (Fig. 90):**

on tergites 2-7 (0); on tergites 3-7 (1); on tergites 4-7 (2); on tergites 5-7 (3); on tergites 6-7 (4); only on tergite 7 (5); 1-7 (6)

See Davis (2008b) for baridine spiculate patch morphology.

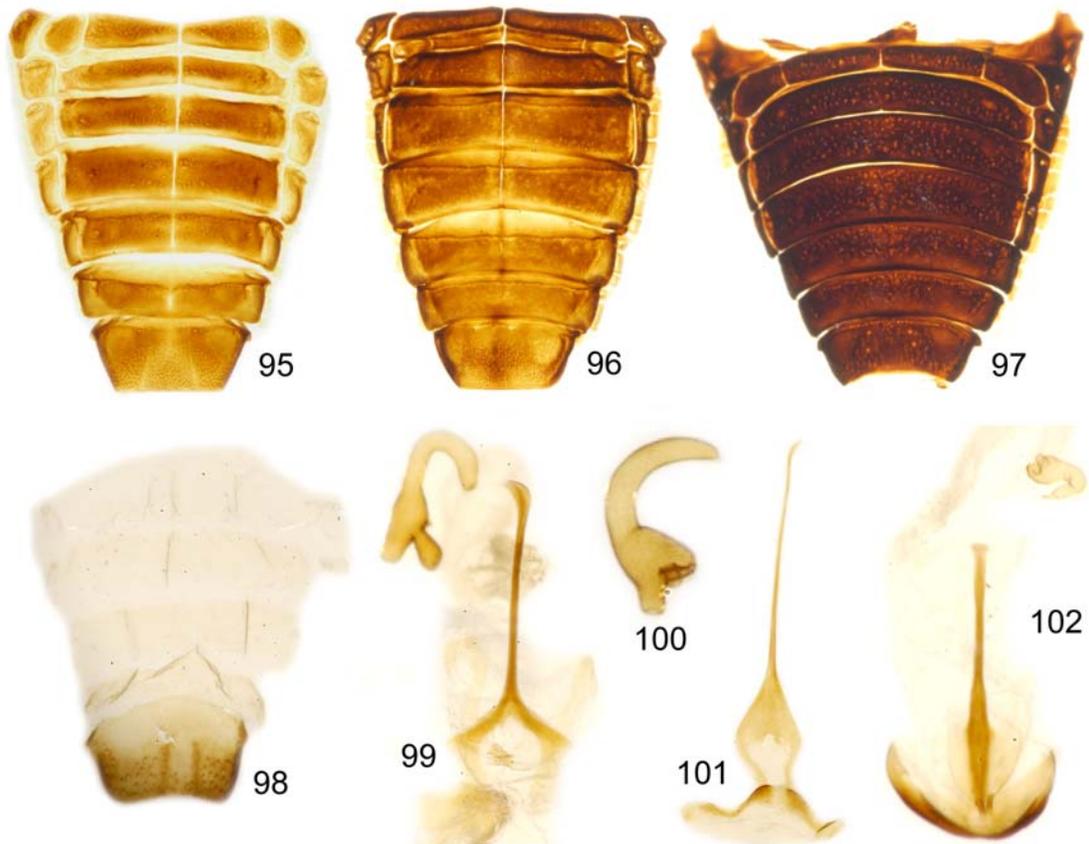
*Female genitalia:*

**105. female, 8th sternite - lateral margin:**

with acute angle (0); with rounded angle (1)

The basal antero-lateral margins of the female 8<sup>th</sup> sternite may be quadrate and angular (Fig. 99) or rounded to reduced or nearly absent (Figs. 101, 102).

**106. female, spermatheca:**



with ramus and collum present (0); only collum present (ramus reduced or absent) (1)

The spermatheca may have both ramus and collum present (with the ramus often developed and elongate) (Fig. 99) or the ramus may be highly reduced or absent (Fig. 100).

*Male genitalia:*

**107. male, aedeagus - internal flagellum:**

absent (0); present (1)

An internal flagellum may be present (Figs. 107, 108) or absent.

**108. male, aedeagus – median struts:**

very short, highly reduced (0); ~as long as aedeagus (1); longer than aedeagus, thin (2)

There is enormous variation in length in the median struts, most being approximately equal in length to the aedeagus (Figs. 103, 105), though they may be highly reduced and shortened (Fig. 104) or several times longer than the aedeagus (Figs. 106-108).

**109. male, aedeagus – median orifice:**

large (0); slightly restricted (1); nearly fused basally (2); opening restricted to apex, fused basally (3)

Most baridines possess a median orifice that is enlarged and opening up to the anterior margin of the median lobe (Figs. 106, 108), and in which the lateral sides of the median lobe are moderately slender. The lateral margins of the median lobe may also be nearly fused (Fig. 103) or completely fused (Fig. 105) forming an enclosed median orifice. Somewhat intermediate between these is a slightly restricted orifice, in which the lateral sides of the median lobe are wide but not to the point of nearly fusing at the anterior end (Fig. 107). This intermediate state may be difficult to distinguish from the completely open state of the median orifice.

**110. male, aedeagus - apical margin:**

concave (0); acutely rounded (1); with small rounded projection (2); round, globular (3)

The apex of the median lobe may be broadly rounded (Fig. 105), acute (Fig. 103), with a central lobed projection, or concave (Fig. 106). Occasionally the apex may be narrowly rounded, falling in between states 1 and 3, and in these cases the taxon was coded as having an acute apex.



**111. male, 9th sternite - apex of spiculum gastrale:**

normal, subequal in width (0); expanded and flattened (1)

The apex of the spiculum gastrale may be straight and bear no modification, but it often bears a hood-like expansion (Fig. 109).

**112. male, tegmen – ventral strut:**

monofurcate, narrow (0); bifurcate (1); monofurcate, wide (2); absent (3); very reduced (4)

The ventral strut often is narrow and elongate in Baridinae, but may be wide, reduced in length, or bifurcate.

**Phylogenetic methods***Parsimony analyses with full dataset*

The full data matrix, consisting of 113 characters and 301 taxa, was compiled in WinClada (Nixon 1999b). Phylogenetic analyses were performed using NONA (Goloboff 1999) and TNT (Tree analysis using New Technology; Goloboff *et al.* 2003). In NONA, two alternative styles were used for ratchet runs (Nixon 1999a) during tree exploration. One ran single ratchet sets for 4,000 iterations while sampling 35 to 50 characters and holding 1 tree per iteration. The second style was utilizing multi-ratchet sets. One set of runs used 2 simultaneous threads and 10 sequential ratchet runs, performing 200 iterations per run while sampling 35 to 45 characters and holding 1 tree per iteration. Another set of runs used 2 simultaneous threads and 20 sequential ratchet runs, performing 100 iterations per run while sampling 35 characters and holding 1 tree per iteration.

Runs in TNT consisted of implementing sectorial searches (SS) with tree drifting (TD) and tree fusing (TF) and ratchet runs with TD and TF. The final strict

consensus tree was computed using TNT by implementing 500 random addition sequences, and 1,000 ratchet iterations, including 100 cycles of both TD and TF per iteration.

#### *Reduced taxon matrix (RTM)*

A reduced taxon dataset, including all 113 characters, but only 140 taxa, was constructed. To do so, exemplar taxa were included from all baridine tribes and subtribes, and all taxa with approximately 50% missing data (due to the inability to dissect type specimens) were removed from the dataset, which did not interfere with obtaining a relatively reasonable sampling from each tribe and subtribe. All outgroup taxa in the full dataset were included in the RTM. The final run was performed in TNT and was conducted using the same settings and procedures as used in the final analysis of the full dataset (see above). Additionally, one of the most-parsimonious trees found is reported for better topological clarity (Fig. 117), as a few of the major nodes collapsed in the strict consensus (Fig. 116).

#### *Clade support analyses*

Bootstrap analyses performed using TNT gave similar results to jackknife runs, and also due to results in previous studies that have reported greater utility of jackknifing to bootstrapping in morphological studies (Hovenkamp 2006), only jackknife values are reported. Previous studies also have preferred bootstrapping over jackknifing because of the uncertainty in percentage of characters (or taxa) to

delete during replications (Soltis and Soltis 2003). Also, because bootstrapping assesses group support in a slightly different manner, by analyzing re-sampled matrices of the same size, and jackknifing assesses more of progress towards obtaining stable results by directly eliminating characters (or taxa) from the analyses (thus inferring the effect on tree topology if more characters were added; Siddall 1995), jackknifing seemed more appropriate for attempts towards a first phylogenetic hypothesis. Jackknife runs were performed using TNT. Final jackknife values were obtained by implementing 100 random addition sequences, and 1,000 ratchet iterations, including 100 cycles of both TD and TF per iteration.

Bremer support values (both absolute and relative) were calculated in TNT. Using the most-parsimonious trees obtained from the final TNT parsimony run, 10,000 trees within 15 steps of the MP tree were searched for and retained.

#### *Character tracing*

Characters of interest and those supporting the monophyly of Baridinae were selected to trace their evolution on the resulting cladogram in WinClada. In each case, tracing was performed under fast optimization (ACCTRAN). These characters include 41 (ascension of the mesepimeron, Fig. 125), 46 (posterior margin of mesonotum, Fig. 122), 54 (lateral margin of postnotum, Fig. 123), and 98 (fusion of lateral tergites, Fig. 124). Although not shared among all Baridinae, character 88 (tergite sclerotization) was also traced (Fig. 121).

### *Character weighting using implied weights*

Character weighting using Goloboff's (1997) implied weights was performed in TNT with both the complete dataset and RTM for varying values (2, 4, 6, 8) of the weighting strength or concavity constant  $K$ . Runs in TNT consisted of 100 random addition sequences, and 1,000 ratchet iterations, including 100 cycles of both TD and TF per iteration.

### *Bayesian analyses*

Bayesian analyses were conducted with both the full dataset and the RTM using the MrBayes software (Ronquist and Huelsenbeck 2002). All runs were performed using the standard discrete (morphology) model (derived from Lewis 2001) using the default settings with 4 chains, except the character sampling coding was set to "variable." Also, a run of 3 million generations was executed for both datasets, and another run of 10 million generations was executed using only the full dataset. Burn-ins consisted of 300,000 generations for the 3 million generation runs and 1,000,000 for the 10 million generation run. The program Tracer software (Rambler and Drummond 2004) was used to construct plots of parameter diagnostics, namely the log likelihoods of the trees (LnL) and the tree lengths (TL).

## **Results**

### *Strict consensus*

The duration of the final TNT run was ~37 hours, and the total rearrangements examined was 3,930,947,747,326. A strict consensus tree (Fig. 111) was calculated from 33 most-parsimonious trees of length 4,509 and  $Ci=5$ ,  $Ri=51$ . The length of the consensus tree is 4,850, with  $Ci=4$ ,  $Ri=48$ . The considerably longer length of the strict consensus is largely due to the poor resolution in the large polytomy present at the apex of the tree. The absolute and relative bremer support values for each clade of the full tree and RTM tree are given in Fig. 111, and jackknife values of 50 and greater are also reported. Characters and character states are mapped onto the branches of the strict consensus tree under fast optimization (Fig. 112), slow optimization (Fig. 113), and showing unambiguous changes only (Fig. 114).

The duration of the RTM run was considerably shorter, a mere ~1.6 hours, and the total rearrangements examined was 135,442,242,201. A strict consensus tree was calculated from 110 most-parsimonious trees of length 2,692. Similar to the strict consensus of the complete analysis, characters and character states for the RTM tree are mapped onto the branches of the strict consensus tree under fast optimization (Fig. 118), slow optimization (Fig. 119), and showing unambiguous changes only (Fig. 120).





According to the current classification of Alonso-Zarazaga and Lyal (1999), a monophyletic Baridinae was not recovered. Falling within various places in the outgroup were the following taxa previously placed within Baridinae: *Calandrinus grandicollis*, *Microcholus puncticollis*, *Oomorphidius leavicollis*, *Eisonyx opaca*, *Eisonyx crassipes*, *Elasmobaris signifer*, *Fishonia brevinasus*, and *Neplaxa illustris*. The sister clade to Baridinae is Oorbitidinae, followed by Conoderinae (though Conoderinae is divided in this result), Curculioninae, Molytinae, and Cryptorhynchinae. The position of Conoderinae in the outgroup is uncertain in this study, although this result may also reflect instability in conoderine phylogeny and classification. The sister-group relationships, relative to Baridinae, obtained in this study are similar to those obtained in Marvaldi *et al.*'s (2002) phylogeny of Curculionoidea.

#### *Character tracing and character evolution*

Although not displayed, characters 99 and 100 share the same topological distribution, and character 101 is similar in distribution. Based on the results of this study, characters 41, 46, 54, and 98-100 appear to be indicative of a monophyletic Baridinae. Character 88 also is shared by most Baridinae. Because the grouping of taxa in the outgroup that was previously included in Baridinae shares some features with Baridinae (as defined here), such as the developed lobe on the lateral margin of the postnotum, its topological position may change with the inclusion of more taxa and examination of more characters. Although this group does appear to possess

plesiomorphic qualities in comparison to the remainder of Baridinae, it is uncertain whether or not these qualities correctly place them outside of Baridinae due to the combination of high homoplasy and small ratio of characters to taxa.

#### *Character weighting using implied weights*

All analyses using implied weights resulted in 1 phylogeny. Phylogenies from analysis of the complete dataset using  $K=2, 4, 6,$  and  $8$  are displayed in Figs. 128-131, respectively. Many of the taxa within the groupings that are defined by the strict consensus tree of the equal weights analysis have moved position in the implied weights analyses. Although the non-baridine taxa largely remain in the outgroup, a few (*Derelomus*, *Balanogastris*, *Telephae*) appear nested within the ingroup.

Phylogenies from analysis of the RTM using  $K=2, 4, 6,$  and  $8$  are displayed in Figs. 132-135, respectively. Similar to the analysis of the full dataset, many taxa within the groupings defined in the strict consensus of the equal weights analysis of the RTM have moved position in the implied weights analyses. Also, the same outgroup taxa (*Derelomus*, *Balanogastris*, *Telephae*) appear nested within the ingroup.

#### *Bayesian analyses*

The bayesian phylogeny produced from analysis of the full dataset using 3 million generations (Fig. 136) is much more concordant with the strict consensus tree produced from the parsimony analysis in TNT (Fig. 110) than is the phylogeny

produced from the bayesian analysis with 10 million generations (Fig. 137). As evident from the Tracer plots (and the posterior probabilities on the trees), even though the tree space of the 10 million generation analysis (Figs. 145-149) was better sampled than that of the 3 million generation analysis (Figs. 140-144), the phylogeny of the 10 million generation run is highly incongruent with the parsimony-produced phylogeny.

The bayesian phylogenies produced from analyses of the RTM using 3 (Fig. 138) and 10 million generations (Fig. 139) were both highly concordant with the strict consensus tree produced from the parsimony analysis in TNT (Fig. 116). Also, none of the outgroup taxa in the bayesian phylogenies fell within the ingroup. The posterior probabilities on the bayesian trees from both runs are identical. As visible from the Tracer plots, the tree space of the 10 million generation analysis (Figs. 155-159) was much better sampled than that of the 3 million generation analysis (Figs. 150-154).

## **Discussion**

It is particularly evident that the dataset compiled in this study results in an extremely homoplasious phylogeny, a phenomenon not exceptional of datasets with large numbers of taxa (Sanderson and Donaghue 1989). Very few synapomorphies were hypothesized and even fewer appeared to withstand a phylogenetic test. Many factors are believed to have contributed to this phenomenon. Due to its size, it is doubtful that the dataset is free of errors. Thus it is possible that phylogenetic noise

was introduced through human error. Another contributing factor is homology assessment. Because of the large number of taxa examined, the diversity in morphological shapes and structures made it difficult to define decisive character states. The resulting cladogram reflects this difficulty in forming hypotheses of homology, and the large degree of homoplasy may indicate that many character states that were hypothesized to be homologous actually are not. Due to the excessive amount of homoplasy in the tree, non-homoplasious synapomorphies for the subfamily are unable to be defined, at least from the results of this study. Synapomorphies nonetheless can be defined, though, which are present in the majority of taxa. The lateral margin of the postnotum of the metanotum is developed and projecting (character 54) in most baridines but reduced and smooth in all outgroup taxa (Fig. 123). The posterior margin of the mesonotum (character 46) is most often developed and projecting (with the projecting apex acute or rounded) in Baridinae, while outgroups possess various forms of a reduced margin which does not form a projecting apex (Fig. 122).

#### *Comparison of complete matrix analysis to RTM*

As has been shown by numerous studies (Hillis 1998; Graybeal 1998), the addition of more taxa to a phylogenetic analysis may increase topological accuracy. The phylogeny of Baridinae provides no exception. In comparing the tree obtained from analysis of the complete data matrix to the tree obtained from analysis of the RTM, a few major differences are evident; however, despite changing taxon

composition, the topology remained similar. Because of the reduction in the number of taxa included in the RTM, the clades present in this tree are fewer than those present in the complete tree. The majority of clades shared in both the complete tree and RTM tree also have similar topological identity, although a few do not.

This result supports previous conclusions that incomplete taxon sampling may bias phylogenetic studies, in which topology may change through the addition of taxa to the analysis. It also indicates, though, and supports evidence suggesting that taxon composition, despite affecting the number of clades present in a phylogenetic tree, has little effect on overall topology (Miller and Hormiga 2004). Thus, although greater taxon sampling is always desired, and certainly is desired with baridines and weevils in general, more rigorous character examination is needed to help resolve baridine phylogeny. Also, although the complete dataset contained more than fifty taxa with approximately 60% missing data, the inclusion of these taxa appeared not to have affected topological accuracy (in comparing the strict consensus tree to the RTM tree). This result supports previous studies that explained differences in the way missing data and missing taxa affect phylogenetic accuracy (Wiens 1998, 2003a, b). Even though large amounts of missing data per taxon in a matrix may greatly affect topological accuracy and phylogenetic resolution, if these missing data is more evenly distributed throughout the matrix so as not to be particular to a few taxa, then the effect on the resulting phylogeny will not be markedly large.

### **Implications towards baridine classification**

Despite the breadth of this study, in which slightly more than half of the extant, described genera were examined, several observations can be made about the evolution of this diverse group. Although it is a definitive goal to revise the baridine classification system, it is believed that this single study is not rigorous enough to propose and adopt a new system, but can be thought of as a starting point towards elucidating the evolution of this group.

As a result of this study, it is evident that the current classification for Baridinae is inadequate. All of the currently recognized tribes and subtribes are shown to be paraphyletic, and a few, such as Madopterini and Baridini, are polyphyletic, particularly the former. It appears, however, that Optatini may represent a valid tribe, with some minor adjustments to the taxa and characters that define it. Also Baridini, despite being polyphyletic, may also represent a real evolutionary grouping in a narrower sense.

The following is a list of groupings (mostly clades) and characters present at these nodes in the full tree that are suggestive of a revised classification of Baridinae (Fig. 111), though no taxonomic rankings will be proposed for these groups.

Although many clades do appear in the strict consensus tree, there are also paraphyletic lineages (groups 2, 6-8, 12-13) that I suggest as possible groupings due to the number of characters they share. The boundaries of these paraphyletic lineages are not delineated randomly, and they share character states that group them together, even though the states may be homoplasious and shared by other groups on the tree. Provided further refinement of characters and more rigorous studies of baridine

phylogeny, these groupings may or may not represent true clades. The characters shared among the indicated paraphyletic groupings also are not only strictly present within those taxa and may be present within adjacent taxa as well. The characters that only provide significant structure to clades (i.e. are possessed by a majority of the taxa) are mentioned below. Although most clades are supported by numerous characters, most of them are homoplasious at lower levels, thus those characters showing the least homoplasy are listed below. Most clades are accounted for; however, a few groupings whose hierarchical rank is dubious are not defined. Character evolution is followed using WinClada's fast optimization.

Group 1 (Baridinae): 41, 46, 48, 54, 98, 99, 100, 101

Group 2: 62, 73, 74, 76

Group 3: 62, 73, 74, 76

Group 4: 20, 21, 50, 55, 63, 74, 90, 91, 95, 104

Group 5: 21, 32, 44, 55, 62, 80, 90, 95, 97

Group 6: 21, 44, 70, 71

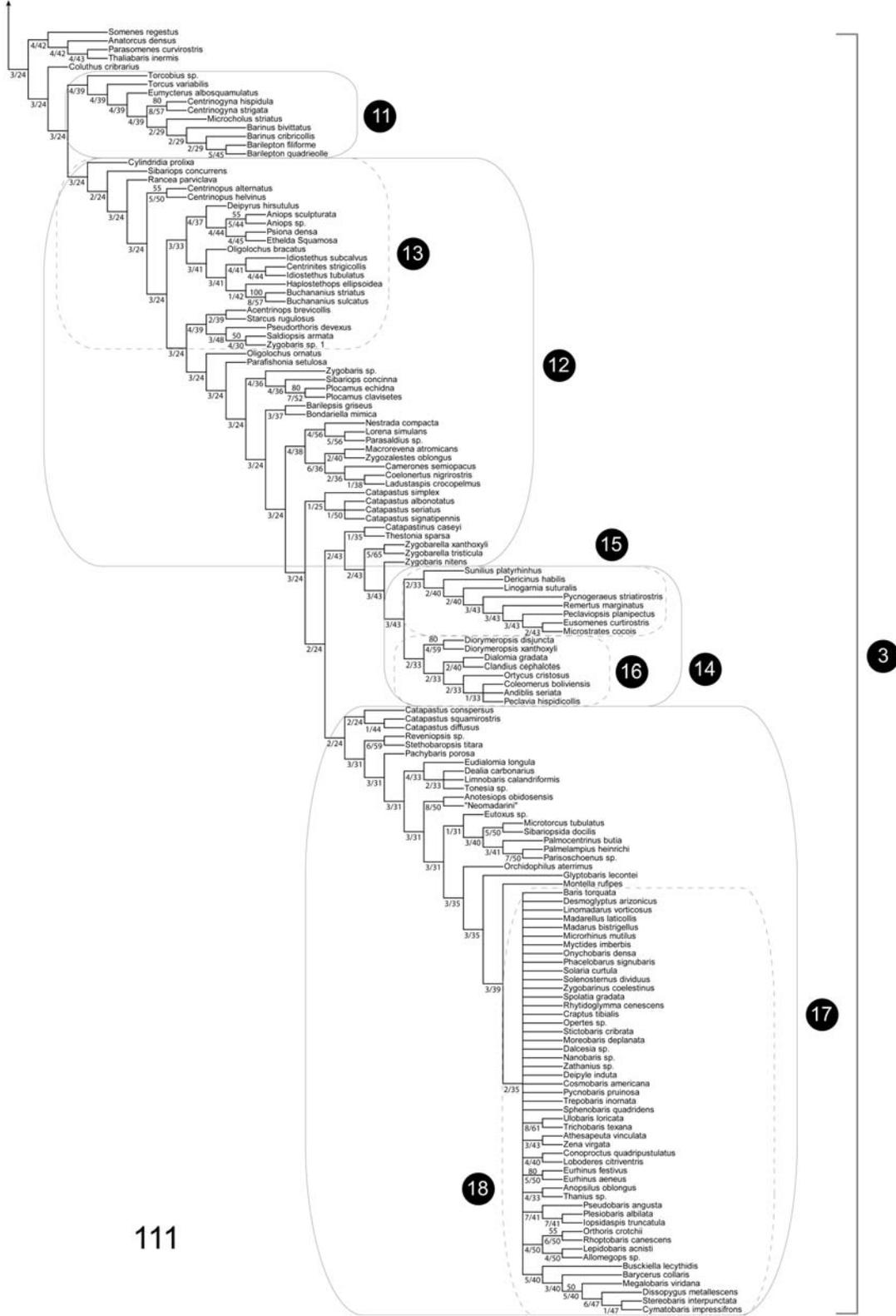
Group 7 (subclade of 6): 30, 32, 33, 37, 94, 95, 96, 97

Group 8: 10, 17, 19, 21, 44, 55, 71, 97, 103, 108, 109

Group 9 (subclade of 8): 3, 4, 23, 32, 33, 38, 39, 47, 54, 59, 64, 66, 68, 78, 89



part 1



111

Group 10: 24, 36, 43, 51, 58, 61, 63, 64, 66, 67, 75, 78, 80, 81, 87, 89, 90, 95,  
101, 108, 111

Group 11: 3, 10, 20, 58, 59, 63, 81, 88, 109

Group 12: 26, 36

Group 13 (subclade of 12): 70, 102

Group 14: 17, 19, 20, 36, 50, 91

Group 15 (subclade of 14): 33, 34

Group 16 (subclade of 14): 63

Group 17: 3, 20, 34

Group 18 (subclade of 17): 17, 58, 61, 63, 73, 82, 83, 86, 89, 95, 96, 102,  
103, 107, 109

Below is a list of groupings (mostly clades) and characters present at these nodes in the RTM tree (Fig. 117). The topology of the RTM tree and the corresponding characters supporting the clades are similar to the full tree, however it is clear that some clades are missing and are different in taxon composition due to the elimination of taxa in the analysis.

Group 1 (Baridinae): 92, 93, 98, 99, 100, 101

Group 2: 62, 72, 73, 74, 75

Group 3: 62, 72, 73, 74, 75

Group 4: 17, 32, 51, 54, 88, 108, 109

Group 5: 19

Group 6 (subclade of 5): 48, 59, 83

Group 7 (subclade of 5): 5, 28, 50, 59, 62

Group 8: 24, 36, 43, 46, 51, 58, 61, 64, 66, 67, 75, 87, 90, 101, 108, 111

Group 9: 36

Group 10 (subclade of 9): 102, 103

Group 11 (subclade of 9): 37, 38, 39, 47, 54, 59, 66, 64, 70, 78, 82, 109

Group 12: 3, 15, 26, 32, 45, 50, 51, 58, 66, 68

Group 13 (subclade of 12): 19, 33, 52, 56, 91

Group 14: 26, 48

Group 15: 112

Group 16: 17, 36, 46, 61, 73, 80, 82, 83, 107, 108

Group 17 (subclade of 16): 3, 10, 51, 56, 86, 91, 94

Group 18 (subclade of 16): 13, 59, 89, 90, 109

Group 19 (subclade of 16): 3, 14, 23, 69, 91

Despite incongruence in results obtained from the implied weights analyses of both full datasets and the RTM, the strict consensus tree (Fig. 111) of the analysis of the full dataset is believed to represent the best hypothesis of baridine evolution to date. Given the data, the RTM analysis derived a strict consensus tree (Fig. 116) with similar topology to that of the full dataset. Regardless of the high amount of homoplasy, several characters support clades and suggested groupings that are present in the analyses of both the full dataset and the RTM. Although jackknife

values and Bremer support values are relatively low at many of the major basal nodes, these types of values can be expected from analyses, such as this one, with a low ratio of characters to taxa. It is believed that with the addition of more characters, not only morphological ones, the phylogeny of Baridinae will obtain greater stability.

### **Biogeography of Baridinae**

From examination of mapping the biogeographic zones onto the strict consensus tree (Fig. 126), no specific distribution patterns or patterns of dispersion are visible. Approximately 75% of the known baridine genera are found in the Neotropics. Because relatively few Old World taxa were included in this study, it is difficult to interpret any biogeographic patterns. In order to definitively assess biogeographic patterns within Baridinae, denser sampling is needed of Old World taxa.

### **Host plant utilization**

All known host records were mapped onto the strict consensus tree (Fig. 127); however, because records are available for extremely few baridine genera, no definitive trends in host plant evolution are evident. It is believed that the superfamily Curculionoidea originated sometime during the early to middle Jurassic (Grimaldi and Engel 2005), with the Curculionidae appearing during the middle Cretaceous (Farrell 1998). From Farrell (1998), it can be estimated that along with the other curculionid subfamilies, Baridinae originated sometime during the late

Cretaceous. These origins, outside of Curculionidae, mostly show weevils as feeding on conifers and cycads, subsequently radiating onto angiosperms. Presently, no baridines are known to feed on gymnosperms. Because the subfamily is believed to have radiated long after the origin of angiosperms, it is unlikely that any patterns exist of transitions from monocotyledons to dicotyledons. Thus, a more complex story must exist for explanation of host plant patterns in Baridinae, one that requires much more biological data than is presently available to answer.

### **Character weighting in baridine phylogenetics**

In the implied weights analyses of both full dataset and the RTM, the higher the value of  $K$ , the greater stability of the tree topologies. Although the trees analyzed with  $K=2$  were quite different in topology to the strict consensus trees analyzed with equal weights, they were much more similar to the subsequent trees analyzed with  $K=4, 6,$  and  $8$ . Aside from the suboptimality of the weighted trees, their topologies are fairly different from the equal weights analyses. Previous studies have reported increased phylogenetic stability by down-weighting homoplasy using implied weights (Goloboff *et al.* 2008). Through analysis of both full datasets and the RTM, this study also appears to corroborate those previous accounts. Stability of clades became more apparent as the value of  $k$  was increased. Because of the high amount of homoplasy in the resulting cladograms under equal weights (~97% of all morphological characters are recognized as homoplasious), the accuracy of the phylogenies under implied weights is uncertain. Weighting schemes based on

homoplasy indices are designed to down-weight homoplasious transformations in characters, causing them to contribute less to the topology of the tree (Goloboff 1997); however, situations involving datasets that produce trees with mostly homoplasious characters have not been explored. In accordance with other studies which argue that homoplasy is a natural biological phenomenon, especially as the number of examined taxa increases, that provides definition to phylogenetic structure (Källersjö *et al.* 1999), if these characters are down-weighted during phylogenetic analysis, there potentially might be a large effect on tree topology. Also, due to uncertainty in how much of the homoplasy present in the equal weight trees constitutes false statements of homology and how much actually represents independent character state origins (Farris 1983), it is difficult to assess phylogenetic accuracy of character weighted analyses.

### **Concordance of bayesian and parsimony analyses**

Because of the highly homoplasious baridine phylogeny, another tree-building method beyond parsimony was implemented (bayesian analysis) to assist in elucidating if this high amount of homoplasy is due to evolutionary history or is a random artifact. These analyses were also conducted to examine the effects of using highly homoplasious data under a bayesian framework.

The results produced from both analyses of the full dataset are rather inconclusive in reference to baridine phylogeny. While it is interesting to note that the bayesian tree produced from the run with 3 million generations is more

concordant with the strict consensus tree produced by parsimony using TNT than is the tree produced from the run with 10 million generations, both of the bayesian-produced trees are still quite incongruent with the parsimony-produced tree.

Although the log likelihoods show more of an asymptotic behavior as the number of generations increased from 3 to 10 million, and the sampled distribution of tree lengths is more normally distributed, the topology appears to have become less congruent with increased generation time.

The results from bayesian analyses of the RTM, on the other hand, are much more topologically similar to the respective parsimony analyses of the RTM. Taxa within the major groupings (defined in Fig. 117) change position between the bayesian runs; however, the groupings remain static and largely concordant with the parsimony-produced tree. These results are quite different from the parsimony analyses, in which both the analysis of the full dataset and of the RTM are topologically congruent.

### **Final thoughts and future directions in baridine phylogenetics**

Indeed, a high amount of homoplasy in phylogenies with large numbers of taxa which are produced from morphological data can be expected and may not be cause for much concern. Because homology is a *post hoc* assessment, those characters which turn out not to be homologous on a phylogeny are homoplasies (Wake 1999). Thus, homoplasies not only give structure to trees as synapomorphies do, they also delineate which characters do not have the same qualities. However, if

homoplasy can be equated to noise (structure created from random data by chance; Wenzel and Siddall 1999), then it is uncertain how much of the homoplasy in the baridine dataset represents noise. If phylogenetic structure is attributed to randomness in the characters then there is no reason why the most-parsimonious tree should be selected as that providing the best hypothesis for evolution within any particular groups (Hillis and Huelsenbeck 1992). Thus, separating the amount of homoplasy that is due to noise and that which is caused by evolutionary history is integral in examining and improving large phylogenetic studies such as this one.

In order to discriminate between phylogenetic signal and noise, and to further assess the quality of the data, future work on baridine phylogenetics may include examination of the distributions of tree-length skewness (Huelsenbeck 1991). Given the results from analyses of the full dataset and RTM, the data appears to be consistent (Hillis 1995), in that addition of more data from the RTM to the full dataset resulted in similar phylogenies. Moreover, convergent results from the bayesian analyses of the RTM datasets illustrate robustness of the data.

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**Appendix I. Character matrix - characters 0 – 36. \* = [0,4]; \$ = [0,1]**

	0	5	10	15	20	25	30	35
Dryophthorinae ( <i>Dryophthorus americanus</i> )	0010000101024010142102010011000001110							
Bagoinae ( <i>Bagous transversus</i> )	0010100201100201231102014011002000110							
Conoderinae ( <i>Cylindrocopturus operculatus</i> )	0010100211001201022112012001102020110							
Conoderinae ( <i>Trichodocerus</i> sp.)	0010100110000301330120010021102000110							
Conoderinae ( <i>Arachnopus gazella</i> )	0112100211200201010031110011002001010							
Conoderinae ( <i>Cyllophorus fausciatus</i> )	1001100211200200010021011011101010110							
Conoderinae ( <i>Metialma straminea</i> )	1010100211200211030121011001002011110							
Conoderinae ( <i>Balanogastriis kolae</i> )	1010100211200201031120011001002011016							
Conoderinae ( <i>Telephae oculata</i> )	1010100211100201230120011021102010106							
Conoderinae ( <i>Cylindrocopturus adspersus</i> )	0010100211000200021130012011002000110							
Conoderinae ( <i>Acoptus suturalis</i> )	0010100211200010000100112011102000116							
Conoderinae ( <i>Lobotrachelus troglodytes</i> )	1010100211100201031110012011002010111							
Conoderinae ( <i>Mecopus trilineatus</i> )	0012110211100200220111111010002001110							
Ceutorhynchinae ( <i>Ceutorhynchus obstructus</i> )	1010100211001201031130213011002010110							
Ceutorhynchinae ( <i>Hypurus bertrandi</i> )	1010100211100200031130013011002000116							
Ceutorhynchinae ( <i>Phytobius oriseomicans</i> )	1010100211200200031130013011002001116							
Ceutorhynchinae ( <i>Mononychus vulpeculus</i> )	1010100211200000031130013021002010116							
Ceutorhynchinae ( <i>Auleutes argentinensis</i> )	1010100211100000031130013011002010116							
Ceutorhynchinae ( <i>Coeliodes flavicaudis</i> )	1010100211100200031130013011002000116							
Curculioninae ( <i>Curculio pardalis</i> )	0010100111000201310010214001002001110							
Molytinae ( <i>Cholus rana</i> )	1010110211100201031112004011102000110							
Molytinae ( <i>Trigonocolus curvipes</i> )	1000100211100121231120213001000122116							
Molytinae ( <i>Conotrachelus fissunguis</i> )	001010021110020120002001001100200111*							
Entiminae ( <i>Cyrtepistomus castaneus</i> )	0010100103100101160112211001002001110							
Derelominae ( <i>Derelomus basalis</i> )	0110000211100211222102014001000011110							
Cryptorhynchinae ( <i>Cryptorhynchus lapathi</i> )	0010100211100201032120010021102010100							
Orobitidinae ( <i>Parorobitis gibbus</i> )	10001102110012012??????10011002020116							
Acenrinops <i>brevicollis</i>	1011110211200201020120000021101010104							

Amercedes subulirostris	1010110011000201020002000021002020104
Amercedes orthorrhinus	1011110011000201020002000021002020114
Anavallius ruficornis	1011110011200200220000010010001011000
Anopsilus oblongus	0011000211200210022100010111000010102
Antesis sparsa	0011110211100211020031000021102020114
Athesapeuta vinculata	0011110211100210020121010011101001013
Barilepsis griseus	0010110211200210030120010011102001111
Barilepton filiforme	0011100202100210030130010011002002013
Barilepton quadrieolle	0011100212100200030100010001102002113
Barinus bivittatus	0012100201100200020130000011101000114
Barinus cribricollis	0010110212100201030120010011101000113
Baris torquata	0010110211100211031110000011001\$11113
Barymerus binaries	011010001100000200030010011101011012
Buchananus striatus	1010100211100201031102010021102010111
Buchananus sulcatus	1010100211100211031132010021102110111
Busckieilla lecythidis	1010000201200020022121000011100112114
Calandrinus grandicollis	001210021120020102013100002110200114
Camelodes leachii	10100002112002110200210000020110020103
Catapastinus caseyi	1011110211200211030120010021002011004
Catapastus conspersus	1010110211200201030120010021002011014
Catapastus squamirostris	1011110211100211030120010021002011014
Catapastus albonotatus	1010110211200211030120010021002021011
Catapastus diffusus	10111102112002110?????010021102021014
Catapastus seriatus	1010110211200211030100010021002021011
Catapastus signatipennis	1010110211200221030122010021002021011
Catapastus simplex	10101102112002010?????010021002011011
Centrinites strigicollis	0010110211100011230121010021002110114
Centrinogyna hispidula	0012110211100211030121010021102101114
Centrinogyna strigata	0012110211100211032121010021101101114
Centrinopsis sp.	1010000211100210022110000011100011013
Centrinopus alternatus	0011100211200010030120010024002011104
Centrinopus helvinus	0010100211200010030110000022102011101
Centrinus curvirostris	1010100211200201220021010020102021105
Coelonertus nigrirostris	0010100211200010020120010021002010104
Coleomerus boliviensis	1011100211000010000000010011101010102
Conoproctus quadripustulatus	0011001211100101220010014011100011114
Crostidia tenuipes	10100102112001010?????014021000021000
Crotanuis trivittatus	00101102111002012?????014023002010114
Cylindridia prolixa	0010100211200201020101000013001001114
Cylindrocerus comma	0010100211100121200000014010000021114
Cyrionyx camelus	1010100211200201030100014021112011014
Dactylocrepis flabellitarsis	00100002111002112?????014013000010103
Dealia carbonarius	00121102112002112?????0000011000001011
Deipyros hirsutulus	0010110211200020030110010021002011014
Demoda vittata	0110110111200101020120010012102011114
Desmoglyptus arizonicus	0010010211100210020102010021000020111
Dialomia gradata	10111102112002100?????010024001010103
Diastethus eurthinoides	1010100212000200000011000011010011110
Dimesus rubricatus	0010110211200111000000010014000011114
Diorymeropsis disjuncta	1011110211200211020030010021101010111
Diorymeropsis xanthoxyli	1011110211200211020000010021101010111
Diorymerus lancifer	10000002110001210?????010004000020110
Dirabius calvus	0012100211100211020121000011100000114
Dirabius rectirostris	0011100211200211020130000011101002114
Dissopygus metallescens	1012000201100020021100000011101021012
Eisonyx crassipes	0010110101100220222111010021101000113
Eisonyx opaca	0010010211100020031102010011100001010
Elasmobaris signifer	00101102011000200?????010011102000114
Embates chaetopus	0010100211000101020110004011002111014
Eugeraeus sp.	0012100211000200000011010120002121003
Eumycterus albosquamulatus	0012100111200211020132000011101001111
Eurhinus festivus	1001000211100221220112000111000010113
Eurhinus aeneus	10010002111002210201120001111000010111
Eusomenes curtirostris	11111102011000200?????010011001001014
Eutoxus sp.	0012010211200201020120010014000021113
Fishonia brevinasus	01101100022002200?????010011101000111
Fryella mutilatus	11100102012002212?????0000011000011011

Garnia sp.	1011010211000101020110010011000020111
Geraeopsis duplocincta	00101102111002110?????010021001010112
Geraeus lineellus	0011110211100201200000014013102021111
Geraeus penicella	1011110011000201000000010021002011004
Glyptobaris lecontei	1011110011200010020030010021100111010
Haplostethops ellipsoidea	0011100211100211030120010021101010114
Idiostethus subcalvus	1010110211100000030100010021002110114
Idiostethus tubulatus	1010110211100001030121010021101110114
Iops bicolor	01101001111000100?????014011001001110
Ladustaspis crocopelmus	00101002122002102?????010021002021004
Lampobaris cicullata	1011010112100210230120000010000011014
Lasiobaris geminata	0010110212200221030120010011102001013
Laurentius bruchi	00101002111002010?????010011001000114
Lepidobaris acnisti	0010110211100211022100000011002011011
Leptoschoinus fucatus	1011100211200101000020010011002011114
Lichnus longulus	0012010212200010020130014011000001110
Limnobaris bicincta	0011110211100200030000010011101011111
Limnobaris calandriiformis	0112010211200221230100010013000011111
Linogeraeus urbanus	1011110211200201000000000011002011111
Linogeraeus viduatus	1011100211200200210020000013002010113
Linomadarus vorticoides	0011100011200211022100010121001011013
Lipancylus brevis	0012100110100010020130004011001001112
Loboderes citriventris	0011110211100111010110010011100011112
Lorena simulans	10121102111000102?????010024102011001
Lydamis cinnamomeus	1010100211200201020110014011102021010
Macrobaris sp.	0010000212100210030110010011000000110
Macrorevena atromicans	10100100112000102?????010021000022114
Madarellus laticollis	1011000211200221020032010111010011013
Madarus bistrigellus	0012100211200211020032010121000011011
Madopteris talpa	0011000211100020020110000011100011115
Megabaris quadriguttata	1010100211200111020030000011102021012
Megavallius auritarsis	1010110211200200220121010011000011114
Melampus basalis	1011110211000211000021010024100020111
Microbaridia delicatula	00101102110002010?????014011002011004
Microcholus puncticollis	0012100211100000030130000011102001011
Microcholus striatus	00121002111000000?????000021100011114
Microforandia uniformis	11101002112000000?????000011002011013
Microrhinus mutilus	1011010201000020222132010001100010110
Microstegotes sp.	1010000211200121220121010011010010110
Microstrates coccois	00101101112000100?????010011001001012
Myctides imberbis	1011101211100020221121004011100011110
Nertinus suturalis	0011100110200201200011014011001001115
Nestrada compacta	10111102112002102?????010023002111002
Nicentrus decipiens	001010021220020002000?010011002011114
Nicentrus grossulus	0012100212100200020000010011102010114
Odontobaris sp.	111000021010020002011?010011001011114
Odontocorynus scutellumalbum	0010100211100210020030000011102021012
Odontocorynus creperus	0010100211100010020030000021102011002
Oligolochus braccatus	1010110211200010030120010021101001115
Oligolochus ornatus	0010110211200010030120010021102021113
Onychobaris densa	1011010211200010022102010011000011011
Oomorhidius leavicollis	0012000211100000030120010011000000111
Opseobaris alba	0012110211100010030121010011101001114
Optatus palmaris	1010100211200101220130004021102010100
Orchidophilus aterrimus	0012110211100010030121010011102011113
Orissus meigenii	10100002112002112?????000020010020113
Orissus christophori	1001000211200211220031000010000020110
Orthoris crotchii	0010110111100211022110010011002021110
Ortycus cristosus	1010110211200?????????010111112110113
Ovanus picipennis	1110010211100211230110010011000010111
Ovanus minutus	1011010211200221032020010011000010113
Pachybaris porosa	1011100211000210220030010011000021011
Pachygeraeus laevirostris	0010110211200210010011000020002011113
Pacomes subglaber	00121001112002002?????000011000001110
Palmelampus heinrichi	0011110011000000030100000022001021011
Pantoteles tenuirostris	00101001102002012?????004011002000110
Parageraeus tumidirostris	0010110211100201200021014013100011115

Parallelosomus amplitarsis	0112100110100010020120000001001001110
Parasaldius sp.	1010110211100200230020000023102011101
Parasomenes curvirostris	0111100211100000220130010011101001113
Pardisomus biplagiatus	1010100211100001021110014011001011110
Parisoschoenus sp.	1011110211200200230101000010101021114
Peclaviopsis planipectus	10101102112000100?????010011101021014
Peridinetus cretaceus	0010100211200201221102004011102010110
Peridinetus irroratus	0010100211200201221102004011102010100
Phacelobarus signubaris	1010110112100221021130010021112011013
Pistus galeatus	1010100211200200032131014021112010100
Platyonyx ornatus	1011110211100101020000010021001021113
Plesiobaris albilata	0010110212200010031132010011102001010
Plocamus echidna	0010100011000200022102010011002021111
Plocamus clavisetes	0010100011000200022100010011002021111
Prodinus sp.	1001010211100211030132010011000010113
Pseudobaris angusta	0011010211200210030112010011000010113
Pseudocentrinus ochraceus	0010100211200201020020010021102010104
Pseudogeraeus macropterus	001011021110000023000001002110211014
Pseudorthoris devexus	0010110211000211030100000011102011014
Pseudotorcus rufipes	0110100111100210020121010012102001113
Psiona densa	00101002111002200?????010011002101014
Pteracanthus smidtii	00101001111002010211200040211120101010
Pycnogeraeus modestus	1010100212200201010001000011102021011
Pycnogeraeus striatirostris	1011110211200210010000010021102121013
Pycnonicentrus gilvivistis	10101102111002110?????014011002011002
Pycnotheantis sp.	1010010211000000230110010011001021113
Ranceoma uniformis	00101101111002000?????014011100020112
Remertus marginatus	101010021000001000?????000011101021113
Ravena sexualis	10111002110002010?????010021000011001
Reveniopsis sp.	10110100120002210?????010011000011011
Rhoptobaris canescens	0010110211100111022110010011002011014
Saldiopsis armata	10111100122002112?????010021102121004
Saldius inaequalis	10101102112002000?????010011102021014
Selasella cuneipennis	10111102110002010?????010121100021001
Sibariops concinna	0011110211200000220100010011002011113
Sibariops concurrens	0010100111200200020101010011101011111
Solaria curtula	1011010011000211022100010111100011011
Solenosternus dividuus	0011010211200010031132000011000011012
Somenes regestus	00101102111002000?????000010102021114
Stereobaris interpunctata	1010010211200020022111010021101021112
Stethobaris commixta	1011010211200121030110010011100010111
Stethobaris laevimargo	101000021120021003012??010011000010011
Stethobaroides nudiventris	1011000211000211030120000011100010011
Stethobaropsis titara	10110102120002210?????00011000012013
Strongylotes squamans	0010100110200200010030004011102001013
Telemus sp.	1010100211000201031110004021112010110
Tenemotes abdominalis	1011000011000010020121010011000010110
Tenemotes parviclava	101010021120001002002?010011001020114
Thaliabaris inermis	01101002111000000?????000011101001114
Torcobius sp.	0012100111100211022131000111101010113
Torcus nigrinus	0111100210100201030030010011002001114
Torcus variabilis	0110100111100011020130000012101011114
Trachymeropsis palmipes	0011100110200211000010004011101002113
Trichodirabius longulus	0011100211200211220121000011102010114
Valdenus laevis	00111002112002210?????000011000000114
Valiopsis squamipes	001011001110020102003?010021001020101
Vallius sulcatus	10100002112002210?????010021010010100
Xystus ater	1010000211000201020000014010000010114
Xystus ruficollis	1010000211000201020000000011000020114
Zena virgata	0010110211100010022121010011101011113
Zygobarella xanthoxyli	1011110211200211030100010021102021014
Zygobarella tristicula	1011110211200211030100010021002021014
Zygobarinus coelestinus	00100102111000100?????000011000011011
Zygobaris sp. 1	1011110211200201030100010021102021004
Zygobaris nitens	1011110211200121030130000021002021011
Zygobaris sp.	0010100211200210030100010011002011013
Zygozalestes oblongus	10101100111000202?????010021000021014

Anatorcus densus	01101102111002200???????10011102001114
Andiblis seriata	11101000110002110???????10011002010112
Aniops sculpturata	00101002011000200???????10011002001014
Anotesiops obidosensis	00111102111002100???????10011101001013
Calorida binocularis	10101102112002000???????10011102011002
Camerones semiopacus	00121002112001102???????10121002021011
Chepagra rotundicollis	0012100212200?00???????10111101021014
Clandius cephalotes	10111002112002110???????10121001010113
Crostis subexplanata	00100102121002212???????10011000011000
Dericinus habilis	10111102112002100???????10021101021001
Ethelda Squamosa	00101002121000100???????10021102011012
Eudialomia longula	00111102110002102???????00011001021011
Forandia duplex	00101001112002010???????10011102011014
Forandiopsis carinulata	00101002112002010???????10011102011014
Iopsidaspis truncatula	00110102122002000?0?????10011100001010
Leptogarnia polita	10110102112002110?0?????10111000021013
Leptoladustes densus	10101102112002010???????10020102021113
Linogarnia suturalis	10011102112002102?0?????10021001021003
Microtorcus tubulatus	00111102111002110?0?????10011101001014
Microzalestes basalis	11010100120002000???????10111000020111
Nedestes sarpedon	10100102110001012???????00022000021010
Neplaxa illustris	10100002011002013???????00000100000110
Nicentridia angusticollis	00101102111000000???????10011002011001
Palocopsis tecta	00111102111000000???????10011002011014
Parafishonia setulosa	01101102112000102???????10021101011013
Peclavia hispidicollis	10111000112002010???????10011102010112
Pseudorancea spissirostris	00111102121002212???????10014100000115
Pseudosaldius conjunctus	10101102122002002???????10015102021110
Rancea parviclava	00101000112000100???????00011101010114
Roalius rufipes	00101002112000?00???????10?10?11102000114
Sibariopsida docilis	00101102111002110?0?????10011101001014
Sodesia sparsa	11111102110000000???????00011002021013
Spolatia gradata	10110102122000200???????10111000011011
Starcus rugulosus	01101002112001?10???????10?21102010114
Sunilius platyrhinus	11111100110002100???????10121101021003
Ternova biartita	00101102122002012???????10011000011004
Thestonia sparsa	11111102111002110???????10011102011011
Zalestes perpolitus	10010102110002110???????00121000010101
Cymatobaris impressifrons	001011020120002003112001012101101113
Pacomes distortus	0010010211100200210120010011000001110
Megalobaris viridana	1010100211200220030120000021001022112
Rhytidoglymma cenescens	0010010211200211031130000011110012011
Craptus tibialis	0010010211200211020130010021000010101
Testalthea sp.	1000000211000121031130010011100020110
Barycerus collaris	1012000201200020020110000011000012011
Opertes sp.	1011100211100210020030010021100010111
Stictobaris cribrata	0010110212100020020130010021102011010
Moreobaris deplanata	0010010211200010020120010021100021013
Ulobaris loricata	0010100211200020031121010021100001010
"Neomadarini"	0011110211100211030130010011100021113
Trichobaris texana	0010110212200020031120010021102021013
Dalcesia sp.	0010000211200211031130000011000000111
Nanobaris sp.	1110110211100010021130010011002000110
Zathanus sp.	1011110212200211020120010021102001011
Allomegops sp.	1010100211100211020120000121002000113
Deipyle induta	1011100211200221020132010011102011011
Cosmobaris americana	0010110212100000031120010021002011013
Thanus sp.	0011000211200211030130010121100010102
Cryptosternum nevermanni	10101002112002110?????0000021102002011
Pycnobaris pruinosa	1011110212200020020111010021102022001
Tonesia sp.	1112010211200211030130010021000001011
Trepobaris inornata	0011010212200020020130010021000000101
Hiotus inflatus	1001000212200211010020010011000020110
Sphenobaris quadridens	1111110211200211020130010111002112011
Coluthus cribrarius	0010100211100201020130010021102010103
Aniops sp.	0010100211100020030120010021002011014
Montella rufipes	10111102112000210???????10011100022010

Palmocentrinus butia	00111002110002110??????10013101021012
Bondariella mimica	00101100110002100??????10021102001011
Eucalus vitticollis	00101002111002010??????10021002001010
Scirpicola chilensis	00101002111002010??????10011102001110
Ortycus setifer	1011100211200201210021010021102122010

### Appendix I (continued). Character matrix - characters 37 – 73

	37	42	47	52	57	62	67	72
Dryophthorinae (Dryophthorus americanus)	0	1	0	0	0	2	3	1
Bagoinae (Bagous transversus)	3	0	1	0	0	0	2	3
Conoderinae (Cylindrocopturus operculatus)	0	1	1	0	0	2	2	1
Conoderinae (Trichodocerus sp.)	3	1	0	0	0	1	4	0
Conoderinae (Arachnopus gazella)	1	2	1	0	0	1	0	1
Conoderinae (Cyllophorus fausciatus)	0	1	0	0	0	0	0	1
Conoderinae (Metialma straminea)	3	1	0	1	0	2	0	0
Conoderinae (Balanogastris kolae)	0	1	0	1	0	2	0	0
Conoderinae (Telephae oculata)	0	1	0	1	0	2	0	0
Conoderinae (Cylindrocopturus adspersus)	1	1	0	1	0	2	0	0
Conoderinae (Acoptus suturalis)	0	1	0	0	0	2	0	0
Conoderinae (Lobotrachelus troglodytes)	1	2	1	0	0	2	0	0
Conoderinae (Mecopus trilineatus)	0	1	2	0	0	2	0	0
Ceutorhynchinae (Ceutorhynchus obstructus)	0	1	0	1	0	2	0	0
Ceutorhynchinae (Hypurus bertrandi)	0	1	0	0	2	0	0	0
Ceutorhynchinae (Phytobius oriseomicans)	0	1	0	2	0	0	0	0
Ceutorhynchinae (Mononychus vulpeculus)	1	1	1	0	2	0	0	0
Ceutorhynchinae (Auleutes argentinensis)	1	1	0	1	0	2	0	0
Ceutorhynchinae (Coeliodes flavicaudis)	1	1	0	1	0	2	0	0
Curculioninae (Curculio pardalis)	0	0	0	0	2	0	0	0
Molytinae (Cholus rana)	0	0	0	0	2	0	0	0
Molytinae (Trigonocolus curvipes)	0	1	0	0	0	2	0	0
Molytinae (Conotrachelus fissunguis)	0	1	0	0	0	2	0	0
Entiminae (Cyrtepistomus castanaeus)	3	0	2	0	0	2	0	0
Derelominae (Derelomus basalis)	3	1	2	0	0	2	0	0
Cryptorhynchinae (Cryptorhynchus lapathi)	1	1	0	0	1	0	2	0
Orobittidinae (Parorobitis gibbus)	1	1	0	0	1	0	2	0
Acentrinops brevicollis	0	2	1	0	1	0	0	0
Amercedes subulirostris	0	2	1	0	1	0	0	0
Amercedes orthorrhinus	0	2	0	1	0	0	0	0
Anavallius ruficornis	0	2	0	1	0	0	0	0
Anopsilus oblongus	2	2	0	1	0	0	0	0
Antesis sparsa	1	2	0	1	0	0	0	0
Athesapeuta vinculata	1	1	0	1	0	0	0	0
Barilepsis griseus	1	2	0	1	0	0	0	0
Barilepton filiforme	0	2	0	1	0	0	0	0
Barilepton quadrieolle	0	1	0	0	1	0	0	0
Barinus bivittatus	0	1	2	0	1	0	0	0
Barinus cribricollis	0	1	1	0	1	0	0	0
Baris torquata	0	2	0	1	0	0	0	0
Barymerus binaries	1	2	0	1	0	0	0	0
Buchananianus striatus	0	2	0	1	0	0	0	0
Buchananianus sulcatus	0	2	0	1	0	0	0	0
Busckiella lecythidis	2	2	0	1	0	0	0	0
Calandrinus grandicollis	1	2	0	1	0	0	0	0
Camelodes leachii	1	2	0	1	0	0	0	0
Catapastinus caseyi	0	2	0	1	0	0	0	0
Catapastus conspersus	0	2	0	1	0	0	0	0

Catapastus squamirostris	0210110001001121000200100220001020001
Catapastus albonotatus	0210110001001010001201000210001022???
Catapastus diffusus	021011000100112100020010022??01022???
Catapastus seriatus	0210110001001010001201000210001022001
Catapastus signatipennis	0210110001001010001201000210001022001
Catapastus simplex	021011000100101000120100021??01020???
Centrinites strigicollis	0200110411011010001200010100011120211
Centrinogyna hispidula	0100110421013011010002000010011122000
Centrinogyna strigata	010011041??1011000001010011011120001
Centrinopsis sp.	0100111020011010201211201020012120110
Centrinopus alternatus	0210110421111011100110010220011122001
Centrinopus helvinus	0100110221011011000110010220011122001
Centrinus curvirostris	1200110211011211000100000120011122110
Coelonertus nigrirostris	1100110011001011100001100121011022001
Coleomerus boliviensis	1210110021001211101100010220011022201
Conoproctus quadripustulatus	1200110200101021200002111110011121100
Crostidia tenuipes	021011052????????????????????1120???
Crotanuis trivittatus	0200111521011111100000110200001122210
Cylindridia prolixa	0210110120001010000102200011011122001
Cylindrocerus comma	1200110411000111201200000011011122110
Cyrionyx camelus	0210111340000010201101001021010122211
Dactylocrepis flabellitarsis	012011004????????????????????11020???
Dealia carbonarius	220011052????????????????????11100???
Deipyros hirsutulus	02101102110110110000011000120011120201
Demoda vittata	0100110021011021001111200220011122110
Desmoglyptus arizonicus	0100110010001011001202201210011132201
Dialomia gradata	021011000????????????????????11022???
Diastethus eurthinoides	1210110541001210100110010011000101110
Dimesus rubricatus	0210111221001120000200000121011122211
Diorymeropsis disjuncta	1200110011001120200100010220011020001
Diorymeropsis xanthoxyli	1210110011001120200101010220011020100
Diorymerus lancifer	1210110521011011001211100001001021110
Dirabius calvus	0100110421001020001100100120011121110
Dirabius rectirostris	0100110121011021000101100020011122110
Dissopygus metallescens	0110110111001020200001001220011022110
Eisonyx crassipes	0210110311111000010012011210021020322
Eisonyx opaca	0210110310111011210202011211021020322
Elasmobaris signifer	021011010????????????????????0011130???
Embates chaetopus	0100110020011020001201200001010122110
Eugeraeus sp.	2210110521010021101101000110010122100
Eumycterus albosquamulatus	1120110510011011010202201010011120001
Eurhinus festivus	0100110040000010001201011210001131100
Eurhinus aeneus	221011034000111101202001210001031200
Eusomenes curtirostris	020011002????????????????????11141???
Eutoxus sp.	2210110011001021200001200210011122100
Fishonia brevinasus	211011041????????????????????11020???
Fryella mutilatus	121011034????????????????????01041???
Garnia sp.	2200110011011211201201000001001022110
Geraeopsis duplocincta	021011042????????????????????11022???
Geraeus lineellus	0200110001001110001000000110011122001
Geraeus penicella	12001105010011110110000000011102110
Glyptobaris lecontei	2200110010000011001012001210011120200
Haplostethops ellipsoidea	0200110120011011201200000210011121001
Idiostethus subcalvus	0210110411011010200201000220011120011
Idiostethus tubulatus	02001104410110100001000??0011120211
Iops bicolor	112011001????????????????????1001022???
Ladustaspis crocopelmus	012011042????????????????????0011022???
Lampobaris cicullata	0210110420111010210012000010011120210
Lasiobaris geminata	0210110111001111201100000120011002210
Laurentius bruchi	020011052????????????????????11100???
Lepidobaris acnisti	1210110520111011000011211210011020200
Leptoschoinus fucatus	120011040100122110110000001011102010
Lichnus longulus	0020110111110201010100200021001122210
Limnobaris bicincta	0210110021001011101000200110011122210
Limnobaris calandriiformis	2200110411001021101200000110011120101
Linogeraeus urbanus	2210110221001111001200000100011122210
Linogeraeus viduatus	0210110421001110001001010100011121100

Linomadarus vorticosus	2210110200001011000212201210011022100
Lipancylus brevirostris	0020110121110011210111201001001121210
Loboderes citriventris	1200110340011021201211200210011020100
Lorena simulans	020011052????????????????????11022???
Lydamis cinnamomeus	0110111520011021111011011001010121110
Macrobaris sp.	0020111111111000201200200021001022210
Macrorevena atromicans	010011052????????????????????11002???
Madarellus laticollis	2210110320000021100012011210010022200
Madarus bistrigellus	2210110340001021001002101220010121210
Madopterus talpa	0020110121100110211101200001011141210
Megabaris quadriguttata	0100110201010011101110000000011122100
Megavallius auritarsis	0200110411011211000201000200011122110
Melampus basalis	2210110521010021001200000220011122110
Microbaridia delicatula	020011000????????????????????11020???
Microcholus puncticollis	0110110011101000110112011210011122322
Microcholus striatus	010011001????????????????????0011122???
Microforandia uniformis	020011051????????????????????11020???
Microrhinus mutilus	1210110311001010001002011210011022001
Microstegotes sp.	1210110521000010000210000021002021110
Microstrates coccois	1210110511001021100001100200011122???
Myctides imberbis	1210110321000011001001101210010022100
Nertinus suturalis	0020110221111000011110200001001021110
Nestrada compacta	120011010????????????????????11022???
Nicentrus decipiens	0100110221001011000011200000011122001
Nicentrus grossulus	0100110521001011000100100100011122101
Odontobaris sp.	1100110121111001210210000120011022110
Odontocorynus scutellumalbum	0120110220000011100200100020011122210
Odontocorynus creperus	0120110221100011200100100020011122110
Oligolochus braccatus	0210110000011011000001010220011120011
Oligolochus ornatus	0210110201000111001100010210011120001
Onychobaris densa	2210110220000021000012111210011120000
Oomorhphidius leavicollis	121011002101????????????????1210011122322
Opseobaris alba	0020110011111010211200200001001121210
Optatus palmaris	0200111540011021001110010001000121110
Orchidophilus aterrimus	2210110030101020000200011210010121110
Orissus meigenii	1200110211011200201110000001000021110
Orissus christophori	2210110511001210200110010001002022110
Orthoris crotchii	0210110221011010000111111210011120001
Ortycus cristosus	120011050????????????????????11022???
Ovanus picipennis	1210110420001111001200000210001122211
Ovanus minutus	1210111110001011001001000220011022211
Pachybaris porosa	2210111001000021001200000210011022001
Pachygeraeus laevirostris	0100110221111011200200000120011122210
Pacomes subglaber	002011010????????????????????00121???
Palmelampus heinrichi	1210110511001011101200000110011022001
Pantoteles tenuirostris	0100111520010021200210200021010120???
Parageraeus tumidirostris	0100111411011011001100000120011122210
Parallelosomus amplitarsis	0120110121110110000110200021011121110
Parasaldius sp.	1200110001001011001201100120011122001
Parasomenes curvirostris	1100110001001011000100200110011122100
Pardisomus biplagiatus	0110111420110011000201111001000121110
Parisoschoenus sp.	1210110511000011100201100110011022000
Peclaviopsis planipectus	021011052????????????????????11022???
Peridinetus cretaceus	0100110441010020001011201001000121110
Peridinetus irroratus	0100110021010020001211201001000122110
Phacelobarus signubaris	1100110100011010000011110210010022100
Pistus galeatus	0210111520001020100100001001010132010
Platyonyx ornatus	1200110211101111100000100020011101110
Plesiobaris albilata	1110110320011011011202011120011020001
Plocamus echidna	2210110501010020211001010210011120001
Plocamus clavisetes	2210110501001011000012010210011120001
Prodinus sp.	011011022001100120020100000011022210
Pseudobaris angusta	1210110120111011001001200120011022000
Pseudocentrinus ochraceus	0100110211001011000200100121011120110
Pseudogeraeus macropterus	0220110201100000201110100000011020110
Pseudorthoris devexus	0200110521011011101010200120011120201
Pseudotorcus rufipes	0200110111101011101100100020011122010

<i>Psiona densa</i>	011011142????????????????????01020???
<i>Pteracanthus smidtii</i>	0100111520010010000101000021000122110
<i>Pycnogeraeus modestus</i>	0120110201001120001100000100011122110
<i>Pycnogeraeus striatirostris</i>	02101105010011201001010000200011122001
<i>Pycnonicentrus gilvivistis</i>	011011011????????????????????11002???
<i>Pycnotheantis sp.</i>	1200110420011021001100010120011020110
<i>Ranceoma uniformis</i>	010011011????????????????????11022???
<i>Remertus marginatus</i>	221011022????????????????????11122???
<i>Ravena sexualis</i>	121011042????????????????????1011022???
<i>Reveniopsis sp.</i>	221011031????????????????????11022???
<i>Rhoptobaris canescens</i>	0210110520011110001200201210011020201
<i>Saldiopsis armata</i>	021011042????????????????????11020???
<i>Saldius inaequalis</i>	021011041????????????????????11020???
<i>Selasella cuneipennis</i>	220011041????????????????????11022???
<i>Sibariops concinna</i>	1210110011001021000011200210011122001
<i>Sibariops concurrens</i>	1210110410001011000100000220011122001
<i>Solaria curta</i>	2210110320001021001101011210010020200
<i>Solenosternus dividius</i>	1210110010101021001012101210011020200
<i>Somenes regeustus</i>	011011012????????????????????11122???
<i>Stereobaris interpunctata</i>	0210110111000010100002001220011020110
<i>Stethobaris commixta</i>	220011011010121120110000220001022211
<i>Stethobaris laevimargo</i>	1210111111101011201201000210011022210
<i>Stethobaroides nudiventris</i>	121011111110122110120000220011022211
<i>Stethobaropsis titara</i>	020011101????????????????????11022???
<i>Strongylotes squamans</i>	0020110021110010011111200001011121110
<i>Telemus sp.</i>	0210111020010020010010011001000121110
<i>Tenemotes abdominalis</i>	0210110521001110201110200001001002210
<i>Tenemotes parviclava</i>	0210110520001111201110000001001002211
<i>Thaliabaris inermis</i>	121011042????????????????????0011122???
<i>Torcobius sp.</i>	0210111120111011101001100220011122001
<i>Torcus nigrinus</i>	2020110221101010010101100021011121210
<i>Torcus variabilis</i>	2200110510011011000101200010011122001
<i>Trachymeropsis palmipes</i>	1120110121112010111000200021001021210
<i>Trichodirabius longulus</i>	1200110520001021100100100210011122110
<i>Valdenus laevis</i>	012011011????????????????????11122???
<i>Valliopsis squamipes</i>	0210110221111111001210000100011022110
<i>Vallius sulcatus</i>	121011052????????????????????00021???
<i>Xystus ater</i>	1210110520011200200110000001010021210
<i>Xystus ruficollis</i>	0210110521011200200110010001002022210
<i>Zena virgata</i>	0100110500100020000001001110001122100
<i>Zygobarella xanthoxyli</i>	1200110001001011000200010210001022001
<i>Zygobarella tristicula</i>	2210110521001011000200010210001122001
<i>Zygobarinus coelestinus</i>	220011033????????????????????0001122???
<i>Zygobaris sp. 1</i>	0210110121011011001010000120011020001
<i>Zygobaris nitens</i>	1210110011000121000200010220001022010
<i>Zygobaris sp.</i>	1110110021001011000001000200011122001
<i>Zygozalestes oblongus</i>	110011002????????????????????11022???
<i>Anatorcus densus</i>	1??011040????????????????????11122???
<i>Andiblis seriata</i>	1??011030????????????????????01042???
<i>Aniops sculpturata</i>	0??011060????????????????????01132???
<i>Anotesiops obidosensis</i>	2??011010????????????????????11022???
<i>Calorida binocularis</i>	0??011041????????????????????11021???
<i>Camerones semiopacus</i>	1??011042????????????????????11022???
<i>Chepagra rotundicollis</i>	0??011022????????????????????11122???
<i>Clandius cephalotes</i>	0??011040????????????????????11022???
<i>Crostis subexplanata</i>	0??012050????????????????????11020???
<i>Dericinus habilis</i>	1??011051????????????????????11022???
<i>Ethelda Squamosa</i>	0??011030????????????????????01022???
<i>Eudialomia longula</i>	2??011042????????????????????11120???
<i>Forandia duplex</i>	0??011022????????????????????11101???
<i>Forandiopsis carinulata</i>	0??012052????????????????????11002???
<i>Iopsidaspis truncatula</i>	1??011042????????????????????11132???
<i>Leptogarnia polita</i>	1??011054????????????????????01020???
<i>Leptoladustes densus</i>	1??011052????????????????????11120???
<i>Linogarnia suturalis</i>	0??011061????????????????????01020???
<i>Microtorcus tubulatus</i>	0??011041????????????????????11122???
<i>Microzalestes basalis</i>	1??011041????????????????????11022???

Nedestes sarpedon	1??012052????????????????????11001???
Nephlaxa illustris	0??000221????????????????????10161???
Nicentridia angusticollis	0??011030????????????????????11122???
Palocopsis tecta	0??011030????????????????????01022???
Parafishonia setulosa	1??011040????????????????????11122???
Peclavia hispidicollis	1??011040????????????????????11022???
Pseudorancea spissirostris	0??011042????????????????????01022???
Pseudosaldius conjunctus	0??011052????????????????????11120???
Rancea parviclava	0??011142????????????????????11021???
Roalius rufipes	3??011021????????????????????00122???
Sibariopsida docilis	0??011040????????????????????11120???
Sodesia sparsa	1??011040????????????????????11120???
Spolatia gradata	1??011010????????????????????00132???
Starcus rugulosus	1??011042????????????????????11120???
Sunilius platyrhinus	2??011001????????????????????11022???
Ternova biartita	0??011054????????????????????11122???
Thestonia sparsa	0??011002????????????????????01022???
Zalestes perpolitus	1??011002????????????????????11122???
Cymatobaris impressifrons	1210110111001021200001001220011122110
Pacomes distortus	0020110421110211201101201001000121110
Megalobaris viridana	0110110601001020201201101220011022100
Rhytidoglymma cenescens	2210110611001021000200101210001132110
Craptus tibialis	1210110520101020101001201210001032100
Testalthea sp.	1210110301010121100201000001001030210
Barycerus collaris	0210110021010021001201001220011030100
Opertes sp.	1210110621001021000202001210011032100
Stictobaris cribrata	0100110221001011000101101210011100100
Moreobaris deplanata	2210110610001010000100101210011020200
Ulobaris loricata	0100110520111011200200011110011120200
"Neomadarini"	1210110001001021000200100220011021001
Trichobaris texana	0100110520101011000210201210001120100
Dalcesia sp.	0100110620211011100202101220011020100
Nanobaris sp.	1210110620001011000111001210001020201
Zathanus sp.	0210110620101020000200101210011020110
Allomegops sp.	1210110520110011000101201210001120210
Deipyle induta	2210110620010020000201001210011020200
Cosmobaris americana	0110110100101011000112201210011020200
Thanius sp.	2200110620011021000201101210001022110
Cryptosternum nevermanni	121011062????????????????????010162???
Pycnobaris pruinosa	1210110501001011001201001210011120110
Tonesia sp.	2210110221001020001011000210011100200
Trepobaris inornata	1100110620001011000012201120010020100
Hiotus inflatus	1200110201011001001111000000011022110
Sphenobaris quadridens	2210110330001010000202001210010122200
Coluthus cribrarius	1100110520011011000200200020011122101
Aniops sp.	0100110001011001000010200121001132211
Montella rufipes	021011030????????????????012?0001122???
Palmocentrinus butia	120011052????????????????0?2?0011102???
Bondariella mimica	120011010????????????????0?2?0011122???
Eucalus vitticollis	300000202????????????????0?1?0031120???
Scirpicola chilensis	300001311????????????????1?0?1011122???
Ortycus setifer	1210110521011020000201000001011122110

**Appendix I (continued). Character matrix - characters 74 - 110. \$ = [2,3].**

	74	79	84	89	94	99	104	109
Dryophthorinae (Dryophthorus americanus)								
	0000012000113002100000000000002?10201							

Bagoinae ( <i>Bagous transversus</i> )	100001010011110310000000000000301????
Conoderinae ( <i>Cylindrocopturus operculatus</i> )	011011020101000510000000111110301????
Conoderinae ( <i>Trichodocerus</i> sp.)	1000211200000003000000000000002110202
Conoderinae ( <i>Arachnopus gazella</i> )	2222322000014000000000000000005??0102
Conoderinae ( <i>Cyllophorus fausciatus</i> )	01102101000101031000000000000002??0111
Conoderinae ( <i>Metialma straminea</i> )	0110200111002004110000000000002010202
Conoderinae ( <i>Balanogastris kolae</i> )	1000210101010002101110001110002110201
Conoderinae ( <i>Telephae oculata</i> )	1000110101010002101110001110002??0102
Conoderinae ( <i>Cylindrocopturus adspersus</i> )	0000110101010003100000000000002010101
Conoderinae ( <i>Acoptus suturalis</i> )	0000110100020003100000000000002111202
Conoderinae ( <i>Lobotrachelus troglodytes</i> )	00001101102010310000000000000211????
Conoderinae ( <i>Mecopus trilineatus</i> )	1010200200015003100000000000002110102
Ceutorhynchinae ( <i>Ceutorhynchus obstrictus</i> )	1110000011012104110000000000002??0101
Ceutorhynchinae ( <i>Hypurus bertrandi</i> )	0000000211012103110000000000002??0112
Ceutorhynchinae ( <i>Phytobius oriseomicans</i> )	000010311101500410000000000003110003
Ceutorhynchinae ( <i>Mononychus vulpeculus</i> )	0110110211015102100000000000002010102
Ceutorhynchinae ( <i>Auleutes argentinensis</i> )	0000100111012003100000000000002010131
Ceutorhynchinae ( <i>Coeliodes flavicaudis</i> )	0110100211012003100000000000002010102
Curculioninae ( <i>Curculio pardalis</i> )	0010210100112002100000000000001??0111
Molytinae ( <i>Cholus rana</i> )	0110111200010005100000000000002??0032
Molytinae ( <i>Trigonocolus curvipes</i> )	1110213111112016110000000000006011210
Molytinae ( <i>Conotrachelus fissunguis</i> )	1000212000110004000000000000003100102
Entiminae ( <i>Cyrtepistomus castanaeus</i> )	111021200011000310000000000000310????
Derelominae ( <i>Derelomus basalis</i> )	2222322000110004101110001111002010111
Cryptorhynchinae ( <i>Cryptorhynchus lapathi</i> )	1110211000101004100000000000003010131
Orobittidinae ( <i>Parorobitis gibbus</i> )	1000110111012012100000001110001??0111
Acentrinops <i>brevicollis</i>	00000010000101110111111111100210????
Amercedes <i>subulirostris</i>	000011100001011?01?????????????010110
Amercedes <i>orthorrhinus</i>	000011110001011?01?????????????010111
Anavallius <i>ruficornis</i>	1010110100012111001111111111003011111
Anopsilus <i>oblongus</i>	000011011101311101110000111111011232
Antesis <i>sparsa</i>	0000111110010111211110001111002000022
Athesapeuta <i>vinculata</i>	0000110011011012101100001111112001032
Barilepsis <i>griseus</i>	000011010001211101111001111002100102
Barilepton <i>filiforme</i>	2222320000010112101111001111003010031
Barilepton <i>quadrieolle</i>	000011000001001211111001111003010031
Barinus <i>bivittatus</i>	00000000001000220111001111003000031
Barinus <i>cribricollis</i>	0000001000010101001111001111002010031
Baris <i>torquata</i>	0010110211014111001110001111112000120
Barymerus <i>binaries</i>	10102101110000110011111111100311????
Buchananius <i>striatus</i>	000001210001010210111110111101000121
Buchananius <i>sulcatus</i>	0000012000010112101111101111101010101
Busckiella <i>lecythidis</i>	001021221101201201111111111112011101
Calandrinus <i>grandicollis</i>	2222321000000103000000001110004000122
Camelodes <i>leachii</i>	1010112200010011?01110001111003??0100
Catapastinus <i>caseyi</i>	0000110100????????????????????00????
Catapastus <i>conspersus</i>	??????1000010111011111001111003010112
Catapastus <i>squamirostris</i>	0000111100010111011111001111002010112
Catapastus <i>albonotatus</i>	??????1100010111001111001111002000101
Catapastus <i>diffusus</i>	??????1100010111011111001111002010112
Catapastus <i>seriatus</i>	0000111100010111011111001111002000101
Catapastus <i>signatipennis</i>	0000000100010111001111001111002000101
Catapastus <i>simplex</i>	??????1100010111??1111001111002000101
Centrinities <i>strigicollis</i>	0000111100010112001110001111003000220
Centrinogyna <i>hispidula</i>	00001110000111021011100011100030?????
Centrinogyna <i>strigata</i>	0000010010011102011110001111003010030
Centrinopsis sp.	0000112000012112101111111111003010030
Centrinopus <i>alternatus</i>	0000010100010111001110001111001010200
Centrinopus <i>helvinus</i>	0000110100010112001110001111003010202
Centrinus <i>curvirostris</i>	1010110200010112001111101111003110101
Coelonertus <i>nigrirostris</i>	000011000001000110000000111100300????
Coleomerus <i>boliviensis</i>	1010111110012111011100001111002000101
Conoproctus <i>quadripustulatus</i>	00101120110120110111111111111102??11\$1
Crostidia <i>tenuipes</i>	??????00000000????????????????????
Crotanius <i>trivittatus</i>	1010110100010111001100001111003??0112
Cylindridia <i>prolixa</i>	10001111100111030011100011110020?0110
Cylindrocerus <i>comma</i>	1010211100010111001111001111111010221

Cyrionyx camelus	1010110200014111101100001110002001200
Dactylocrepis flabellitarsis	??????020000011?00??????????????????
Dealia carbonarius	??????00000100??????????????????????
Deipyrus hirsutulus	000011200001011?00????????????????0111
Demoda vittata	1010210100010011211111001111003??0101
Desmoglyptus arizonicus	0000112200004112101110001111112011120
Dialomia gradata	??????10000100??????????????????????
Diastethus eurthinoides	1010112200010111101000001111002010201
Dimesus rubricatus	1000110100010111011111001111113010112
Diorymeropsis disjuncta	001011110001011100111100111100201????
Diorymeropsis xanthoxyli	00101111000101111111100111100200????
Diorymerus lancifer	111021210000001210111111111111?0111
Dirabius calvus	0010110100010012001111001111002000010
Dirabius rectirostris	0010111111010012201111001111002000010
Dissopygus metallescens	001011121101401211110001111112001111
Eisonyx crassipes	22223210000110021000000011111120?0230
Eisonyx opaca	2222320000014103100000001111103000130
Elasmobaris signifer	??????00000131??????????????????????
Embates chaetopus	1110210200010011001110001110003000201
Eugeraeus sp.	101011320001011110111100111100310????
Eumycterus albosquamulatus	000000101100210?10000000000000??1131
Eurhinus festivus	001021011101211111111000111111001211
Eurhinus aeneus	00101101110141111111000111111011231
Eusomenes curtirostris	??????10100100??????????????????????
Eutoxus sp.	10102111000101110111111111102??0221
Fishonia brevinasus	??????10000101??????????????????????
Fryella mutilatus	??????22100130??0??????????????????
Garnia sp.	10101121000100110111111111113??0131
Geraeopsis duplocincta	??????02000100??????????????????????
Geraeus lineellus	0000010100014111211110001111002000110
Geraeus penicella	0010110100010111011110001111002010211
Glyptobaris lecontei	000001110000211300111111111112000220
Haplostethops ellipsoidea	00000111000101020011111111110300????
Idiostethus subcalvus	1000111100010102001111111111103000112
Idiostethus tubulatus	0000111010010102001111001111003000112
Iops bicolor	??????2001012113101111101111113??0121
Ladustaspis crocopolmus	??????010001011110110000111100310????
Lampobaris cicullata	1010112100014113001111111111113??1101
Lasiobaris geminata	101011100001001210111111111113??0031
Laurentius bruchi	??????02000100??????????????????????
Lepidobaris acnisti	0010112211014012101100001111112000110
Leptoschoinus fucatus	1000110211012111011100001111102??0102
Lichnus longulus	0010001111001113101111001111112011131
Limnobaris bicincta	0000010000012011001100001111002??0131
Limnobaris calandriiformis	0000011010010011201110001111002000202
Linogeraeus urbanus	0000110100010011211110001111002000210
Linogeraeus viduatus	0010110200010111201110001111002000100
Linomadarus vorticosus	0000110211102111011110001111112001131
Lipancylus brevirostris	1011213111002013011111101111113010132
Loboderes citriventris	0010110011012011011110001111101??0222
Lorena simulans	??????11000100??????????????????????
Lydamis cinnamomeus	11102102000100111011100011100031?0200
Macrobaris sp.	1010011000000114101111001111113010131
Macrorevena atromicans	??????020001101?10??????????????????
Madarellus laticollis	0000112211012111011110001111111011221
Madarus bistrigellus	000011111101211111110000111111001121
Madopteris talpa	1011211211013113001111111111113010131
Megabaris quadriguttata	0010110210010111211110001111003100022
Megavallius auritarsis	1010210200010112011111111111110201????
Melampius basalis	1010211100010112201111001111002??0111
Microbaridia delicatula	??????1100??????????????????????????
Microcholus puncticollis	22223200000110030000000000000030?0101
Microcholus striatus	??????10000101??????????????????????
Microforandia uniformis	??????30000100??????????????????????
Microrhinus mutilus	0000111011012012101100001111112011112
Microstegotes sp.	1010112200010112001100001111101??0211
Microstrates cocois	??????0010012011111111001111002100131

Myctides imberbis	00001101110120121111100011111111?1232
Nertinus suturalis	101021010001311111111111111111113100231
Nestrada compacta	??????31000100????????????????????
Nicentrus decipiens	0000000000010112211110001111002000102
Nicentrus grossulus	0000110100010111211110001111002??0112
Odontobaris sp.	001011001101011210111111111111113110112
Odontocorynus scutellumalbum	1010110011010111001100001111002000101
Odontocorynus creperus	1010110100010011001100001111002000012
Oligolochus braccatus	000011110001111200111101111103111102
Oligolochus ornatus	000001110001011110111100111100211????
Onychobaris densa	0000110111013111011100001111112011221
Oomorphidius leavicollis	2222320000010004101110001111003000101
Opseobaris alba	101021011001011111111111111111113010131
Optatus palmaris	111021020001001111111100111000210????
Orchidophilus aterrimus	000011000001211100111111111111211????
Orissus meigenii	1010210200010111101100001111111010220
Orissus christophori	101021210001011110100000111002010201
Orthoris crotchii	000000001101411210111000111111211231
Ortycus cristosus	??????12000100????????????????????
Ovanus picipennis	0000011000011111001111111111113100111
Ovanus minutus	0000010100000111011111111111112010001
Pachybaris porosa	1000111000010111201111101111002??0211
Pachygeraeus laevirostris	101011020001010200111001111002??0101
Pacomes subglaber	??????12111100????????????????????
Palmelampus heinrichi	00101130000120110111111111111102??0122
Pantoteles tenuirostris	??????020001001110110000111000201102
Parageraeus tumidirostris	101011110001011320111000111100201????
Parallelosomus amplitarsis	101121001101111301111111111111113110111
Parasaldius sp.	1010110110010111001110001111002??0201
Parasomenes curvirostris	101011100101011111111100111100200????
Pardisomus biplagiatus	1010110200010012101110001110003000202
Parisoschoenus sp.	000011311101201101111111111102010132
Peclaviopsis planipectus	??????10000100????????????????????
Peridinetus cretaceus	1111112200014012101111001110002000200
Peridinetus irroratus	1111210200010012101111101110002??0200
Phacelobarus signubaris	0101110100004011111110001111101??1131
Pistus galeatus	1010110200010111101100001110001011200
Platyonyx ornatus	0010110101000113001100001111003100102
Plesiobaris albilata	0000011010002105000000001111114011222
Plocamus echidna	0000011000010011101000001111001110201
Plocamus clavisetes	000000200001111101111001111001000022
Prodinus sp.	1010110100002111001111111111113010201
Pseudobaris angusta	0000003011003111001100001111002??1212
Pseudocentrinus ochraceus	1010110100010111101111001111002100022
Pseudogeraeus macropterus	1010110111012111011110001111003000200
Pseudorthoris devexus	0000001111011111????????????????0031
Pseudotorcus rufipes	1010110100010111201111001111002000111
Psiona densa	??????21000000????????????????????
Pteracanthus smidtii	1111211200011112101111001110002001101
Pycnogeraeus modestus	101011011101011?01????????????????1111
Pycnogeraeus striatirostris	0010001100010111211110001111002100001
Pycnonicentrus gilvivistis	??????0100????????????????????????
Pycnotheantis sp.	101011110001011110111000111100311????
Ranceoma uniformis	??????11000000????????????????????
Remertus marginatus	??????01000100????????????????????
Ravena sexualis	??????010001001121111001111003??0111
Reveniopsis sp.	??????1200000111001111001111003??0211
Rhoptobaris canescens	000011001101411210111000111112011230
Saldiopsis armata	??????11000100????????????????????
Saldius inaequalis	??????10000100????????????????????
Selasella cuneipennis	??????11000101????????????????????
Sibariops concinna	00000010000001110111000111100200????
Sibariops concurrens	000011110001011101111000111100300????
Solaria curtula	0000111111013111001100001111113000031
Solenosternus dividuus	0000111011012011011100001111113011222
Somenes regestus	??????11010100????????????????????
Stereobaris interpunctata	0010111211014011111110001111112001121

Stethobaris commixta	000000000001011111111001111101100020
Stethobaris laevimargo	001010100001011210111111111112000101
Stethobaroides nudiventris	0000111011004111111111111111120?0021
Stethobaropsis titara	??????11000101????????????????????
Strongylotes squamans	10102102100100121011111111111211????
Telemus sp.	111021220001001110111000111000211????
Tenemotes abdominalis	11102102000101111111111111111210????
Tenemotes parviclava	10101102000101131011111111111121????
Thaliabaris inermis	??????10110121????????????????????
Torcobius sp.	0000101100000011201000001111002??1131
Torcus nigrinus	1010110011010002200000001111102??0012
Torcus variabilis	1000101000010102210000001111103010202
Trachymeropsis palmipes	00100111000101121011111111111310????
Trichodirabius longulus	0000111000010112001111001111002010111
Valdenus laevis	??????21110010????????????????????
Valliopsis squamipes	1010210200012112201111111111002??0110
Vallius sulcatus	??????210000011?00????????????????
Xystus ater	1010110200010111001000001111003000200
Xystus ruficollis	1010110200000011001000001111003??0101
Zena virgata	0010110111014012101100001111112010031
Zygobarella xanthoxyli	000001110001011?00?????????????000221
Zygobarella tristicula	000011110001011?00?????????????000221
Zygoabarinus coelestinus	??????11010131????????????????????
Zygoabaris sp. 1	0000001100010111201111001111001000101
Zygoabaris nitens	101011100001011?00?????????????0100
Zygoabaris sp.	0000001000010111201111001111003001101
Zygozalestes oblongus	??????11000100????????????????????
Anatorcus densus	??????110100001????????????????????
Andiblis seriata	??????110001011????????????????????
Aniops sculpturata	??????110001011????????????????????
Anotesiops obidosensis	??????110101011????????????????????
Calorida binocularis	??????020001001????????????????????
Camerones semiopacus	??????110001001????????????????????
Chepagra rotundicollis	??????010001001????????????????????
Clandius cephalotes	??????110001011????????????????????
Crostis subexplanata	??????30010101????????????????????
Dericinus habilis	??????100001001????????????????????
Ethelda Squamosa	??????110001001????????????????????
Eudialomia longula	??????110001001????????????????????
Forandia duplex	??????011001201????????????????????
Forandiopsis carinulata	??????010002011????????????????????
Iopsidaspis truncatula	??????110000011????????????????????
Leptogarnia polita	??????010001001????????????????????
Leptoladustes densus	??????010001011????????????????????
Linogarnia suturalis	??????010001001????????????????????
Microtorcus tubulatus	??????110001001????????????????????
Microzalestes basalis	??????110001011????????????????????
Nedestes sarpedon	??????021001001????????????????????
Neplaxa illustris	??????000001000????????????????????
Nicentridia angusticollis	??????010001011????????????????????
Palocopsis tecta	??????010002011????????????????????
Parafishonia setulosa	??????110001001????????????????????
Peclavia hispidicollis	??????110001001????????????????????
Pseudorancea spissirostris	??????110001011????????????????????
Pseudosaldius conjunctus	??????010001001????????????????????
Rancea parviclava	??????110001011????????????????????
Roalius rufipes	??????010001001????????????????????
Sibariopsida docilis	??????110001001????????????????????
Sodesia sparsa	??????110001011????????????????????
Spolatia gradata	??????111001401????????????????????
Starcus rugulosus	??????100001001????????????????????
Sunilius platyrhinus	??????110001011????????????????????
Ternova biartita	??????110001011????????????????????
Thestonia sparsa	??????000001011????????????????????
Zalestes perpolitus	??????010001001????????????????????
Cymatobaris impressifrons	001011221101401211111000111111001120
Pacomis distortus	101021121000111400111111111112100112

Megalobaris viridana	0010110211014112111110001111112001123
Rhytidoglymma cenescens	001011121001311410111000111111201????
Craptus tibialis	0000110211013012011100001111111011202
Testalthea sp.	1010110100012114001111101111113010101
Barycerus collaris	0010110211014111111110001111110001133
Opertes sp.	0010210211012112011100001111111011201
Stictobaris cribrata	0010111111013112101110001111111001101
Moreobaris deplanata	0000111211014112101110001111111001210
Ulobaris loricata	0000101111012112001110001111111000131
"Neomadarini"	0010101111010111201111001111000110012
Trichobaris texana	0010110111014013101000001111112010130
Dalcesia sp.	0010110211012011101110001111112001212
Nanobaris sp.	0000011111013012101110001111112001132
Zathanus sp.	0000113111012112101100001111111001102
Allomegops sp.	0010113211012012101100001111111??1111
Deipyle induta	0000113110012012101110001111111011232
Cosmobaris americana	00001100100111112001110001111101101111
Thanius sp.	0010111211013111111100001111110??1202
Cryptosternum nevermanni	??????110001311????????????????????
Pycnobaris pruinosa	0000110111013111001110001111111000032
Tonesia sp.	0010111100010111201111001111000??0232
Trepobaris inornata	0000111111012112001100001111111001212
Hiotus inflatus	10101101000001111010000011111011????
Sphenobaris quadridens	00001131100021121011111111111111????
Coluthus cribrarius	0010111100010112201100001111001??1101
Aniops sp.	0000101100010113001111001111112000102
Montella rufipes	??????100001011210111111111111??0121
Palmocentrinus butia	??????11110120132111111111111102??0212
Bondariella mimica	??????0100010113201111001111002??0101
Eucalus vitticollis	??????0111012004010000001111113010122
Scirpicola chilensis	??????0100010003001111111111112010131
Ortycus setifer	1010211200010111001111111111110110132

**Appendix I (continued). Character matrix - characters 111 – 112.**

	111
Dryophthorinae (Dryophthorus americanus)	00
Bagoinae (Bagous transversus)	??
Conoderinae (Cylindrocopturus operculatus)	??
Conoderinae (Trichodocerus sp.)	13
Conoderinae (Arachnopus gazella)	00
Conoderinae (Cyllophorus fausciatus)	00
Conoderinae (Metialma straminea)	14
Conoderinae (Balanogastris kolae)	10
Conoderinae (Telephae oculata)	10
Conoderinae (Cylindrocopturus adspersus)	00
Conoderinae (Acoptus suturalis)	00
Conoderinae (Lobotrachelus troglodytes)	??
Conoderinae (Mecopus trilineatus)	00
Ceutorhynchinae (Ceutorhynchus obstrictus)	12
Ceutorhynchinae (Hypurus bertrandi)	02
Ceutorhynchinae (Phytobius oriseomicans)	04
Ceutorhynchinae (Mononychus vulpeculus)	00
Ceutorhynchinae (Auleutes argentinensis)	04
Ceutorhynchinae (Coeliodes flavicaudis)	00
Curculioninae (Curculio pardalis)	00

Molytinae ( <i>Cholus rana</i> )	14
Molytinae ( <i>Trigonocolus curvipes</i> )	10
Molytinae ( <i>Conotrachelus fissunguis</i> )	00
Entiminae ( <i>Cyrtepistomus castaneus</i> )	??
Derelominae ( <i>Derelomus basalis</i> )	00
Cryptorhynchinae ( <i>Cryptorhynchus lapathi</i> )	10
Orobitidinae ( <i>Parorobitis gibbus</i> )	04
<i>Acentrinops brevicollis</i>	??
<i>Amercedes subulirostris</i>	10
<i>Amercedes orthorrhinus</i>	10
<i>Anavallius ruficornis</i>	10
<i>Anopsilus oblongus</i>	10
<i>Antesis sparsa</i>	10
<i>Athesapeuta vinculata</i>	12
<i>Barilepsis griseus</i>	10
<i>Barilepton filiforme</i>	00
<i>Barilepton quadrieolle</i>	00
<i>Barinus bivittatus</i>	00
<i>Barinus cribricollis</i>	00
<i>Baris torquata</i>	12
<i>Barymerus binaries</i>	??
<i>Buchananius striatus</i>	10
<i>Buchananius sulcatus</i>	00
<i>Busckiella lecythidis</i>	00
<i>Calandrinus grandicollis</i>	00
<i>Camelodes leachii</i>	10
<i>Catapastinus caseyi</i>	??
<i>Catapastus conspersus</i>	00
<i>Catapastus squamirostris</i>	00
<i>Catapastus albonotatus</i>	00
<i>Catapastus diffusus</i>	00
<i>Catapastus seriatus</i>	10
<i>Catapastus signatipennis</i>	10
<i>Catapastus simplex</i>	10
<i>Centrinites strigicollis</i>	10
<i>Centrinogyna hispidula</i>	??
<i>Centrinogyna strigata</i>	10
<i>Centrinopsis sp.</i>	00
<i>Centrinopus alternatus</i>	10
<i>Centrinopus helvinus</i>	10
<i>Centrinus curvirostris</i>	10
<i>Coelonertus nigrirostris</i>	??
<i>Coleomerus boliviensis</i>	00
<i>Conoproctus quadripustulatus</i>	00
<i>Crostidia tenuipes</i>	??
<i>Crotanius trivittatus</i>	10
<i>Cylindridia prolixa</i>	10
<i>Cylindrocercus comma</i>	00
<i>Cyrionyx camelus</i>	00
<i>Dactylocrepis flabellitarsis</i>	??
<i>Dealia carbonarius</i>	??
<i>Deipyryrus hirsutululus</i>	10
<i>Demoda vittata</i>	10
<i>Desmoglyptus arizonicus</i>	00
<i>Dialomia gradata</i>	??
<i>Diastethus eurthinoides</i>	10
<i>Dimesus rubricatus</i>	00
<i>Diorymeropsis disjuncta</i>	??
<i>Diorymeropsis xanthoxyli</i>	??
<i>Diorymerus lancifer</i>	00
<i>Dirabius calvus</i>	10
<i>Dirabius rectirostris</i>	10
<i>Dissopygus metallescens</i>	10
<i>Eisonyx crassipes</i>	02
<i>Eisonyx opaca</i>	10
<i>Elasmobaris signifer</i>	??
<i>Embates chaetopus</i>	10

<i>Eugeraeus</i> sp.	??
<i>Eumycterus albosquamulatus</i>	?0
<i>Eurhinus festivus</i>	00
<i>Eurhinus aeneus</i>	10
<i>Eusomenes curtirostris</i>	??
<i>Eutoxus</i> sp.	10
<i>Fishonia brevinasus</i>	??
<i>Fryella mutilatus</i>	??
<i>Garnia</i> sp.	00
<i>Geraeopsis duplocincta</i>	??
<i>Geraeus lineellus</i>	00
<i>Geraeus penicella</i>	10
<i>Glyptobaris lecontei</i>	10
<i>Haplostethops ellipsoidea</i>	??
<i>Idiostethus subcalvus</i>	00
<i>Idiostethus tubulatus</i>	10
<i>Iops bicolor</i>	00
<i>Ladustaspis crocopelmus</i>	??
<i>Lampobaris cicullata</i>	10
<i>Lasiobaris geminata</i>	00
<i>Laurentius bruchi</i>	??
<i>Lepidobaris acnisti</i>	10
<i>Leptoschoinus fucatus</i>	02
<i>Lichnus longulus</i>	10
<i>Limnobaris bicincta</i>	10
<i>Limnobaris calandriiformis</i>	10
<i>Linogeraeus urbanus</i>	10
<i>Linogeraeus viduatus</i>	10
<i>Linomadarus vorticosus</i>	10
<i>Lipancylus brevirostris</i>	10
<i>Loboderes citriventris</i>	00
<i>Lorena simulans</i>	??
<i>Lydamis cinnamomeus</i>	00
<i>Macrobaris</i> sp.	00
<i>Macrorevena atromicans</i>	??
<i>Madarellus laticollis</i>	12
<i>Madarus bistrigellus</i>	00
<i>Madopterus talpa</i>	10
<i>Megabaris quadriguttata</i>	10
<i>Megavallius auritarsis</i>	??
<i>Melampus basalis</i>	00
<i>Microbaridia delicatula</i>	??
<i>Microcholus puncticollis</i>	00
<i>Microcholus striatus</i>	??
<i>Microforandia uniformis</i>	??
<i>Microrhinus mutilus</i>	10
<i>Microstegotes</i> sp.	10
<i>Microstrates cocois</i>	00
<i>Myctides imberbis</i>	00
<i>Nertinus suturalis</i>	10
<i>Nestrada compacta</i>	??
<i>Nicentrus decipiens</i>	10
<i>Nicentrus grossulus</i>	10
<i>Odontobaris</i> sp.	10
<i>Odontocorynus scutellumalbum</i>	10
<i>Odontocorynus creperus</i>	10
<i>Oligolochus braccatus</i>	10
<i>Oligolochus ornatus</i>	??
<i>Onychobaris densa</i>	00
<i>Oomorphidius leavicollis</i>	10
<i>Opseobaris alba</i>	10
<i>Optatus palmaris</i>	??
<i>Orchidophilus aterrimus</i>	??
<i>Orissus meigenii</i>	10
<i>Orissus christophori</i>	10
<i>Orthoris crotchii</i>	10
<i>Ortycus cristosus</i>	??

<i>Ovanus picipennis</i>	12
<i>Ovanus minutus</i>	00
<i>Pachybaris porosa</i>	10
<i>Pachygeraeus laevirostris</i>	00
<i>Pacomes subglaber</i>	??
<i>Palmelampus heinrichi</i>	00
<i>Pantoteles tenuirostris</i>	00
<i>Parageraeus tumidirostris</i>	??
<i>Parallelosomus amplitarsis</i>	10
<i>Parasaldius</i> sp.	10
<i>Parasomenes curvirostris</i>	??
<i>Pardisomus biplagiatus</i>	10
<i>Parisoschoenus</i> sp.	10
<i>Peclaviopsis planipectus</i>	??
<i>Peridinetus cretaceus</i>	10
<i>Peridinetus irroratus</i>	00
<i>Phacelobarus signubaris</i>	10
<i>Pistus galeatus</i>	00
<i>Platyonyx ornatus</i>	10
<i>Plesiobaris albilata</i>	10
<i>Plocamus echidna</i>	00
<i>Plocamus clavisetes</i>	00
<i>Prodinus</i> sp.	00
<i>Pseudobaris angusta</i>	10
<i>Pseudocentrinus ochraceus</i>	10
<i>Pseudogeraeus macropterus</i>	00
<i>Pseudorthoris devexus</i>	10
<i>Pseudotorcus rufipes</i>	10
<i>Psiona densa</i>	??
<i>Pteracanthus smidtii</i>	00
<i>Pycnogeraeus modestus</i>	10
<i>Pycnogeraeus striatirostris</i>	11
<i>Pycnonicentrus gilvivistis</i>	??
<i>Pycnotheantis</i> sp.	??
<i>Ranceoma uniformis</i>	??
<i>Remertus marginatus</i>	??
<i>Ravena sexualis</i>	00
<i>Reveniopsis</i> sp.	00
<i>Rhoptobaris canescens</i>	10
<i>Saldiopsis armata</i>	??
<i>Saldius inaequalis</i>	??
<i>Selasella cuneipennis</i>	??
<i>Sibariops concinna</i>	??
<i>Sibariops concurrens</i>	??
<i>Solaria curtula</i>	00
<i>Solenosternus dividuus</i>	10
<i>Somenes regestus</i>	??
<i>Stereobaris interpunctata</i>	10
<i>Stethobaris commixta</i>	02
<i>Stethobaris laevimargo</i>	02
<i>Stethobaroides nudiventris</i>	02
<i>Stethobaropsis titara</i>	??
<i>Strongylotes squamans</i>	??
<i>Telemus</i> sp.	??
<i>Tenemotes abdominalis</i>	??
<i>Tenemotes parviclava</i>	??
<i>Thaliabaris inermis</i>	??
<i>Torcobius</i> sp.	10
<i>Torcus nigrinus</i>	00
<i>Torcus variabilis</i>	10
<i>Trachymeropsis palmipes</i>	??
<i>Trichodirabius longulus</i>	10
<i>Valdenus laevis</i>	??
<i>Valiopsis squamipes</i>	10
<i>Vallius sulcatus</i>	??
<i>Xystus ater</i>	10
<i>Xystus ruficollis</i>	00

<i>Zena virgata</i>	01
<i>Zygobarella xanthoxyli</i>	00
<i>Zygobarella tristicula</i>	00
<i>Zygobarinus coelestinus</i>	??
<i>Zygobaris</i> sp. 1	10
<i>Zygobaris nitens</i>	00
<i>Zygobaris</i> sp.	00
<i>Zygozalestes oblongus</i>	??
<i>Anatorcus densus</i>	??
<i>Andiblis seriata</i>	??
<i>Aniops sculpturata</i>	??
<i>Anotesiops obidosensis</i>	??
<i>Calorida binocularis</i>	??
<i>Camerones semiopacus</i>	??
<i>Chepagra rotundicollis</i>	??
<i>Clandius cephalotes</i>	??
<i>Crostis subexplanata</i>	??
<i>Dericinus habilis</i>	??
<i>Ethelda Squamosa</i>	??
<i>Eudialomia longula</i>	??
<i>Forandia duplex</i>	??
<i>Forandiopsis carinulata</i>	??
<i>Iopsidaspis truncatula</i>	??
<i>Leptogarnia polita</i>	??
<i>Leptoladustes densus</i>	??
<i>Linogarnia suturalis</i>	??
<i>Microtorcus tubulatus</i>	??
<i>Microzalestes basalis</i>	??
<i>Nedestes sarpedon</i>	??
<i>Neplaxa illustris</i>	??
<i>Nicentridia angusticollis</i>	??
<i>Palocopsis tecta</i>	??
<i>Parafishonia setulosa</i>	??
<i>Peclavia hispidicollis</i>	??
<i>Pseudorancea spissirostris</i>	??
<i>Pseudosaldius conjunctus</i>	??
<i>Rancea parviclava</i>	??
<i>Roalius rufipes</i>	??
<i>Sibariopsida docilis</i>	??
<i>Sodesia sparsa</i>	??
<i>Spolatia gradata</i>	??
<i>Starcus rugulosus</i>	??
<i>Sunilius platyrhinus</i>	??
<i>Ternova biartita</i>	??
<i>Thestonia sparsa</i>	??
<i>Zalestes perpolitus</i>	??
<i>Cymatobaris impressifrons</i>	12
<i>Pacomes distortus</i>	00
<i>Megalobaris viridana</i>	10
<i>Rhytidoglymma cenescens</i>	??
<i>Craptus tibialis</i>	10
<i>Testalthea</i> sp.	00
<i>Barycerus collaris</i>	12
<i>Opertes</i> sp.	10
<i>Stictobaris cribrata</i>	02
<i>Moreobaris deplanata</i>	00
<i>Ulobaris loricata</i>	12
"Neomadarini"	10
<i>Trichobaris texana</i>	12
<i>Dalcesia</i> sp.	12
<i>Nanobaris</i> sp.	10
<i>Zathanius</i> sp.	10
<i>Allomegops</i> sp.	10
<i>Deipyle induta</i>	10
<i>Cosmobaris americana</i>	12
<i>Thanius</i> sp.	10
<i>Cryptosternum nevermanni</i>	??

Pycnobaris pruinosa	12
Tonesia sp.	10
Trepobaris inornata	10
Hiotus inflatus	??
Sphenobaris quadridens	??
Coluthus cribrarius	10
Aniops sp.	10
Montella rufipes	00
Palmocentrinus butia	10
Bondariella mimica	00
Eucalus vitticolis	00
Scirpicola chilensis	10
Ortycus setifer	10

### Figure captions

**Figs. 1-13.** 1-9, adult images. 1, *Barinus bivittatus* (dorsal view); 2, *Orissus christophori* (dorsal view); 3, *Orissus meigenii* (lateral view); 4, *Nertinus suturalis* (lateral view); 5, *Parallelosomus amplitarsis* (lateral view); 6, *Peridinetus suturalis* (dorsal view); 7, *Loboderes citriventris* (dorsal view); 8, *Madarellus laticollis* (dorsal view); 9, *Prodinus* sp. (lateral view). 10-13, adult head and rostrum, lateral view. 10, *Centrinogyna strigata*; 11, *Pardisomus biplagiatus*; 12, *Strongylotes squamans*; 13, *Myctides imberbis*.

**Figs. 14-17.** Antennae. 14-15, *Oligolochus braccatus*; 15, enlargement of apical end; 16-17, *Camelodes leachii*; 17, enlargement of apical end.

**Figs. 18-26.** Mouthparts. 18, *Oligolochus ornatus*, right mandible; 19, *Plocamus clavisetes*, right mandible; 20, *Eisonyx opaca*, right mandible; 21, *Parallelosomus*

*amplitarsis*, right mandible; 22, *Torcus nigrinus*, right mandible; 23, *Coleomerus boliviensis*, right mandible; 24, *Oligolochus bracatus*, right maxilla; 25, *Anthinobaris* sp., right maxilla; 26, *Loboderes citriventris*, right maxilla.

**Figs. 27-33.** 27-32, mouthparts. 27, *Linogeraeus viduatus*, right maxilla; 28, *Xystus ruficollis*, right maxilla; 29, *Anthinobaris* sp., labium; 30, *Linogeraeus viduatus*, labium; 31, *Loboderes citriventris*, labium; 32, *Microcholus punticollis*, labium; 33, *Peridinetus irroratus*, head and rostrum (anterior aspect).

**Figs. 34-43.** 34, *Pertorcus* sp.; 35, *Odontocorynus creperus*; 36, *Pachybaris porosa*. 37-38, *Centrinus curvirostris*. 37, adult lateral view; 38, prosternum; 39, *Orissus meigenii*, horn sheath; 40, *Demoda vittata*, horn sheath; 41, *Demoda vittata*, adult lateral view; 42-43, *Eutoxus* sp.; 42, adult lateral view; 43, prosternum.

**Figs. 44-54.** 44-45, *Geraeus lineellus*. 44, adult lateral view; 45, prosternum; 46, *Catapastus squamirostris*, pronotum (SEM); 47, *Trichodirabius longulus*, pronotum (SEM); 48, *Vallius sulcatus*, adult lateral view; 49-51, posterior margin of pronotum and mesoscutellum. 49, *Trichodirabius longulus*; 50, *Pycnogeraeus modestus*; 51, *Pertorcus* sp.; 52-53, *Zygobaris nitens*. 52, prosternum (photograph); 53, prosternum (illustration); 54, *Xystus ruficollis*, prosternum (mesosternal process).

**Figs. 55-59.** Prosterna (mesosternal process). 55, *Limnobaris calandriformis*; 56, *Loboderes citriventris*; 57, *Madopterus talpa*; 58, *Parallelosomus amplitarsis*; 59, *Peridinetus cretaceus*.

**Figs. 60-64.** 60, *Zygobarella zanthoxyli*, sclerolepidia (SEM); 61, *Lydamis cinnamomeus*, sclerolepidia (SEM). 62-64, mesoscutellum. 62, *Pertorcus* sp.; 63, *Pycnogeræus striatirostris*; 64, *Pachybaris porosa*.

**Figs. 65-73.** 65, *Pycnogeræus ochraceus*, mesonotum; 66, *Garnia* sp., mesonotum; 67-68, generalized types of prescuta. 69-73, metanotum. 69, *Leptoschoinus fucatus*; 70, *Garnia* sp.; 71, *Centrinus curvirostris*; 72, *Peridinetus irroratus*; 73, *Camelodes leachii*.

**Figs. 74-77.** 74, *Madopterus talpa*, metanotum; 75-77, metendosternite. 75, *Leptoschoinus fucatus*; 76, *Pardisomus biplagiatus*; 77, *Madopterus talpa*.

**Figs. 78-82.** 78, *Madarus bistrigellus*, apical tibial uncus; 79, *Demoda vittata*, apical tibial uncus; 80, *Zygobarella zanthoxyli*, connate pre-tarsal unguis; 81, *Anthinobaris* sp., connate pre-tarsal unguis; 82, *Baris* sp., diverging pre-tarsal unguis.

**Figs. 83-86.** 83, generalized baridine hind wing venation. 84-86, hind wings. 84, *Cryptorhynchus lapathi* (Cryptorhynchinae); 85, *Cholus rana* (Molytinae); 86, *Cylindrocopturus adpersus* (Conoderinae).

**Figs. 87-89.** 87-88, elytra. 87, *Odontocorynus creperus*; 88, *Coleomerus boliviensis*; 89, *Idiostethus tubulatus*, ventrites.

**Figs. 90-94.** 90-91, *Acythopeus* sp. 90, tergites and spiculate patches; 91, enlargement of tergites 4-7; 92, *Pycnogeraeus modestus*, tergite 7; 93, *Deipyryus hirsutulus*, plectra on tergite 7; 94, *Diastethus eurthinoides*, plectra on tergite 7.

**Figs. 95-102.** 95-98, tergites. 95, *Centrinus curvirostris*; 96, *Peridinetus irroratus*; 97, *Xystus ruficollis*; 98, *Calandrinus grandicollis*. 99-102, female genitalia. 99, *Limnobaris* sp., spermatheca and sternite 8; 100, *Strongylotes squamans*, spermatheca; 101, *Parasomenes curvirostris*, sternite 8; 102, *Zena* sp., spermatheca and sternite 8.

**Figs. 103-109.** Male genitalia. 103-108, aedeagus. 103, *Stethobaroides nudiventris*; 104, *Barilepton filiforme*; 105, *Garnia* sp.; 106, *Pardisomus biplagiatus*; 107, *Solenosternus dividius*; 108, *Pteracanthus smidtii*; 109, *Stereobaris interpunctata*.

**Fig. 110.** Strict consensus tree of length 4,850 steps (of 33 most-parsimonious trees of length 4,509 steps) produced in TNT, with old classification, including tribes and subtribes, indicated.

**Fig. 110** (continued). Strict consensus tree of length 4,850 steps (of 33 most-parsimonious trees of length 4,509 steps) produced in TNT, with old classification, including tribes and subtribes, indicated.

**Fig. 111.** Strict consensus tree with suggested revised classification. Numbers above nodes indicate jackknife values, numbers below nodes indicate bremer values (absolute bremer/relative bremer).

**Fig. 112.** Strict consensus tree with characters (below branches) and character states (above branches) mapped onto branches using WinClada's fast optimization (ACCTRAN).

**Fig. 112** (continued). Strict consensus tree with characters (below branches) and character states (above branches) mapped onto branches using WinClada's fast optimization (ACCTRAN).

**Fig. 112** (continued). Strict consensus tree with characters (below branches) and character states (above branches) mapped onto branches using WinClada's fast optimization (ACCTRAN).

**Fig. 112** (continued). Strict consensus tree with characters (below branches) and character states (above branches) mapped onto branches using WinClada's fast optimization (ACCTRAN).

**Fig. 112** (continued). Strict consensus tree with characters (below branches) and character states (above branches) mapped onto branches using WinClada's fast optimization (ACCTRAN).

**Fig. 112** (continued). Strict consensus tree with characters (below branches) and character states (above branches) mapped onto branches using WinClada's fast optimization (ACCTRAN).

**Fig. 113**. Strict consensus tree with characters (below branches) and character states (above branches) mapped onto branches using WinClada's slow optimization (DELTRAN).

**Fig. 113** (continued). Strict consensus tree with characters (below branches) and character states (above branches) mapped onto branches using WinClada's slow optimization (DELTRAN).

**Fig. 113** (continued). Strict consensus tree with characters (below branches) and character states (above branches) mapped onto branches using WinClada's slow optimization (DELTRAN).

**Fig. 113** (continued). Strict consensus tree with characters (below branches) and character states (above branches) mapped onto branches using WinClada's slow optimization (DELTRAN).

**Fig. 113** (continued). Strict consensus tree with characters (below branches) and character states (above branches) mapped onto branches using WinClada's slow optimization (DELTRAN).

**Fig. 113** (continued). Strict consensus tree with characters (below branches) and character states (above branches) mapped onto branches using WinClada's slow optimization (DELTRAN).

**Fig. 114.** Strict consensus tree with characters (below branches) and character states (above branches) mapped onto branches using WinClada and showing unambiguous changes only (no optimization).

**Fig. 114** (continued). Strict consensus tree with characters (below branches) and character states (above branches) mapped onto branches using WinClada and showing unambiguous changes only (no optimization).

**Fig. 114** (continued). Strict consensus tree with characters (below branches) and character states (above branches) mapped onto branches using WinClada and showing unambiguous changes only (no optimization).

**Fig. 114** (continued). Strict consensus tree with characters (below branches) and character states (above branches) mapped onto branches using WinClada and showing unambiguous changes only (no optimization).

**Fig. 114** (continued). Strict consensus tree with characters (below branches) and character states (above branches) mapped onto branches using WinClada and showing unambiguous changes only (no optimization).

**Fig. 114** (continued). Strict consensus tree with characters (below branches) and character states (above branches) mapped onto branches using WinClada and showing unambiguous changes only (no optimization).

**Fig. 115.** 1 of 110 most-parsimonious trees produced from the reduced taxon matrix (RTM) of length 2,692 produced in TNT, with old classification, including tribes and subtribes, indicated.

**Fig. 116.** Strict consensus tree of length (of 110 most-parsimonious trees of length 2,692) produced from the RTM. Numbers above nodes indicate jackknife values, numbers below nodes indicate bremer values (absolute bremer/relative bremer).

**Fig. 117.** 1 of 110 most-parsimonious trees produced from the RTM with suggested revised classification.

**Fig. 118.** 1 of 110 most-parsimonious trees produced from the RTM with characters (below branches) and character states (above branches) mapped onto branches using WinClada's fast optimization (ACCTRAN).

**Fig. 118** (continued). 1 of 110 most-parsimonious trees produced from the RTM with characters (below branches) and character states (above branches) mapped onto branches using WinClada's fast optimization (ACCTRAN).

**Fig. 118** (continued). 1 of 110 most-parsimonious trees produced from the RTM with characters (below branches) and character states (above branches) mapped onto branches using WinClada's fast optimization (ACCTRAN).

**Fig. 118** (continued). 1 of 110 most-parsimonious trees produced from the RTM with characters (below branches) and character states (above branches) mapped onto branches using WinClada's fast optimization (ACCTRAN).

**Fig. 119**. 1 of 110 most-parsimonious trees produced from the RTM with characters (below branches) and character states (above branches) mapped onto branches using WinClada's slow optimization (DELTRAN).

**Fig. 119** (continued). 1 of 110 most-parsimonious trees produced from the RTM with characters (below branches) and character states (above branches) mapped onto branches using WinClada's slow optimization (DELTRAN).

**Fig. 119** (continued). 1 of 110 most-parsimonious trees produced from the RTM with characters (below branches) and character states (above branches) mapped onto branches using WinClada's slow optimization (DELTRAN).

**Fig. 119** (continued). 1 of 110 most-parsimonious trees produced from the RTM with characters (below branches) and character states (above branches) mapped onto branches using WinClada's slow optimization (DELTRAN).

**Fig. 120.** 1 of 110 most-parsimonious trees produced from the RTM with characters (below branches) and character states (above branches) mapped onto branches using WinClada and showing unambiguous changes only (no optimization).

**Fig. 120** (continued). 1 of 110 most-parsimonious trees produced from the RTM with characters (below branches) and character states (above branches) mapped onto branches using WinClada and showing unambiguous changes only (no optimization).

**Fig. 120** (continued). 1 of 110 most-parsimonious trees produced from the RTM with characters (below branches) and character states (above branches) mapped onto branches using WinClada and showing unambiguous changes only (no optimization).

**Fig. 120** (continued). 1 of 110 most-parsimonious trees produced from the RTM with characters (below branches) and character states (above branches) mapped onto branches using WinClada and showing unambiguous changes only (no optimization).

**Fig. 121.** Character 88 (sclerotization of tergites) mapped onto strict consensus tree.

**Fig. 122.** Character 46 (posterior margin of mesonotum), supporting monophyly of Baridinae, mapped onto strict consensus tree.

**Fig. 123.** Character 54 (lateral margin of postnotum), supporting monophyly of Baridinae, mapped onto strict consensus tree.

**Fig. 124.** Character 98 (abdominal lateral tergite), supporting monophyly of Baridinae, mapped onto strict consensus tree.

**Fig. 125.** Character 41 (mesepimeron), supporting monophyly of Baridinae, mapped onto strict consensus tree.

**Fig. 126.** Biogeographic regions mapped onto strict consensus tree.

**Fig. 126 (continued).** Biogeographic regions mapped onto strict consensus tree.

**Fig. 127.** Known host plant groups mapped onto strict consensus tree.

**Fig. 127 (continued).** Known host plant groups mapped onto strict consensus tree.

**Fig. 128.** Most parsimonious tree obtained through analysis of full dataset using implied weights in TNT; k=2; implied weights best score=92.57134; L=5287 steps, Ci=4, Ri=43.

**Fig. 129.** Most parsimonious tree obtained through analysis of full dataset using implied weights in TNT; k=4; implied weights best score=86.71261; L=5224 steps, Ci=4, Ri=43.

**Fig. 130.** Most parsimonious tree obtained through analysis of full dataset using implied weights in TNT; k=6; implied weights best score=82.15793; L=5192 steps, Ci=4, Ri=44.

**Fig. 131.** Most parsimonious tree obtained through analysis of full dataset using implied weights in TNT; k=8; implied weights best score=78.30540; L=5130 steps, Ci=4, Ri=44.

**Fig. 132.** Most parsimonious tree obtained through analysis of RTM using implied weights in TNT; k=2; implied weights best score=89.40104; L=3041 steps, Ci=7, Ri=43.

**Fig. 133.** Most parsimonious tree obtained through analysis of RTM using implied weights in TNT; k=4; implied weights best score=81.77424; L=3022 steps, Ci=7, Ri=43.

**Fig. 134.** Most parsimonious tree obtained through analysis of RTM using implied weights in TNT; k=6; implied weights best score=75.89121; L=2949 steps, Ci=7, Ri=44.

**Fig. 135.** Most parsimonious tree obtained through analysis of RTM using implied weights in TNT; k=8; implied weights best score=70.88550; L=2916 steps, Ci=7, Ri=45.

**Fig. 136.** Phylogeny produced by bayesian analysis, with 3 million generations, using full dataset. Values at nodes represent bayesian posterior probabilities.

**Fig. 136 (continued).** Phylogeny produced by bayesian analysis, with 3 million generations, using full dataset. Values at nodes represent bayesian posterior probabilities.

**Fig. 137.** Phylogeny produced by bayesian analysis, with 10 million generations, using full dataset. Values at nodes represent bayesian posterior probabilities.

**Fig. 137** (continued). Phylogeny produced by bayesian analysis, with 10 million generations, using full dataset. Values at nodes represent bayesian posterior probabilities.

**Fig. 138.** Phylogeny produced by bayesian analysis, with 3 million generations, using RTM. Values at nodes represent bayesian posterior probabilities.

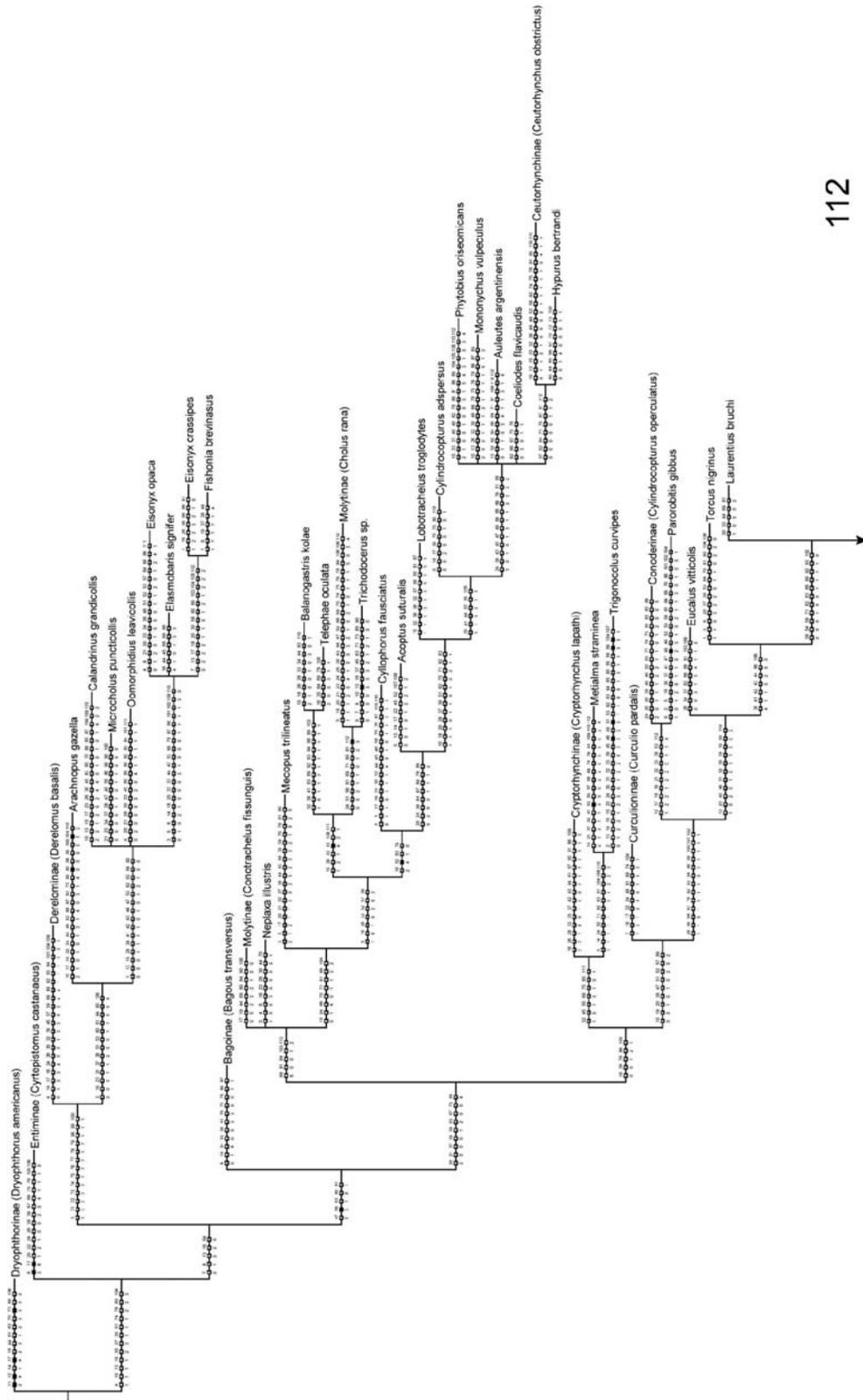
**Fig. 139.** Phylogeny produced by bayesian analysis, with 10 million generations, using RTM. Values at nodes represent bayesian posterior probabilities.

**Figs. 140-144.** Histograms for the bayesian analysis of the full dataset with 3 million generations. 140, frequency plotted against tree log likelihood; 141, frequency plotted against tree length; 142, log likelihood plotted against generation time; 143, tree length plotted against generation time; 144, tree length plotted against log likelihood.

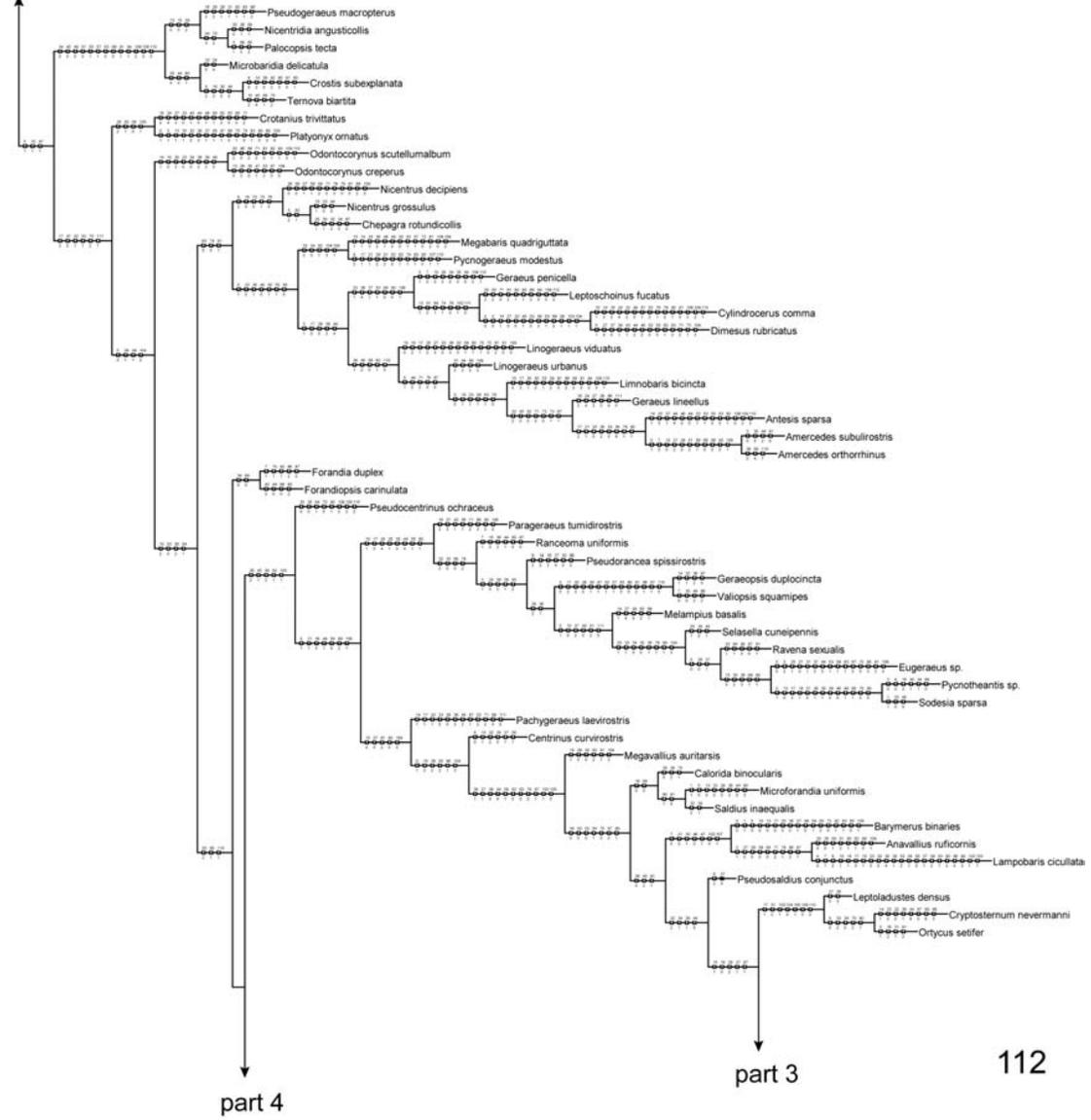
**Figs. 145-149.** Histograms for the bayesian analysis of the full dataset with 10 million generations. 145, frequency plotted against tree log likelihood; 146, frequency plotted against tree length; 147, log likelihood plotted against generation time; 148, tree length plotted against generation time; 149, tree length plotted against log likelihood.

**Figs. 150-154.** Histograms for the bayesian analysis of the RTM with 3 million generations. 150, frequency plotted against tree log likelihood; 151, frequency plotted against tree length; 152, log likelihood plotted against generation time; 153, tree length plotted against generation time; 154, tree length plotted against log likelihood.

**Figs. 155-159.** Histograms for the bayesian analysis of the RTM with 10 million generations. 155, frequency plotted against tree log likelihood; 156, frequency plotted against tree length; 157, log likelihood plotted against generation time; 158, tree length plotted against generation time; 159, tree length plotted against log likelihood.

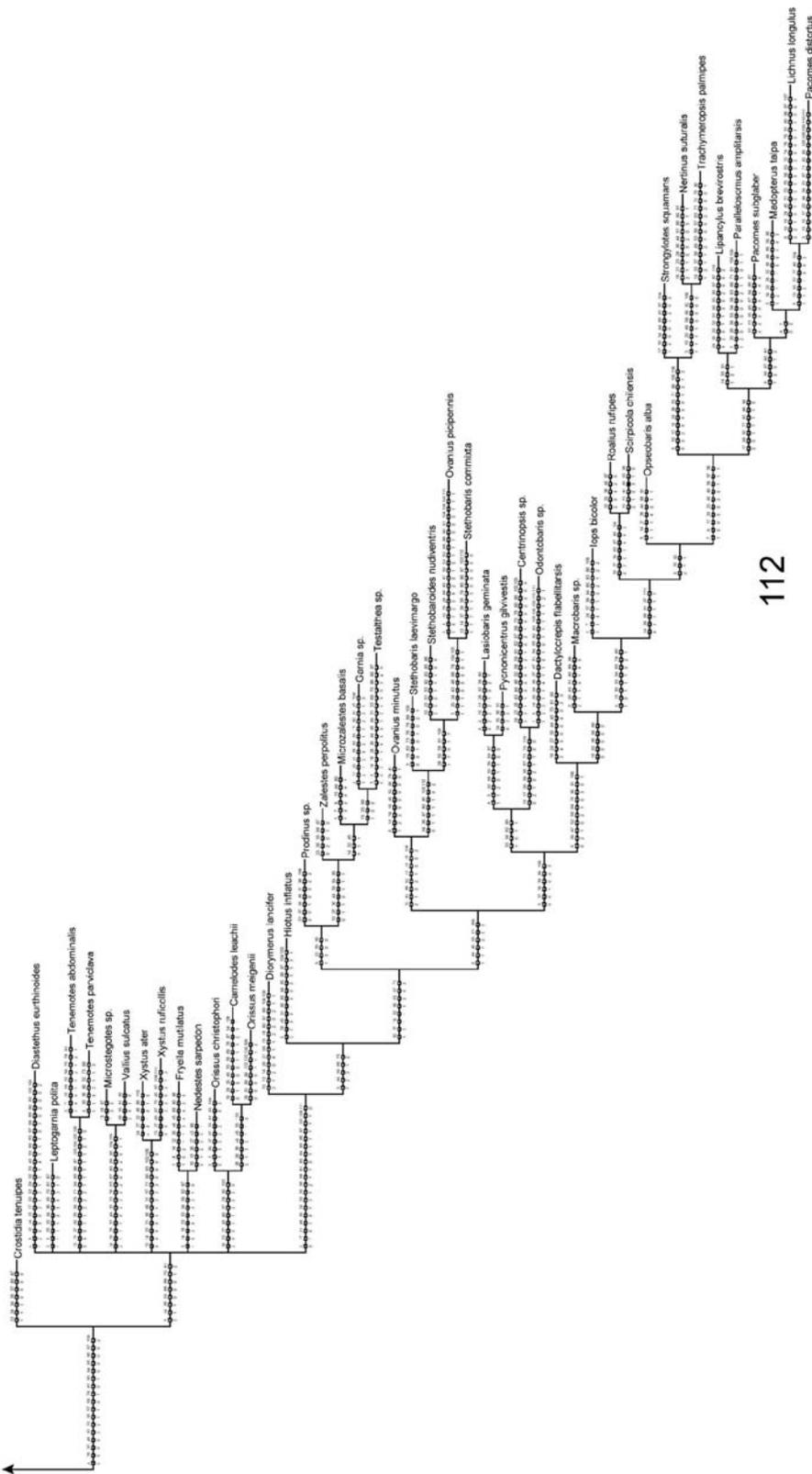


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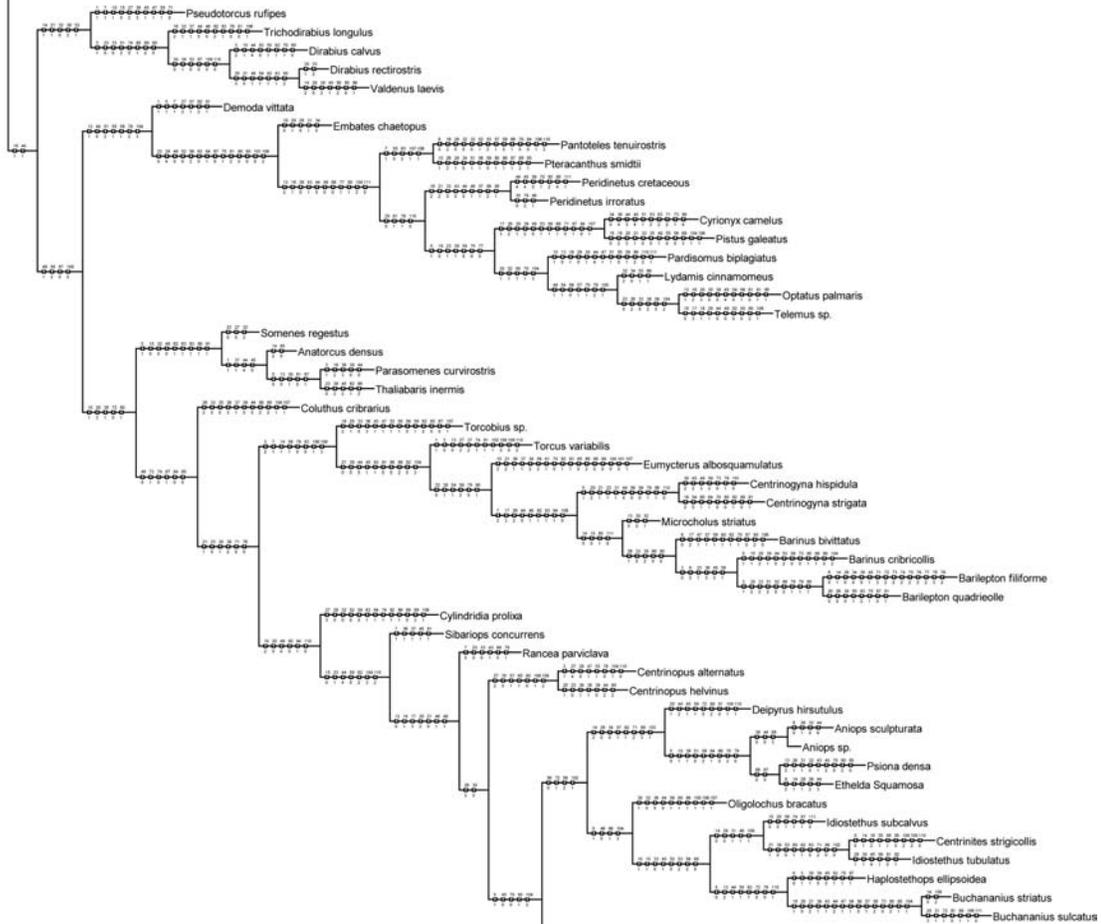
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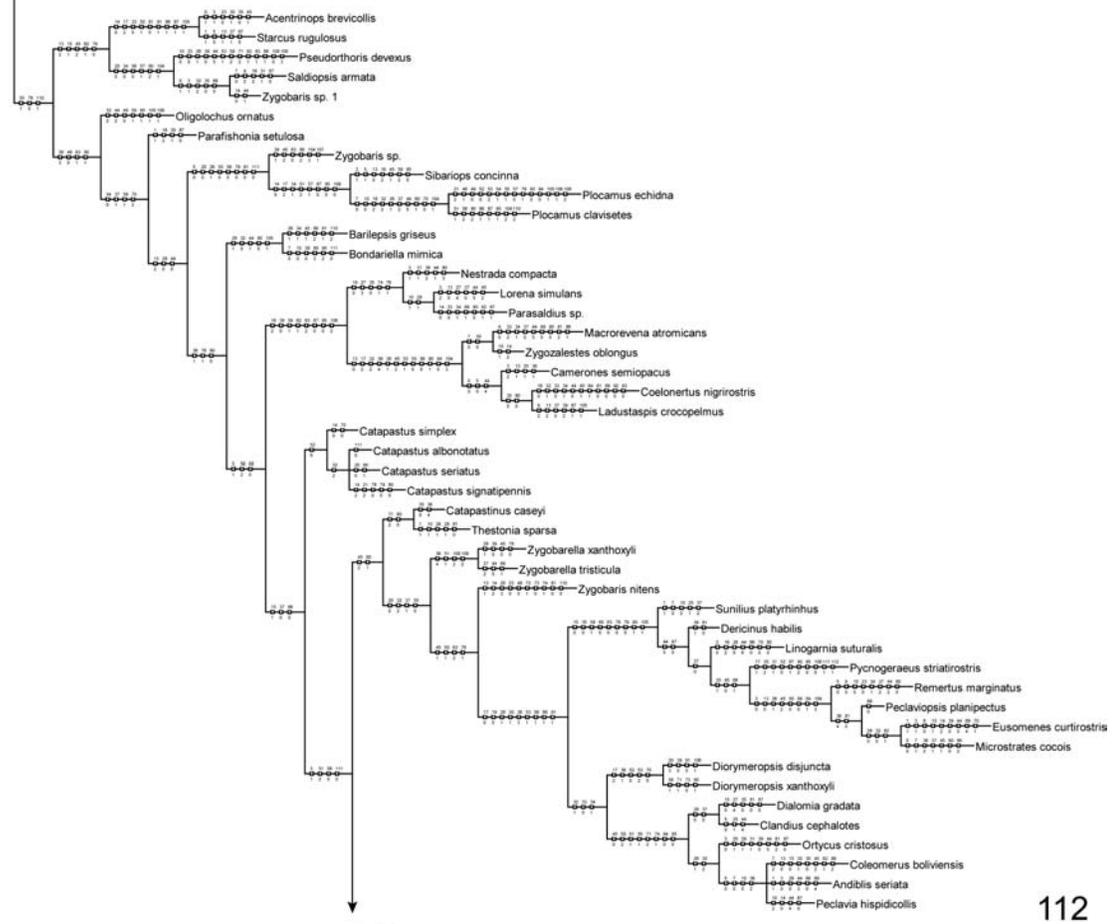
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part 5

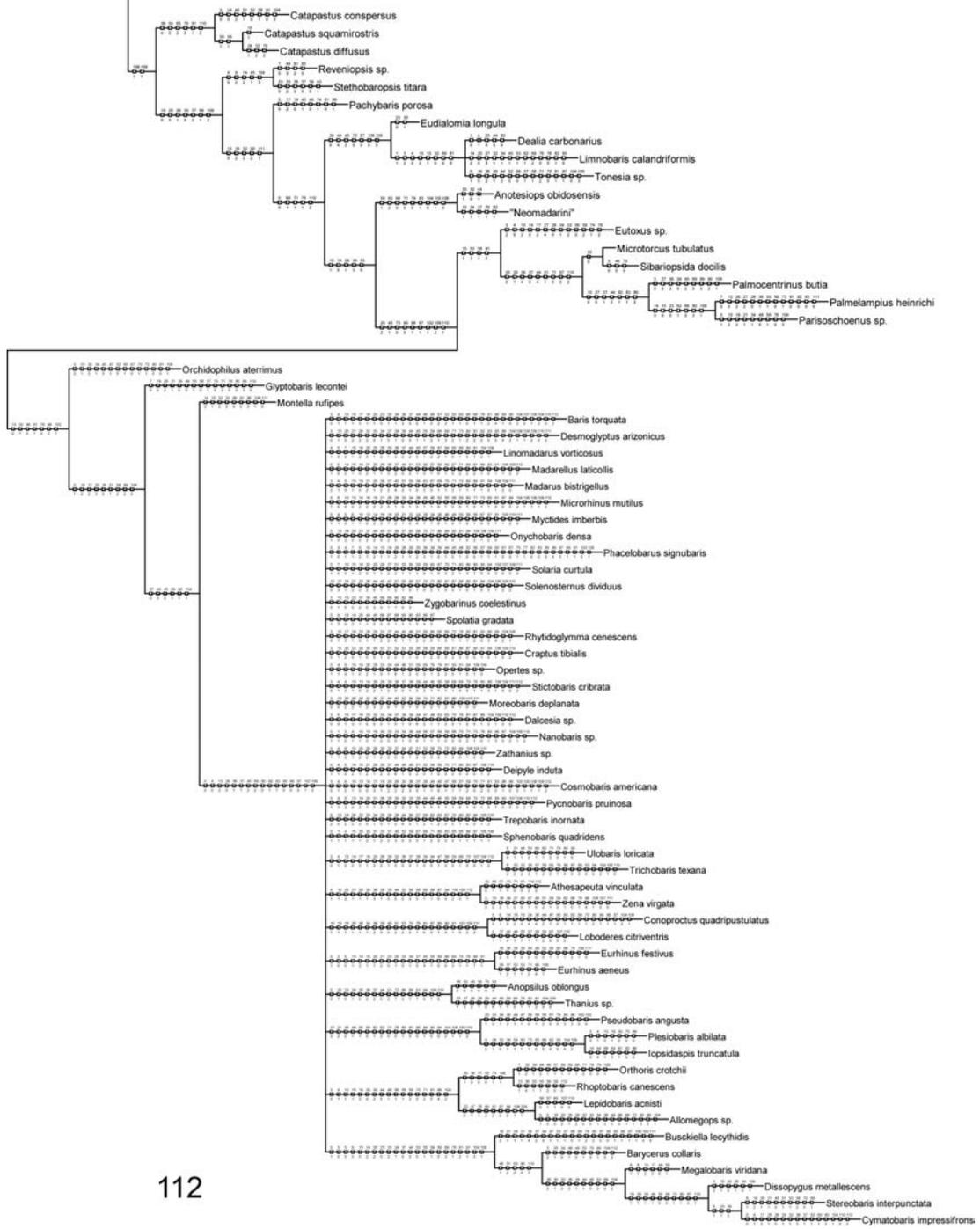
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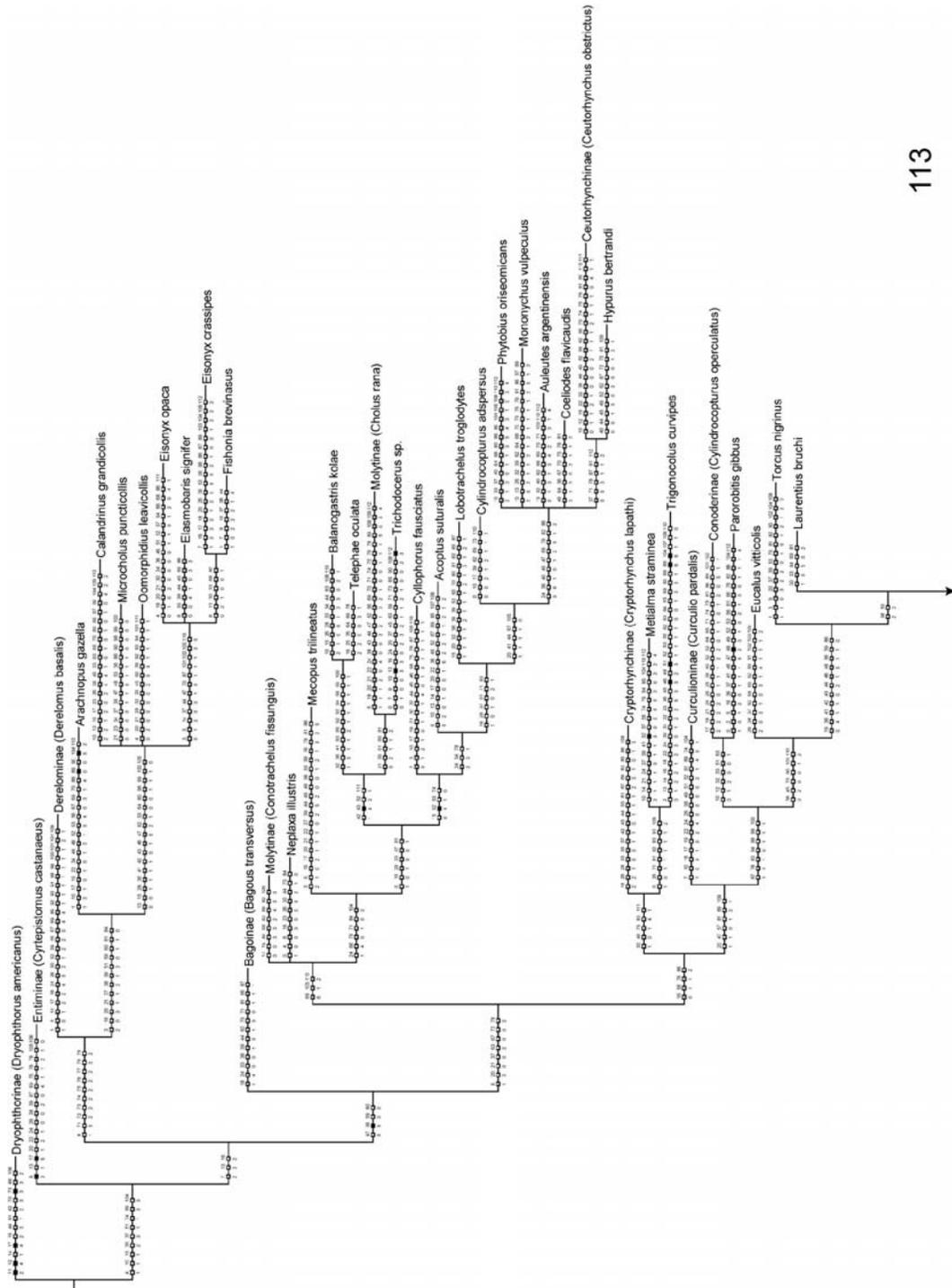


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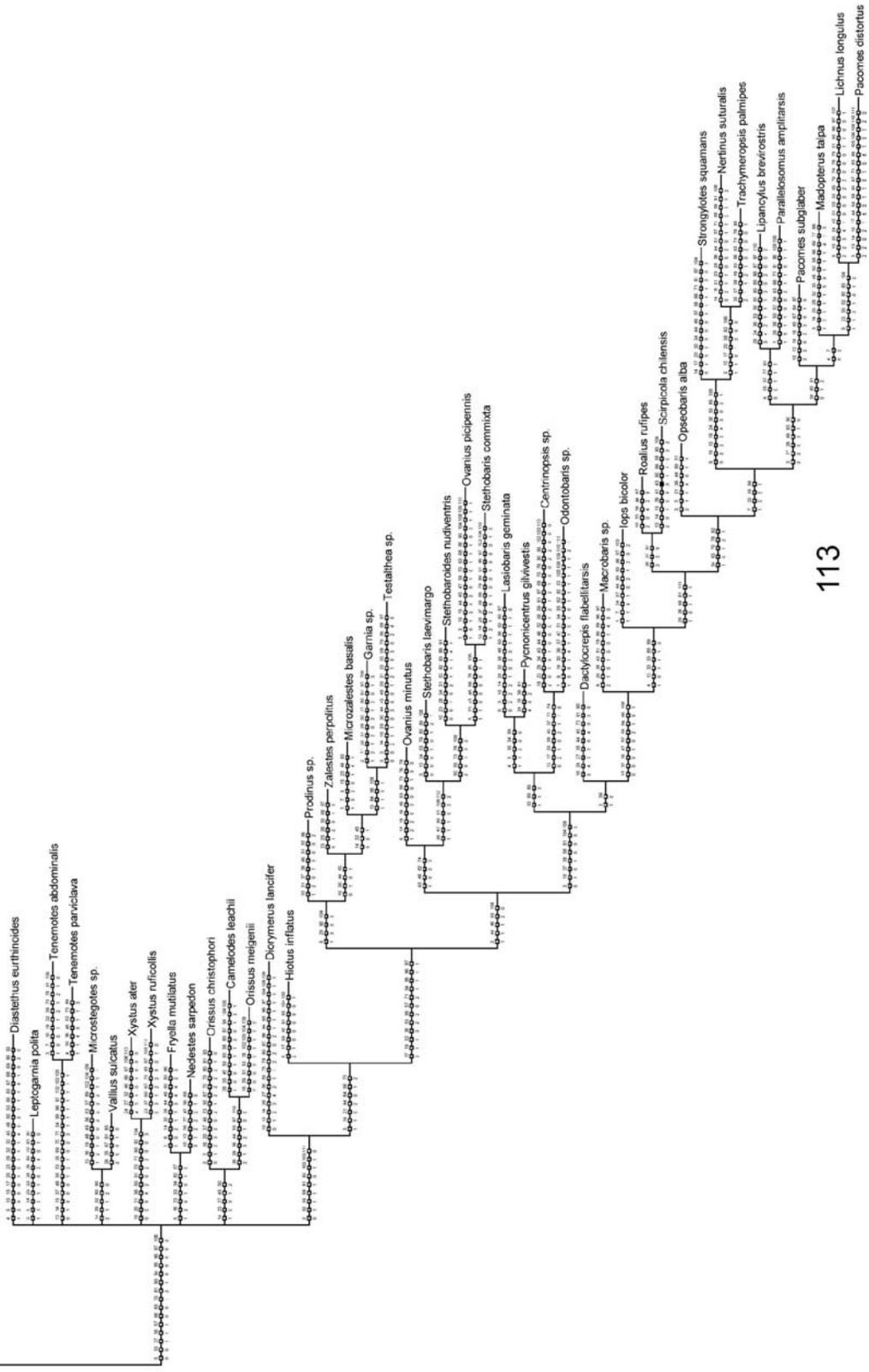


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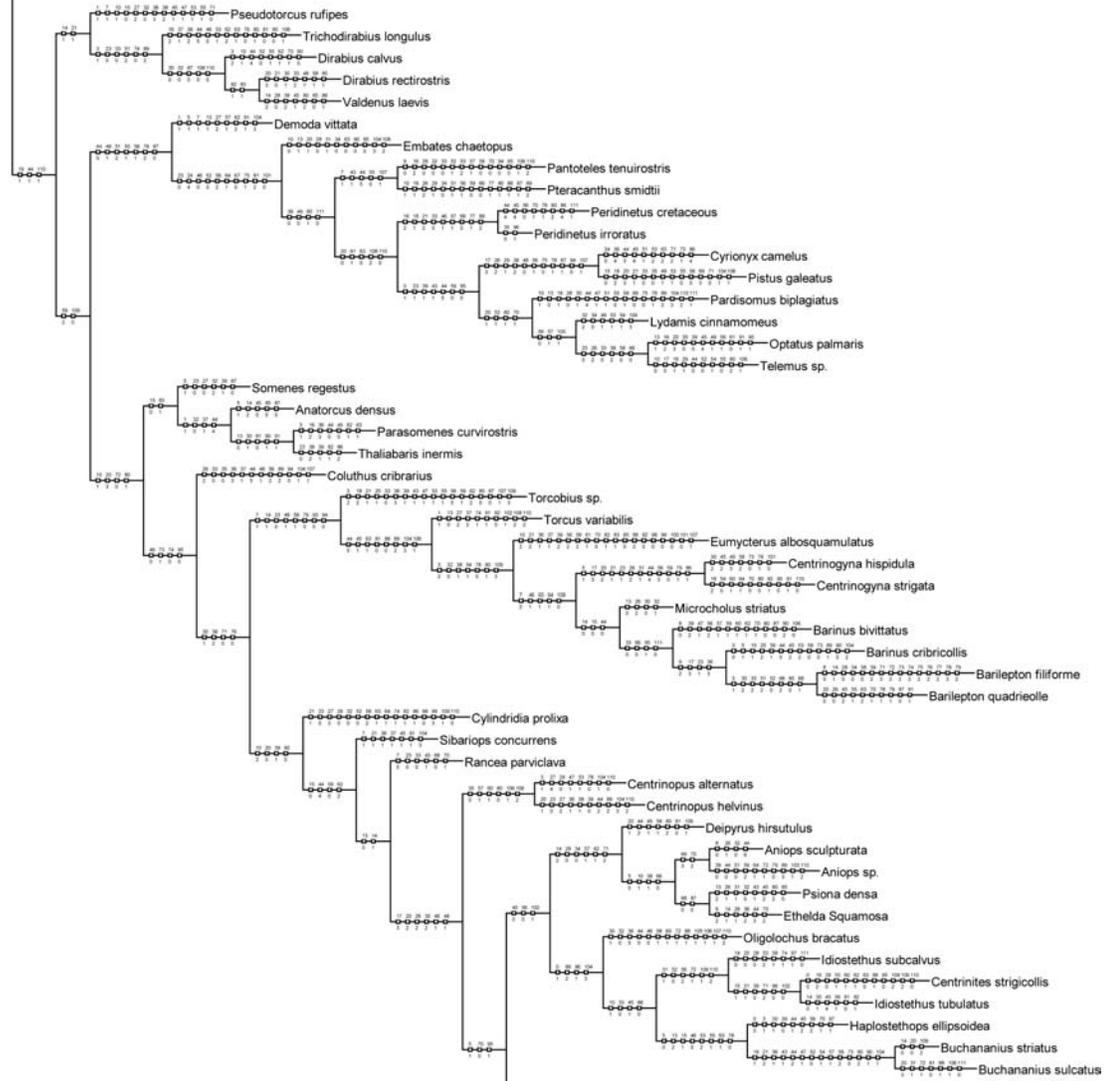


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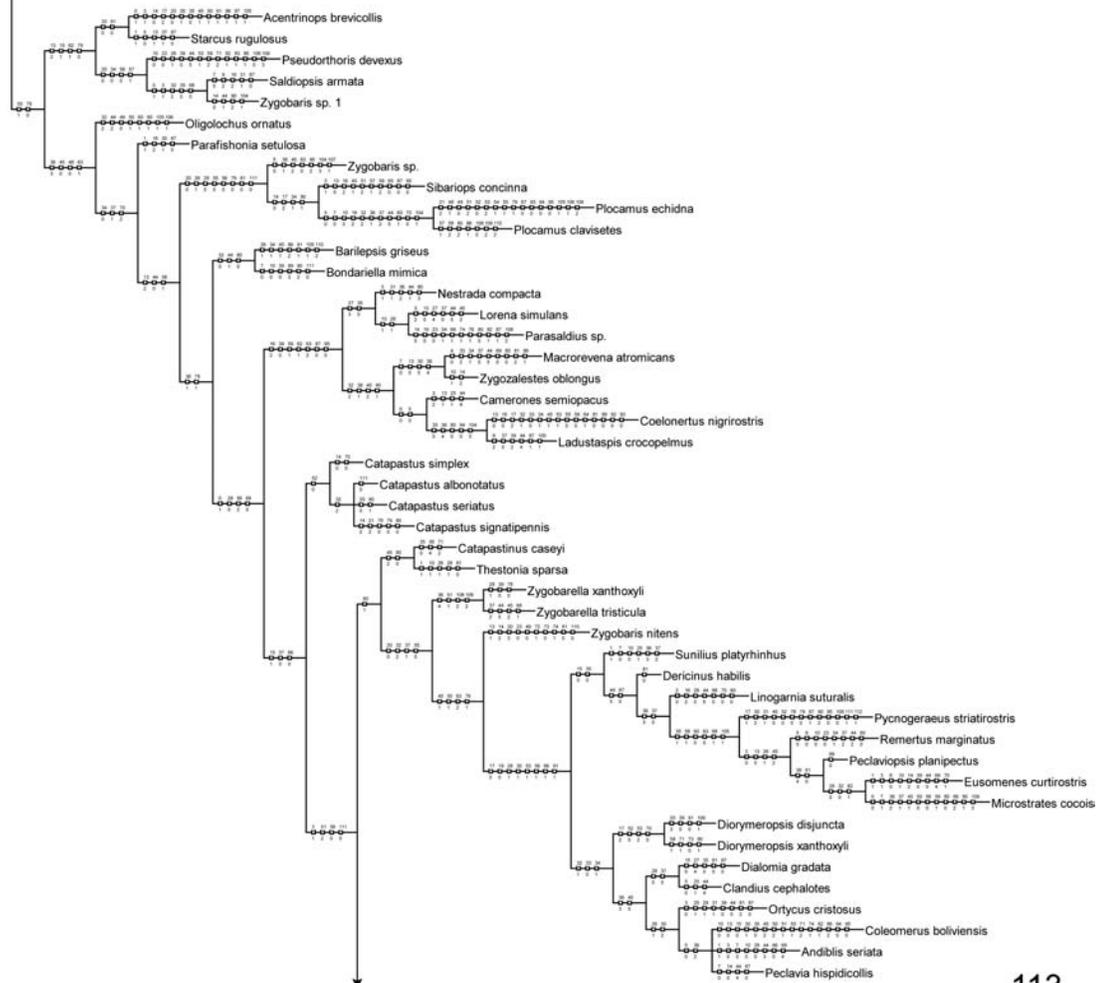
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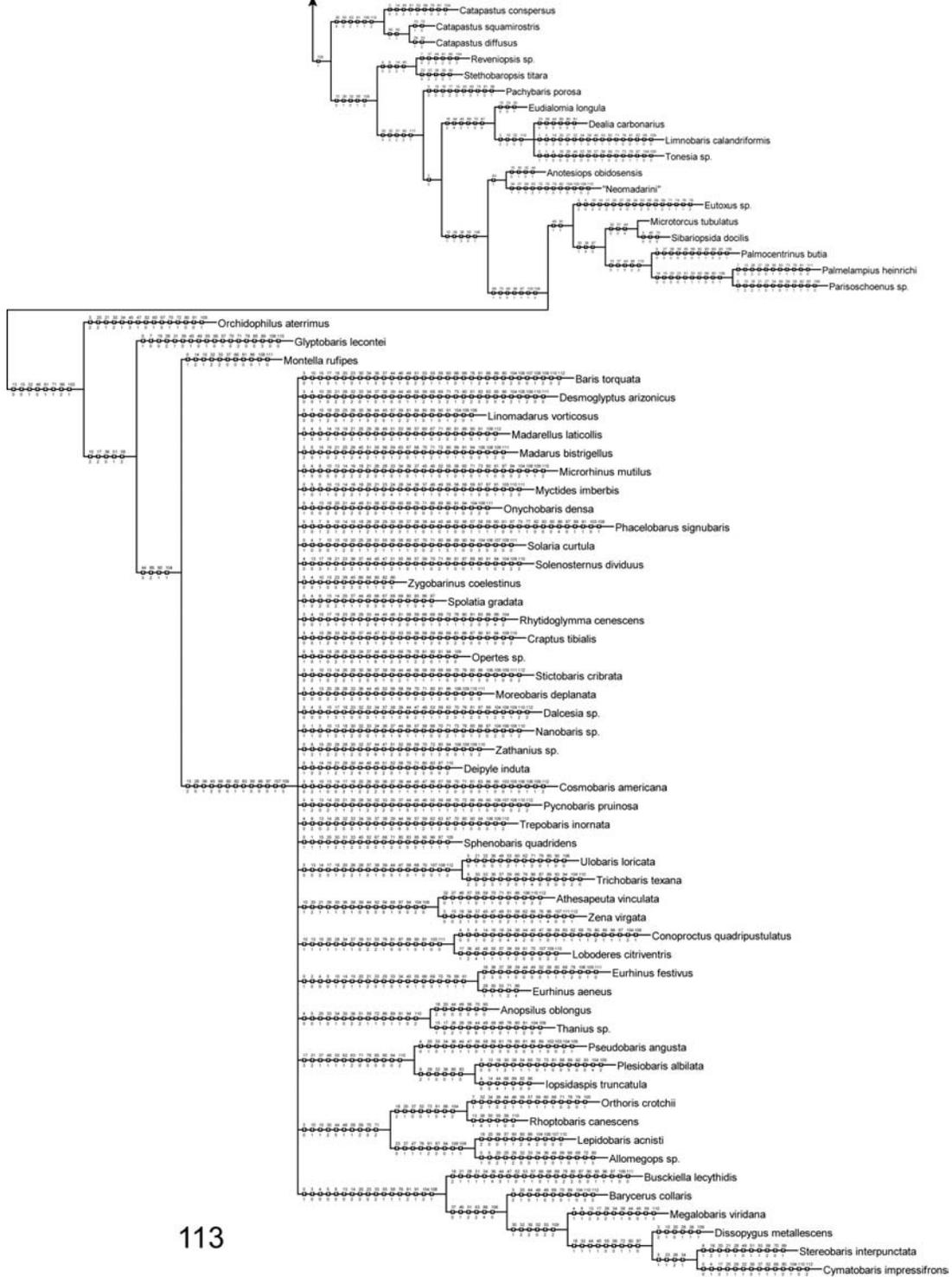
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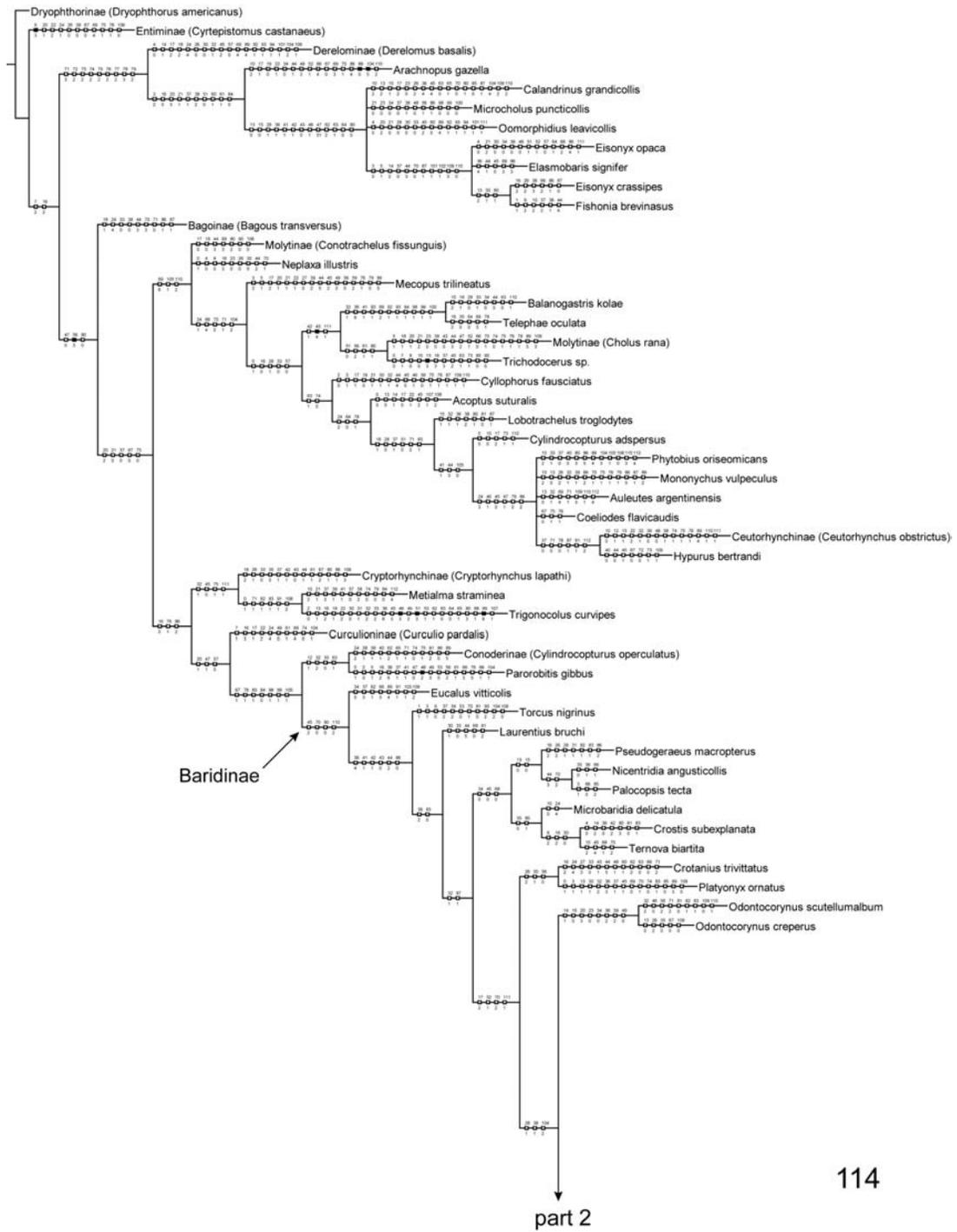


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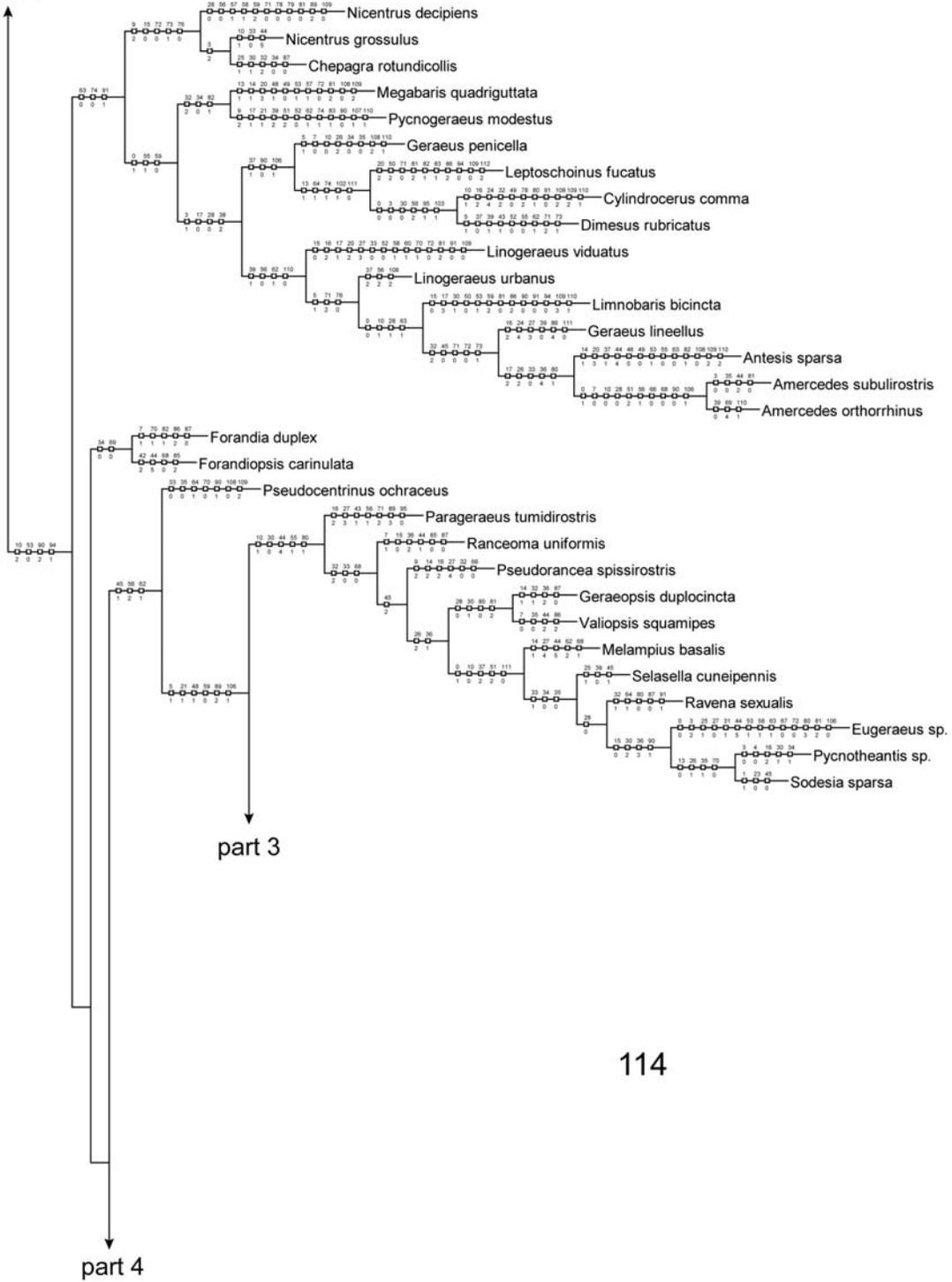
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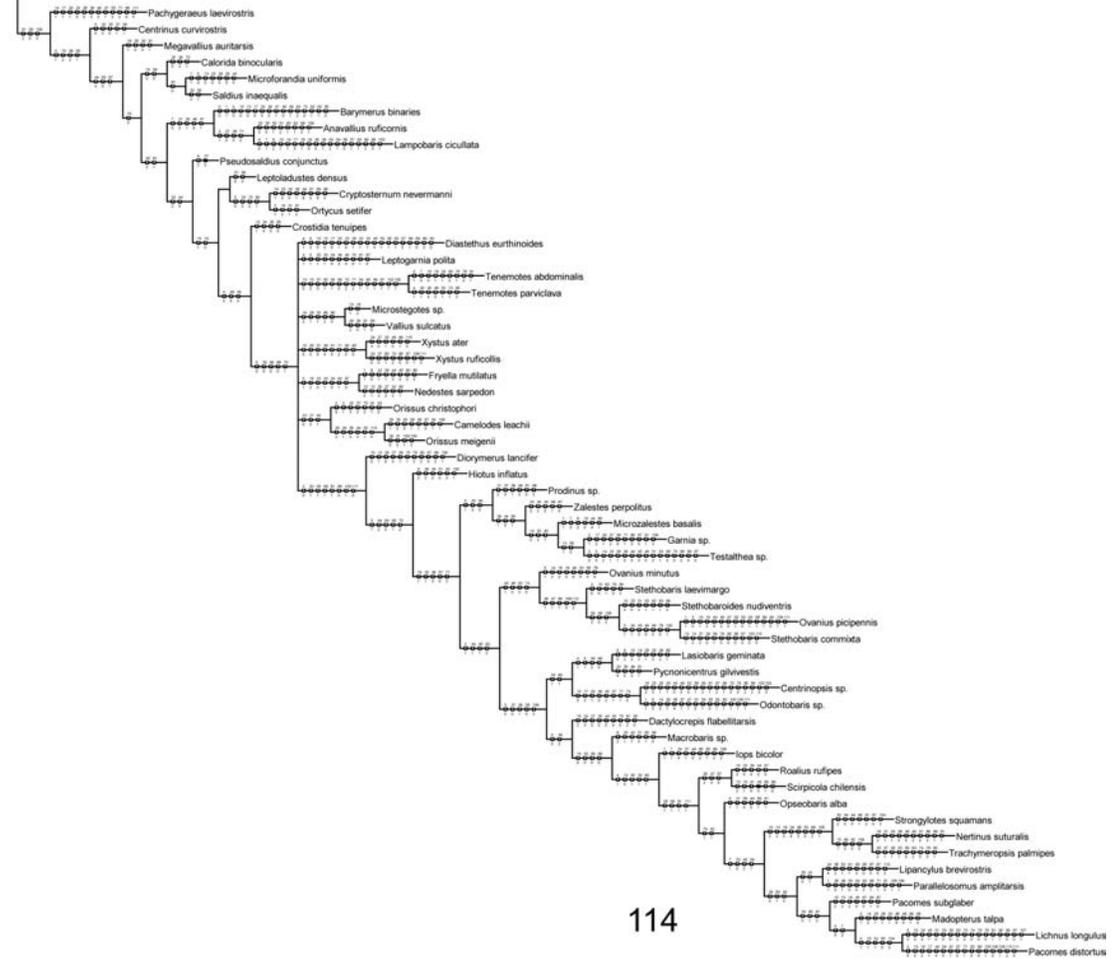
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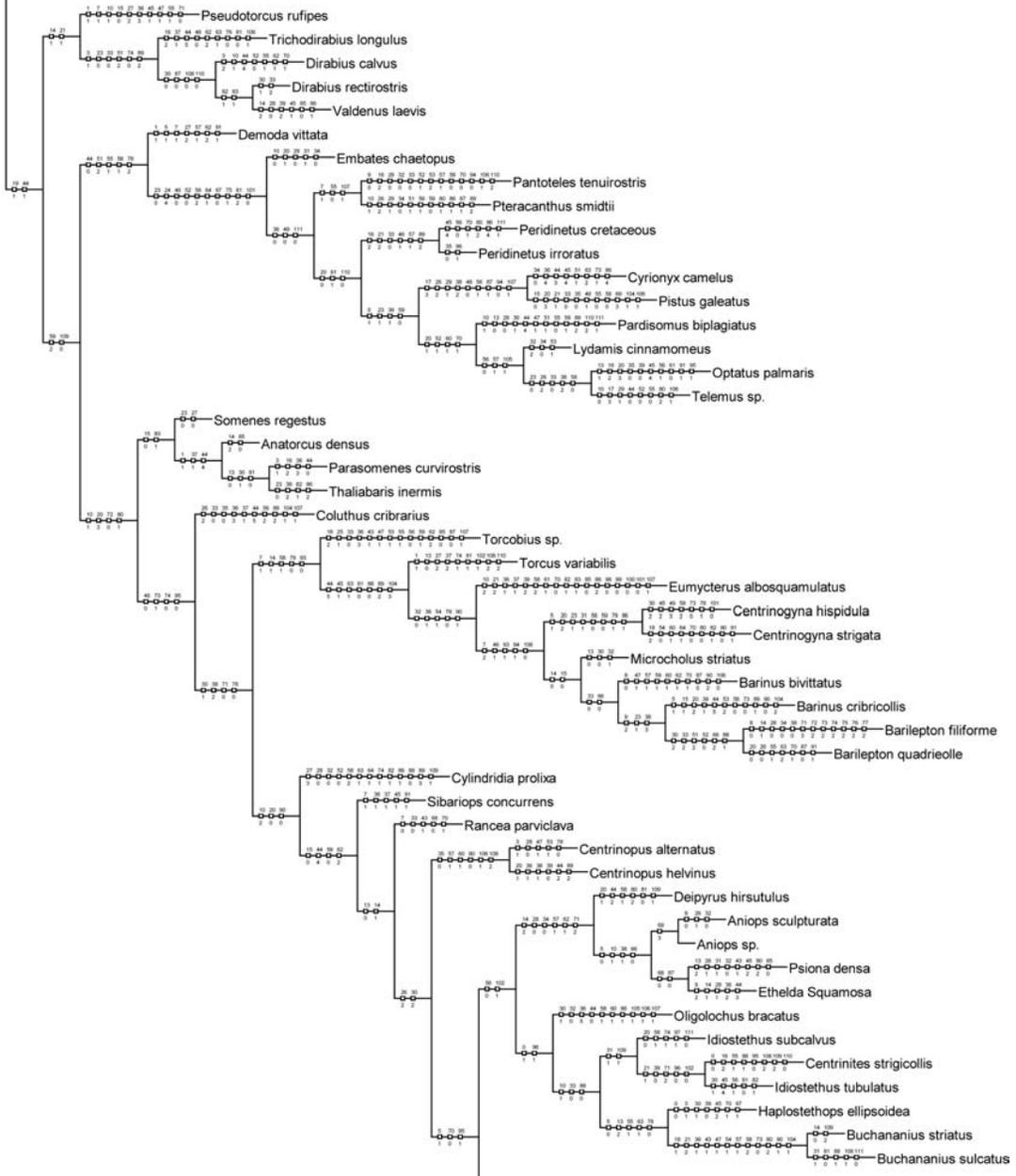


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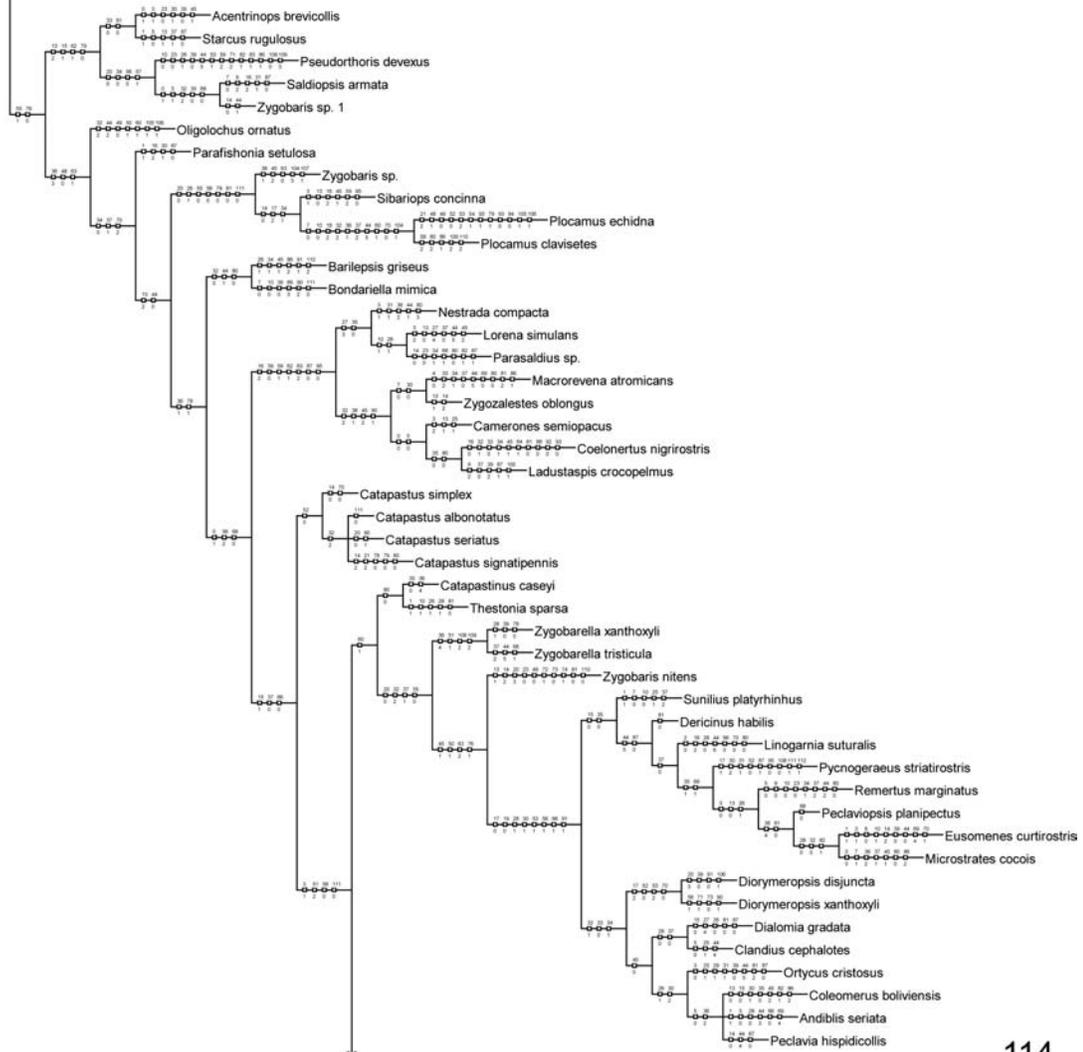
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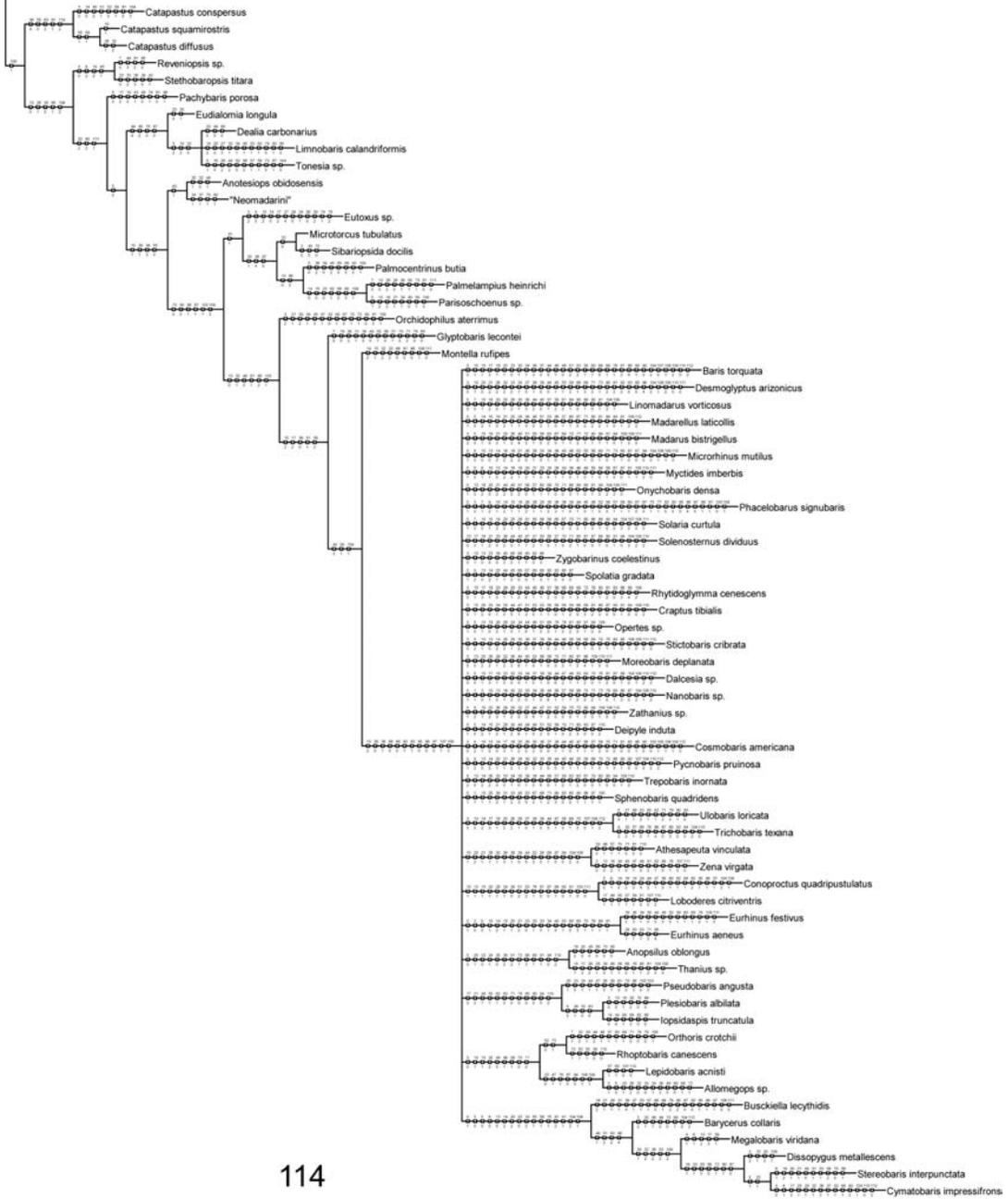
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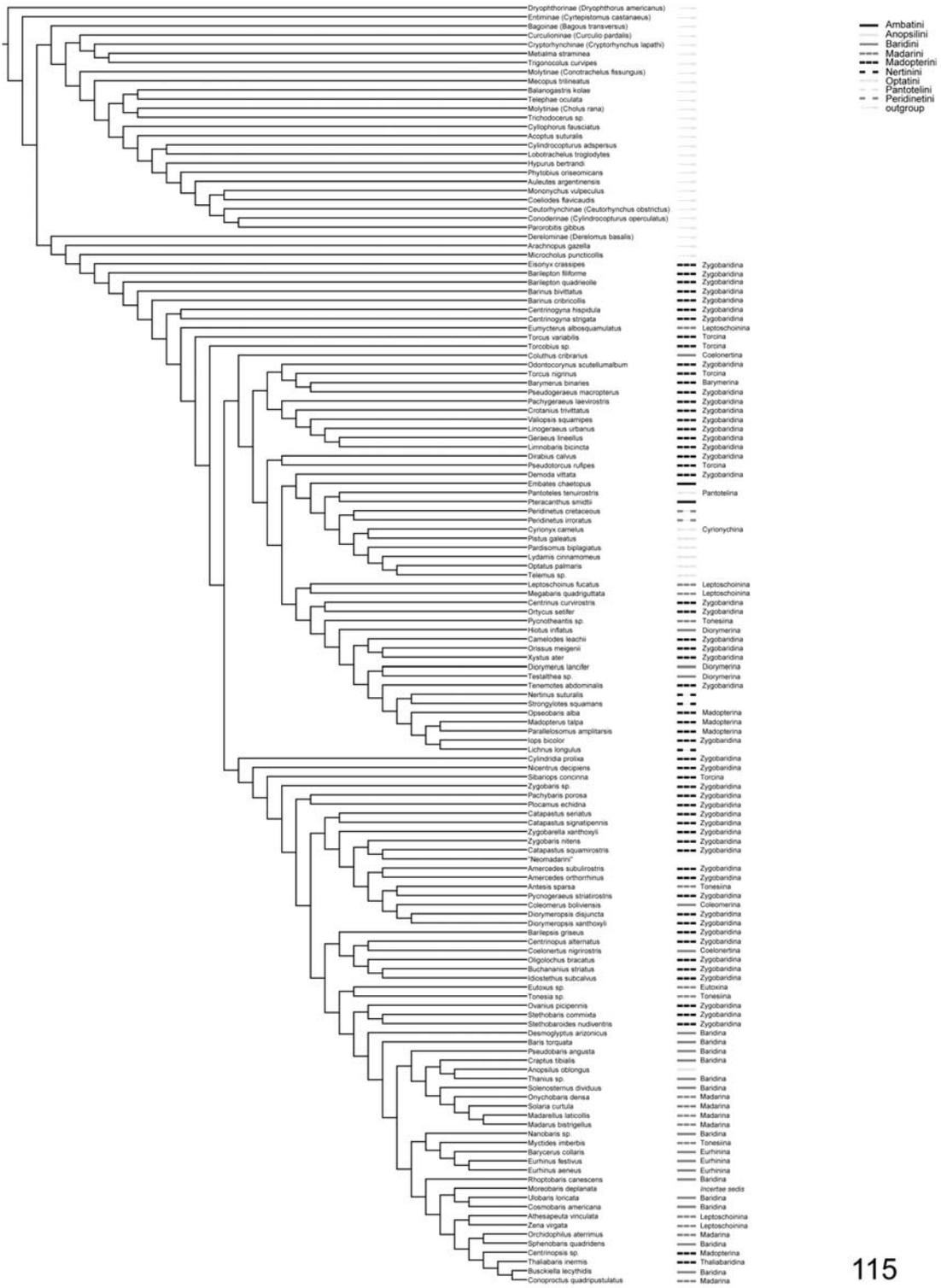


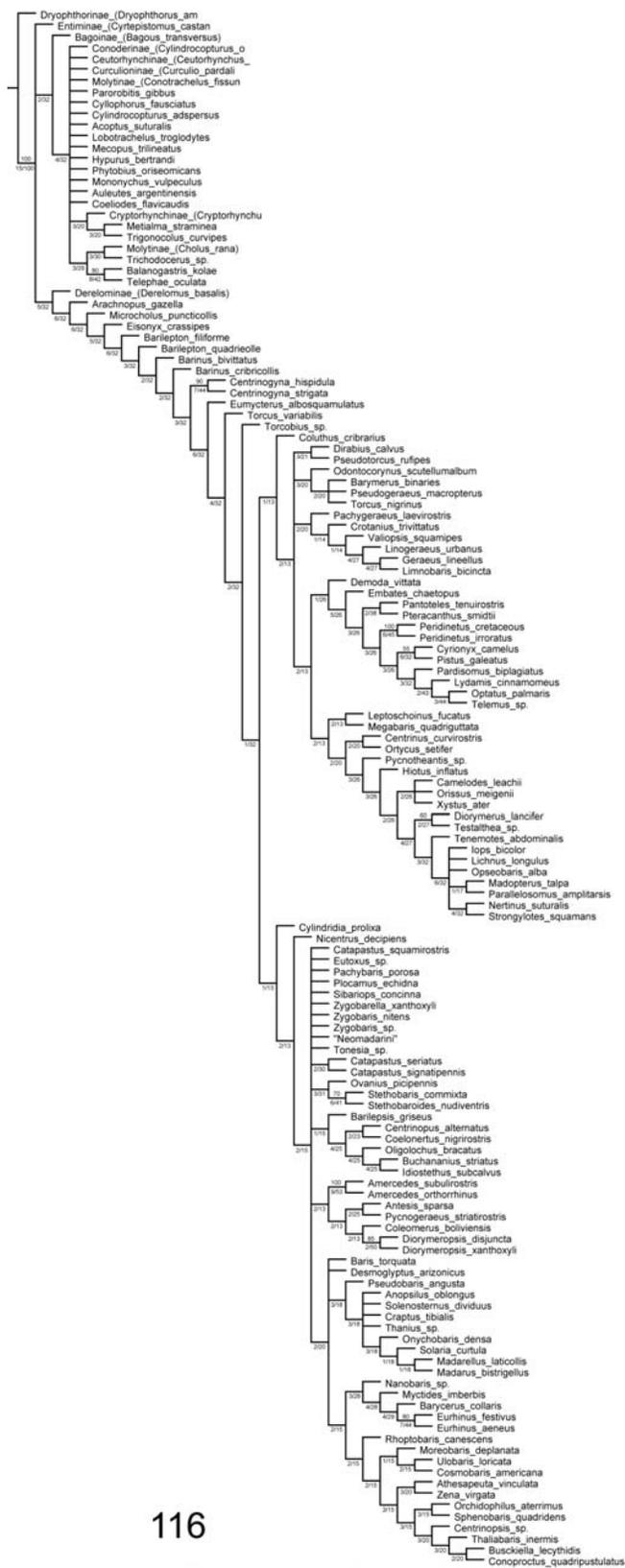
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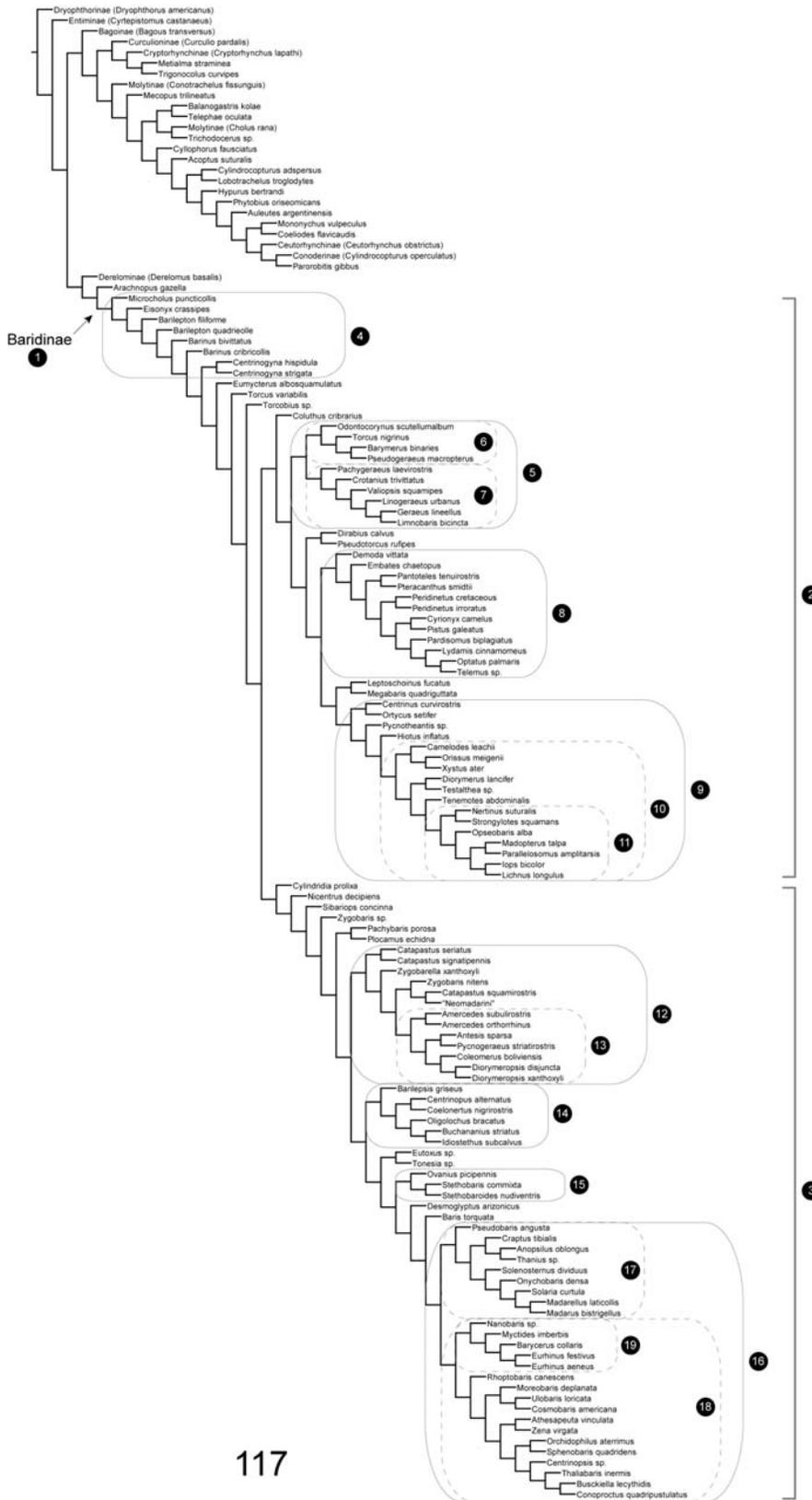
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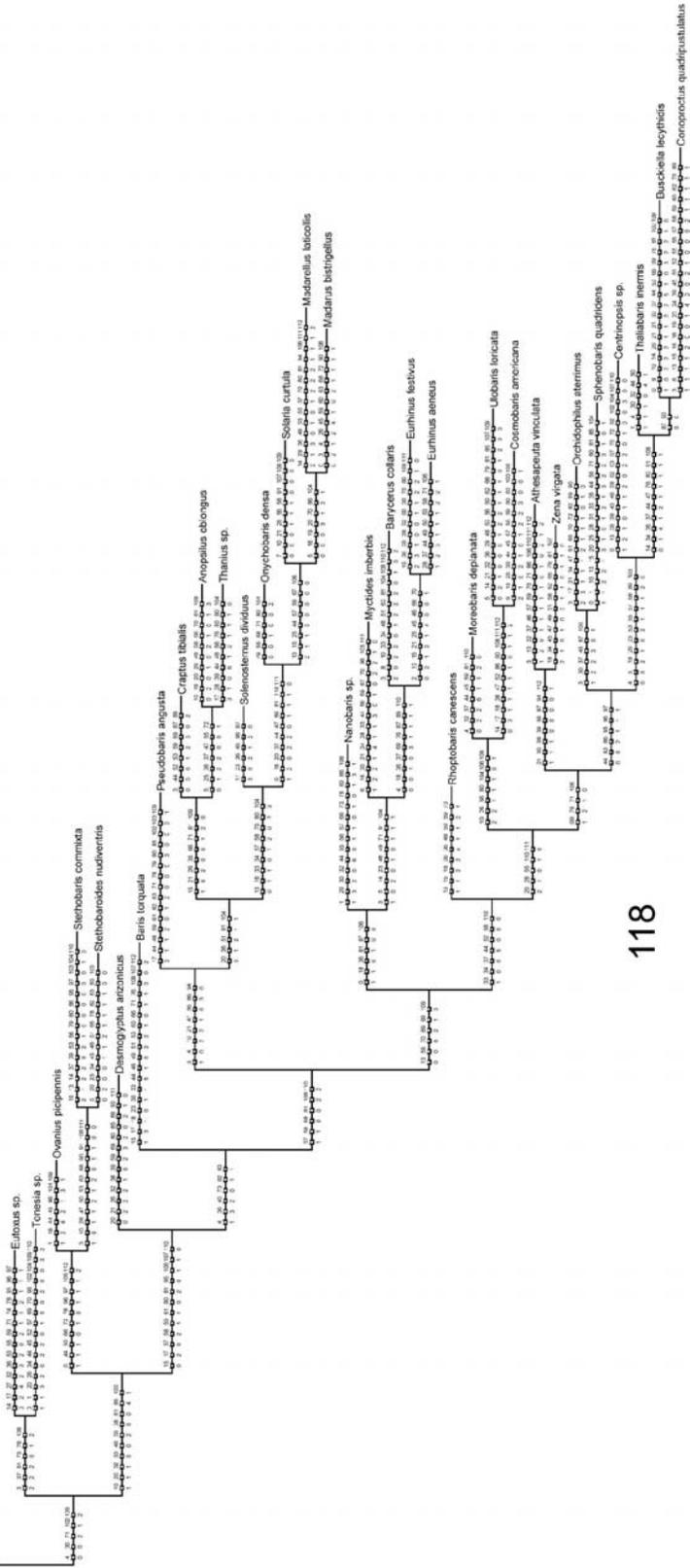




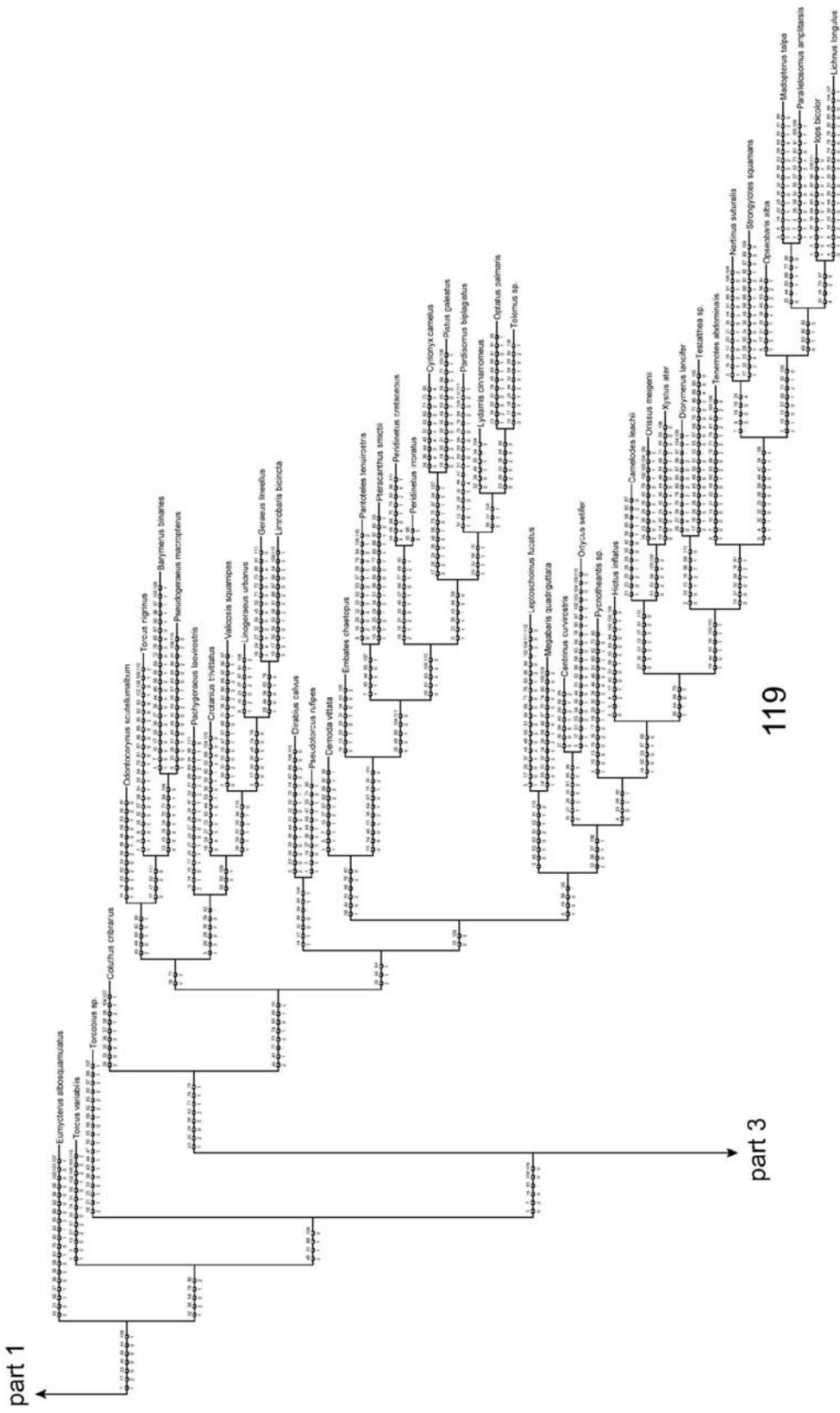




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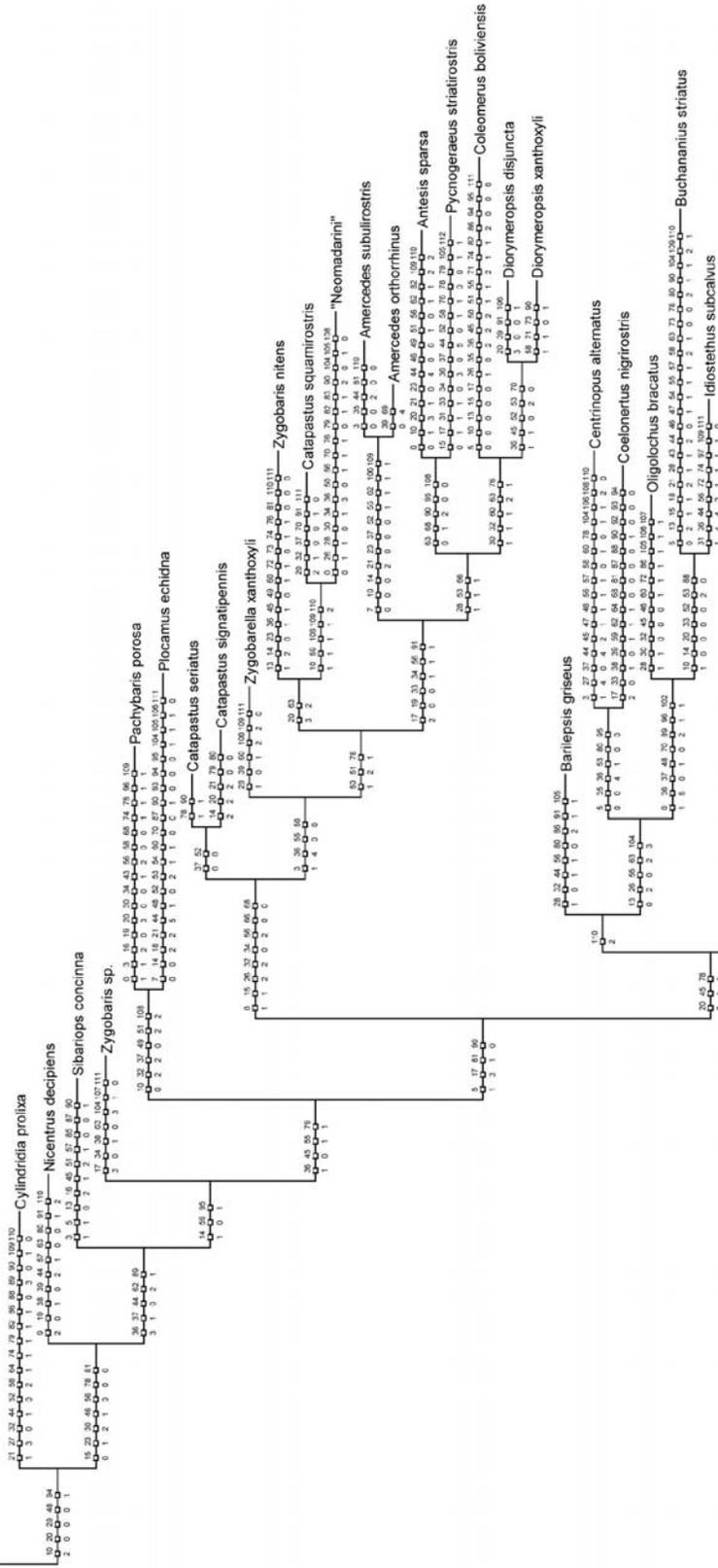






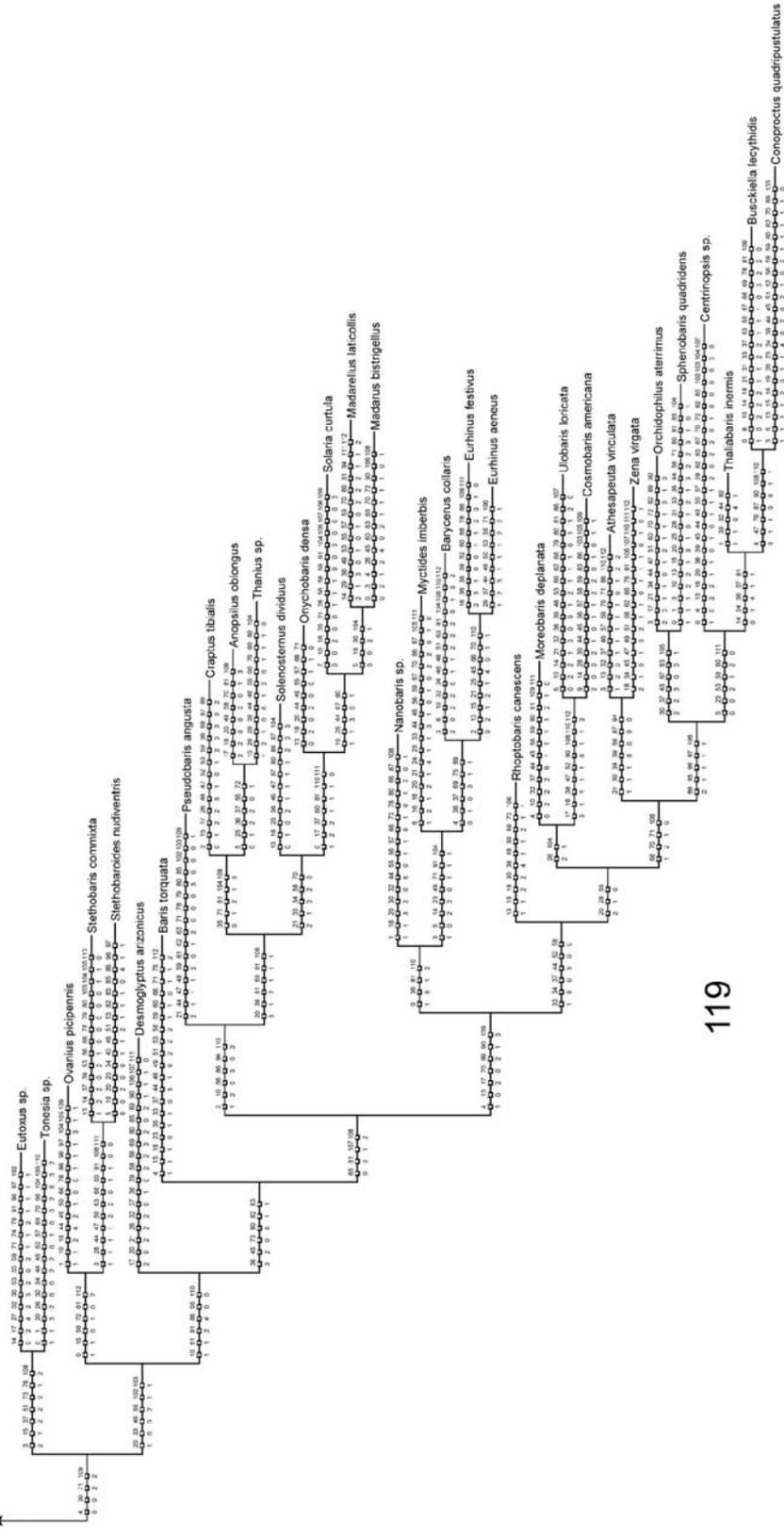
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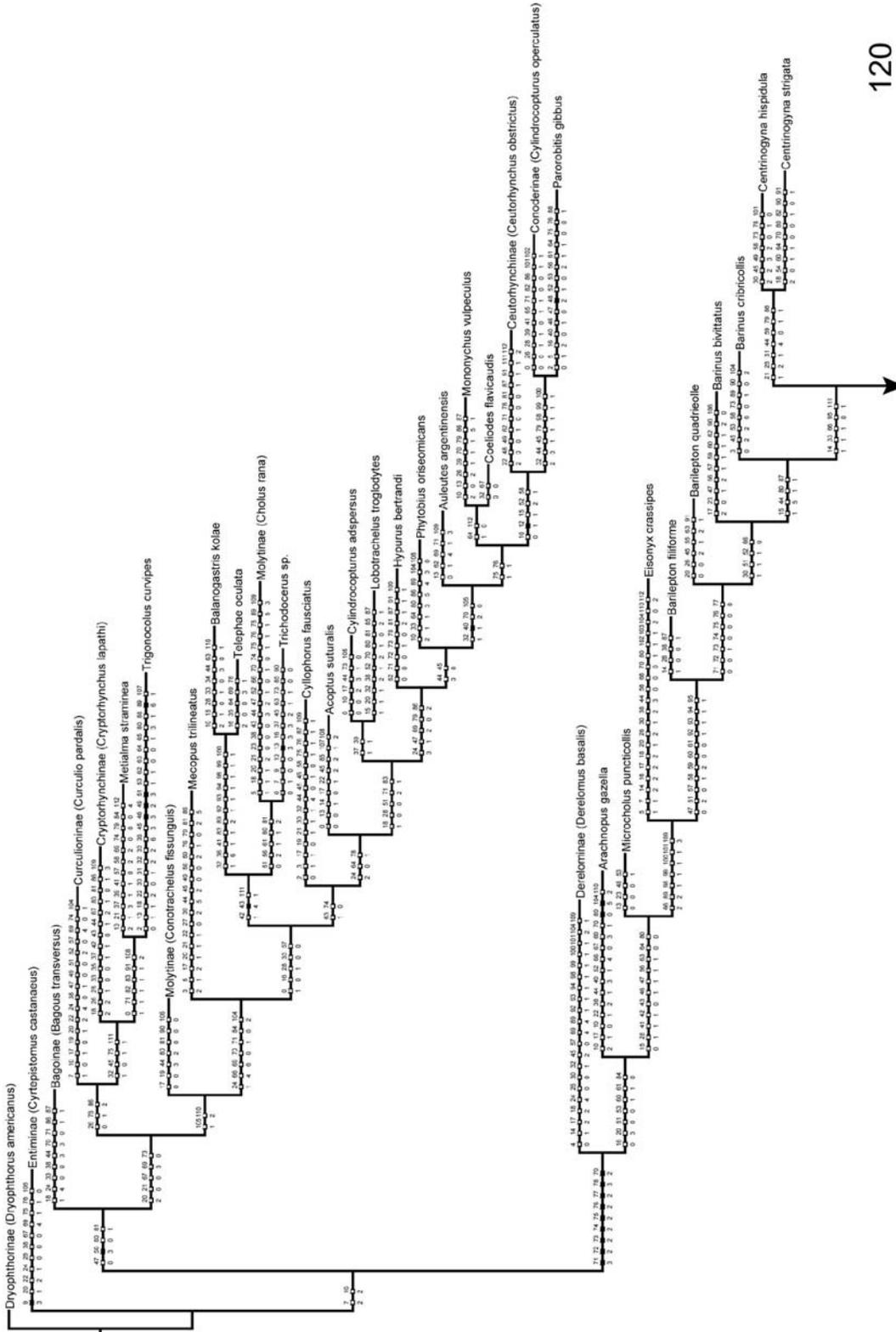
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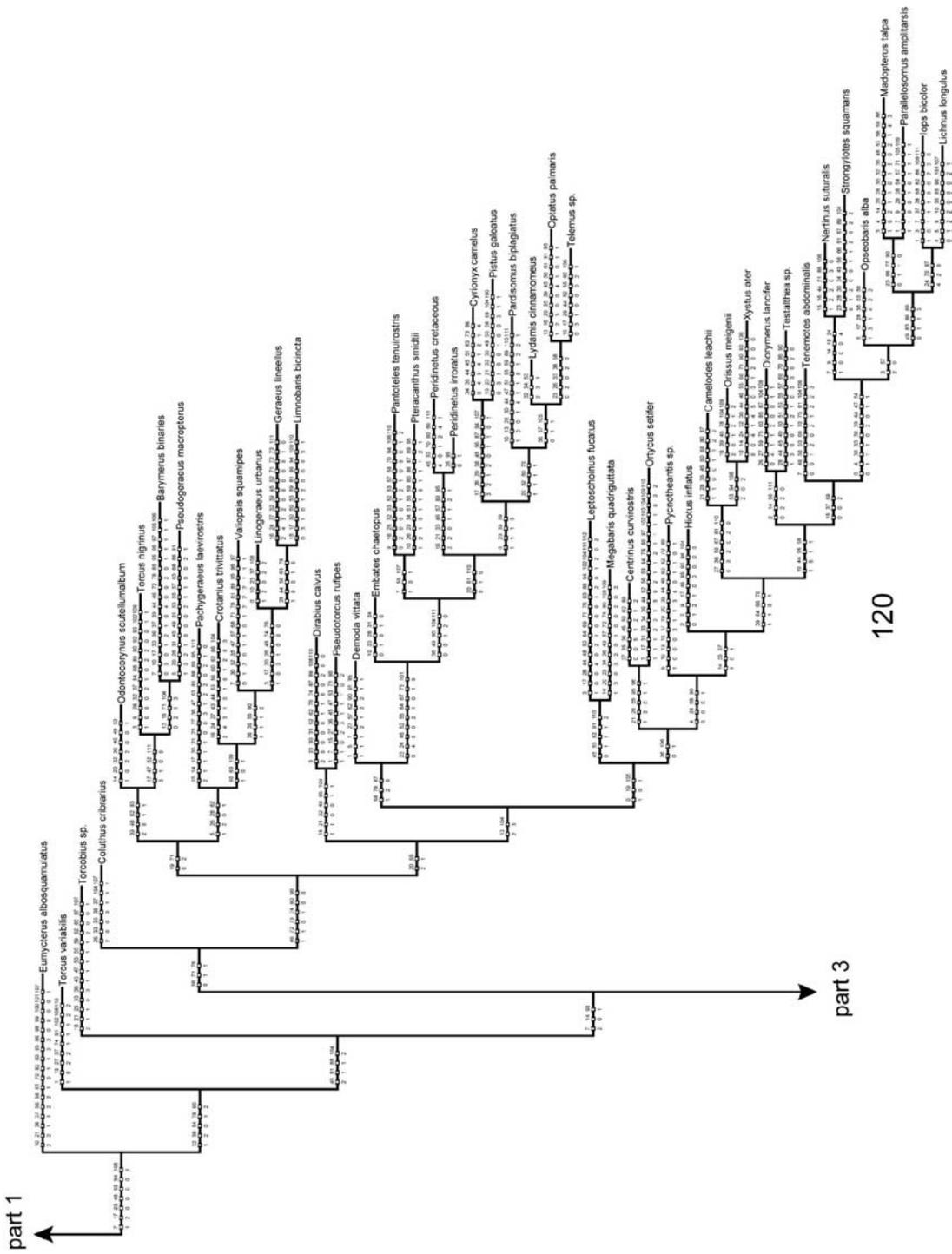
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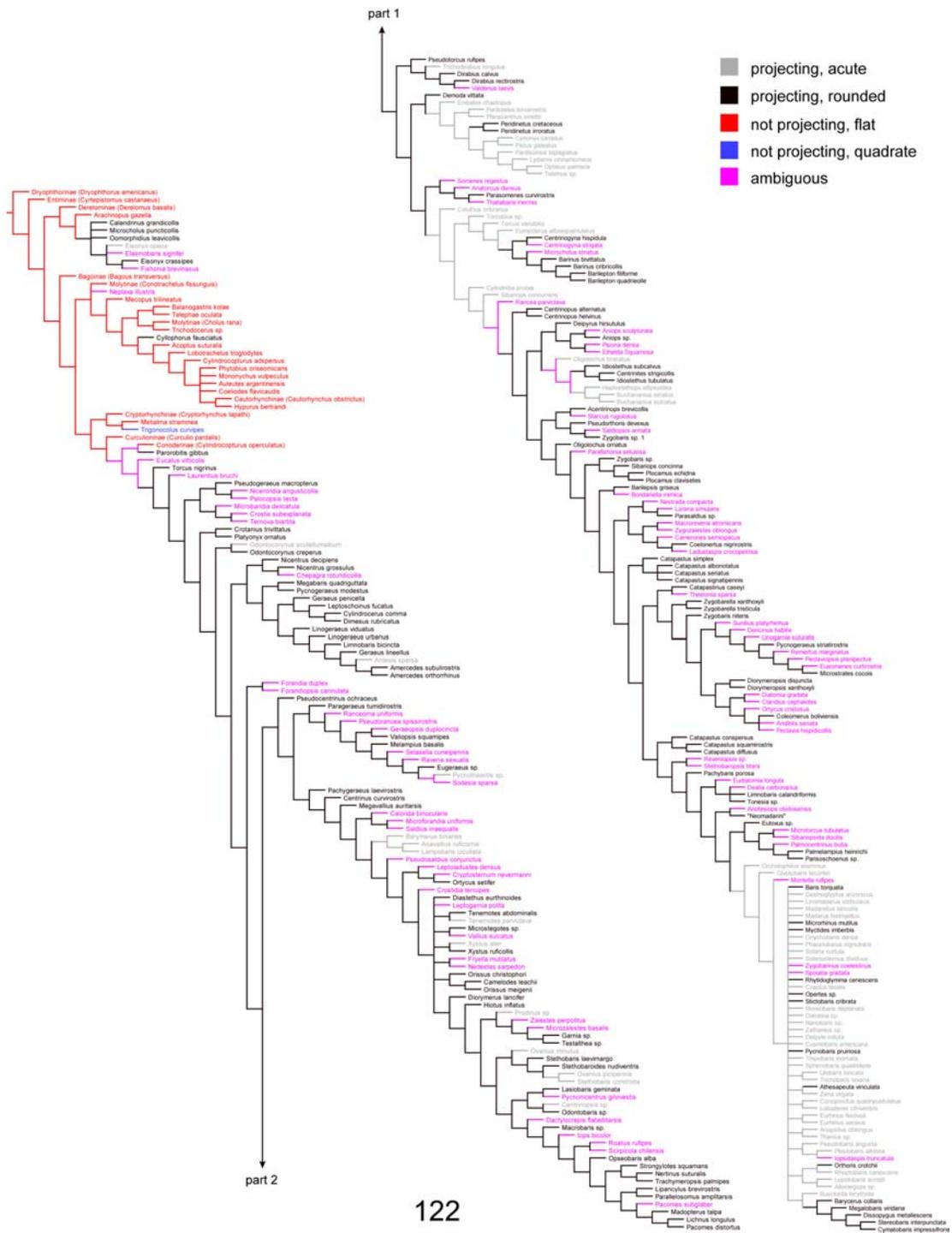


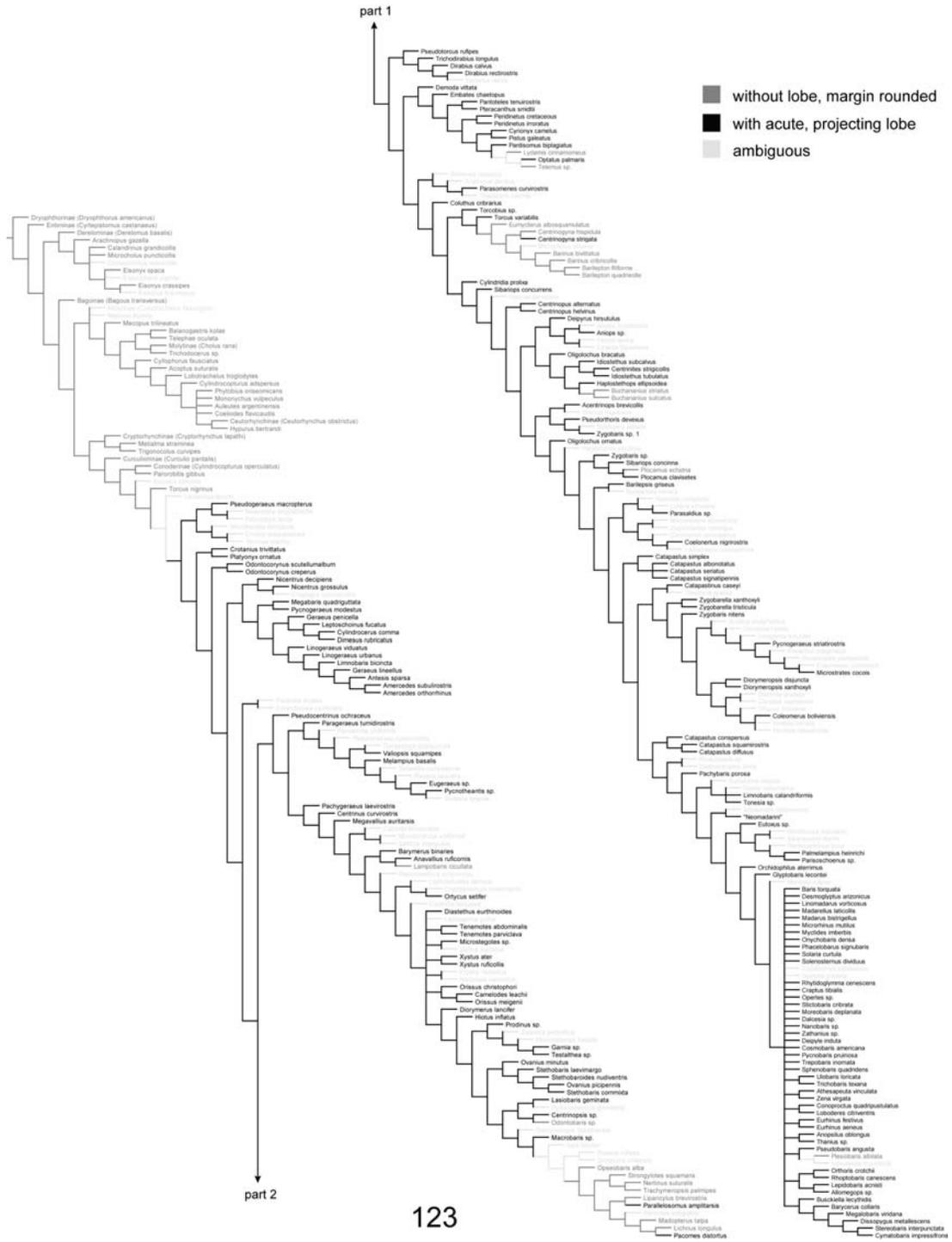
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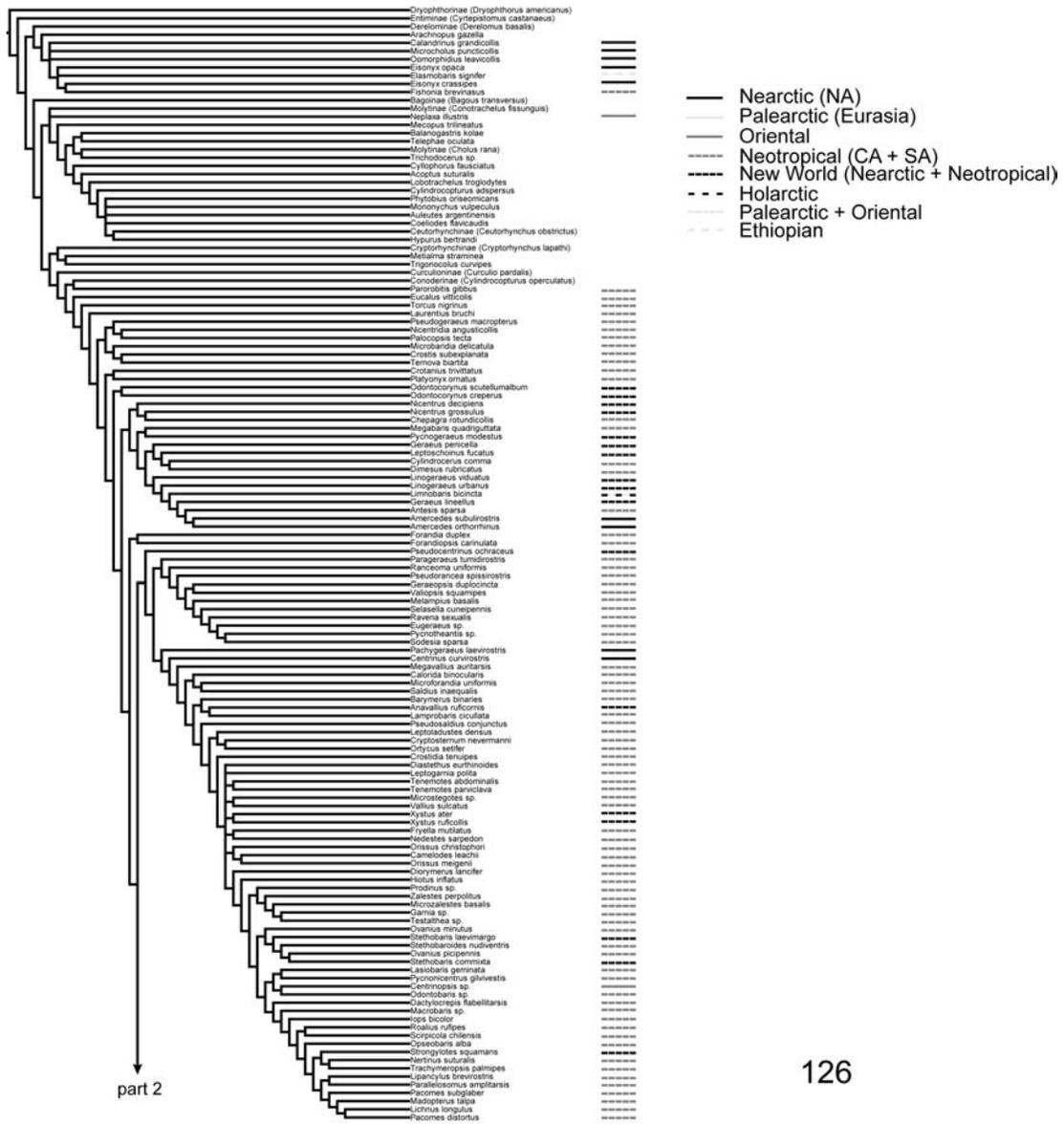








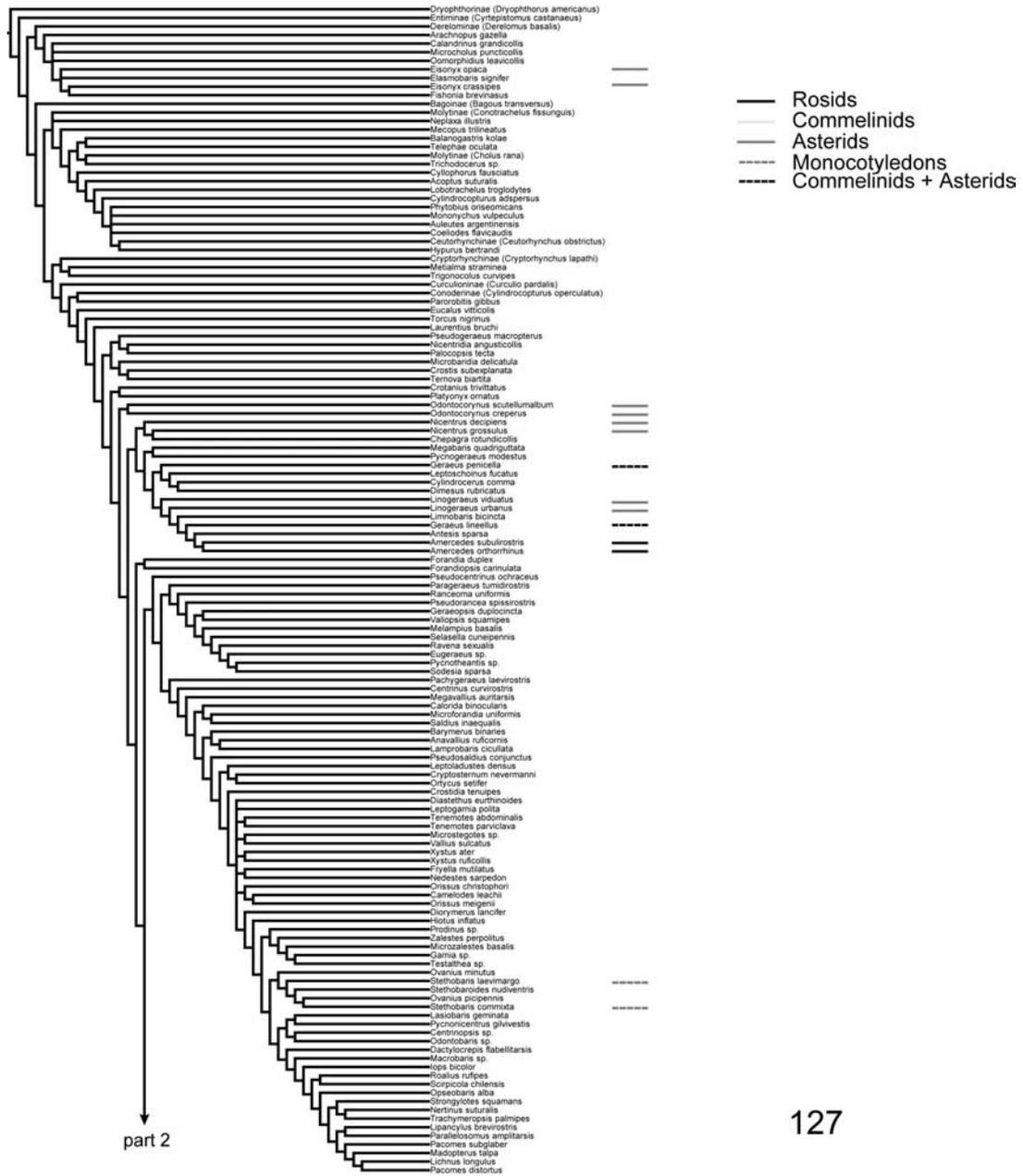




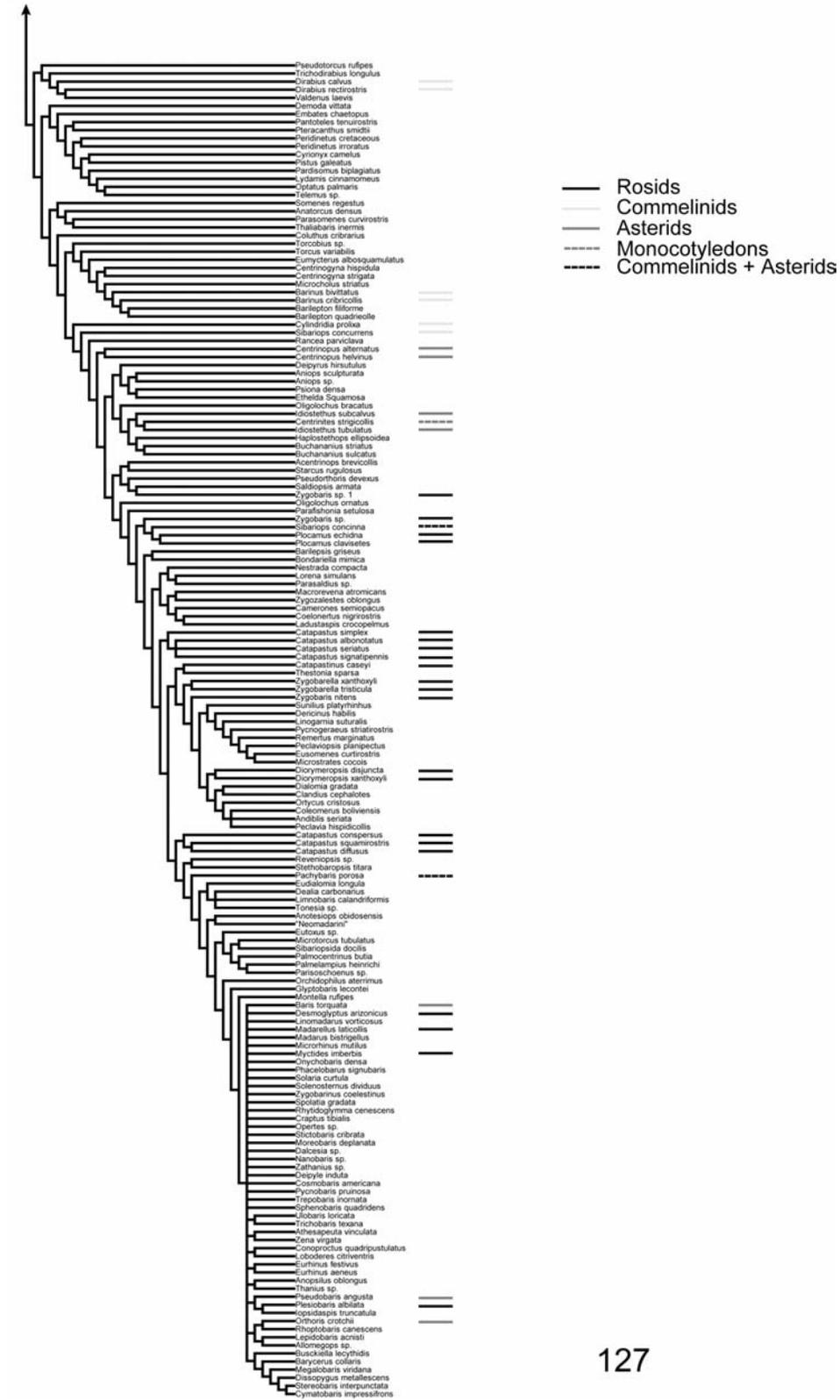
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- Nearctic (NA)
- Palearctic (Eurasia)
- Oriental
- Neotropical (CA + SA)
- New World (Nearctic + Neotropical)
- - - Holarctic
- Palearctic + Oriental
- - - Ethiopian

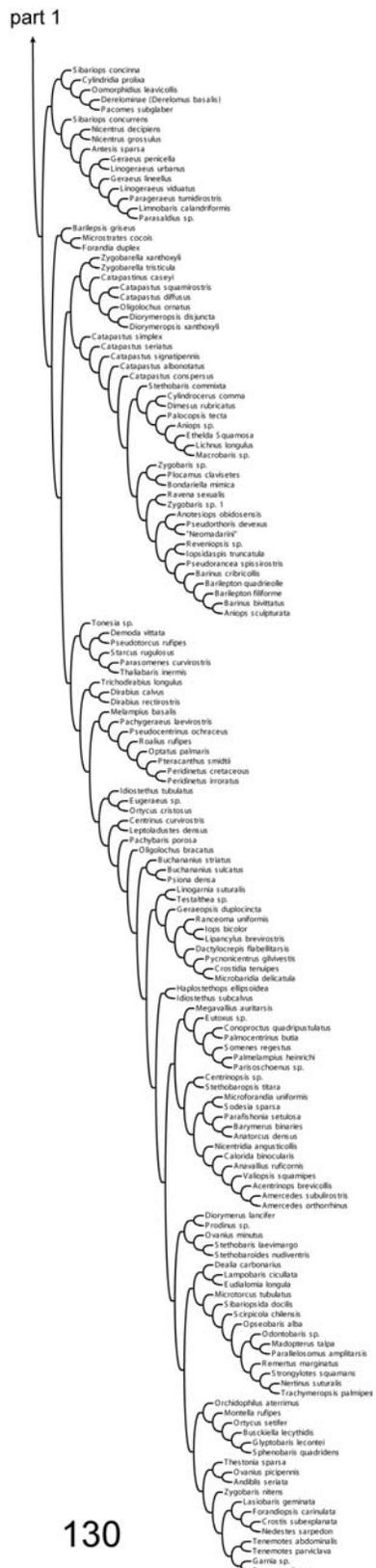
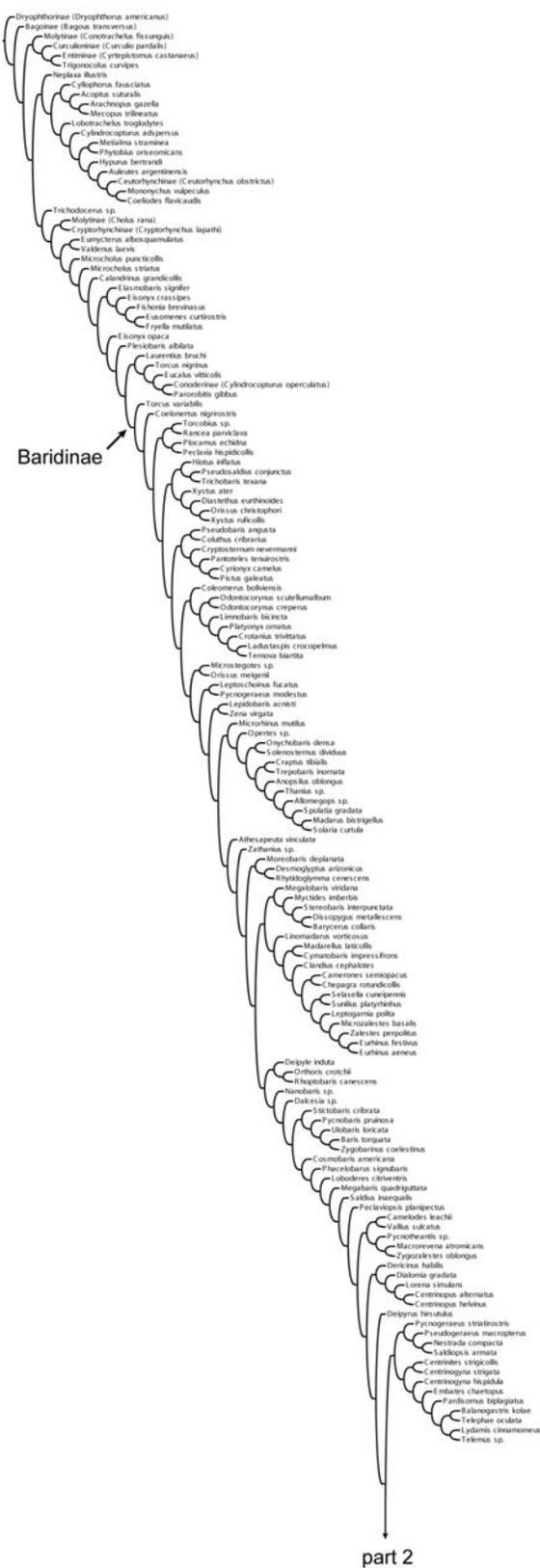


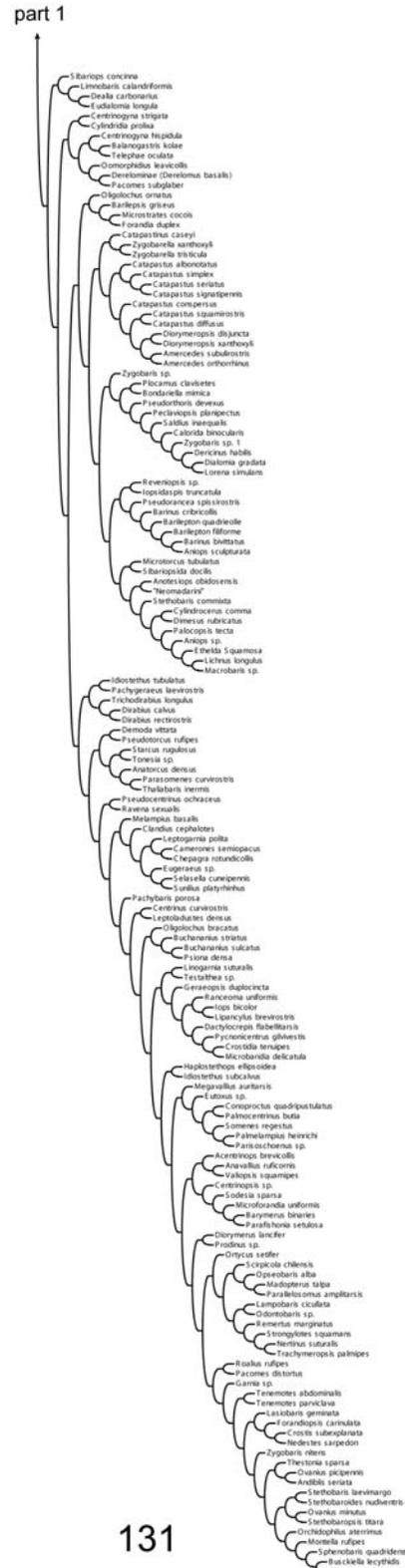
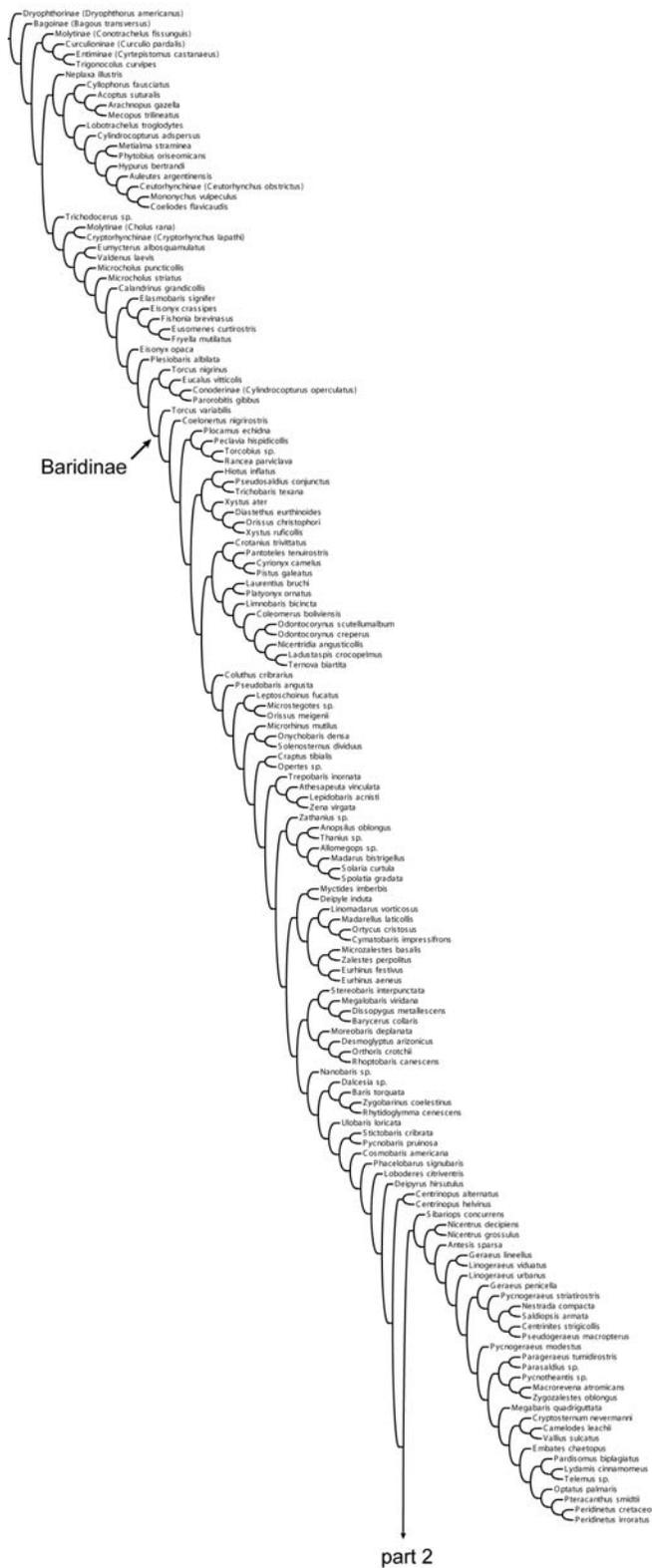
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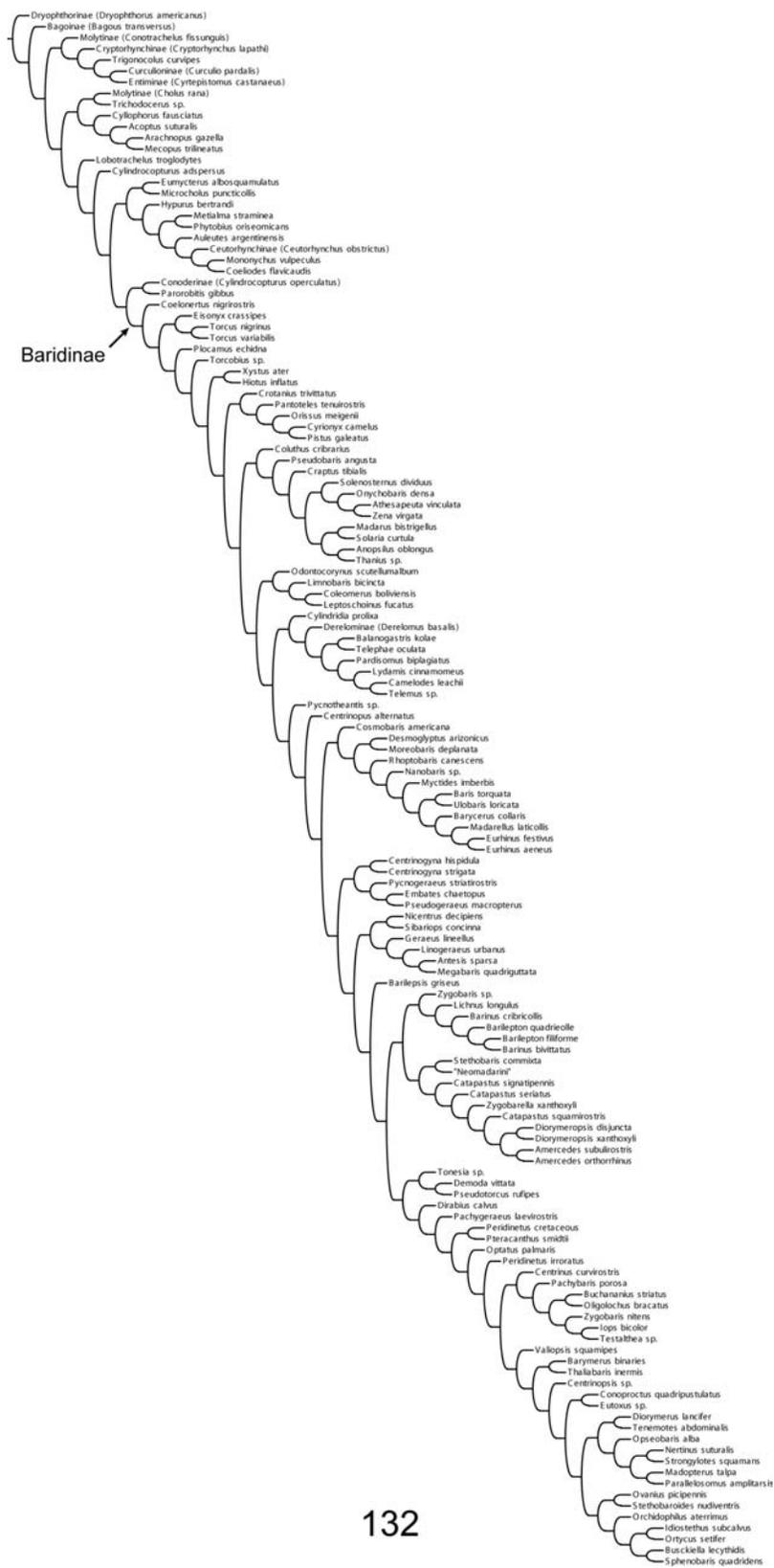


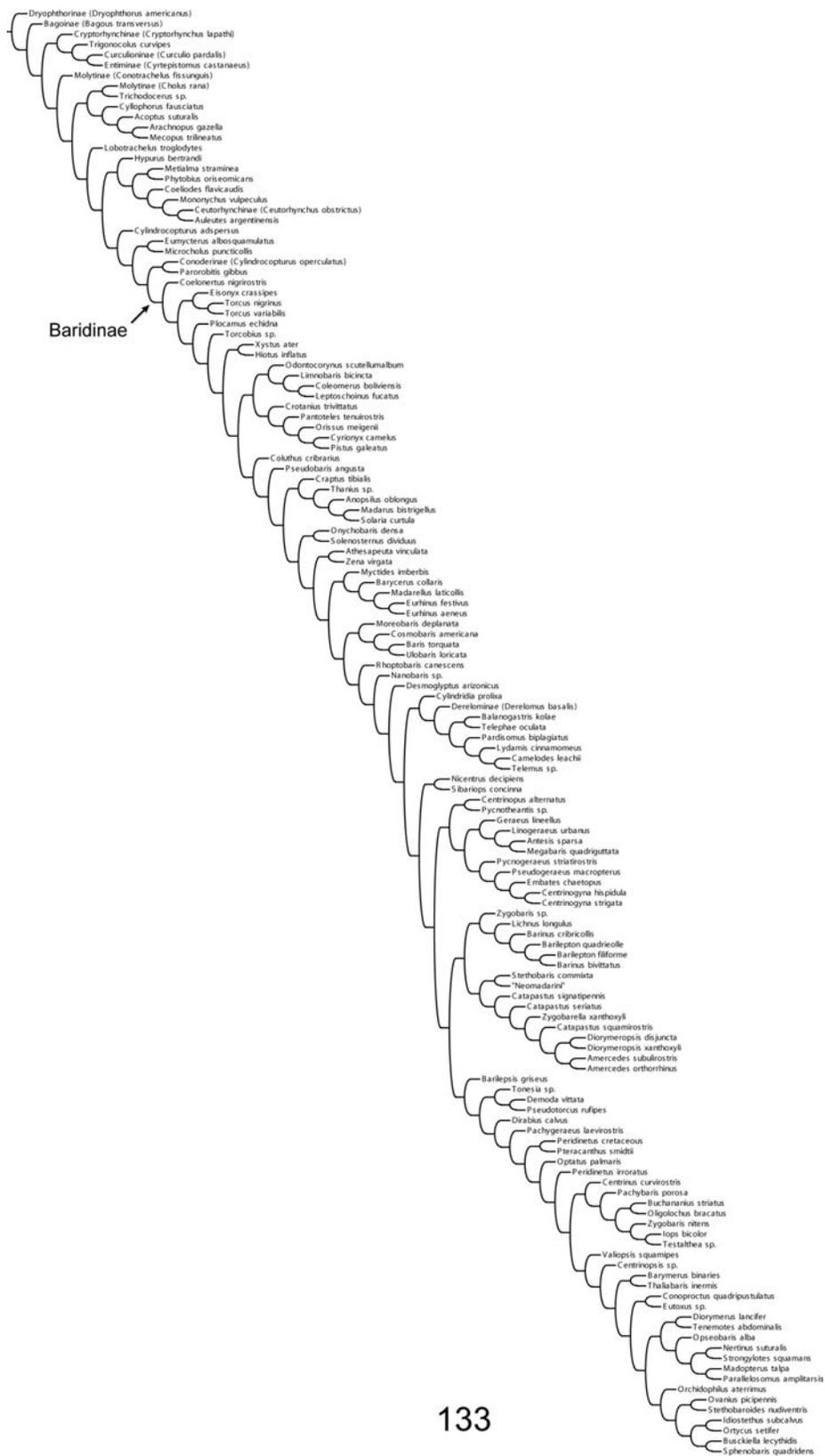


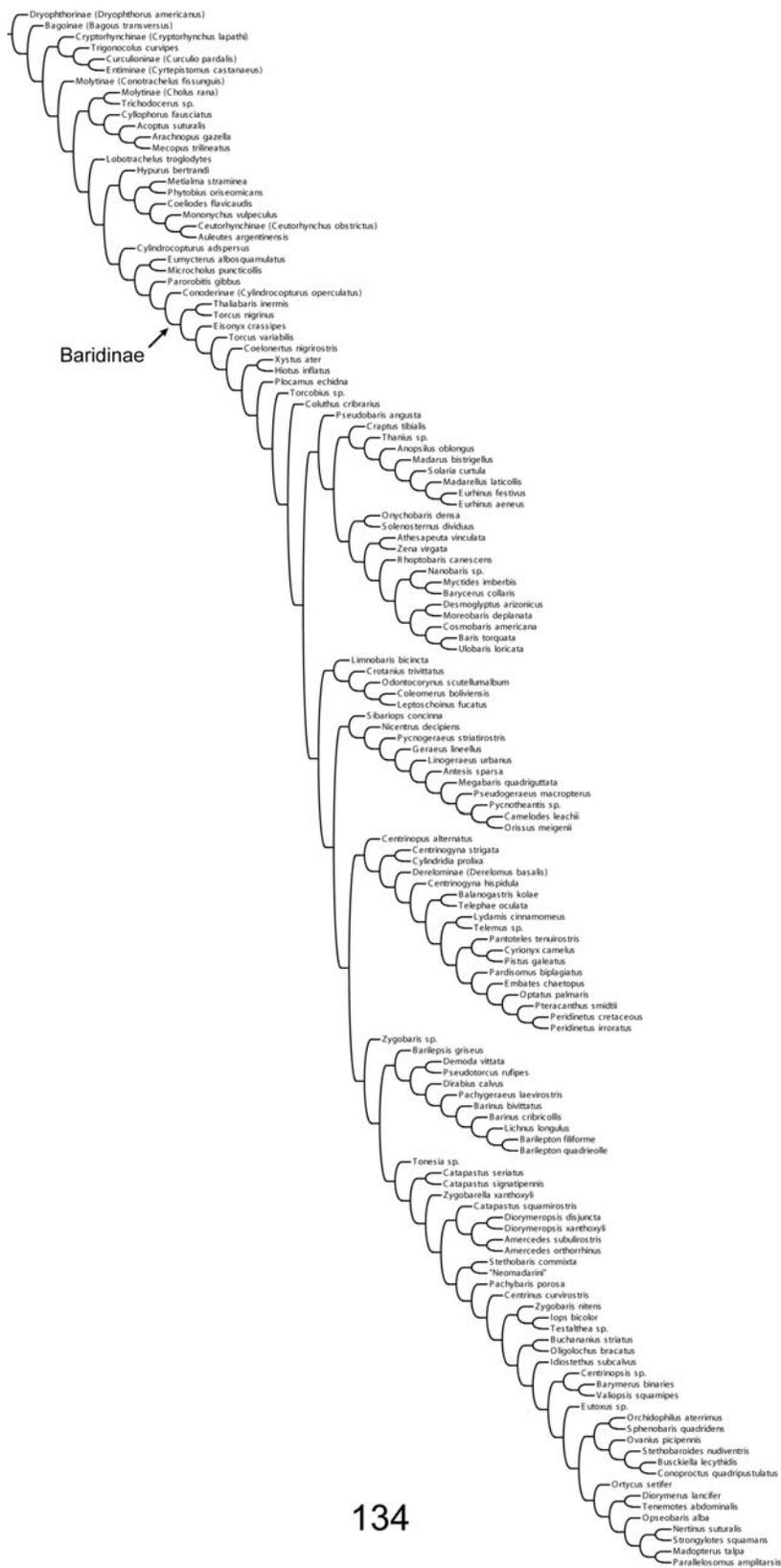








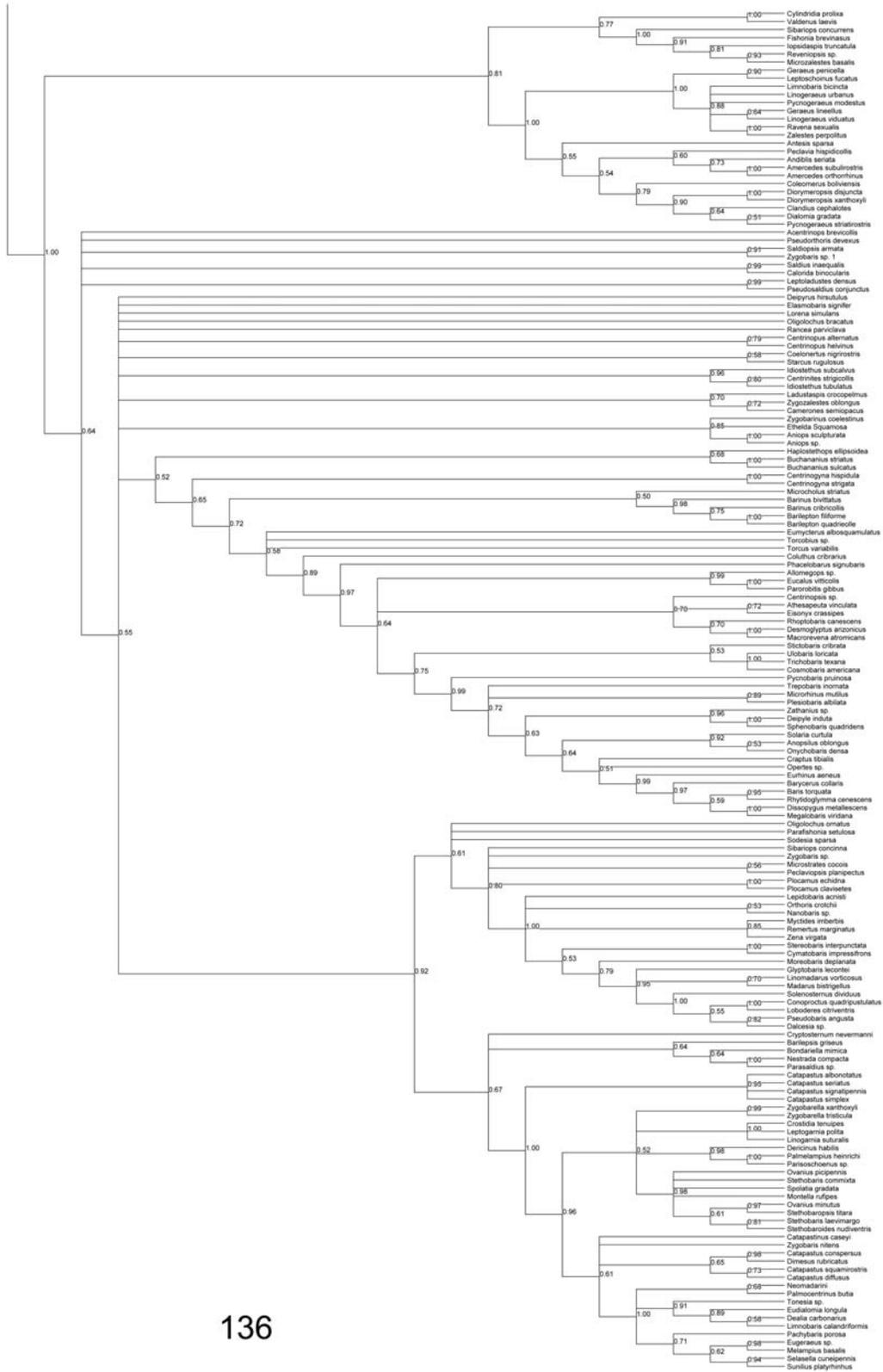








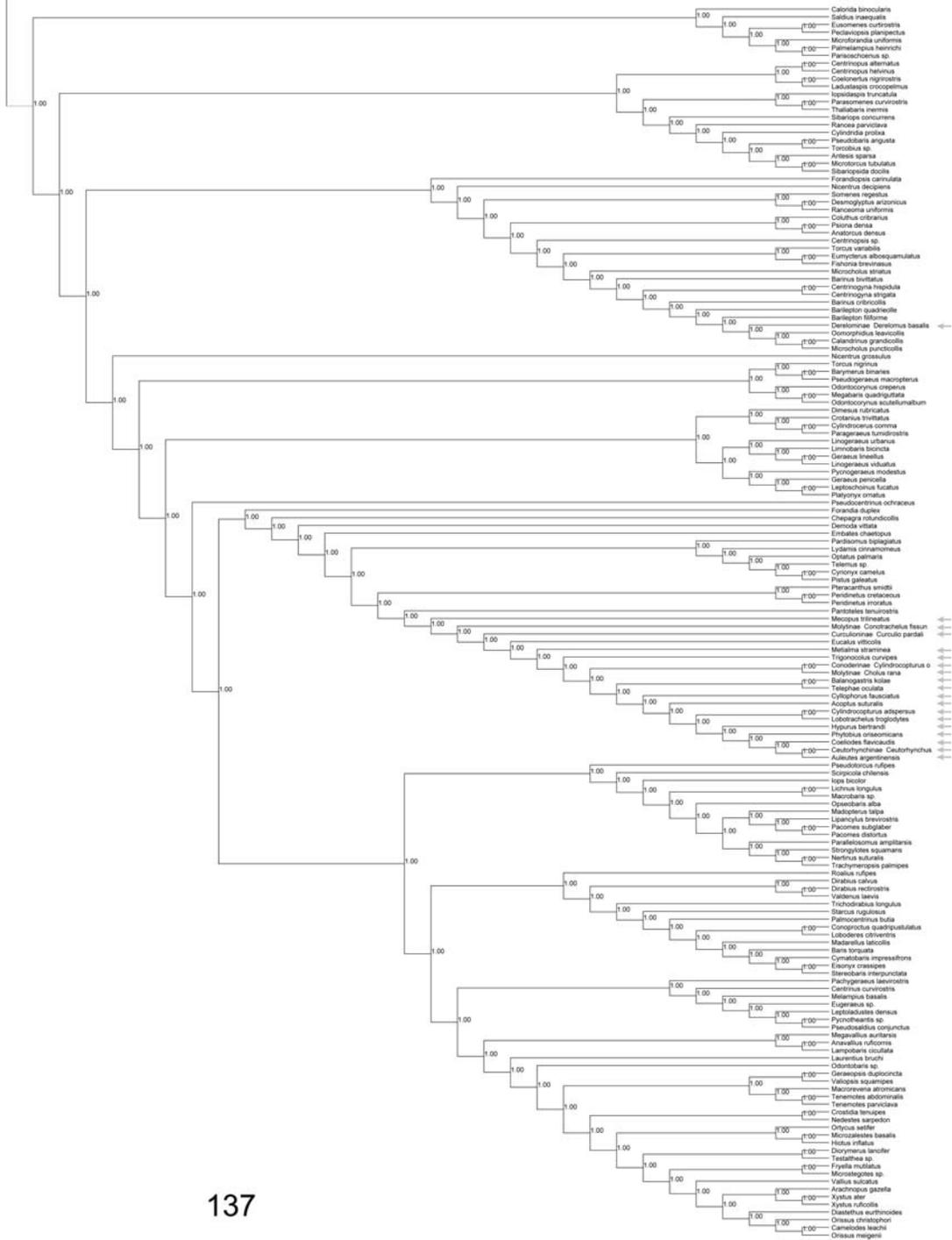
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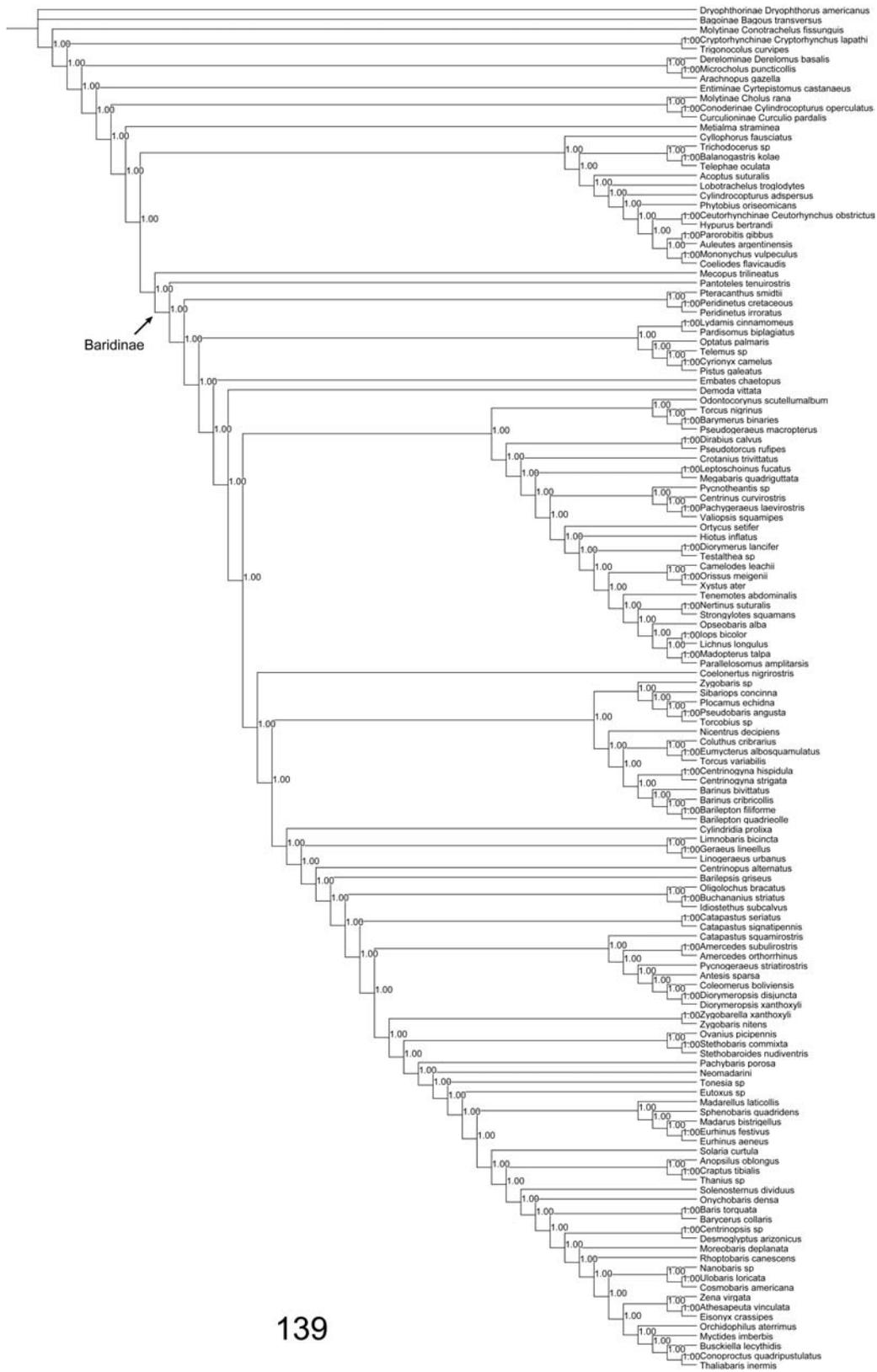


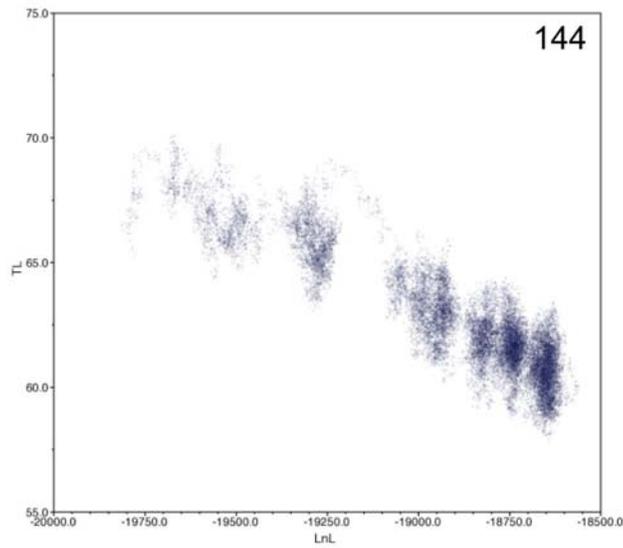
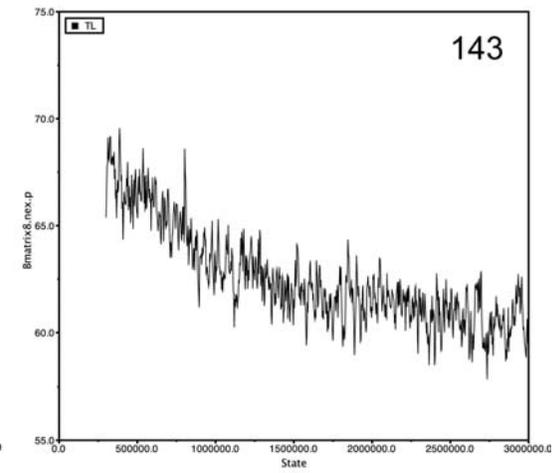
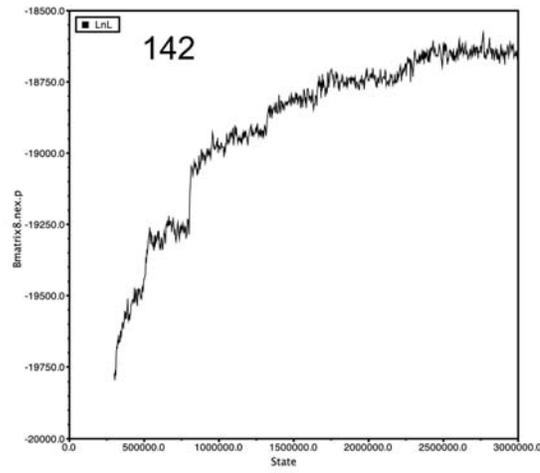
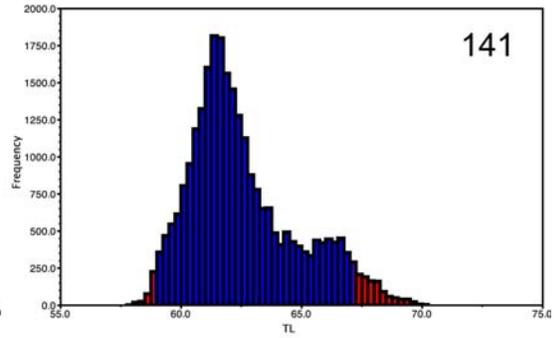
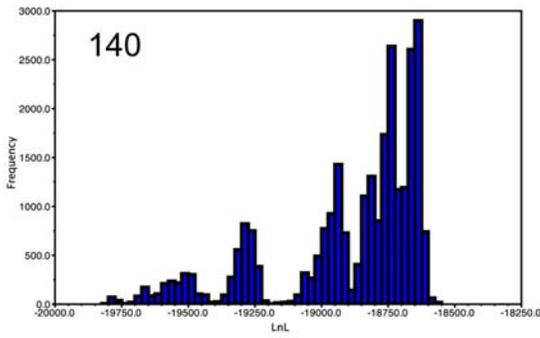
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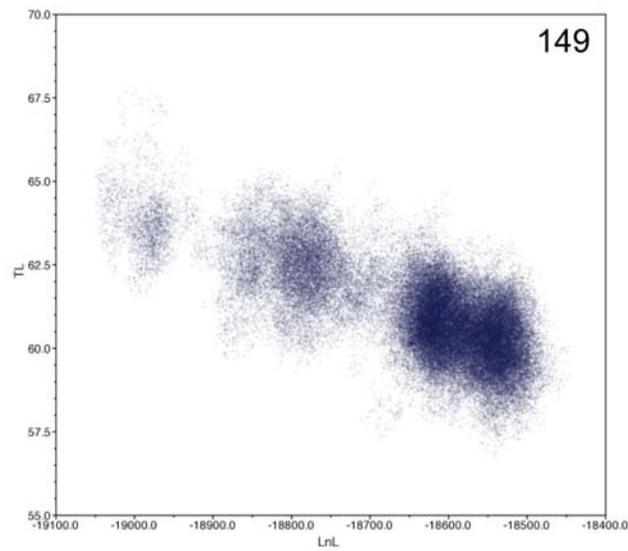
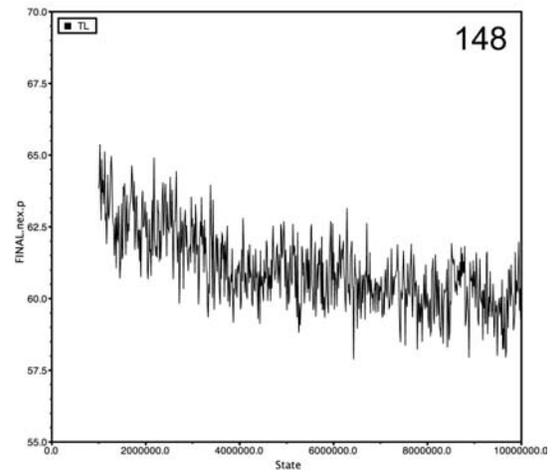
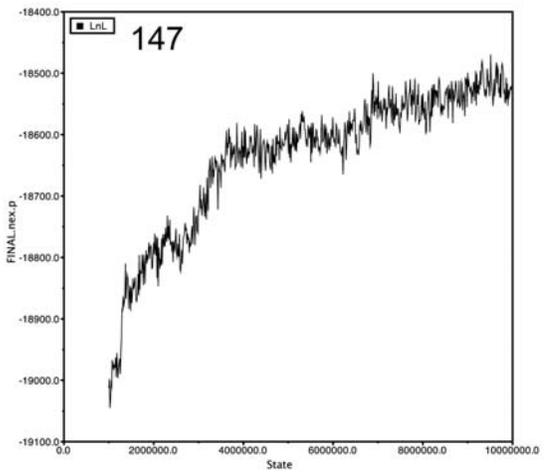
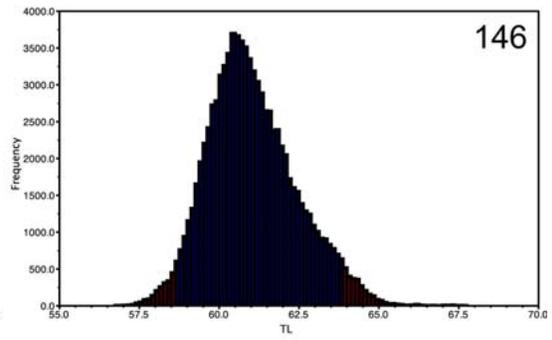
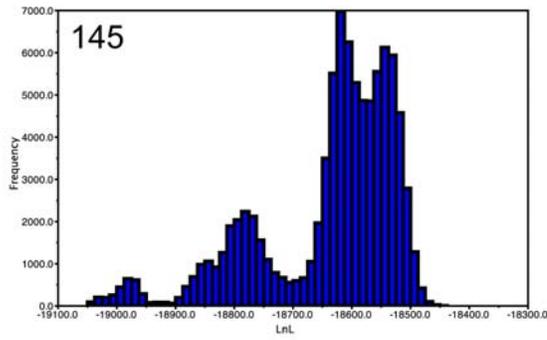


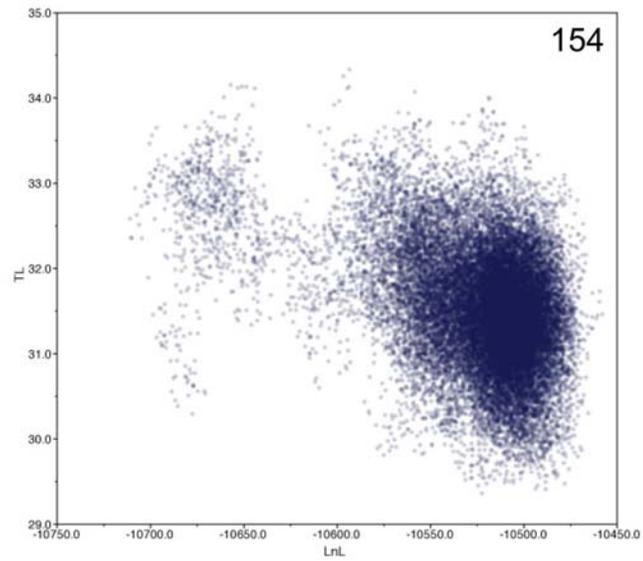
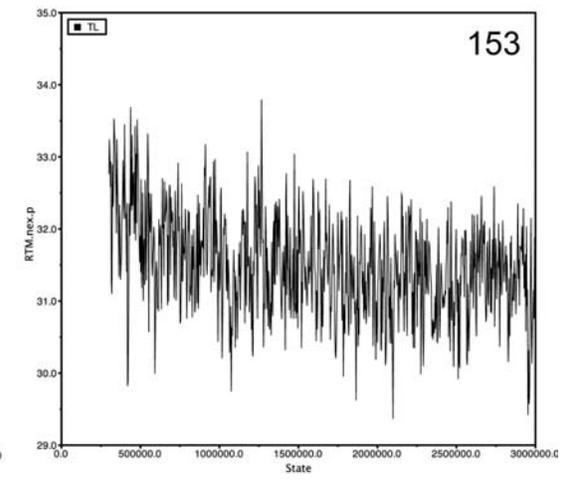
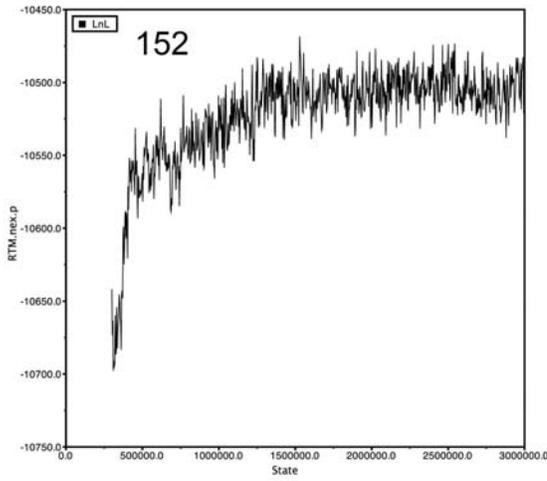
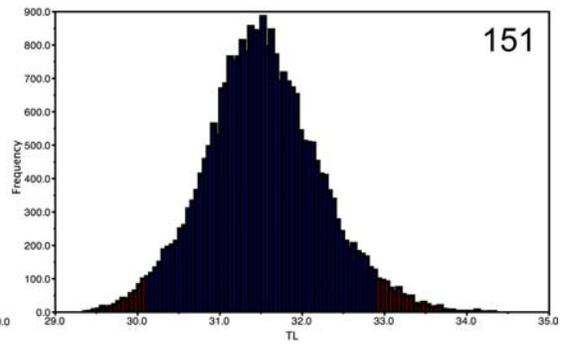
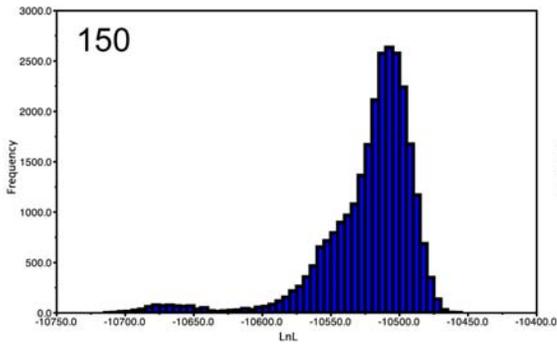
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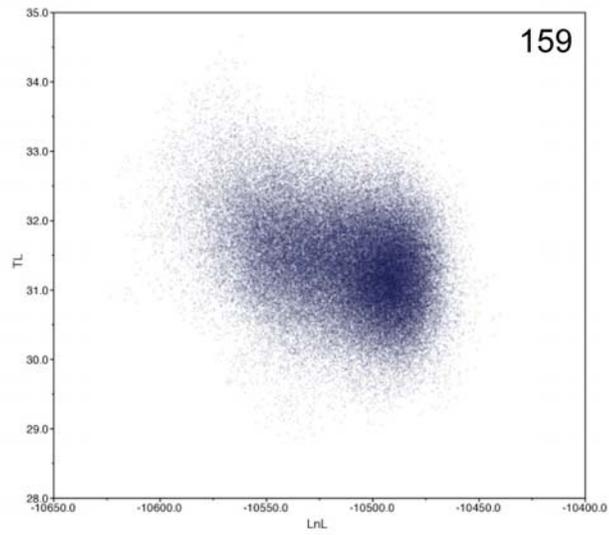
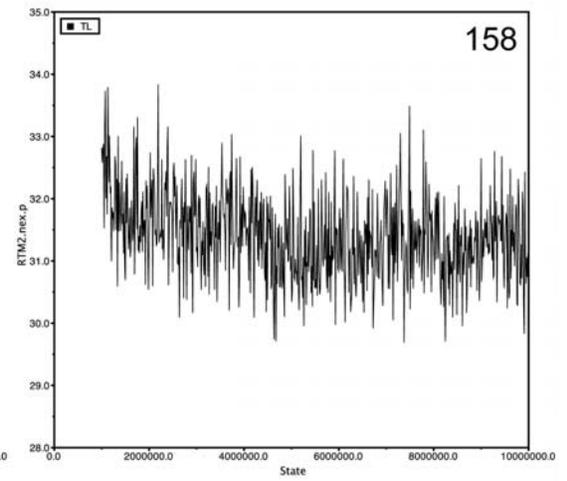
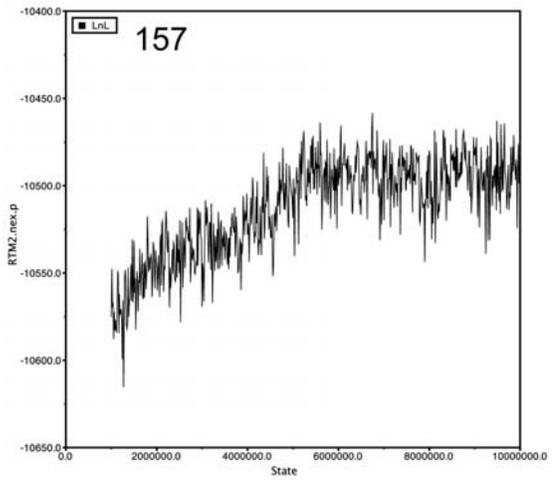
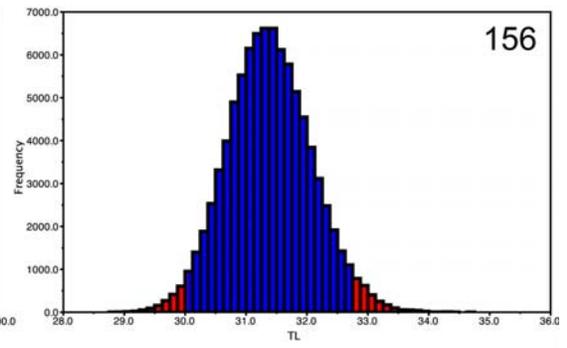
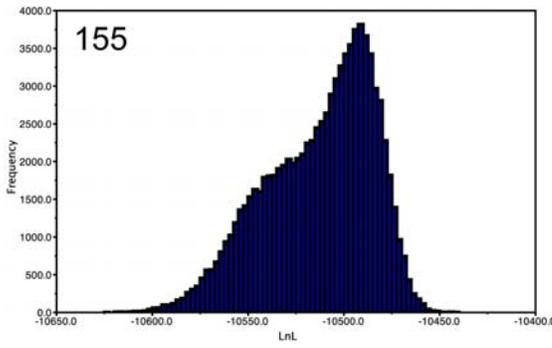












## **Chapter III: Evolution of pro-sternal horns in baridine weevils (Coleoptera: Curculionidae)**

### **Abstract**

Weevils (family Curculionidae) are one of the most diverse groups of extant organisms, with approximately 60,000 described species. They are extremely important economically, being of great agricultural significance because they are associated with all major groups of plants and plant parts. The weevil subfamily Baridinae is one of the larger weevil lineages. It is distributed worldwide, consists of 548 genera, approximately 9,000 described species, and is considered most in need of systematic study. Like the remainder of Curculionidae, there exists no phylogenetic hypothesis for the evolution of Baridinae. In order to provide stability to the group and to define the major lineages, the first phylogenetic hypothesis, based on morphological data, was constructed, providing a framework for the subfamily from which all future research on this group will be derived. The construction of a phylogenetic hypothesis then permits examination of the evolution of certain traits in the organisms, such as the defensive horns that are present in many baridine species. These horns, like those present in other beetles, are used during male-male competition, in which males spar with them in order to gain female mating rights. The fighting exhibited by these weevils, however, is unlike any other known in the insects. Moreover, it appears that horns have evolved multiple times in the

subfamily, as illustrated by their structural differences, and the evolution of other traits, such as stridulation, may be closely associated.

**Keywords:** Baridinae, horns, mating behavior, male intra-specific competition

## **Introduction**

Modification of the body and appendages for use in conspecific battles during mating is common in insects. Pro-thoracic horns have evolved numerous times in insects, most notably in the beetles (Coleoptera). Of these numerous, independent evolutionary events, horns have evolved from certain modified appendages and can be found in various locations on the beetle pro-thorax, namely on the pro-notum, as in Scarabaeidae, on the mandibles, as in Lucanidae (Stag beetles), and on the pro-sternum, as in weevils (Curculionidae). The presence of horns at these different locations, together with their morphological structure, determine specific functions. For example, horns present on the mobile head and immobile horns present on the pro-notum serve a clamping function, often used to lift an opponent and clamp it between the pair of horns. Horns evolved from modified mandibles move laterally in a scissor-like fashion and also are used to capture and immobilize an opponent between them. Those beetles with elongate, straight horns, often projecting from the pro-notum, are used to dislodge the opponent from a surface through a lifting action (Eberhard and Garcia-C. 2000).

Weevils are considered one of the largest groups of organisms on the planet, comprising approximately 60,000 described species. In weevils, the legs most often are modified for intraspecific male-male fighting. For example, in *Rhinostomus barbirostris*, the males possess elongate fore-legs that function to pry an opponent off of a female and push it off of a substrate (often vegetation). In *Macromerus bicinctus*, the male uses its swollen tibiae to strike opponents (Weislo and Eberhard 1989). In the weevil subfamily Baridinae, including a few genera in closely-related subfamilies (Conoderinae), males have evolved horns on the pro-sternum that function in male-male combat, though other functions may be likely. These horns vary in development among males of different sizes (the smaller males possessing smaller horns) and vary in morphological structure (Figs. 1-61, 67-73). Many species possessing horns, though not all, also possess an invagination between them (Figs. 62-66), referred to as the horn sheath. Few studies have examined the evolution of beetle horns using phylogenies. Those that have (Emlen *et al.* 2005) did so with scarab beetles (Scarabaeidae), which possess dorsal horns on the pro-notum.

## **Materials and methods**

### *Scanning Electron Microscopy:*

All SEM images were captured using a LEO 1550 FESEM. Specimens were mounted on an SEM stub using Leit-C-Plast adhesive and an isopropanol-based colloidal graphite. Whole specimens were placed on insect pins or glued to paper points, securing the pin or point on an SEM stub using Leit-C-Plast. Dissected parts

were mounted on a stub by securing them with a thin layer of colloidal graphite. After the desired parts were mounted, coating was performed using gold.

*Taxon sampling:*

Following Alonso-Zarazaga and Lyal (1999), species were sampled from each of the 9 tribes and 17 subtribes in Baridinae, with a total of 283 baridine species, representing 270 genera (out of a total of 546 genera), included in the analysis. A total of 29 species were sampled for the outgroup, consisting of 12 subfamilies outside of Baridinae. The final analysis included a total of 301 taxa. Outgroup selection was based on phylogenies produced by Marvaldi *et al.* (2002), and previous baridine classifications by Zherikhin and Egorov (1990), and Zherikhin and Gratshev (1995).

Taxa were borrowed from the following institutions:

USNM – National Museum of Natural History (United States National Museum),  
Smithsonian Institution, Washington, D.C., USA.

SEMC – Snow Entomological Museum, University of Kansas, Lawrence, Kansas,  
USA.

CMNC – Canadian Museum of Nature, Ottawa, Canada.

IZCAS – Institute of Zoology, Chinese Academy of Sciences, Beijing, China.

CAS – California Academy of Sciences, San Francisco, California, USA.

FMNH – Field Museum of Natural History, Chicago, Illinois, USA.

*Phylogenetic analysis:*

The data matrix was compiled in WinClada. Phylogenetic analyses were performed using NONA and TNT (Tree search implementing New Technology). In NONA, two alternative styles were used for ratchet runs during tree exploration. One ran single ratchet sets for 4,000 iterations while sampling 35 to 50 characters and holding 1 tree per iteration. The second style was utilizing multi-ratchet sets. One set of runs used 2 simultaneous threads and 10 sequential ratchet runs, performing 200 iterations per run while sampling 35 to 45 characters and holding 1 tree per iteration. Another set of runs used 2 simultaneous threads and 20 sequential ratchet runs, performing 100 iterations per run while sampling 35 characters and holding 1 tree per iteration.

The trees presented are those obtained through analyses in TNT. Runs in TNT consisted of implementing sectorial searches (SS) with tree drifting (TD) and tree fusing (TF) and ratchet runs with TD and TF. The final tree was computed using TNT by implementing 500 sequential ratchet runs of 1,000 iterations, including 100 cycles of both TD and TF per iteration.

**Behavior of male baridines possessing horns**

Of the 47 baridine genera that have been found to possess pro-sternal horns (Table 1), the fighting behavior of one species that possesses horns, *Parisoschoenus expositus* Champion, has been thoroughly documented (Eberhard and Garcia-C.

2000). Aggressive behavior in *P. expositus* assumes usually when a male is courting or mating with a female and another male approaches the pair. The first aggressive behavior displayed by the approaching male is to use its rostrum to move or lift the courting male away from the female. The horns, however, never have been observed to perform this lifting or shoving action. When the courting male is separated from the female, the two males will then face each other and rapidly move the apex of their abdomen in an anterior-posterior fashion. This behavior is believed to produce warning sounds that are generated from the interaction of sound producing structures located at the apex of the body. A file is present on the inner apical margin of each elytron and corresponding rows of plectra are present on the last visible abdominal tergite (the 7<sup>th</sup> tergite). When the plectra move across the surface of the file they produce a sound (which to the present time has not been recorded from weevils). This rapid movement of the abdominal apex only occurs during male-male fighting, and it is hypothesized that these weevils only produce sound during aggressive encounters (as opposed to during courtship). At this time the male pair may resume to strike each other with their rostra or they may then engage in horn-locking. In the latter situation, each male will tilt its body sideways and proceed to push its horns into the opponents horn sheath. If one of the males does not tilt its body, horn-locking will fail, as each male's horn sheath can only receive the opponents horn when their bodies are tilted in an appropriate orientation. Thus, the horn of one male can only enter the sheath of the opponent when the opponent's horn is oriented correctly to enter the other male's sheath. When the horns of each male have

interlocked, the orientation of either male does not greatly change, though one male may partially lift his opponent from the substrate. The purpose of this type of fighting, however, appears not to be to lift the opponent up or to flip him over. Rather, the strength of the male seems to be assessed by his ability to push the opponent. Once it is clear which of the males is greater in strength, the lesser weevil most often disperses from the site.

### **Types and diversity of horns**

Five general types of pro-sternal horns have been included in the phylogeny associated with this study, although more have been observed in Baridinae. These types are: 1) horns long, invagination (horn sheath) reduced/shallow to absent, 2) horns long, horn sheath developed and bifurcate, 3) horns long, horn sheath developed and simple, 4) horns short/reduced, horn sheath reduced/shallow to absent, and 5) horns fused, horn sheath developed and simple. In addition to these types, one other has been observed within the genus *Groatus*, in which there are two horn sheaths, one adjacent to each horn. Within these general types, a wealth of diversity exists between genera as well as among species within genera. For instance, species of *Dactylocrepis* possess spade-like horns that are laterally flattened (Figs. 15-17). The genus *Theantis* (not included in the phylogeny), similar to *Limnobaris* (Figs. 37-39), possesses horns which are elevated on a shelf-like projection of the pro-sternum and are dorso-ventrally flattened. It is without a doubt that many more horn types will be discovered upon further examination of other baridine genera.

### **Evolution of pro-sternal horns in Baridinae**

In contrast to previous studies involving baridines that possess relatively long horns and elongate horn sheaths, a great diversity of horns and horn sheaths have evolved multiple times throughout the subfamily (Fig. 74). As the phylogenetic results hypothesize, the 5 general types of horns have evolved multiple times. Although it is possible that all ancestral baridines possessed horns and were subsequently lost in a large majority of the extant taxa, it is much more parsimonious and likely that most ancestral baridine species did not possess pro-sternal horns, and many taxa have independently evolved them. This latter hypothesis is also supported by the inter-generic morphological differences seen in the horns. These differences also may be a result of behavioral differences. The behavior of only a few species has been studied, and in a large number of taxa it is possible that these horns play an insignificant role in male-male aggression.

Correlation between the presence of the different types of horns and the presence of plectra (sound-producing stridulatory structures) on the 7<sup>th</sup> tergite of the abdomen was also examined, as it is known that the presence of both are strongly associated with the display of aggressive behavior in males. These characters were mapped onto the strict consensus tree and adjacently aligned (Fig. 74). As apparent from the aligned trees, the presence of horns strongly correlates with the presence of plectra. Also, the taxa that possess horns which are reduced in size usually also possess the sparsely-arranged form of plectra, and the taxa that possess long horns

usually also possess the densely-arranged form of plectra. This correlation may indicate that species with small (nearly absent) horns also either do not stridulate as much (due to the reduced form of the plectra and file) or produce much different sounds than do species which possess the densely-arranged form of plectra (and file). Conversely, the species with long, well-developed horns may either stridulate better or produce different sounds than the species that possess the reduced form of plectra.

Since many more baridine genera (and non-baridine) possess horns than were examined in this study, the accuracy of the phylogeny and evolutionary history of the horns presented here is uncertain. Future research that will provide insight into baridine horn evolution should include examination of the development and developmental pathways of the horns in different taxa (Emlen *et al.* 2006, 2007). These types of studies will help elucidate the feasibility of multiple gains and losses of pro-sternal horns in weevils.

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### **Acknowledgements**

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### **Figure captions**

**Figs. 1-8.** Adult photographs. 1-3, *Camelodes leachii*. 1, lateral view; 2, dorsal view; 3, ventral view of pro-sternum. 4-6, *Centrinus curvirostris*. 4, lateral view; 5, dorsal view; 6, ventral view of pro-sternum. 7-8, *Crotanius trivittatus*. 7, lateral view; 8, dorsal view.

**Figs. 9-16.** Adult photographs. 9, *Crotanius trivittatus*, ventral view of pro-sternum. 10-11, *Cylindridia prolixa*. 10, lateral view; 11, dorsal view. 12-14, *Cylindrocercus*

*comma*. 12, lateral view; 13, dorsal view; 14, ventral view of pro-sternum. 15-16, *Dactylocrepis flabellitarsis*. 15, lateral view; 16, dorsal view.

**Figs. 17-24.** Adult photographs. 17, *Dactylocrepis flabellitarsis*, ventral view of pro-sternum. 18-19, *Demoda vittata*. 18, lateral view; 19, dorsal view. 20-21, *Dialomia gradata*. 20, lateral view; 21, dorsal view. 22-24, *Dimesus rubricatus*. 22, lateral view; 23, dorsal view. 24, *Diorymerus lancifer*.

**Figs. 25-32.** Adult photographs. 25, *Diorymerus lancifer*, dorsal view. 26-28, *Eugeraeus* sp. 26, lateral view; 27, dorsal view; 28, ventral view of pro-sternum. 29-31, *Eutoxus* sp. 29, lateral view; 30, dorsal view; 31, ventral view of pro-sternum. 32, *Geraeus lineellus*, lateral view.

**Figs. 33-40.** Adult photographs. 33-34, *Geraeus lineellus*. 33, dorsal view; 34, ventral view of pro-sternum. 35-36, *Lampobaris cicullata*. 35, lateral view; 36, dorsal view. 37-39, *Limnobaris calandriiformis*. 37, lateral view; 38, dorsal view; 39, ventral view of pro-sternum. 40, *Linogeraeus viduatus*, lateral view.

**Figs. 41-48.** Adult photographs. 41, *Linogeraeus viduatus*, dorsal view. 42-43, *Nestrada compacta*. 42, lateral view; 43, dorsal view. 44-46, *Orissus christophori*. 44, lateral view; 45, dorsal view; 46, ventral view of pro-sternum. 47-48, *Orissus meigenii*. 47, lateral view; 48, dorsal view.

**Figs. 49-56.** Adult photographs. 49, *Orissus meigenii*, ventral view of pro-sternum. 50-51, *Pachygeraeus laevirostris*. 50, lateral view; 51, ventral view of pro-sternum. 52-54, *Pachygeraeus tumidirostris*. 52, lateral view; 53, dorsal view; 54, ventral view of pro-sternum. 55-56, *Parasaldius* sp. 55, lateral view; 56, dorsal view.

**Figs. 57-66.** Adult photographs. 57-58, *Torcus variabilis*. 57, lateral view; 58, dorsal view. 59-61, *Xystus ater*. 59, lateral view; 60, dorsal view; 61, ventral view of pro-sternum. 62-66, pro-notum, posterior view, showing horn sheaths. 62-63, *Orissus meigenii*. 62, posterior view; 63, lateral view. 64, *Orissus christophori*; 65, *Demoda vittata*; 66, *Pseudotorcus rufipes*.

**Figs. 67-73.** SEM's. 67-68, *Centrinopus alternatus*. 67, adult, lateral view; 68, enlargement of horns. 69-70, *Cylindridia prolixa*. 69, adult, lateral view; 70, enlargement of horns. 71-72, *Geraeus lineellus*. 71, lateral view; 72, enlargement of horn base. 73, *Demoda vittata*.

**Fig. 74.** Strict consensus tree of Baridinae (see Chapter II for details), with horn evolution mapped onto the left phylogeny and plectra evolution mapped onto the right phylogeny.

**Table 1.** List of genera known to possess pro-sternal horns. Species listed include those examined (but this is not an exhaustive list of examined taxa).

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Mecopus trilineatus  
Crotanius trivittatus  
Cylindrocerus comma  
Dimesus rubricatus  
Linogeraeus viduatus  
Geraeus lineellus  
Parageraeus tumidirostris  
Pseudorancea spissirostris  
Melampius basalis  
Eugeraeus spp.  
Pachygeraeus laevirostris  
Centrinus curvirostris  
Anavallius ruficornis  
Lampobaris cicullata  
Pseudosaldius conjunctus  
Leptoladustes densus  
Xystus ater  
Nedestes sarpedon  
Orissus christophori  
Camelodes leachii  
Diorymerus lancifer  
Dactylocrepis flabellitarsis  
Pseudotorcus rufipes  
Demoda vittata  
Somenes regestus  
Torcus variabilis  
Cylindridia prolixa  
Centrinopus alternatus  
Nestrada compacta  
Lorena simulans  
Parasaldius longipes  
Dialomia gradata  
Limnobaris calandriiformis  
Eutoxus spp.  
Palmocentrinus butia  
Palmelampius heinrichi  
Parisoschoenus spp.  
Linonotus regalis  
Nedestes sarpedon

Dimesus thoracicus  
Centrinaspis spp.  
Pycnotheantis spp.  
Palistes spp.  
Groatus spp.  
Theantis spp.  
Stegotes spp.  
Stegotidius spp.

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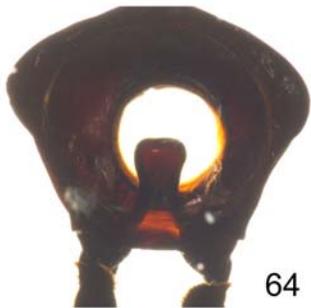
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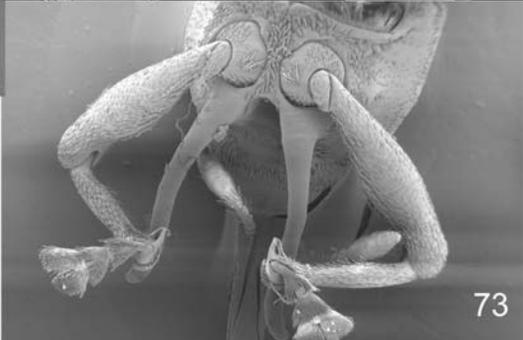
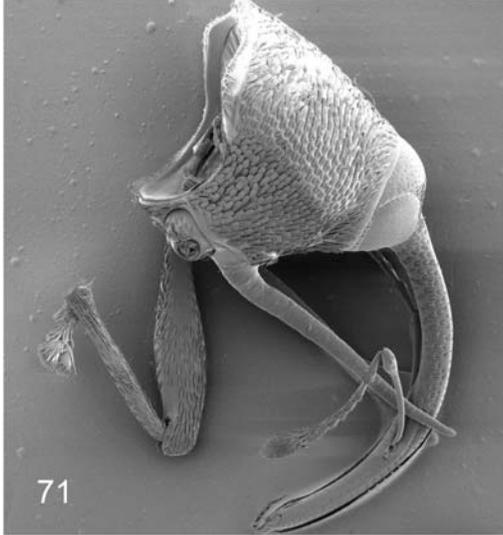
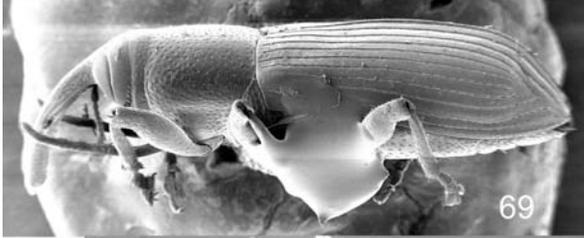
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## **Chapter IV: Sclerolepidia in baridine weevils (Coleoptera: Curculionidae)**

### **Abstract**

In a few families of Curculionoidea and within several subfamilies of Curculionidae, peculiarly modified scales are present along the suture between the metasternum and metepisternum. These scales are specifically known as sclerolepidia and their exact function remains unknown. Previous studies have broadly surveyed the presence of sclerolepidia in Curculionoidea (Lyal *et al.* 2006). The types of sclerolepidia present within Baridinae are described and illustrated in detail here, and the evolution of these types are traced on a phylogeny of Baridinae.

**Keywords:** modified scales, sensory receptors in insects, insect sutures.

### **Introduction**

While conducting a phylogenetic analysis based on morphology and searching through the relatively small amount of literature on baridine weevils, it appears that there are many features of this group that yet await elucidation. Of these features are specialized scales, arranged linearly, along the suture between the metasternum and metepisternum. Through extensive examination of 231 of the 550 total genera presently included in Baridinae (Table 2), it was hypothesized that the presence of these scales, known as sclerolepidia, are a synapomorphy defining the subfamily.

However, upon examination of taxa outside of Baridinae, scales of similar structure were found in Cryptorhynchinae, Cossoninae, and Scolytidae. Sclerolepidia are also found in other subfamilies as well (Lyal *et al.* 2006). Although appearing similar to those found in Baridinae, the homology of sclerolepidia is uncertain due to their apparent sparse presence within Curculionoidea. Few weevil phylogenetic studies have utilized sclerolepidia as characters, and those that have (Kuschel 1995; Marvaldi *et al.* 2002) did so by only noting their absence or presence. The purpose of this study was to describe and characterize the presence and absence of sclerolepidia in weevils, particularly within the curculionid subfamily Baridinae. Their function and significance remain unknown.

### **Materials and methods**

Of the 21 families included in Curculionoidea (Alonso-Zarazaga and Lyal 1999), 11 were examined for this study, and all of the 16 subfamilies included in Curculionidae were examined (Table 1). 231 of the 550 genera in Baridinae were examined. In total, 283 baridine species were examined. Digital photographs were taken using a Microptix photo system, and SEM images were captured using a LEO 1550 FESEM.

### **Description of sclerolepidia in Baridinae**

All of the baridine genera studied possess sclerolepidia, thus it is hypothesized that probably all baridines have them. Two types of sclerolepidia are found in

Baridinae. Using the terminology of Lyal *et al.* (2006) they are the digitate (flat and small) and peg-like (projecting and large) types. From this study, the most common type in Baridinae is the digitate type, with the peg-like type present in fewer taxa. Although the digitate type is relatively uniform throughout all taxa that possess it, a few possess a form which is furcated more or has more digits, appearing feather-like (*Scirpicola chilensis*). Although the number and size of sclerolepidia present may be loosely associated with the density of scales present, nearly glabrous species may also possess many, large sclerolepidia, though the opposite usually is less common (densely covered with scales and possessing few, small sclerolepidia). As noted by Lyal *et al.*, there often are holes or notches in the cuticle along the margin of the metepisternal suture below each sclerolepidion. This structural feature indicates that they may have a secretory function.

### **Evolution of sclerolepidia in Baridinae**

As hypothesized by Lyal *et al.*, it appears that the digitate type preceded the peg-like type in baridine evolution (Fig. 65). The peg-like type also seems not to be homologous among all of the taxa that possess it, indicating convergent evolution, in which several similar forms have arisen multiple times. This result also corroborates the hypothesis of Lyal *et al.* that sclerolepidia probably are not homologous among the Curculionidae due to their patchy distribution. It should also be noted, though, that there have been no phylogenetic hypotheses examining the distribution of the different types of sclerolepidia. Lyal *et al.* based their hypothesis of sclerolepidion

homology on the classification of Alonso-Zarazaga and Lyal (1999). According to the baridine phylogeny, it is unclear what sclerolepidion type is ancestral to Baridinae. Although the conoderine type precedes Baridinae in the tree, it is a clade forming an independent evolutionary trajectory. However, due to lack of phylogenetic hypotheses for Conoderinae (and the majority of curculionid subfamilies), and its current polyphyletic structure, the sister-group of Baridinae remains uncertain, and thus the ancestral baridine sclerolepidion type also remains as such.

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## **Figure captions**

**Figs. 1-8.** 1-2, *Megavallius auritarsis*. 1, adult, lateral view; 2, enlargement of metepisternum. 3-4, *Amercedes subulirostris*. 3, adult, lateral view (SEM); 4, enlargement of metepisternum (SEM). 5-6, *Zygobarella zanthoxyli*. 5, thorax, lateral view; 6, enlargement of sclerolepidia. 7-8, *Stethobaroides nudiventris*. 7, metepisternum and sclerolepidia, dorsal view; 8, enlargement of sclerolepidia.

**Figs. 9-16.** SEM's. 9-15, *Pseudocentrinus ochraceus*. 9, adult, lateral view; 10, enlargement of metepisternum; 11-15, enlargements of sclerolepidia, dorsal view. 16, *Odontocorynus creperus*, metepisternum, lateral view.

**Figs. 17-24.** SEM's. 17, *Coleomerus boliviensis*, metepisternum, lateral view; 18, *Lipancylus brevirostris*, metepisternum, lateral view. 19-22, *Lydamis cinnamomeus*. 19, metepisternum, lateral view; 20, enlargement of sclerolepidia, lateral view; 21-22, enlargements of sclerolepidia, dorsal view. 23, *Baris torquata*, metepisternum, lateral view; 24, *Sibariops concurrens*, metepisternum, lateral view.

**Figs. 25-32.** SEM's. 25-26, *Geraeus lineellus*. 25, metepisternum, lateral view; 26, enlargement of sclerolepidia. 27, *Madarus bistrigellus*, metepisternum, lateral view; 28, *Cylindrocerus comma*, metepisternum, lateral view. 29-30, *Demoda vittata*. 29, metepisternum, lateral view; 30, enlargement of sclerolepidia. 31, *Amercedes subulirostris*, enlargement of sclerolepidia; 32, *Lixus concavus*, thorax, lateral view.

**Figs. 33-40.** 33, *Lixus concavus*, enlargement of metepisternum. 34-35, *Cholus rana*. 34, thorax, lateral view; 35, enlargement of metepisternum. 36-37, *Homoeolabus analis* (Attelabidae). 36, thorax, lateral view; 37, enlargement of suture between metasternum and metepisternum. 38-39, *Platypus parallelus* (Platypodinae). 38, thorax, lateral view; 39, enlargement of suture between metasternum and metepisternum. 40, *Apion longirostre* (Apionidae).

**Figs. 41-48.** SEM's, thorax, lateral view. 41, *Hypera punctata* (Hyperinae); 42-43, *Cossonus impressifrons* (Cossoninae). 42, thorax, lateral view; 43, enlargement of suture between metasternum and metepisternum. 44-45, *Hylurgops planirostris*

(Scolytinae). 44, thorax, lateral view; 45, enlargement of suture between metasternum and metepisternum. 46-49, *Cryptorhynchus lapathi* (Cryptorhynchinae). 46, thorax, lateral view; 47-48, enlargements of suture between metasternum and metepisternum.

**Figs. 49-56.** SEM's, thorax, lateral view. 49, *Cryptorhynchus lapathi* (Cryptorhynchinae), enlargements of suture between metasternum and metepisternum; 50, *Ceutorhynchus obstrictus* (Ceutorhynchinae); 51, *Curculio pardalis* (Curculioninae); 52, *Magdalis armicollis* (Mesoptilinae); 53, *Cyrtepidomus castaneus* (Entiminae); 54, *Derelomus basalis* (Derelominae); 55-56, *Dryophthorus americanus* (Dryophthorinae). 55, thorax, lateral view; 56, enlargement of suture between metasternum and metepisternum.

**Figs. 57-64.** SEM's, thorax, lateral view. 57, *Bagous transversus* (Bagoinae); 58, *Cylindrocopturus operculatus* (Conoderinae); 59, *Rhodobaenus tredecimpunctatus* (Dryophthorinae); 60, *Eudiagogus pulcher* (Entiminae); 61, *Rhigopsis effracta* (Entiminae); 62, *Trigonorhinus* sp. (Anthribidae); 63, brentid sp. (Brentidae); 64, *Conotrachelus fissunguis* (Molytinae).

**Fig. 65.** Strict consensus tree with sclerolepidia character mapped onto it.

**Fig. 65 (continued).** Strict consensus tree with sclerolepidia character mapped onto it.

**Table 1.** List of taxa examined within Curculionoidea (not including those examined in Baridinae). \* = list of taxa found in Table 2.

Family	Subfamily	Taxon	Metepisternal scales present?
Curculionidae	Conoderinae	<i>Cylindrocopturus operculatus</i>	-
		<i>Pseudopiazurus centraliamericanus</i>	-
		Heller	
	Orthognathinae	<i>Rhodoaenus tredecimpunctatus</i>	-
	Entiminae	<i>Eudiagogus pulcher</i>	-
		<i>Eupagoderes argentatus</i>	-
		<i>Rhigopsis effracta</i> Lec.	-
		<i>Cydianerus</i> sp.	-
		<i>Holonychus aeruginus</i>	-
		Fahr.	
		<i>Exophthalmus verecundus</i> Chev.	-
		<i>Otiorrhynchus morio</i>	-
		Fabricius	
		<i>Compsus argyreus</i> L.	-
		<i>Cyrtepistomus castanaeus</i>	-

Lixinae	<i>Lixus concavus</i> Say	-
	<i>Cyphocleonus</i> sp.	-
Cyclominae	<i>Listronotus scapularis</i>	-
	Casey	
	<i>Chrysolophus</i>	-
	<i>spectabilis</i>	
Cryptorhynchinae	<i>Cophes texanus</i> Sleeper	-
	<i>Macromerus bicinctus</i>	-
	Champion	
	<i>Coelosternus leporinus</i>	-
	Champion	
	<i>Cryptorhynchus</i>	X
	<i>melastomae</i> Champion	
	<i>Cryptorhynchus lapathi</i>	X
Ceutorhynchinae	<i>Ceutorhynchus</i>	-
	<i>obstrictus</i> Marsh	
Molytinae	<i>Conotrachelus</i> sp.	X
	<i>Conotrachelus</i>	X
	<i>fissunguis</i> LeConte	
	<i>Cholus rana</i>	-
	<i>Homalinotus coriaceus</i>	-
	Gyll.	
	<i>Hylobius abietis</i>	-
Cossoninae	<i>Cossonus impressifrons</i>	X
	Boh.	
Curculioninae	<i>Curculio pardalis</i>	-

	Mesoptilinae	<i>Magdalis armicollis</i> Say	-
	Hyperinae	<i>Hypera punctata</i> Fab.	-
	Rhyncophorinae	<i>Dynamis borassi</i> Fab.	-
	Derelominae	<i>Derelomus basalis</i>	-
	Bagoinae	<i>Bagous transversus</i>	-
	Baridinae*		X
Dryophthoridae	Dryophthorinae	<i>Dryophthorus</i> <i>americanus</i>	-
Eurhynchidae		<i>Aporhina bispinosus</i> Boisd.	-
Ithyceridae		<i>Ithycerus</i> <i>noveboracensis</i> Forster	-
Attelabidae	Attelabinae	<i>Homoelabus analis</i> Illiger	-
Platypodidae	Platypodinae	<i>Platypus parallelus</i> Fab.	-
Apionidae	Apioninae	<i>Apion longirostre</i> Oliver	-
Anthribidae	Anthribinae	<i>Trigonorhinus</i> sp.	-
Scolytidae	Scolytinae	<i>Hylurgops planirostris</i> Chapius	X
Brentidae		Brentid sp.	-
Brachyceridae	Brachycerinae	<i>Brachyceris granosus</i> Gyll.	-



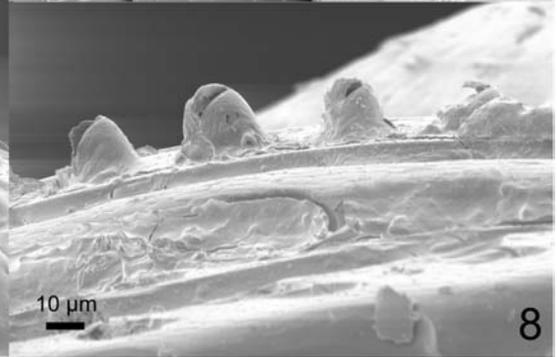
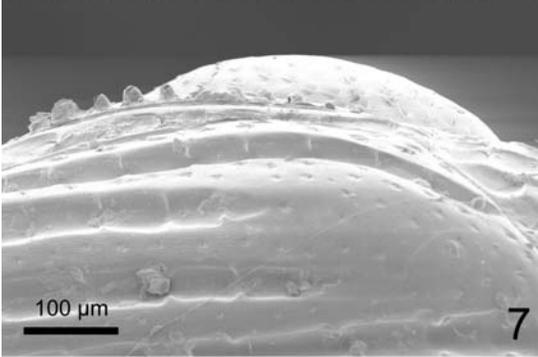
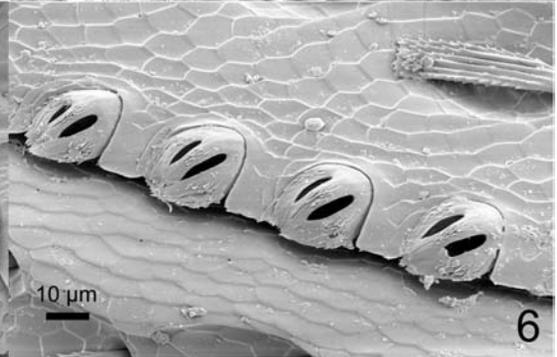
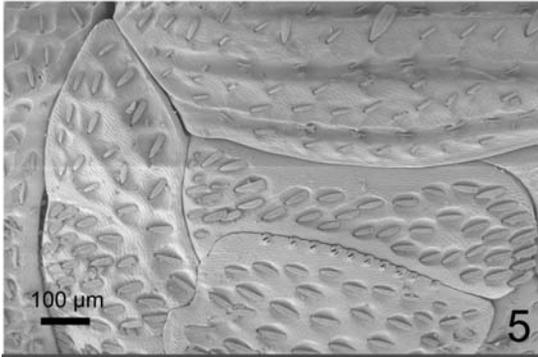
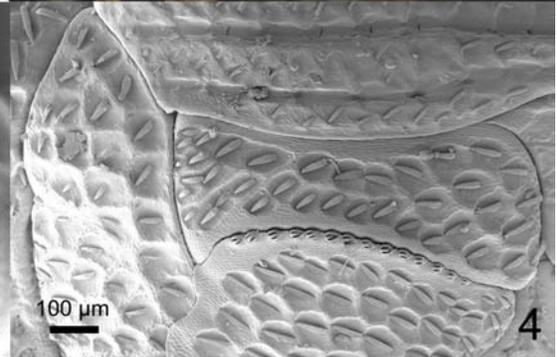
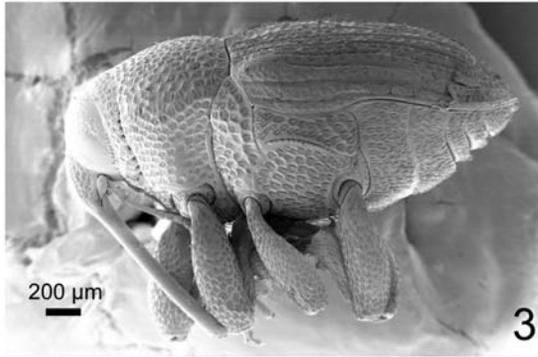
		<i>Pycnotheantis</i> sp. <i>Parisoschoenus</i> sp.
Nertinini		<i>Nertinus suturalis</i> <i>Strongylotes squamans</i> <i>Lichnus longulus</i>
Optatini		<i>Lydamis cinnamomeus</i> <i>Optatus palmaris</i> <i>Telemus</i> sp. <i>Pardisomus biplagiatus</i> <i>Pistus galeatus</i>
Pantotelini	Pantotelina Cyrionychina	<i>Pantoteles tenuirostris</i> <i>Cyrionyx camelus</i>
Peridinetini		<i>Peridinetus cretaceous</i> <i>Peridinetus irroratus</i>
Madopterini	Madopterina  Apostasimerina Thaliabaridina Torcina  Zygobaridina	<i>Azygides</i> sp. <i>Centrinopsis</i> sp. <i>Iasides</i> sp. <i>Lipancylus brevirostris</i> <i>Madopterus talpa</i> <i>Opseobaris alba</i> <i>Pacomes subglaber</i> <i>Parallelosomus amplitarsis</i> <i>Trachymeropsis palmipes</i> <i>Apostasimerus</i> sp. <i>Thaliabaris inermis</i> <i>Anatorcus densus</i> <i>Microtorcus tubulatus</i> <i>Paratorcus</i> sp. <i>Pseudotorcus rufipes</i> <i>Sibariops concinna</i> <i>Sibariops concurrens</i> <i>Sibariopsida docilis</i> <i>Torcobius</i> sp. <i>Torcus nigrinus</i> <i>Torcus variabilis</i> <i>Acanthobaris</i> sp. <i>Acentrinops brevicollis</i> <i>Amercedes subulirostris</i> <i>Anavallius ruficornis</i> <i>Andiblis seriata</i> <i>Aniops sculpturata</i> <i>Anotesiops obidosensis</i> <i>Apinocis deplanatus</i> <i>Barilepis griseus</i> <i>Barilepton filiforme</i> <i>Barinus bivittatus</i> <i>Buchananius striatus</i> <i>Calandrinus grandicollis</i> <i>Calorida binocularis</i> <i>Camelodes leachii</i> <i>Camerones semiopacus</i> <i>Catapastinus caseyi</i> <i>Catapastus conspersus</i>

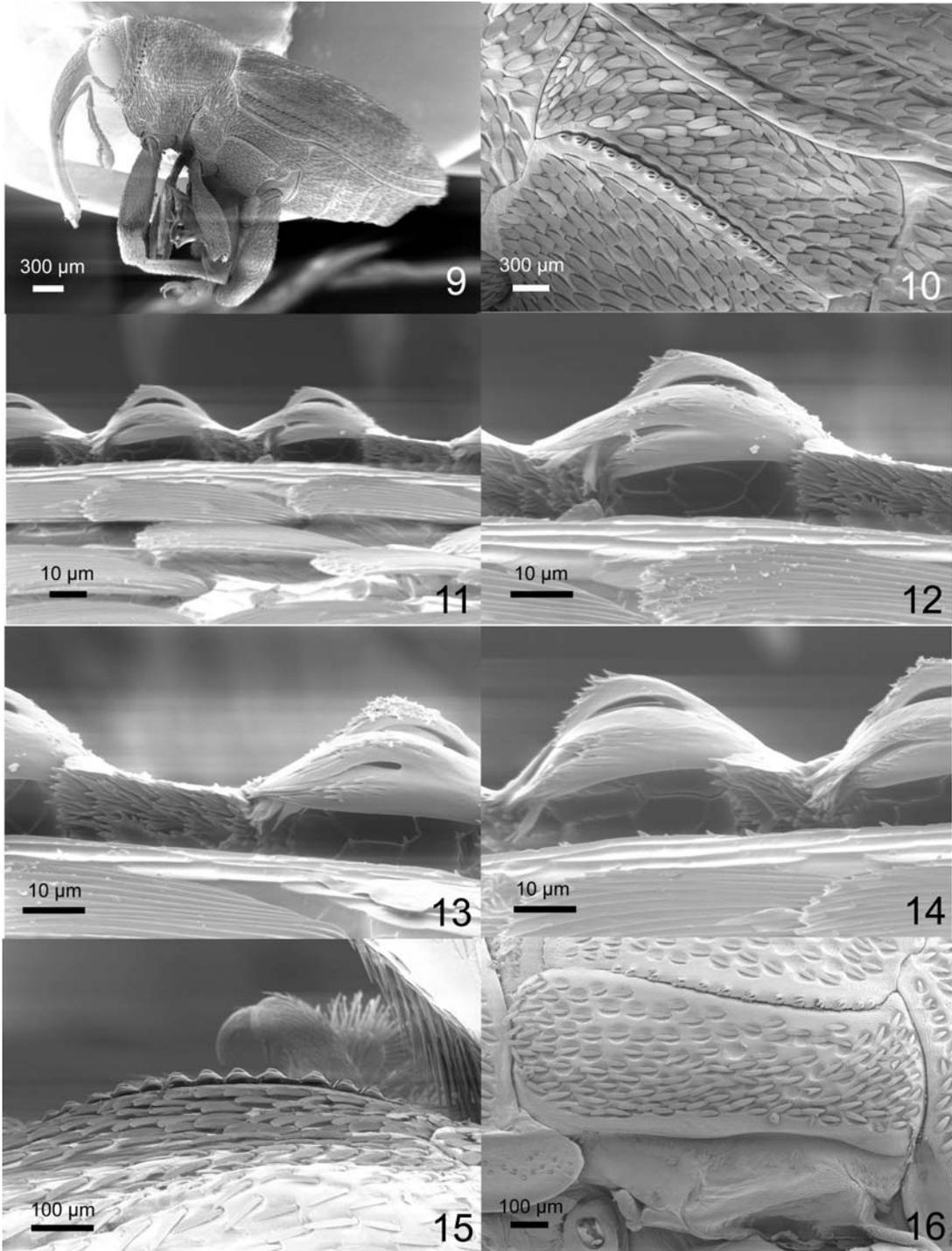
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*Centrinoides* sp.  
*Centrinopus alternatus*  
*Centrinus curvirostris*  
*Chepagra rotundicollis*  
*Clandius cephalotes*  
*Crostidia tenuipes*  
*Crostis subexplanata*  
*Crotanium trivittatus*  
*Cylindridia prolixa*  
*Cylindrocercus comma*  
*Dactylocrepis flabellitarsis*  
*Dealina carbonarius*  
*Deipyrus hirsutulus*  
*Demoda vittata*  
*Dericinus habilis*  
*Dialomia gradata*  
*Diastethus eurthinoides*  
*Dimesus rubricatus*  
*Diorymeropsis disjuncta*  
*Diorymeropsis xanthoxyli*  
*Dirabius calvus*  
*Dirabius rectirostris*  
*Eisonyx crassipes*  
*Eisonyx opaca*  
*Elliptobaris* sp.  
*Ethelda squamosa*  
*Eudialomia longula*  
*Eugeraeus unifasciatus*  
*Eusomenes curtirostris*  
*Fishonia brevinasus*  
*Forandia duplex*  
*Forandiopsis carinulata*  
*Fryella mutilatus*  
*Garnia* sp.  
*Geraeopsis duplocincta*  
*Geraeus lineellus*  
*Haplostethops ellipsoidea*  
*Idiostethus subcalvus*  
*Iops bicolor*  
*Iopsidaspis truncatula*  
*Ladustaspis crocopelmus*  
*Ladustes* sp.  
*Lamprobaris cicullata*  
*Lasiobaris geminata*  
*Laurentius bruchi*  
*Leptogarnia polita*  
*Leptoladustes densus*  
*Limnobaris bicincta*  
*Limnobaris calandriiformis*  
*Linogarnia suturalis*  
*Linogeraeus urbanus*

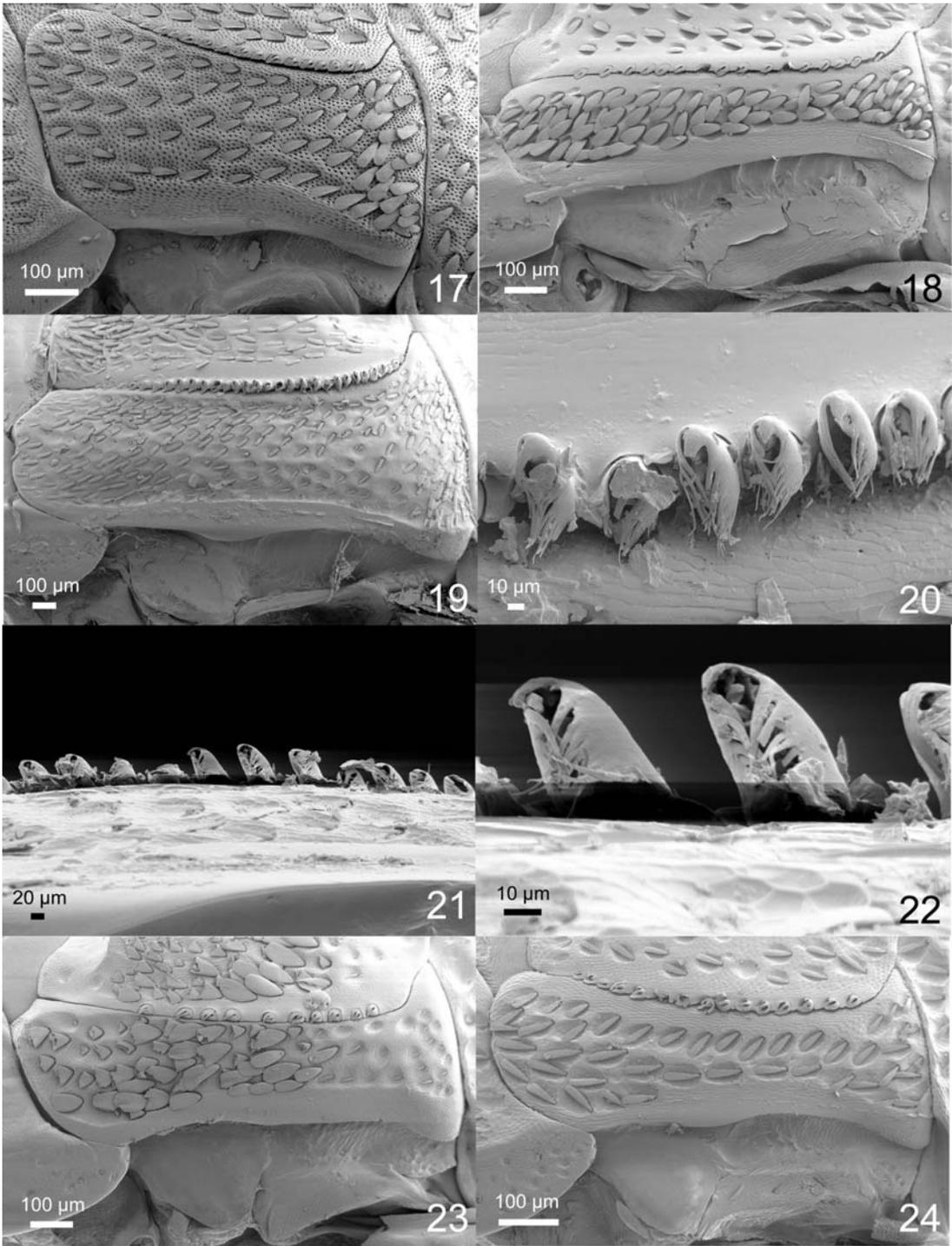
*Linogeraeus viduatus*  
*Liocentrinus* sp.  
*Lissobaris nigropicea*  
*Lissomenes* sp.  
*Lorena simulans*  
*Macrorevena atromicans*  
*Megavallius auritarsis*  
*Melampius basalis*  
*Microbaridia delicatula*  
*Microcholus puncticollis*  
*Microcholus striatus*  
*Microforandia uniformis*  
*Microrevena* sp.  
*Microstegotes* sp.  
*Microzalestes basalis*  
*Nedestes sarpedon*  
*Neocratus* sp.  
*Neplaxa illustris*  
*Nestrada compacta*  
*Nicentridia angusticollis*  
*Nicentrus decipiens*  
*Nicentrus grossulus*  
*Odontocorynus scutellumalbum*  
*Odontocorynus creperus*  
*Oligolochus braccatus*  
*Oligolochus ornatus*  
*Oomorphidius leavicollis*  
*Orissus meigenii*  
*Ortycus cristosus*  
*Ovanus picipennis*  
*Ovanus minutus*  
*Pachybaris porosa*  
*Pachygeraeus laevirostris*  
*Palocopsis tecta*  
*Parafishonia setulosa*  
*Parageraeus tumidirostris*  
*Parasaldius* sp.  
*Parasomenes curvirostris*  
*Peclavia hispidicollis*  
*Peclaviopsis planipectus*  
*Phacelobarus signubaris*  
*Plocamus echidna*  
*Plocamus clavisetes*  
*Pseudocentrinus ochraceus*  
*Pseudogeraeus macropterus*  
*Pseudorancea spissirostris*  
*Pseudorthoris devexus*  
*Pseudosaldius conjunctus*  
*Psiona densa*  
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*Pycnogeraeus striatirostris*  
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*Rancea parviclava*

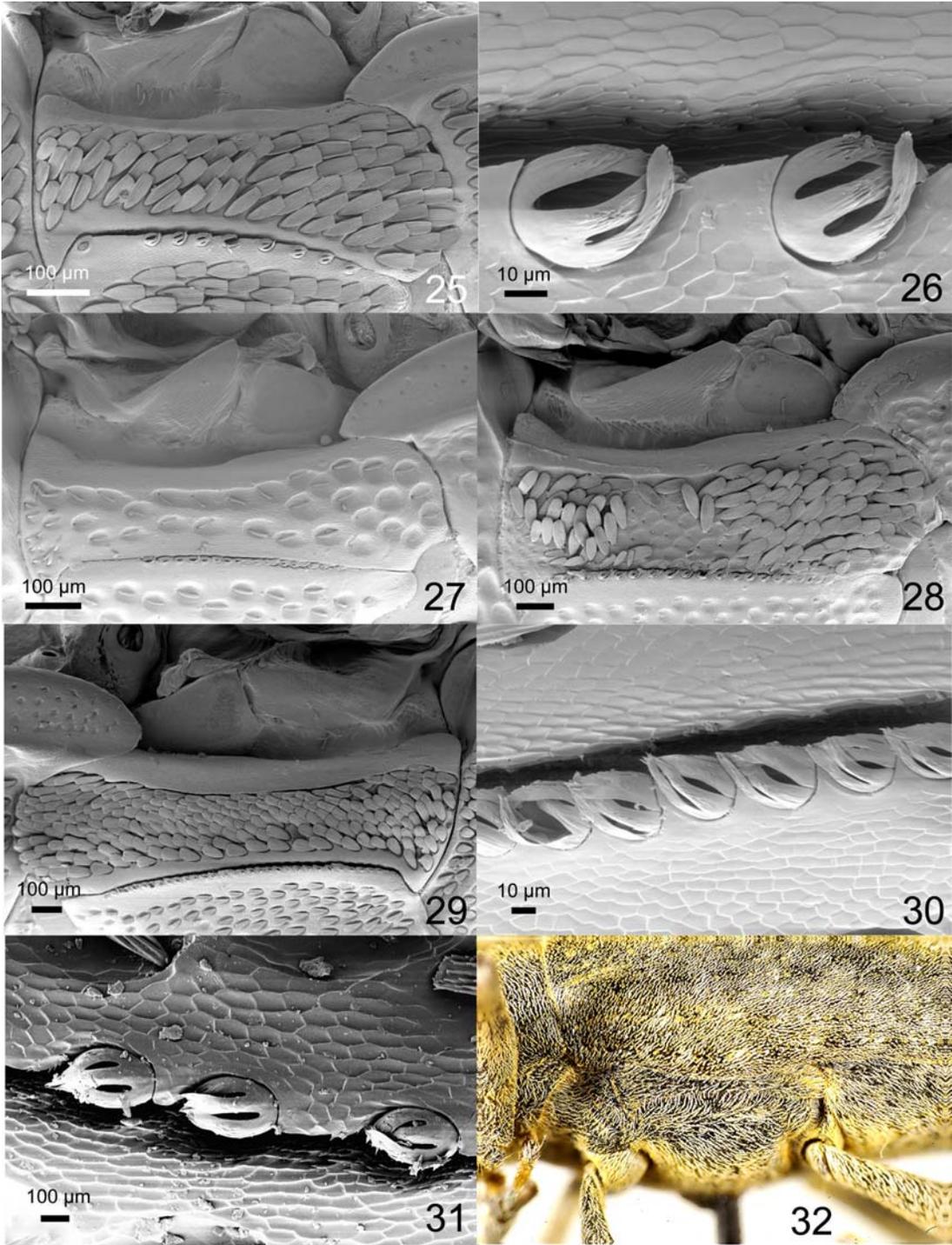
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*Saldiopsis armata*  
*Saldius inaequalis*  
*Selasella cuneipennis*  
*Sodesia sparsa*  
*Somenes regestus*  
*Spolatia gradata*  
*Starcus rugulosus*  
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*Tenemotes abdominalis*  
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*Ternova biartita*  
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*Trichodirabius longulus*  
*Valdenus laevis*  
*Valiopsis squamipes*  
*Vallius sulcatus*  
*Xystus ater*  
*Xystus ruficollis*  
*Zaglyptoides* sp.  
*Zalestes perpolitus*  
*Zygobarella xanthoxyli*  
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*Zygozalestes oblongus*

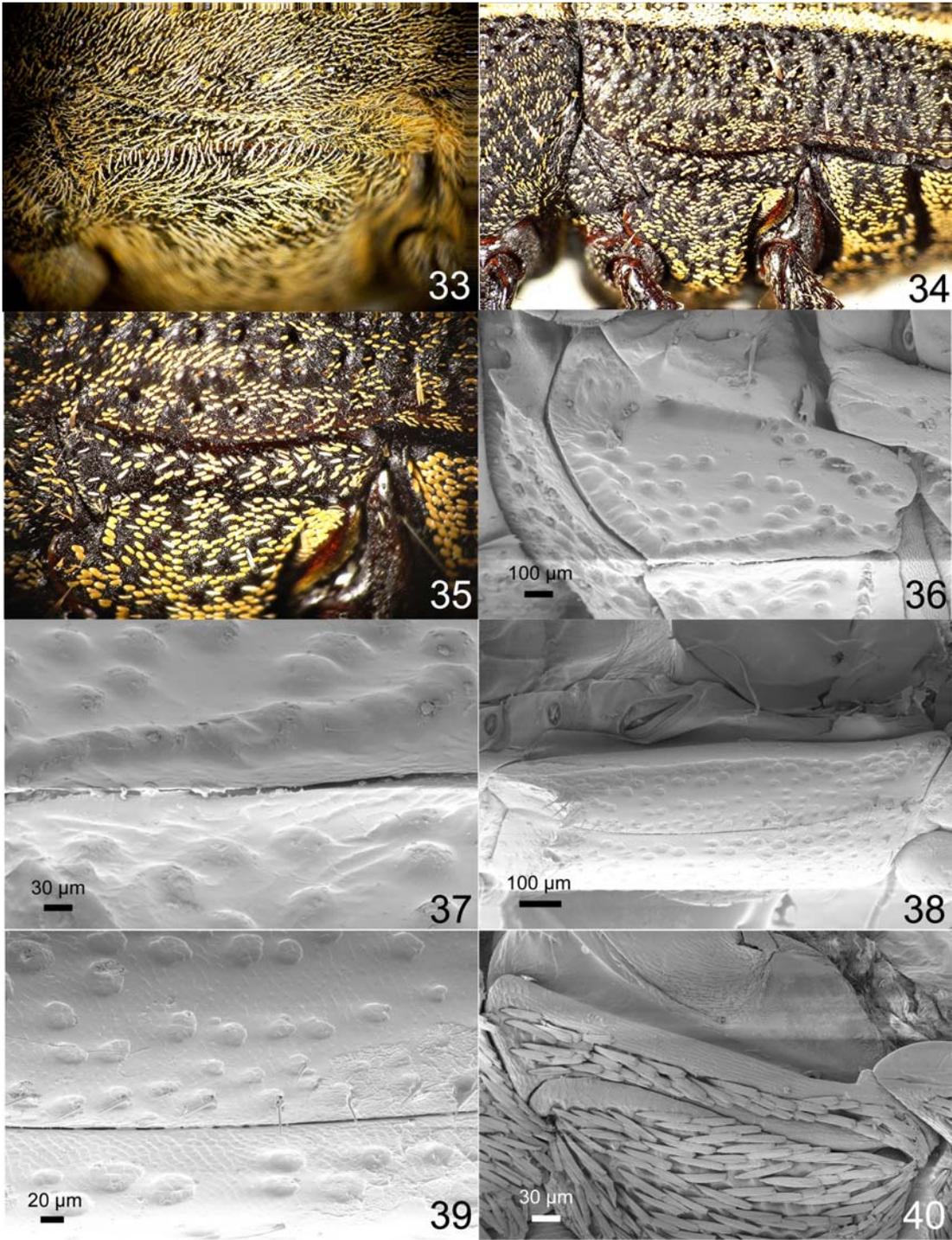
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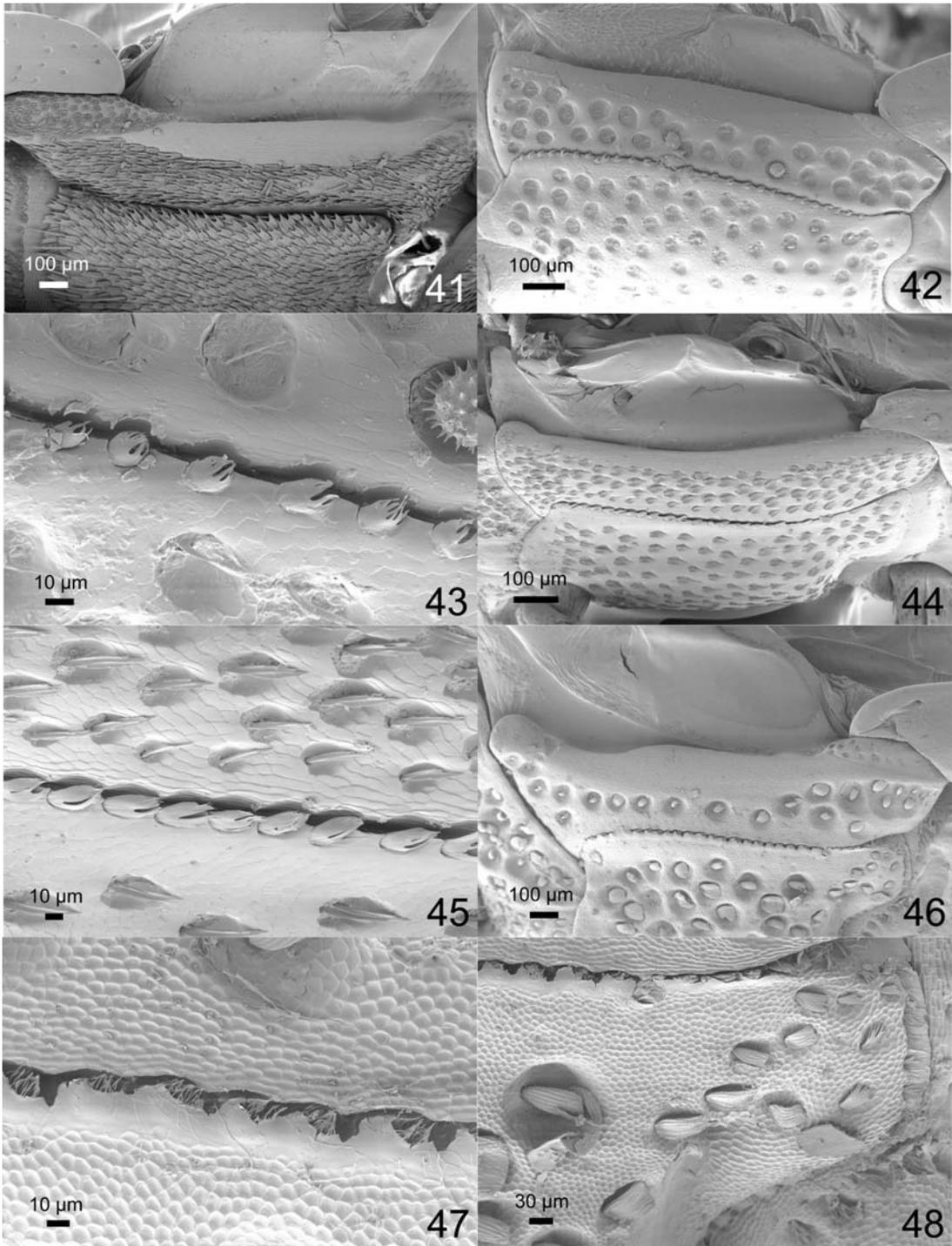


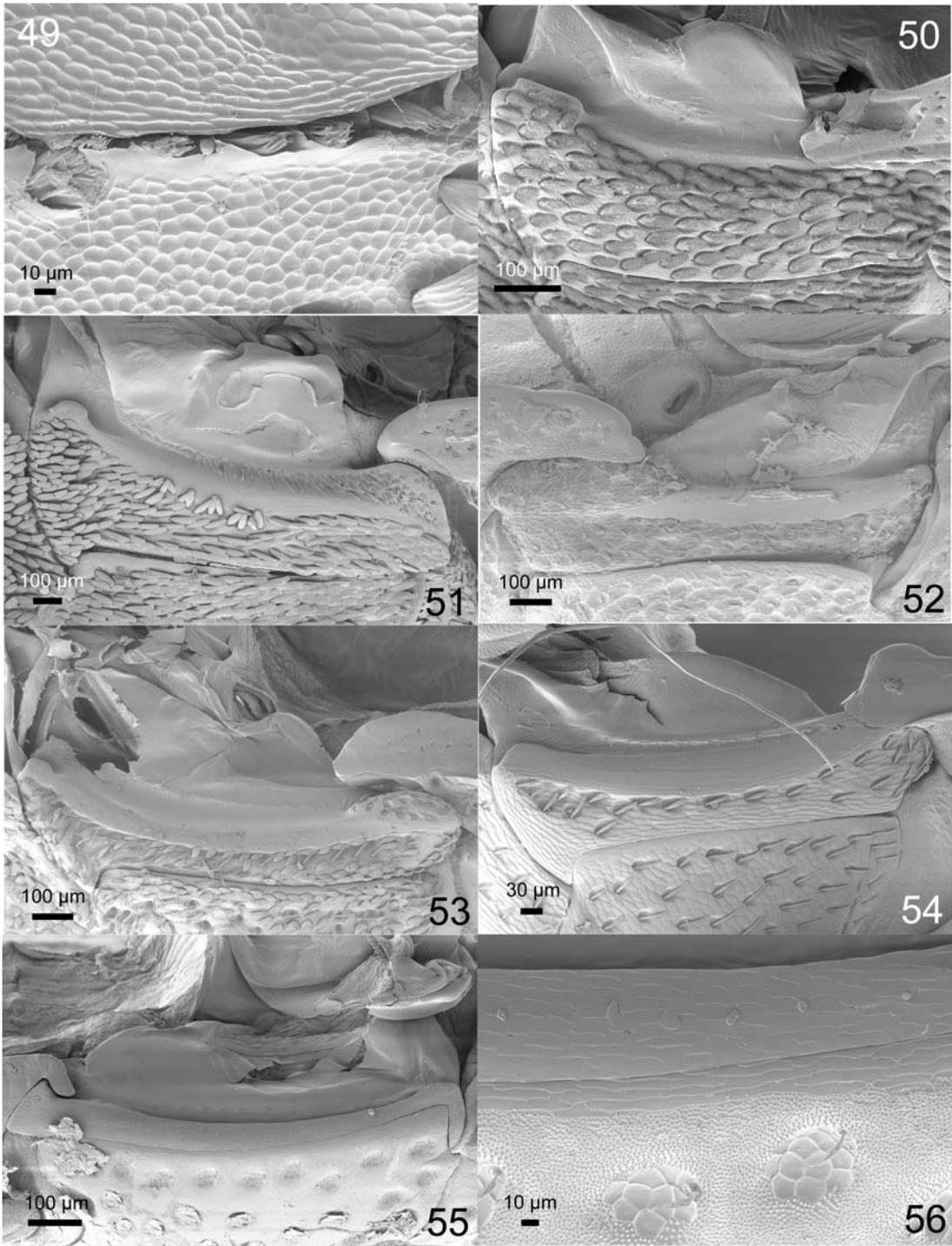


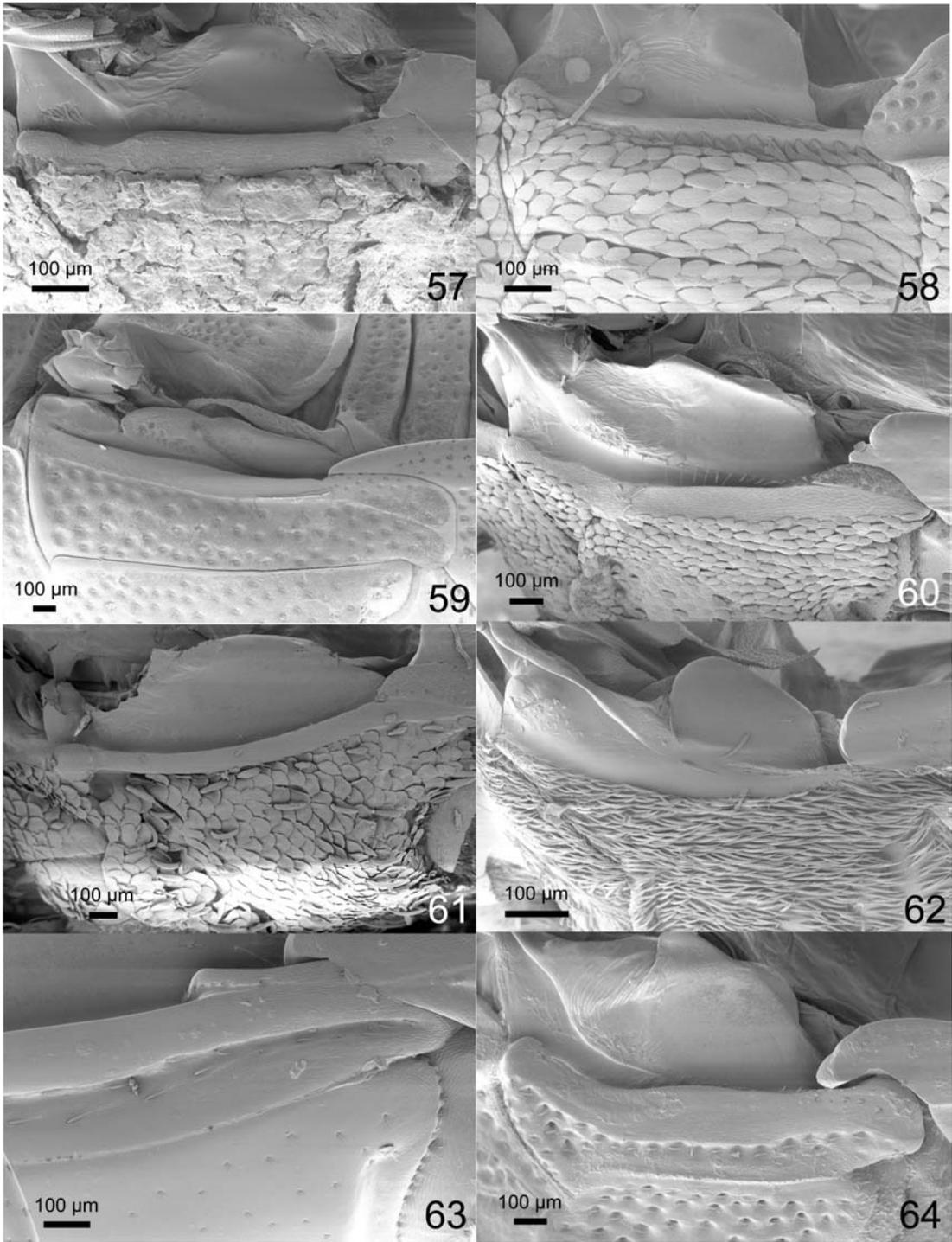


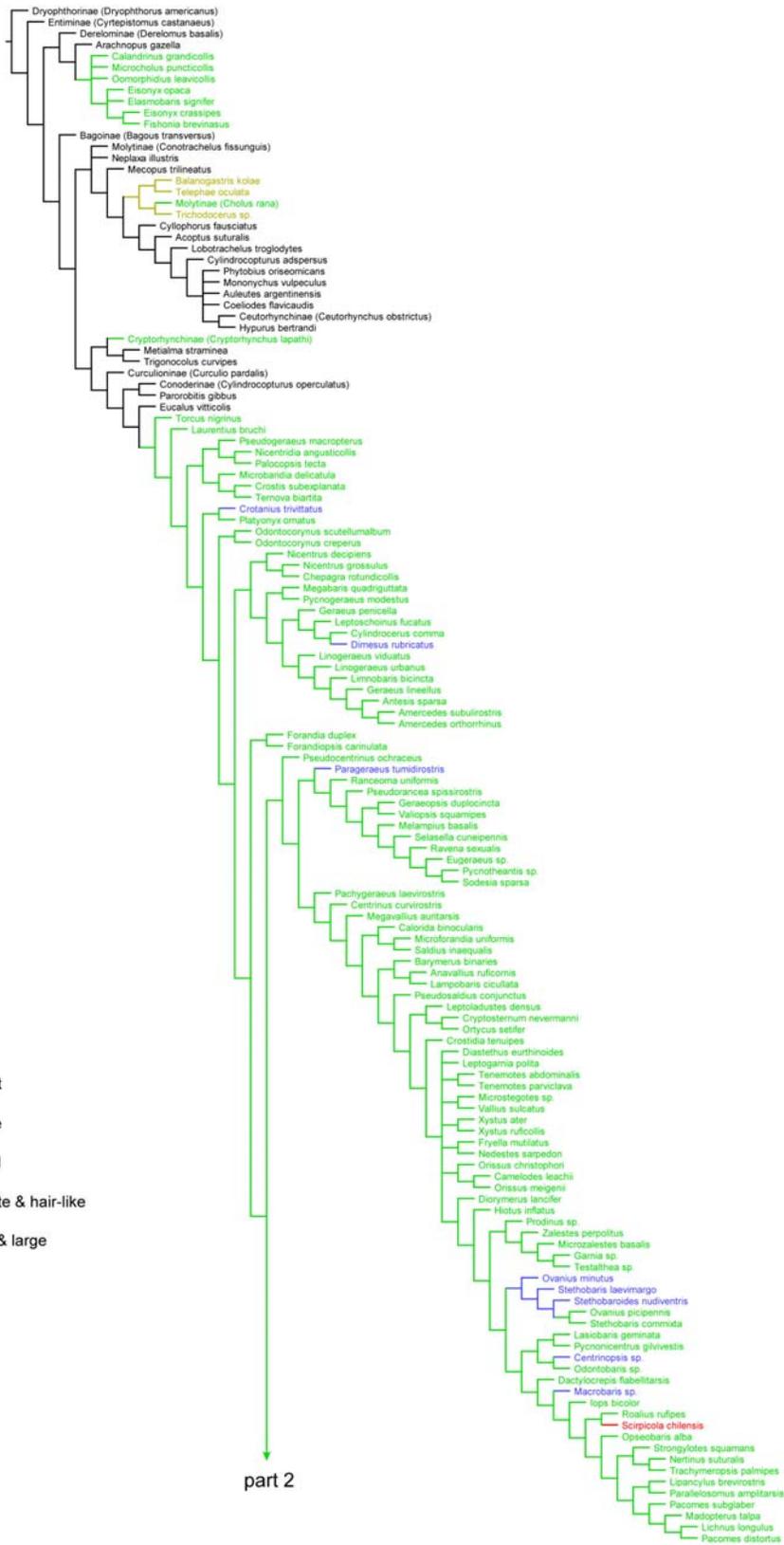




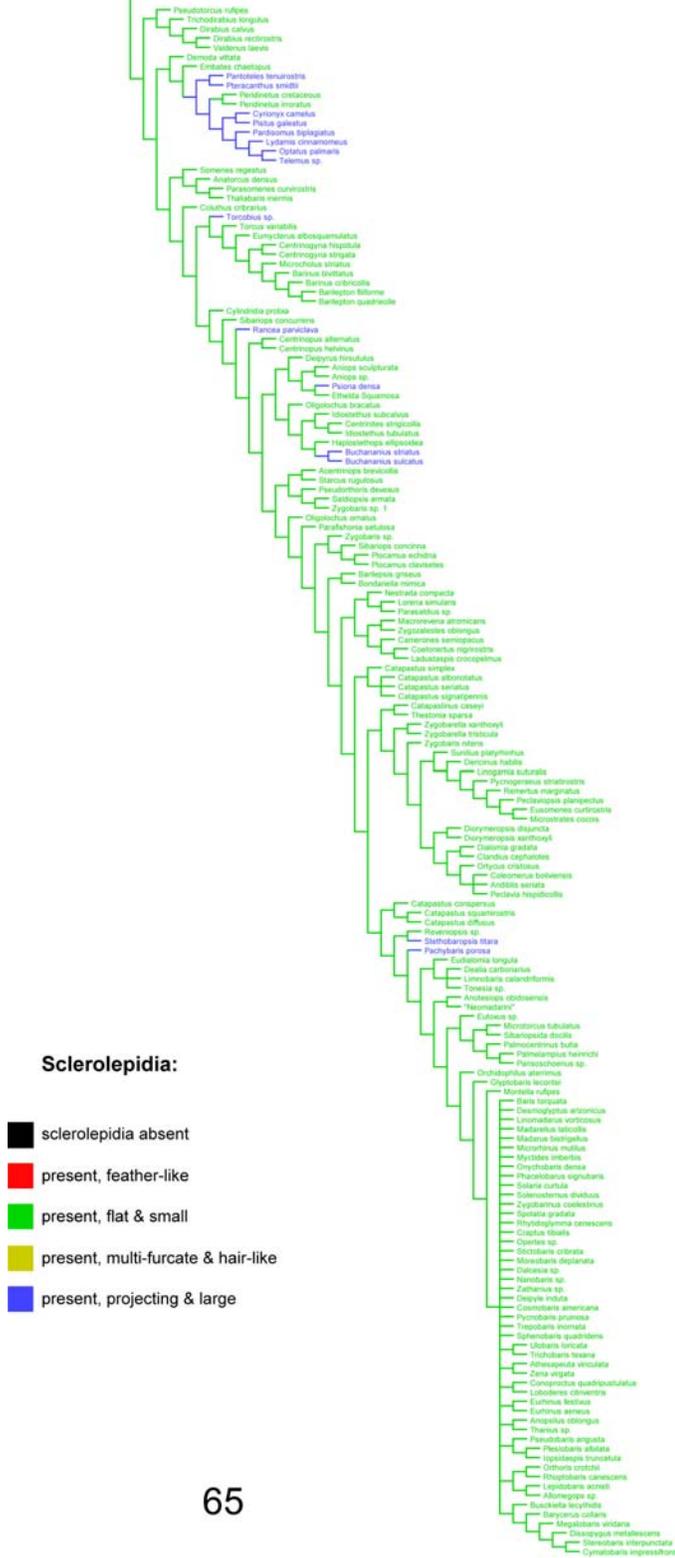








part 1



## **Chapter V: Probabilistic fasteners and wing-locking mechanisms in baridine weevils (Coleoptera: Curculionidae)**

### **Abstract**

It is known that many groups of insects, such as beetles, fasten their elytra to the abdomen utilizing an array of friction-based locking mechanisms, cuticular outgrowths, and microstructures, such as microtrichia. Few studies have examined the ultrastructure of these morphological structures, and there has been no examination of these mechanisms in weevils. Considered one of the largest families of insects, with over 60,000 species described to date, exploration of weevil diversity is still in its infancy. Thus, an investigation of wing locking mechanisms in the subfamily baridinae has been carried out to further understand the morphological variation within this superdiverse insect group, to reveal the ultrastructure of these different mechanisms, and to compare some of the mechanisms found in weevils to those found within other insect groups.

**Keywords:** Parabolic elements, beetle ultrastructure, spiculate patches, wing-fastening.

### **Introduction**

Insects employ a diverse array of cuticular outgrowths and attachment devices for various morphological and mechanical functions depending on the insect, such as for adhesion to surfaces, rapid mobilization and alert movements, and fastening and locking extremities. To accomplish these functions, various cuticular attachment systems have been developed, consisting of hooks, clamps, locks, and diverse frictional surfaces (Gorb *et al.* 2002).

Among the insect lineages that have convergently developed the ability to fasten their wings to the abdomen include the Lepidoptera, Diptera, Dermaptera, Hymenoptera, Heteroptera, and Coleoptera. Among the Coleoptera, and particularly in Baridinae (Coleoptera: Curculionidae), various modified frictional surfaces have evolved for fastening the fore- (elytra) and hind-wings to the abdomen. Known as probabilistic fasteners, these surfaces have modified setae and microtrichia that come together (Gorb 1999; Gorb *et al.* 2002; Gorb and Popov 2002). Although these surfaces do not converge with precise positioning, such as the teeth in zippers, they produce high frictional forces by converging less precisely, similar to the process by which the surfaces of velcro adhere, thereby forming a lock under a certain range of applied force and also permitting fast and easy attachment and detachment (Gorb and Popov 2002).

Although the presence of these microtrichia fields have been broadly surveyed and characterized in many beetle groups, there have been no previous studies examining them in weevils. The purpose of this study is to describe those wing-

fastening structures in the weevil subfamily Baridinae, and contrast them to those present outside of Baridinae.

### **Probabilistic wing fasteners in Baridinae**

In Baridinae, cuticular outgrowths in the form of various modified microtrichia are present on the dorsal surface of the thorax (Figs. 28-87), the abdominal tergites (Figs. 1-5, 9-27, 88-136), the inner surface of the elytra (Figs. 137-216), and the dorsal and ventral surfaces of the hind wings at the folded state (Figs. 217-244). Those on the thorax are mostly of the lamellate type, in which broad, scale-like lamellae interlock (Fig. 7). Sometimes, as on the elytra, these lamellae bear digitiform or lobe-like processes along their apical margin. The microtrichia on the abdominal tergites and spiracular sclerites are the most impressive and developed, forming large patches of large, dense spines from tergites 1-7, although they are most notable on tergites 4-7. These spiculate patches on the abdominal tergites and spiracular sclerites have corresponding patches on the inner surface of the elytra. When these two surfaces, composed of spiniform probabilistic fasteners (Fig. 6), come in contact they lock due to high frictional forces. Because the hind-wings cover most of the abdomen when folded (Figs. 1, 2, 4), only the microtrichial patches on the spiracular sclerites and tergite 7 come in contact with the elytra during rest. Although tergite 7 is the only one to interlock with the elytra during rest, the spiculate patches on tergites 5 and 6 often are well-developed as well for reasons unknown. In order to allow the hind-wings to lay securely fastened over the abdomen, microtrichia are

present along the costal region and ventral region (when folded) on the hind wings. The microtrichia along the center region on tergites 1-6 are also oriented in a different direction than those present along the spiracular sclerites and tergite 7, most likely facilitating the re-opening of the hind-wings during flight.

Also present on tergite 7 of the abdomen of many genera in Baridinae are plectral tubercles (Figs. 88, 90, 94-95, 98, 105, 121, 123-124, 126, 130-131), which stridulate against a file of different forms on the inner apex of the elytra (Figs. 137, 140-141, 146, 156, 184, 192), as shown by the model (Fig. 8). Although mainly used for sound production and communication (Lyal and King 1996), it is also believed that these stridulating structures can also perform some function in fastening the elytra to the abdomen, as they also serve as a type of probabilistic fastener, albeit a weak one.

### **Probabilistic wing fasteners outside of Baridinae**

Other subfamilies in Curculionidae, outside of Baridinae, possess similar wing-fastening structures on the tergites, thorax, elytra, and hind wings. Those in Baridinae, however, tend to be less developed. For instance, the spiculate patches on the tergites usually are present in most other subfamilies, if not all, and they typically are relatively large. The patches in Baridinae, though, often are smaller. This size reduction in spiculate patches may be correlated with the increased sclerotization of the tergites in the majority of Baridinae. If the surfaces of the tergites and the ventral

side of the elytra make complete contact, as they do in Baridinae as a result of the rigid tergites, then it is probably that a smaller surface area of spicules is needed to arrest the elytra and flight wings. In the other curculionid subfamilies, which possess relatively weakly sclerotized tergites, the surfaces of the tergites and elytra may not meet as completely as they do in Baridinae, thus requiring a greater surface area of spicules to arrest the elytra and flight wings.

The microtrichia fields present on the thorax, and particularly on the metascutum, of other curculionids typically are less developed than those in Baridinae. The metascutum in Baridinae is somewhat more defined and larger than that in other subfamilies, which possibly creates a better contact surface for the elytra.

The microtrichia fields on the apico-ventral surface of the elytra and on the hind wings are similar throughout Curculionidae. Although many differences are present, there appear to be no general differences between Baridinae and other curculionids.

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### **Figure captions**

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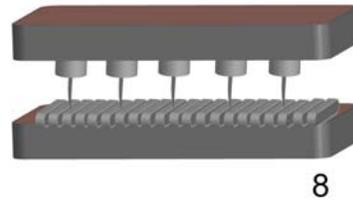
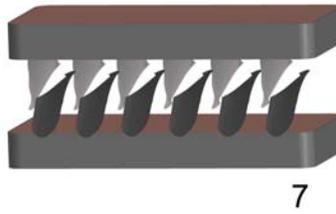
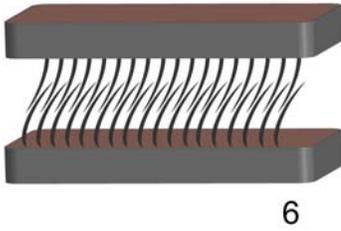
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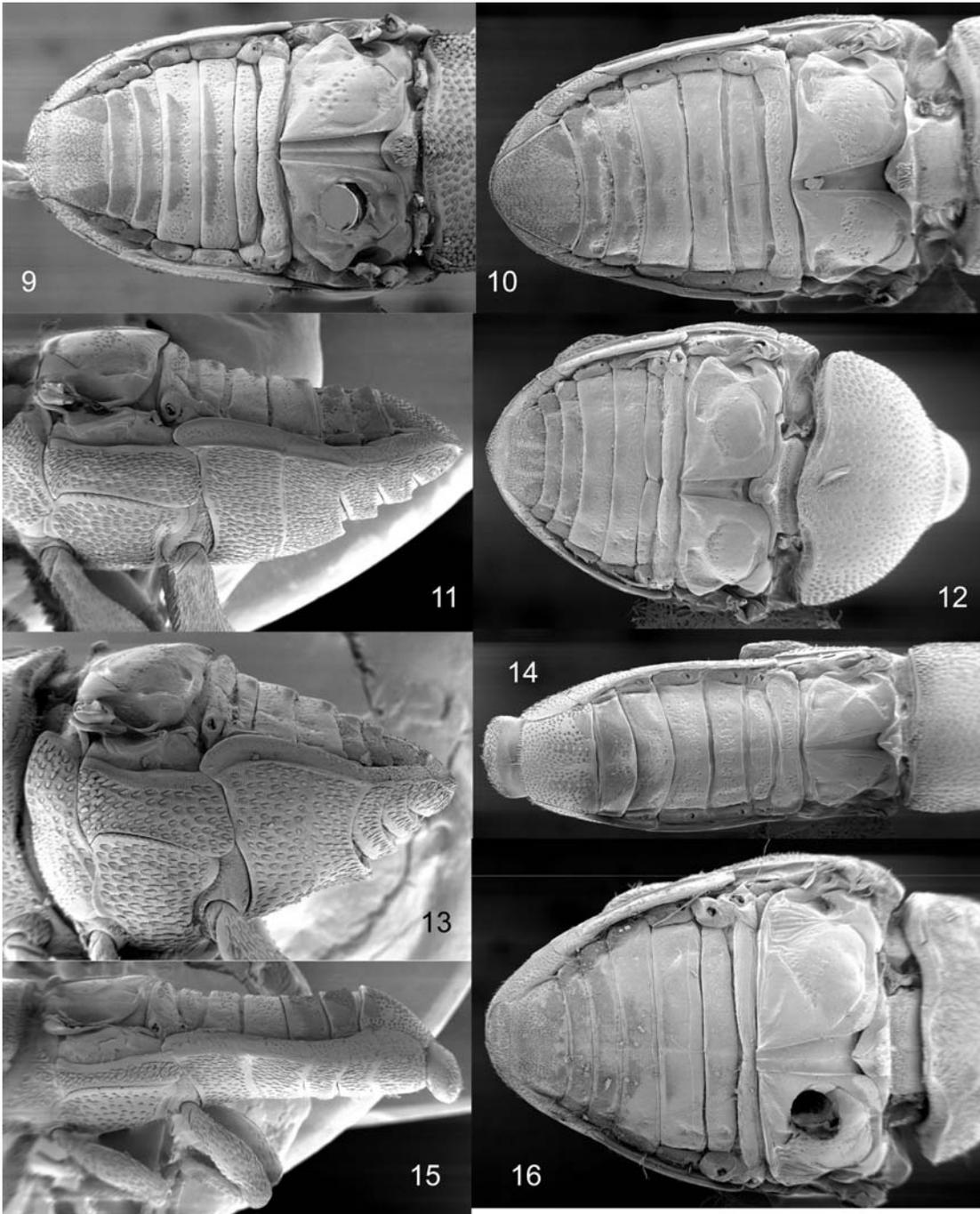
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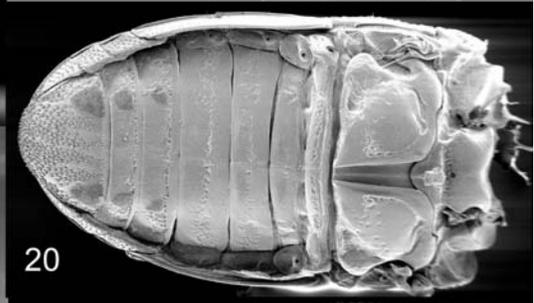
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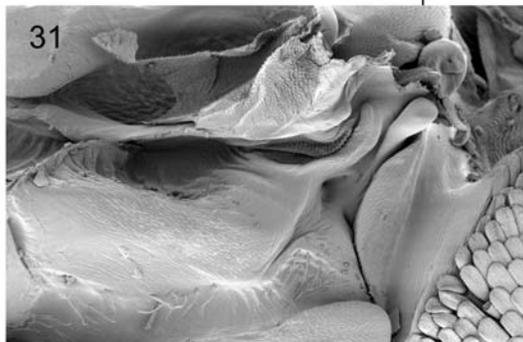
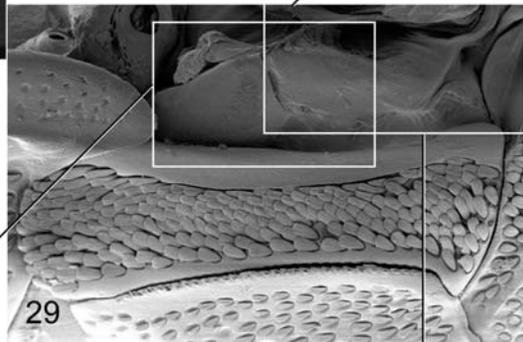
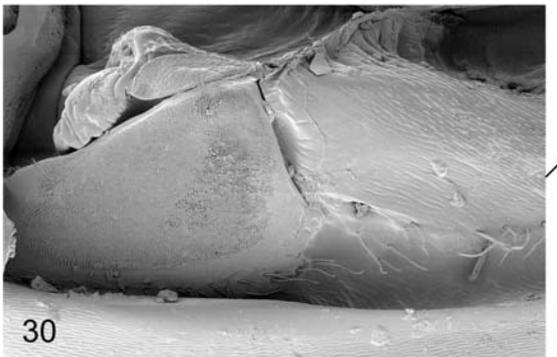
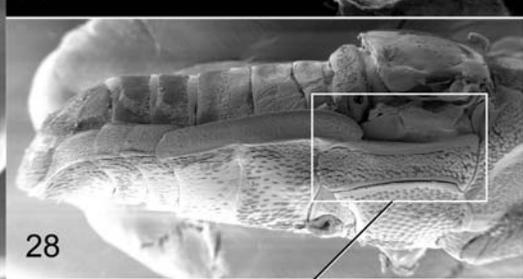
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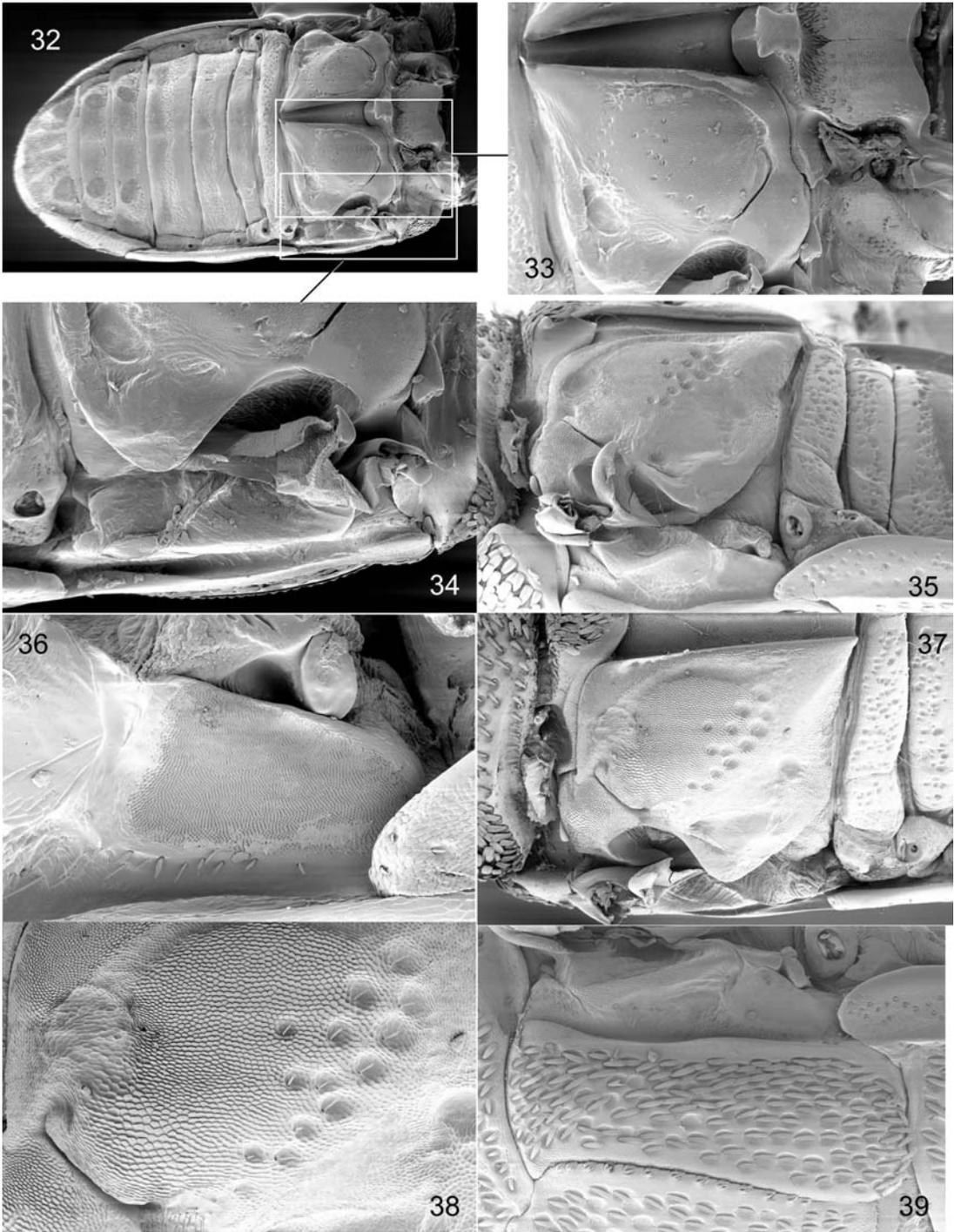
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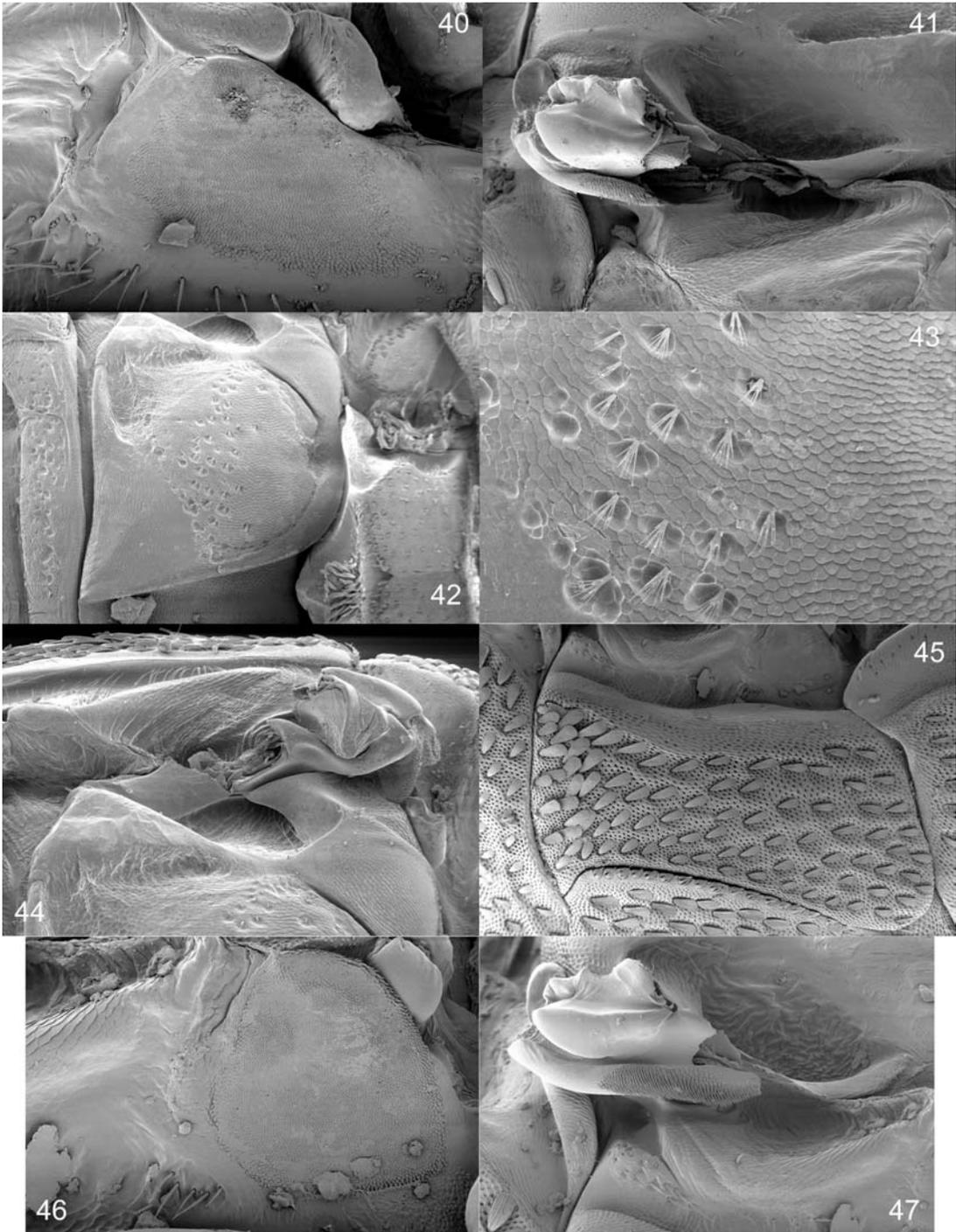




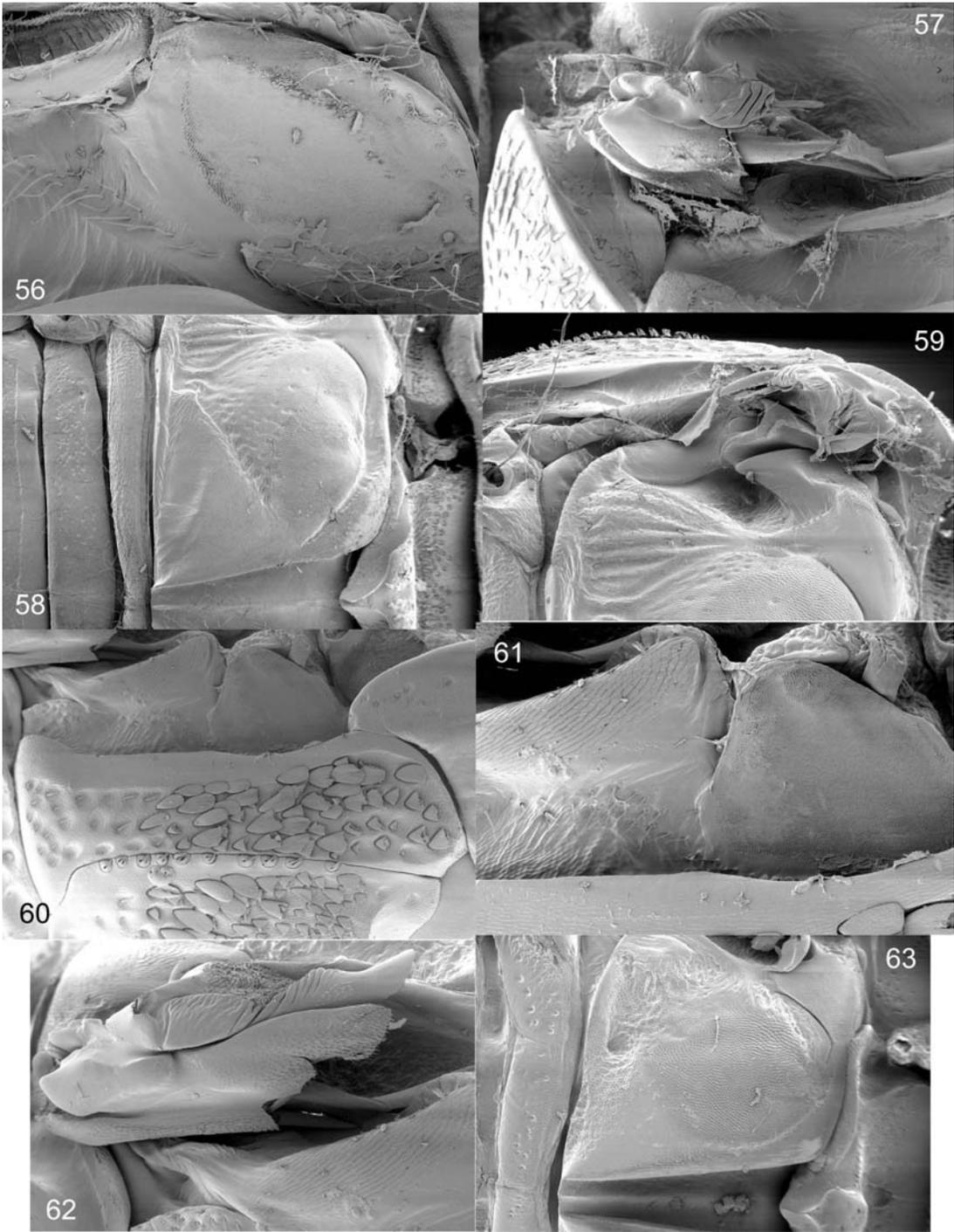


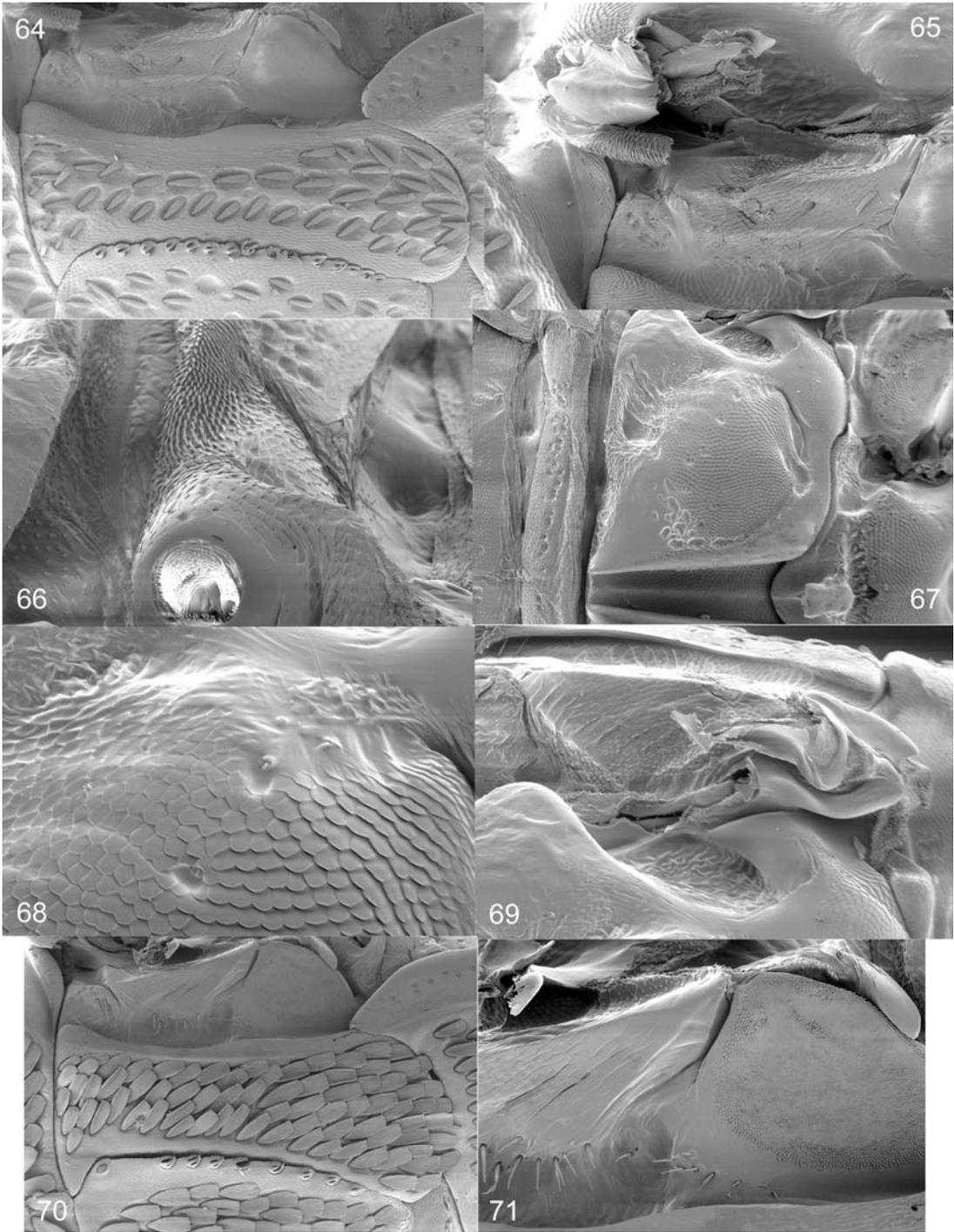


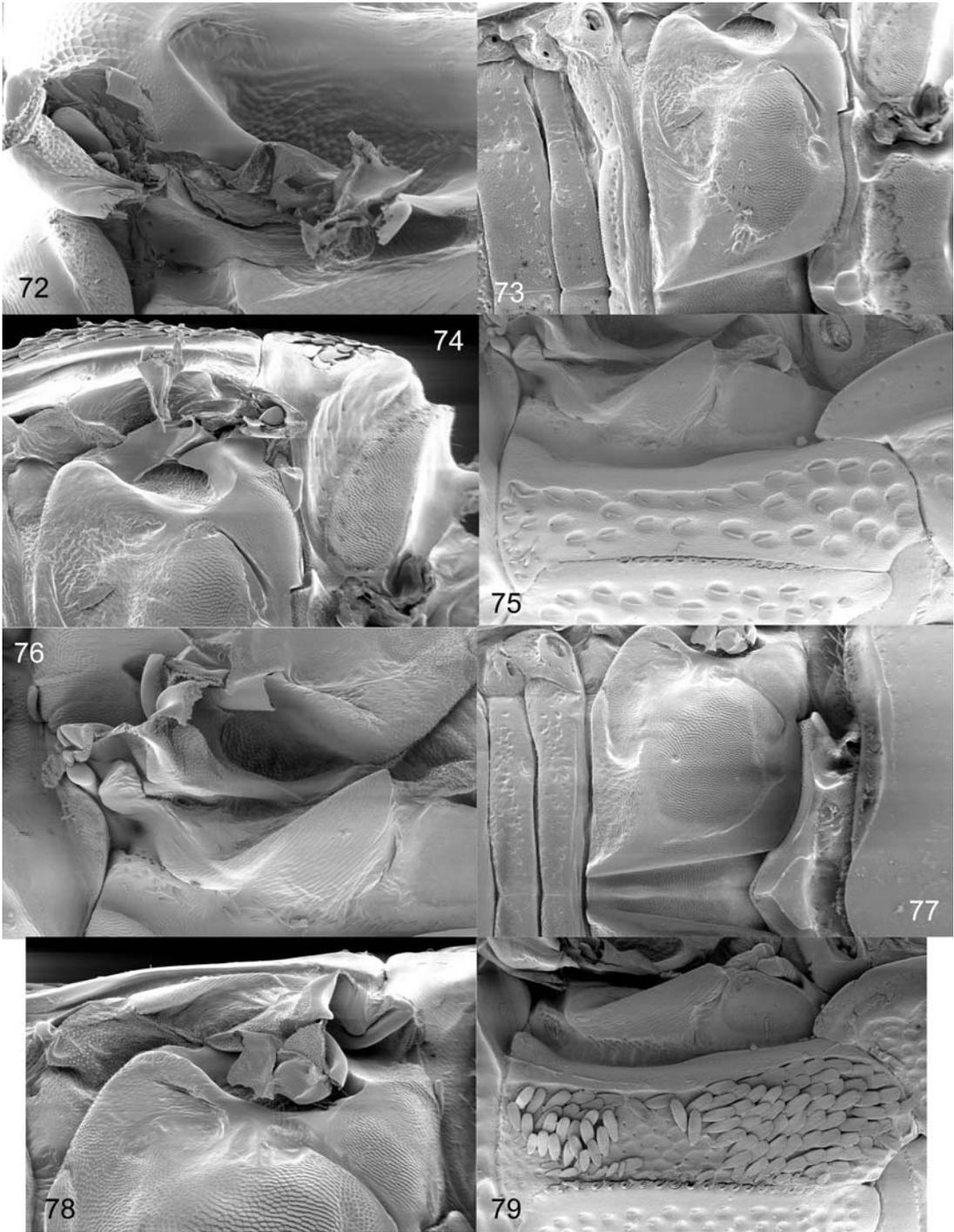


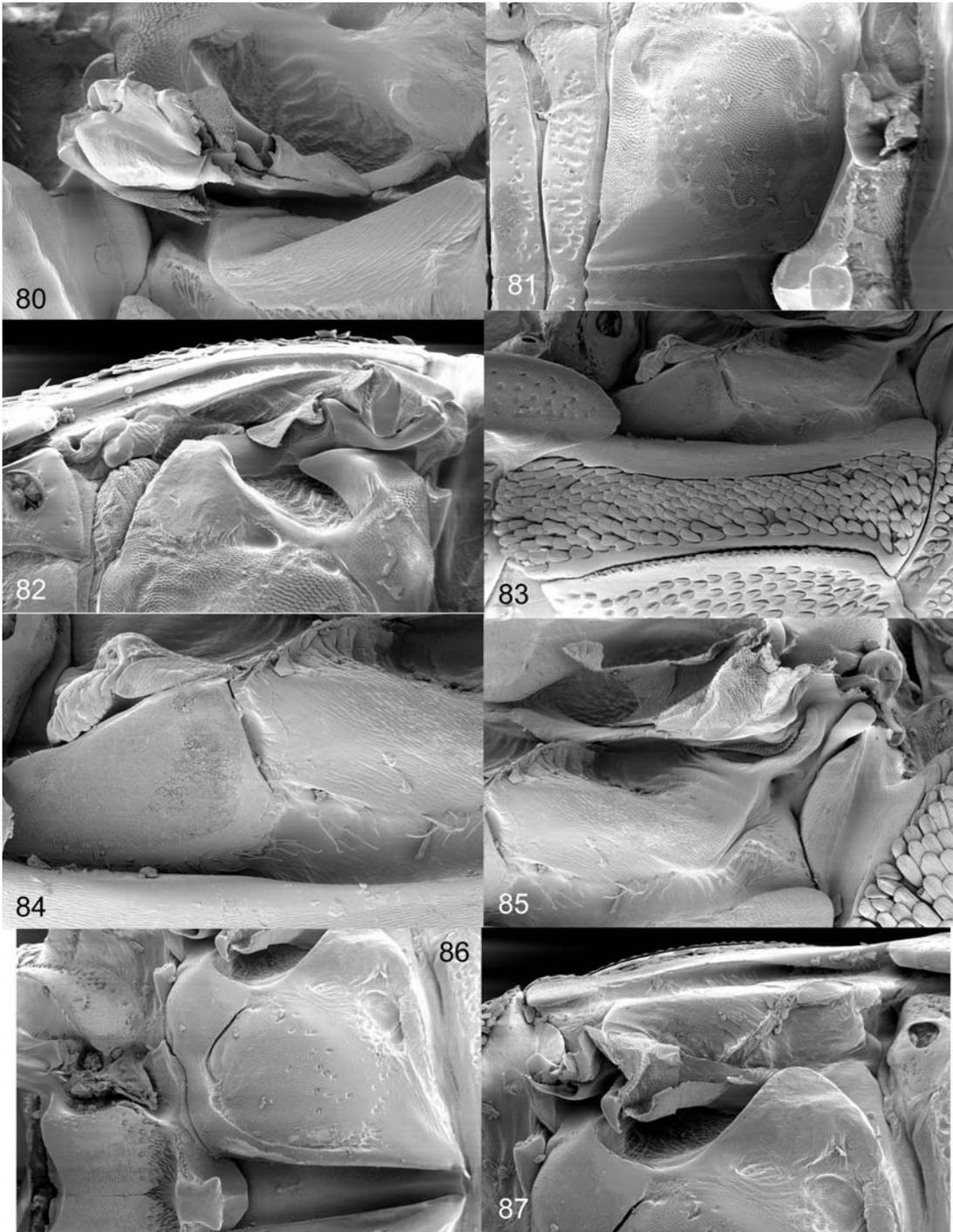


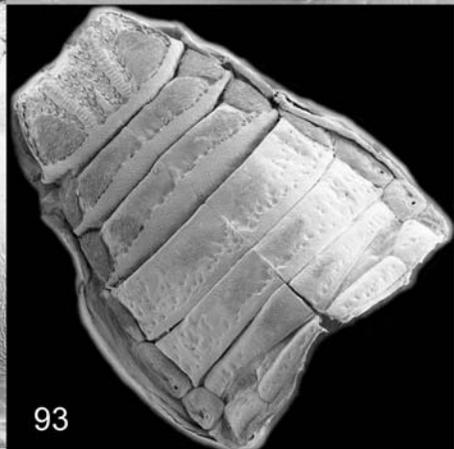
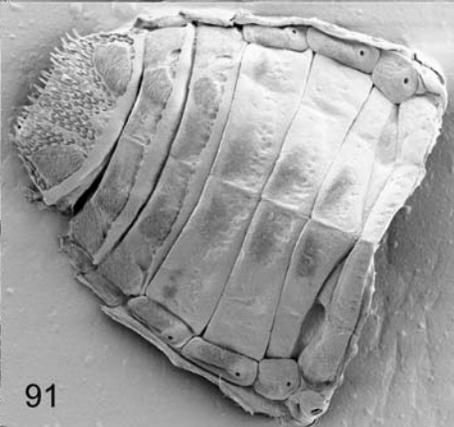
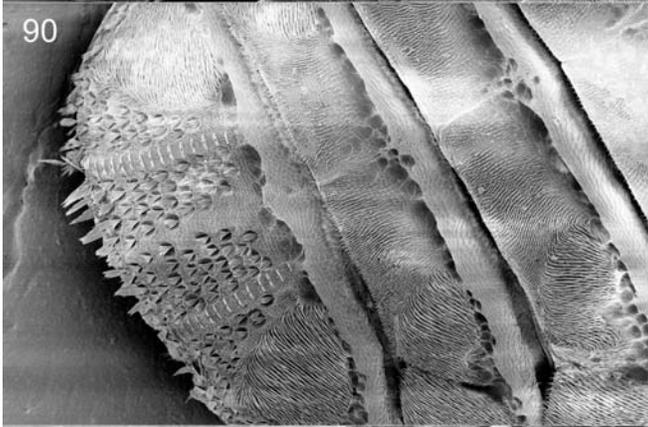
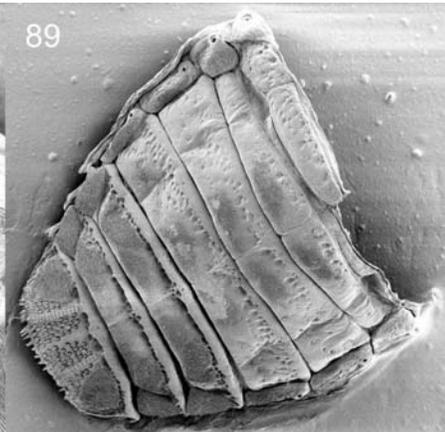
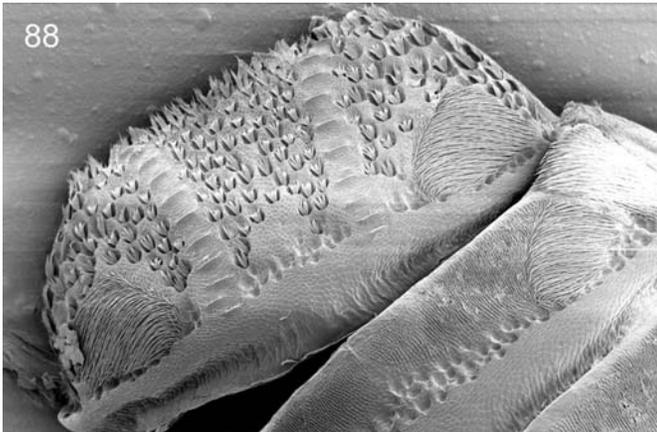


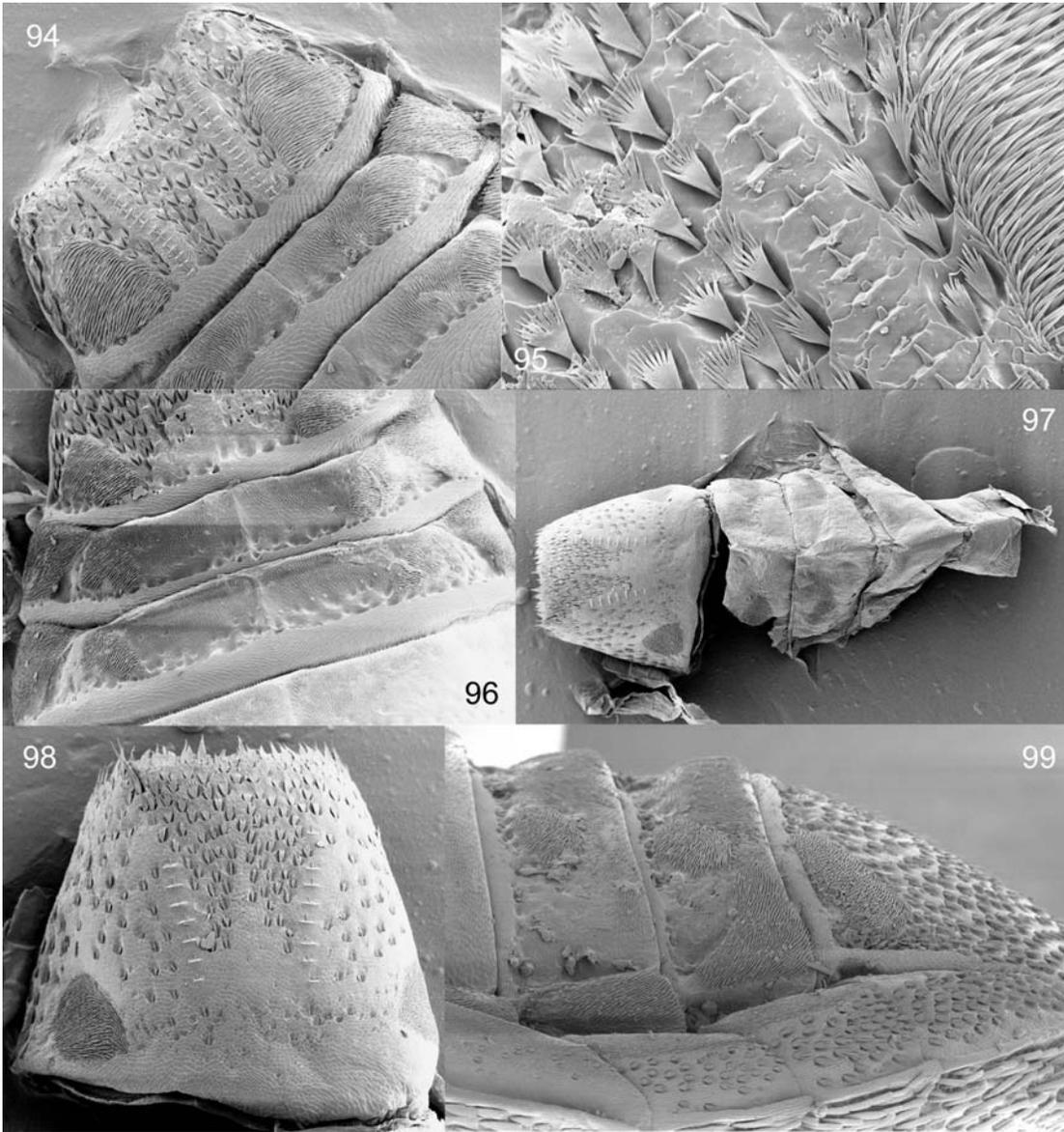


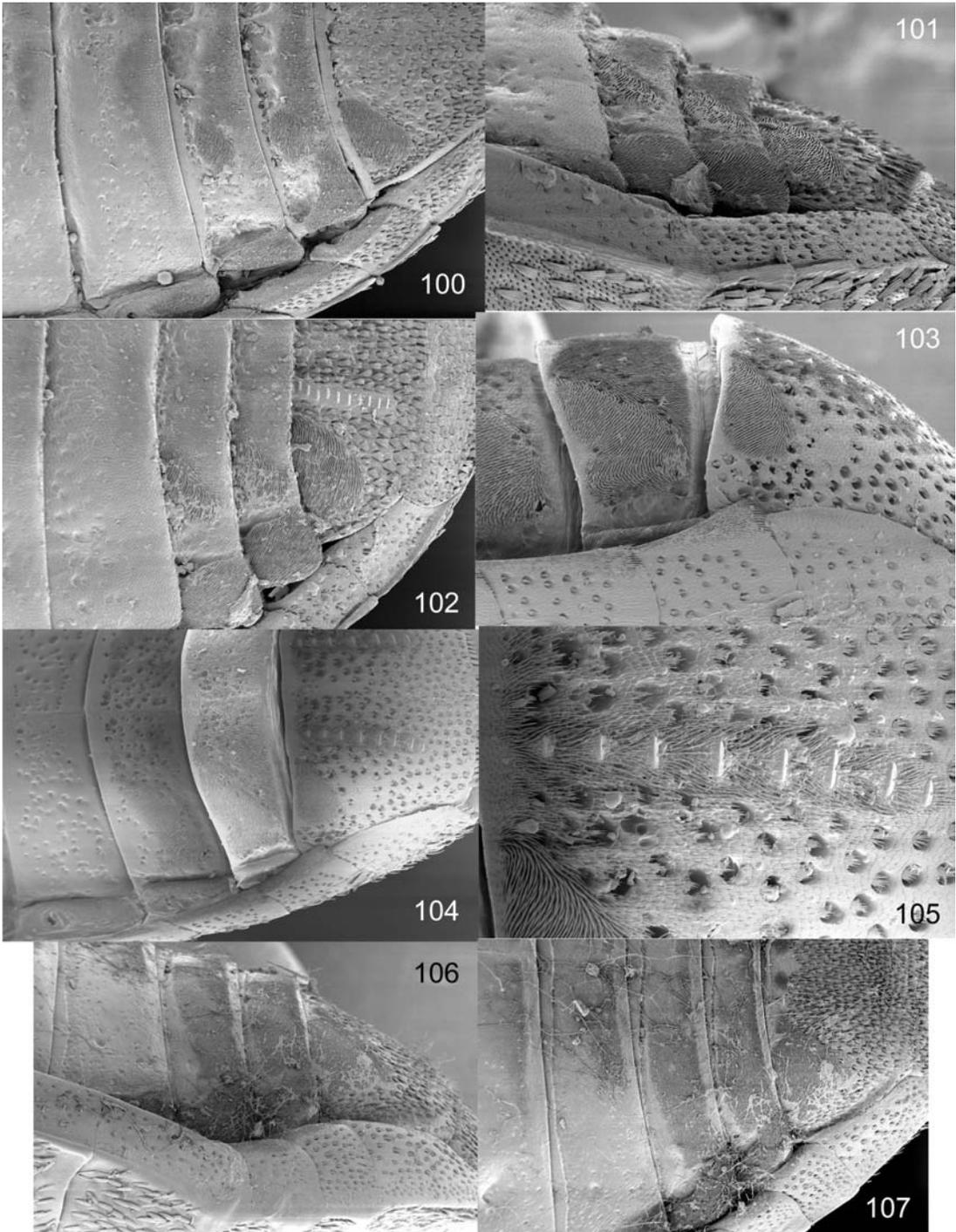


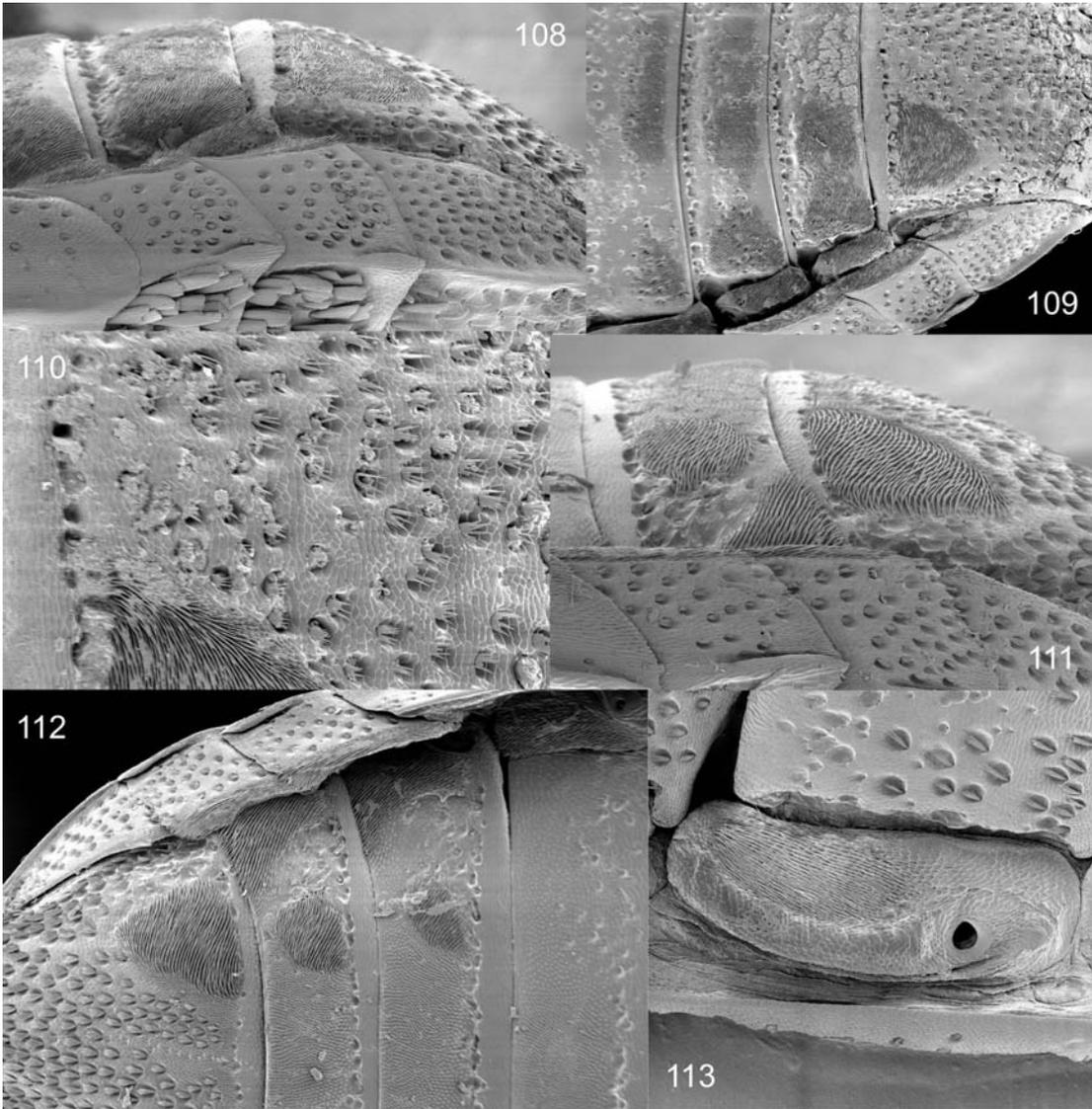


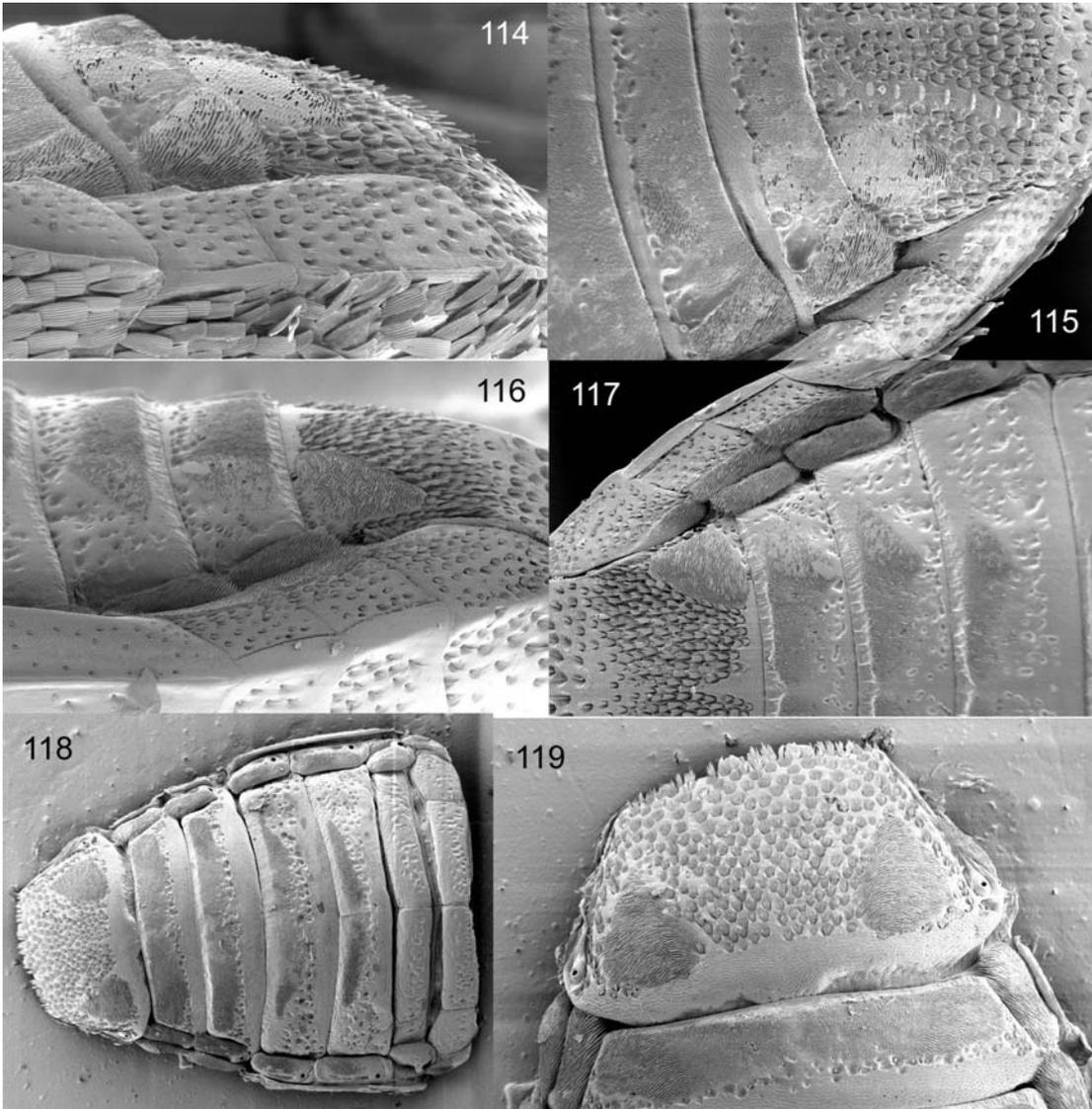


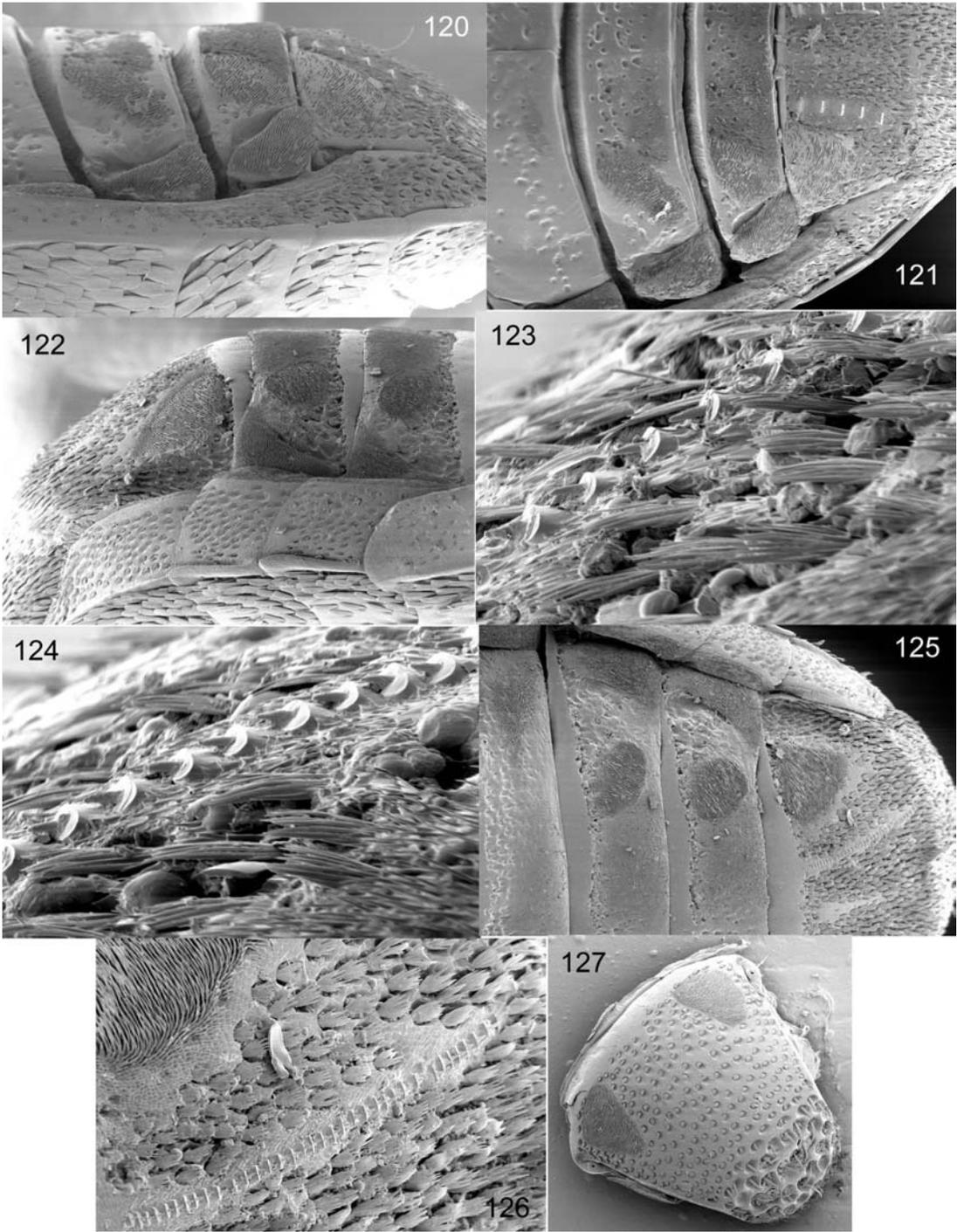


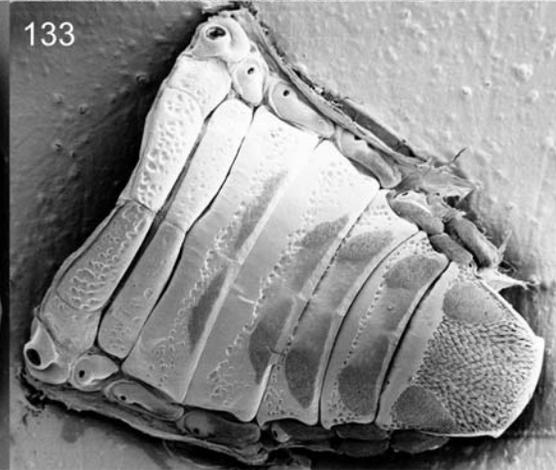
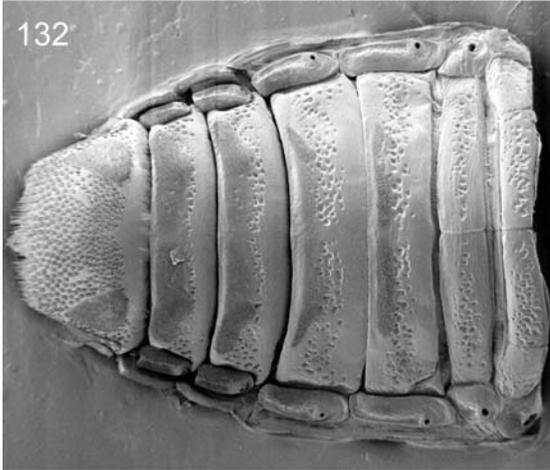
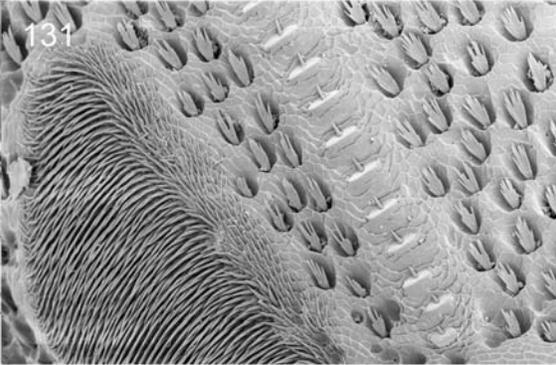
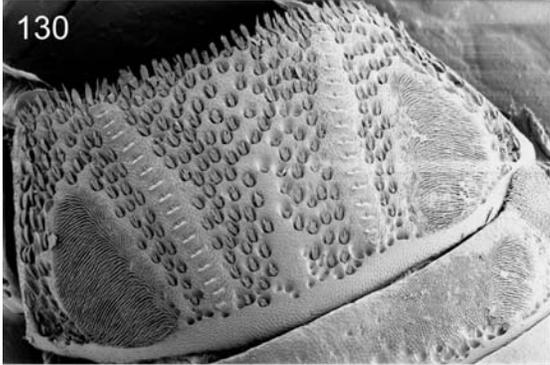
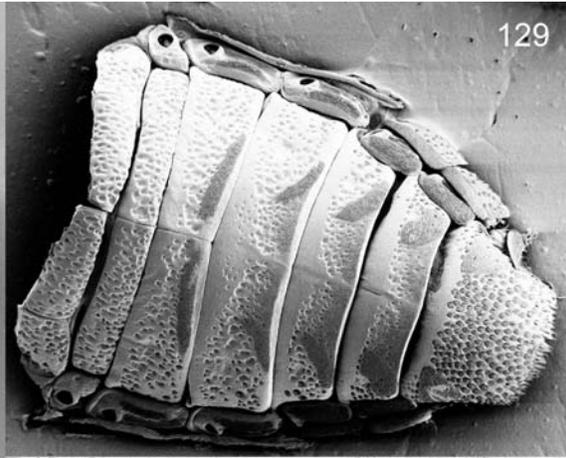
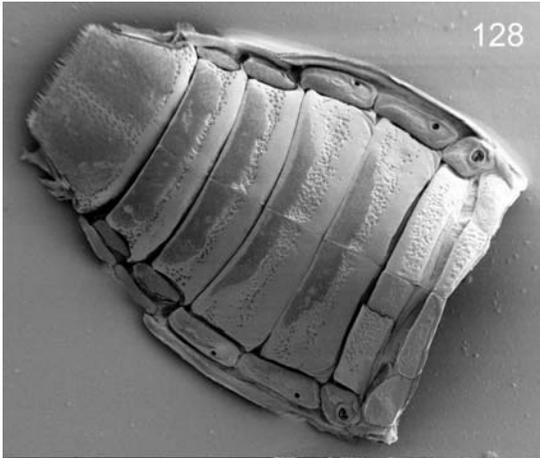






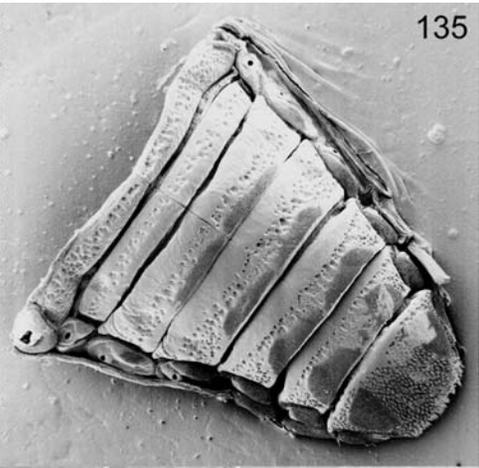




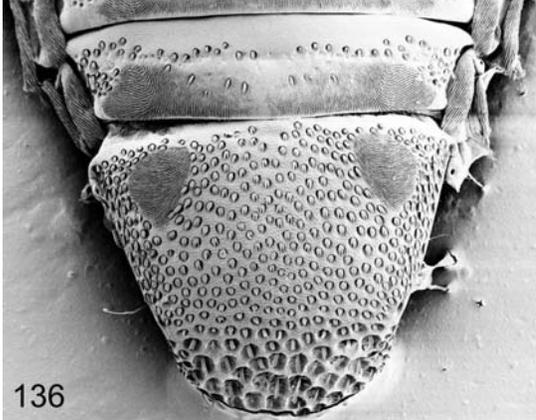




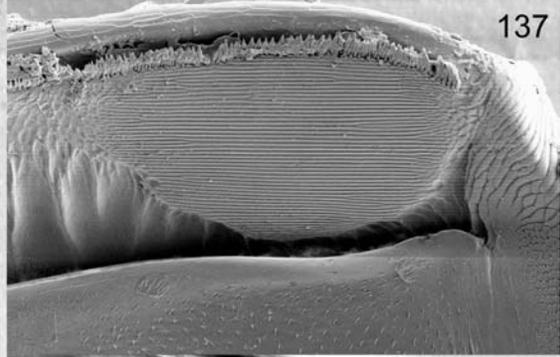
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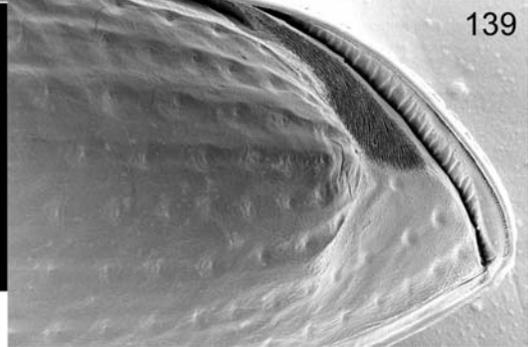
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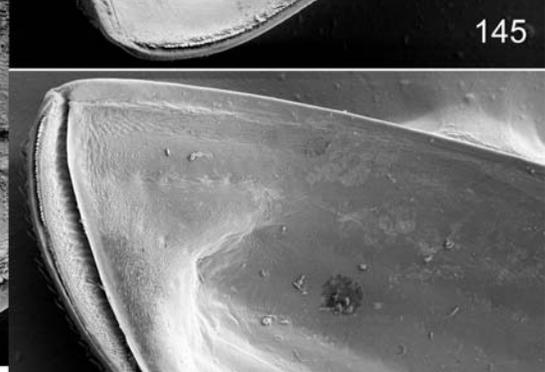
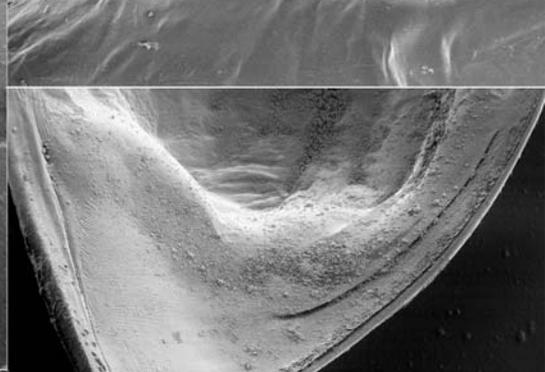
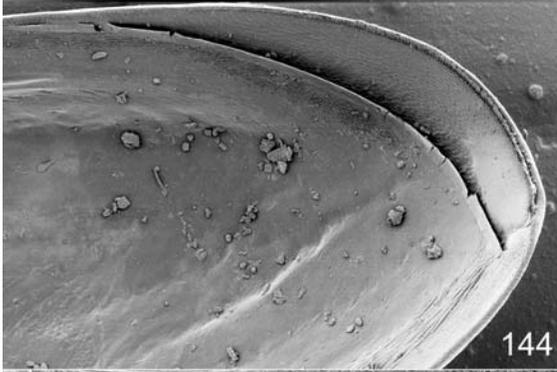
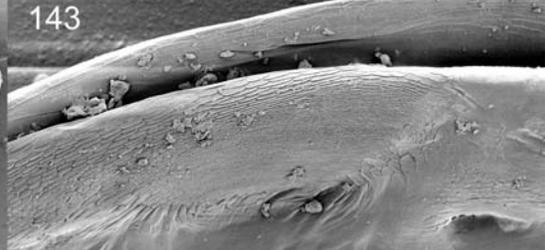
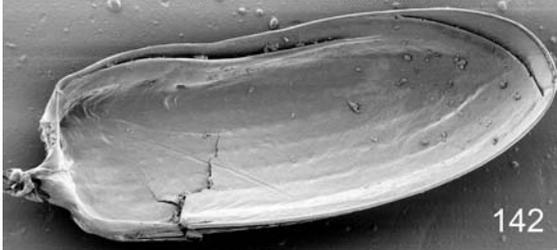
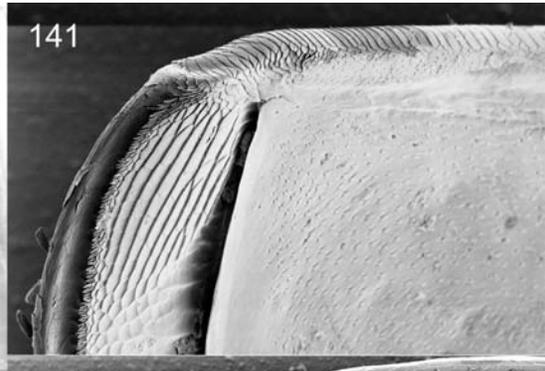
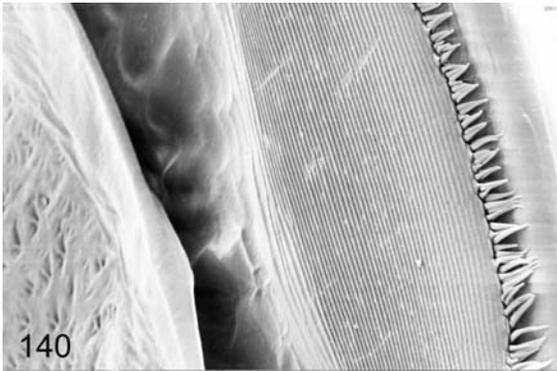
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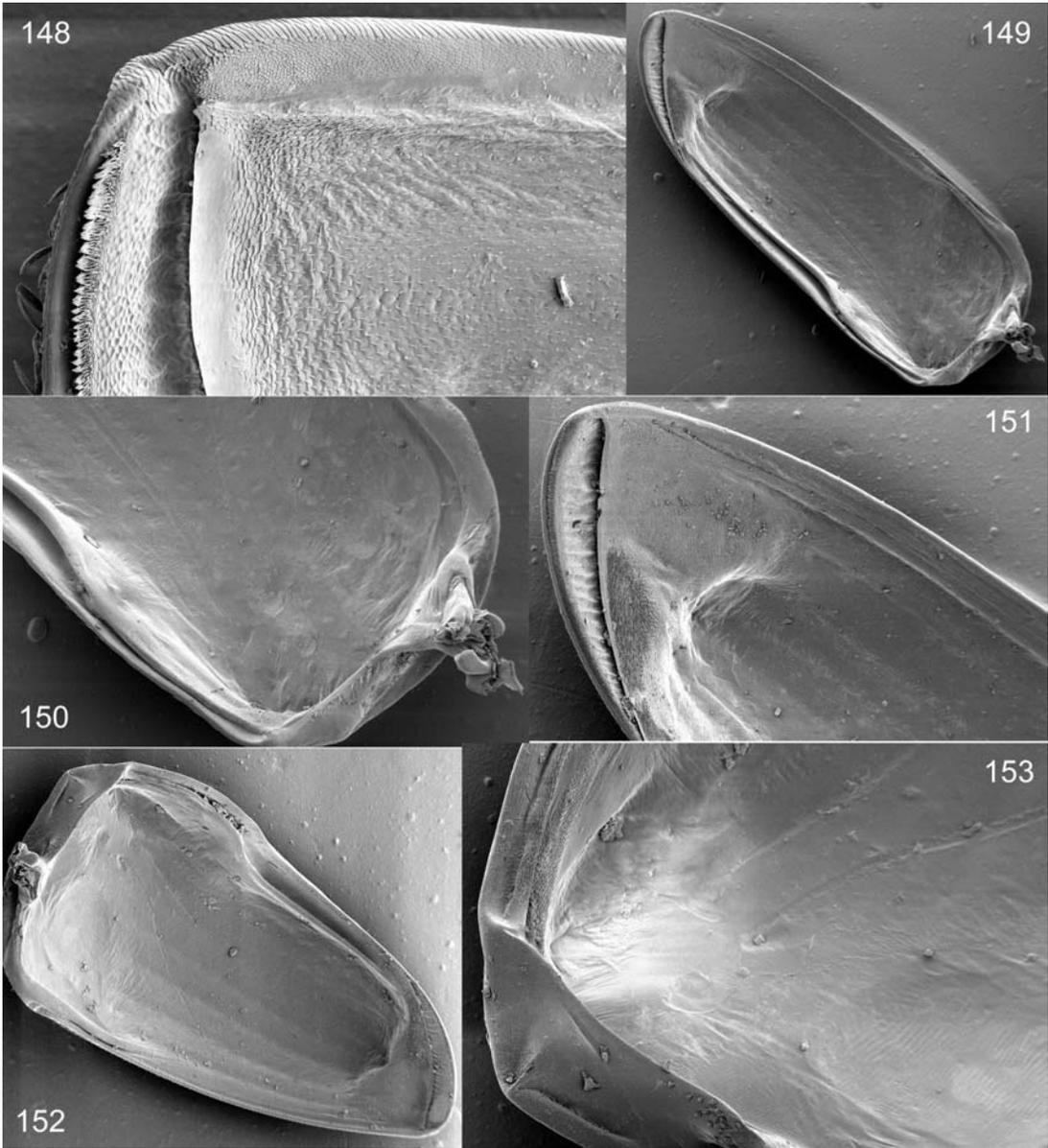


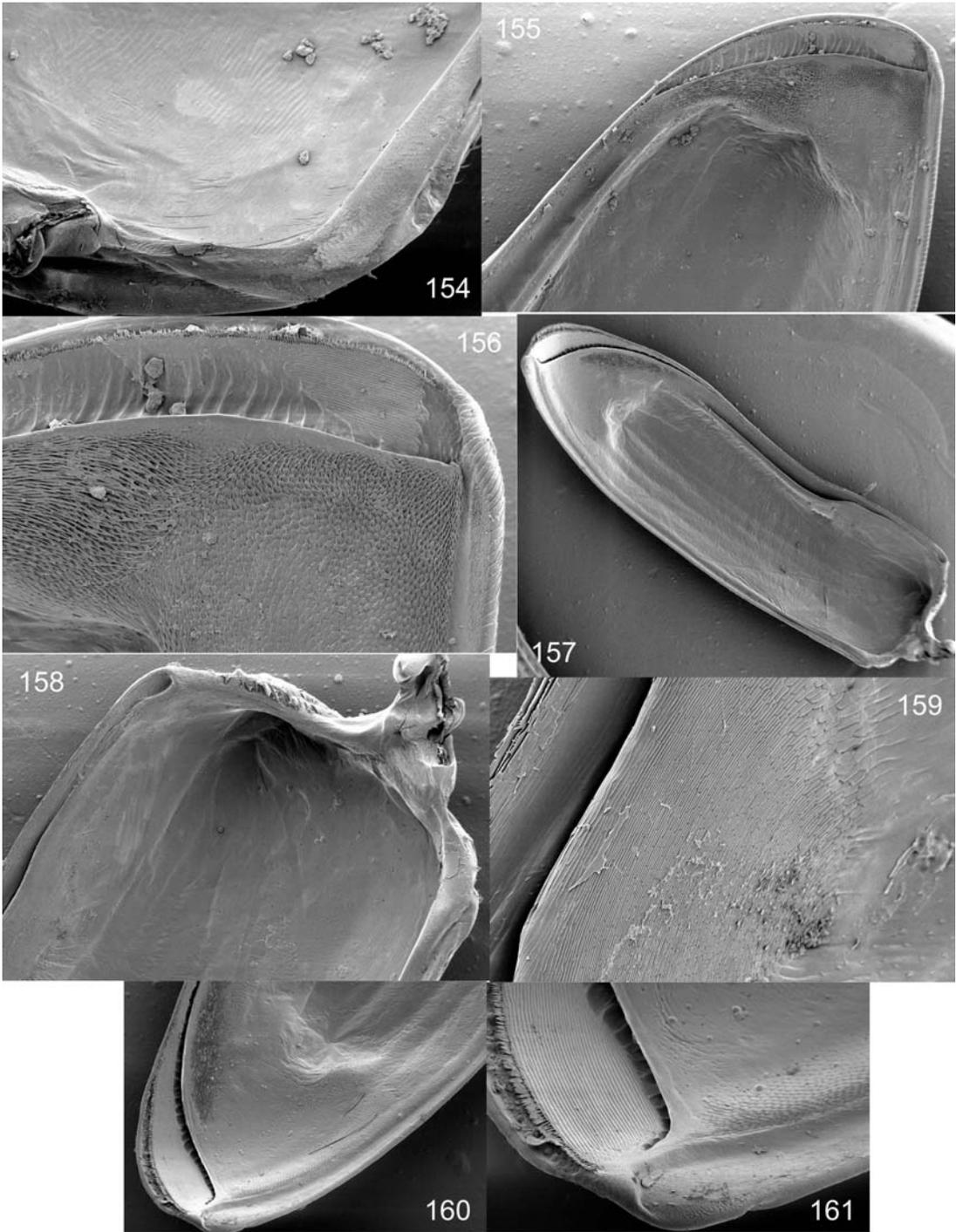
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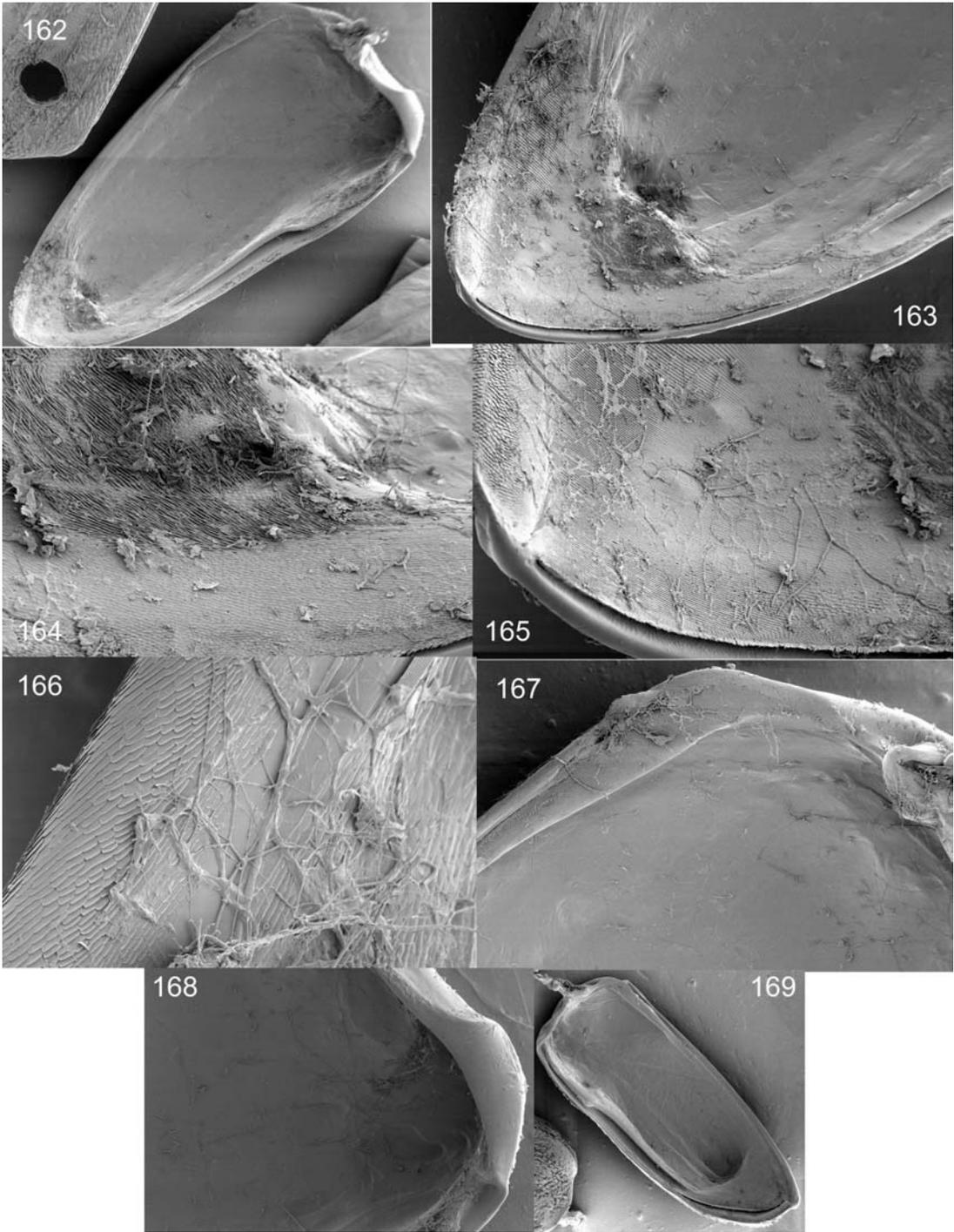


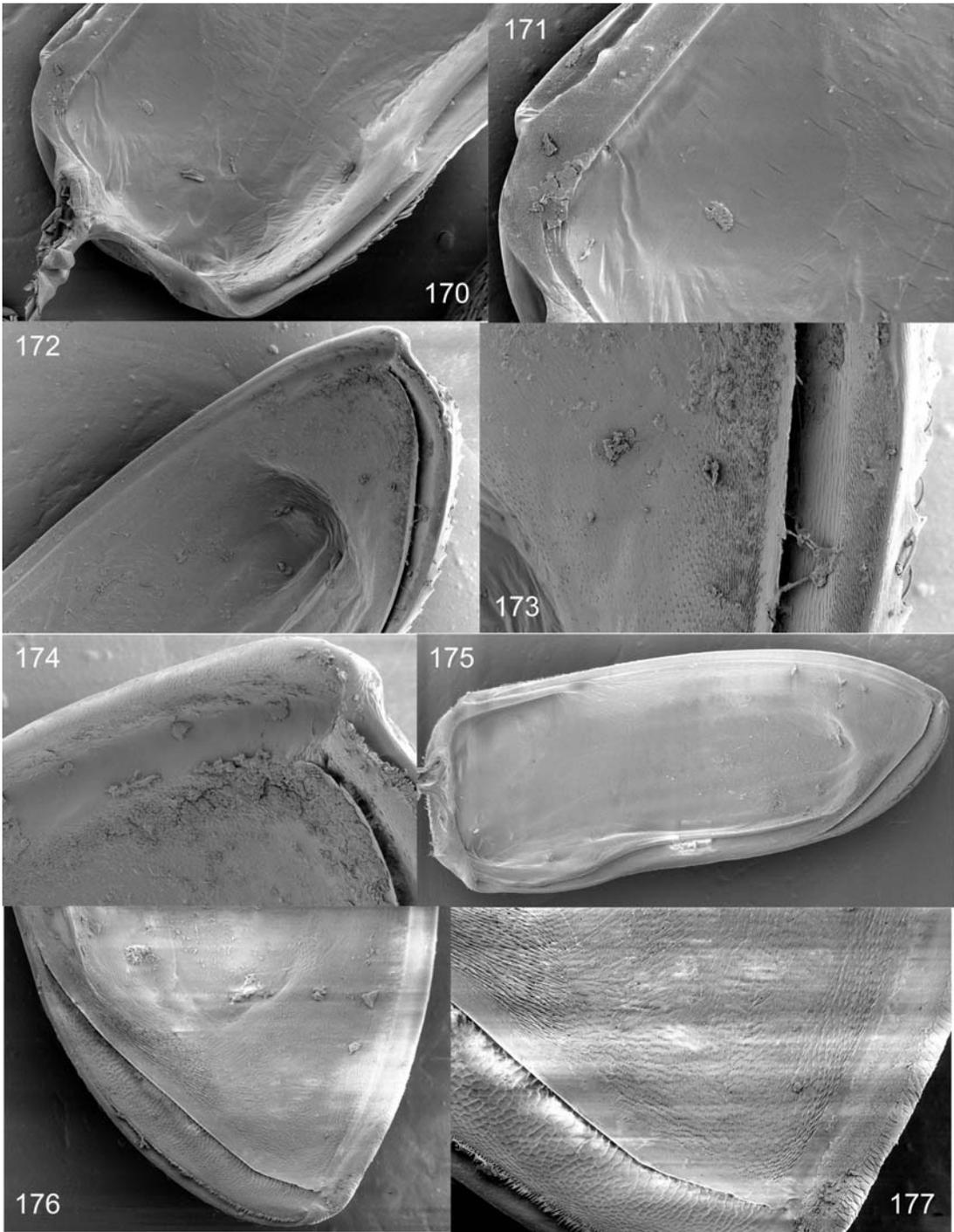
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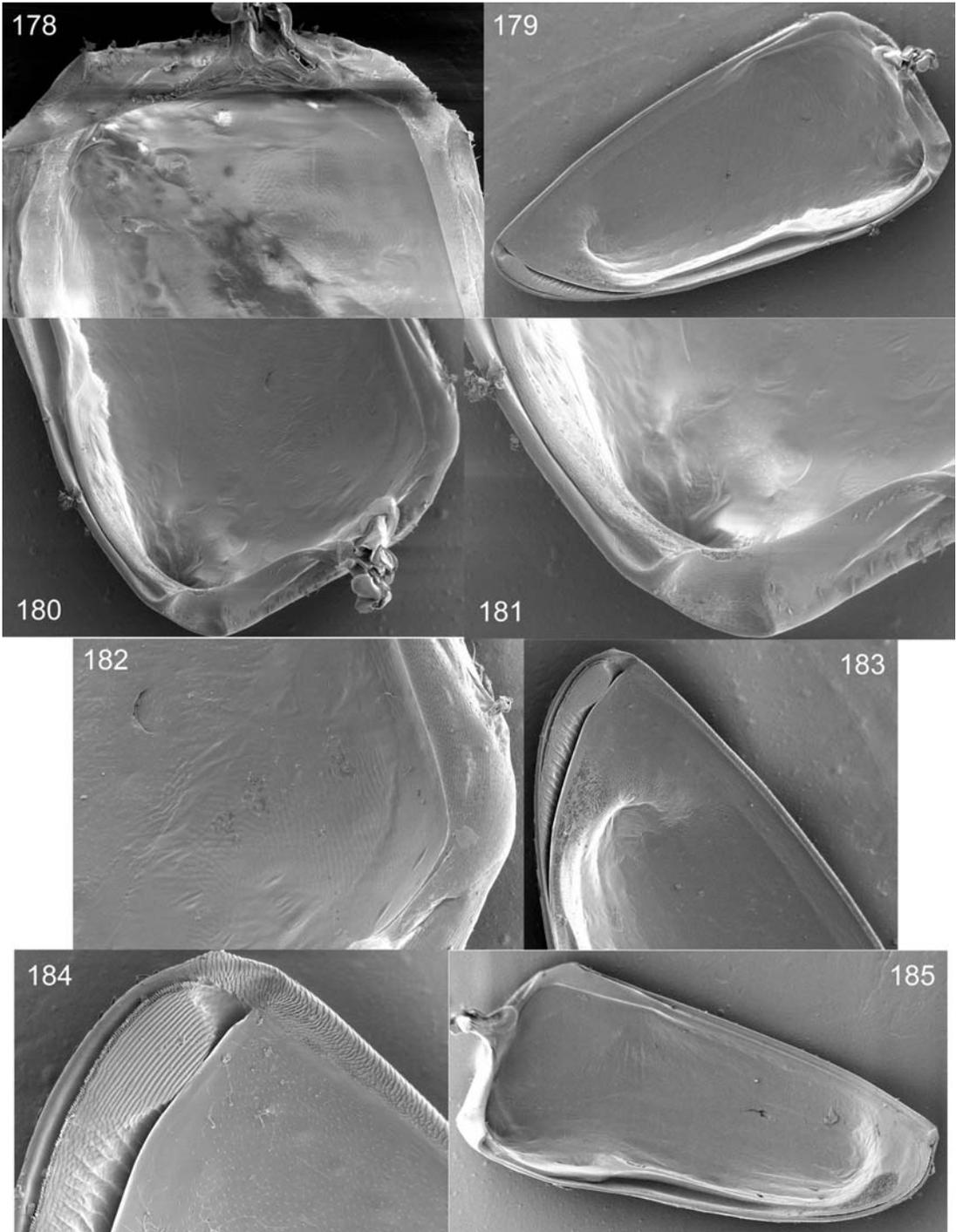


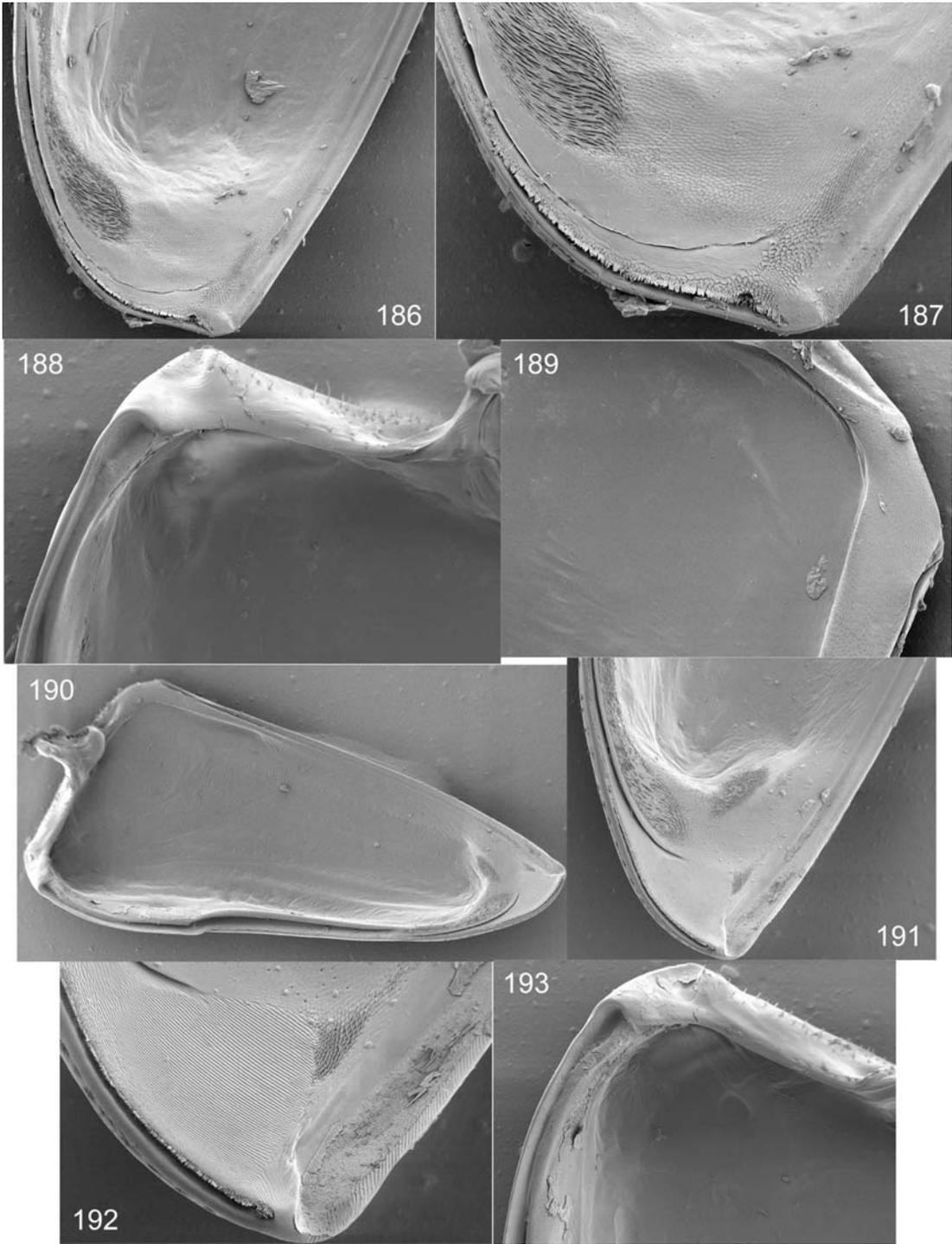


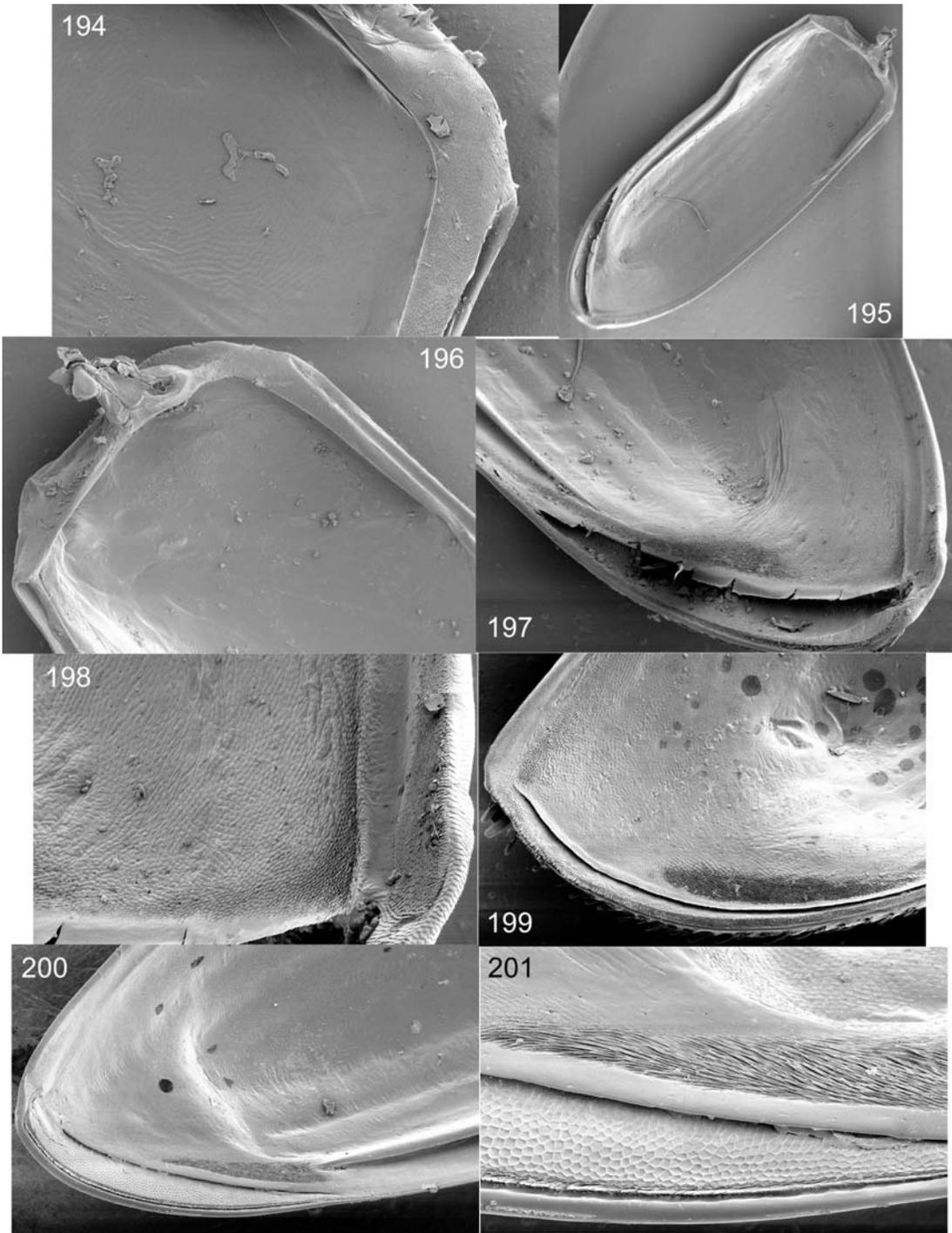


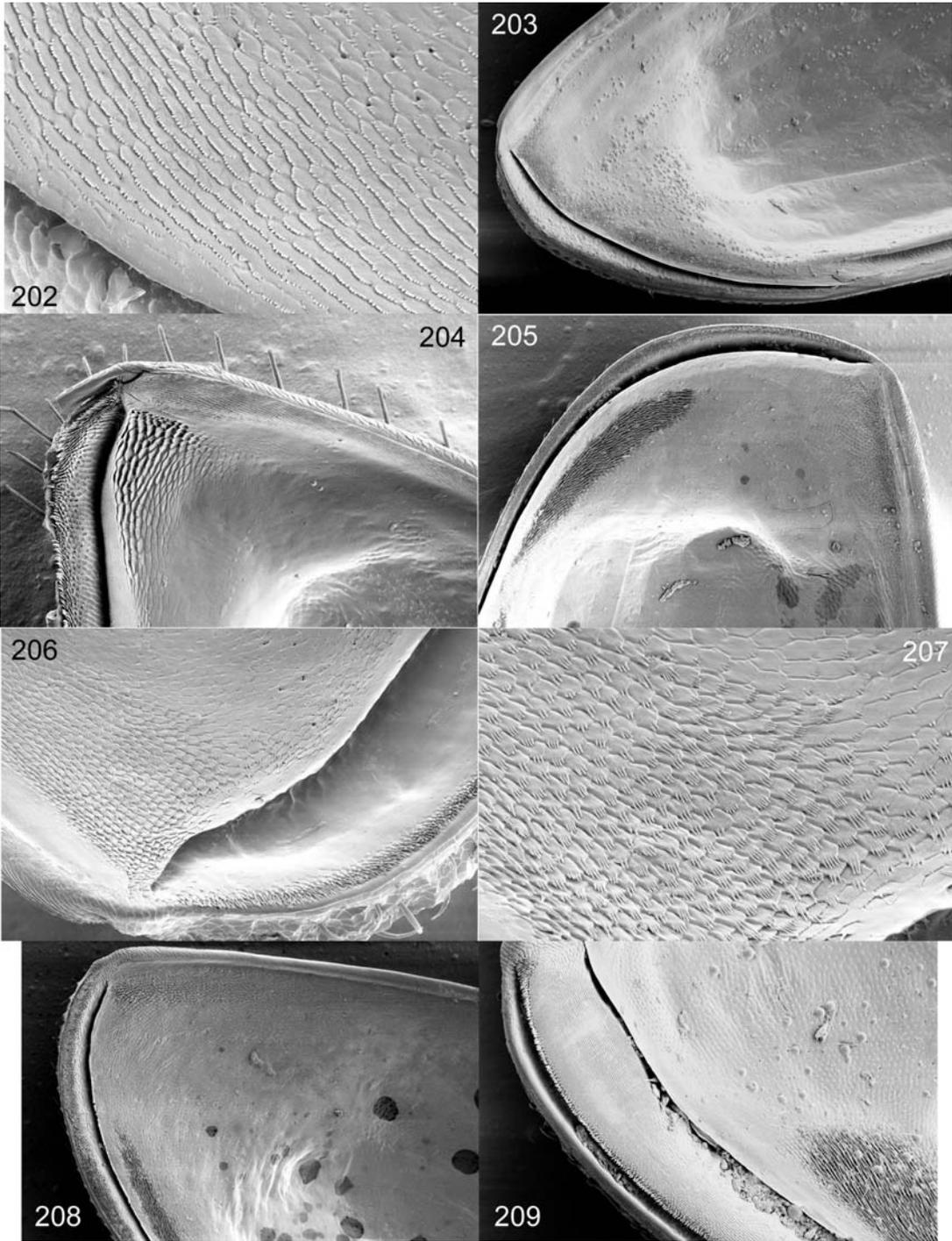


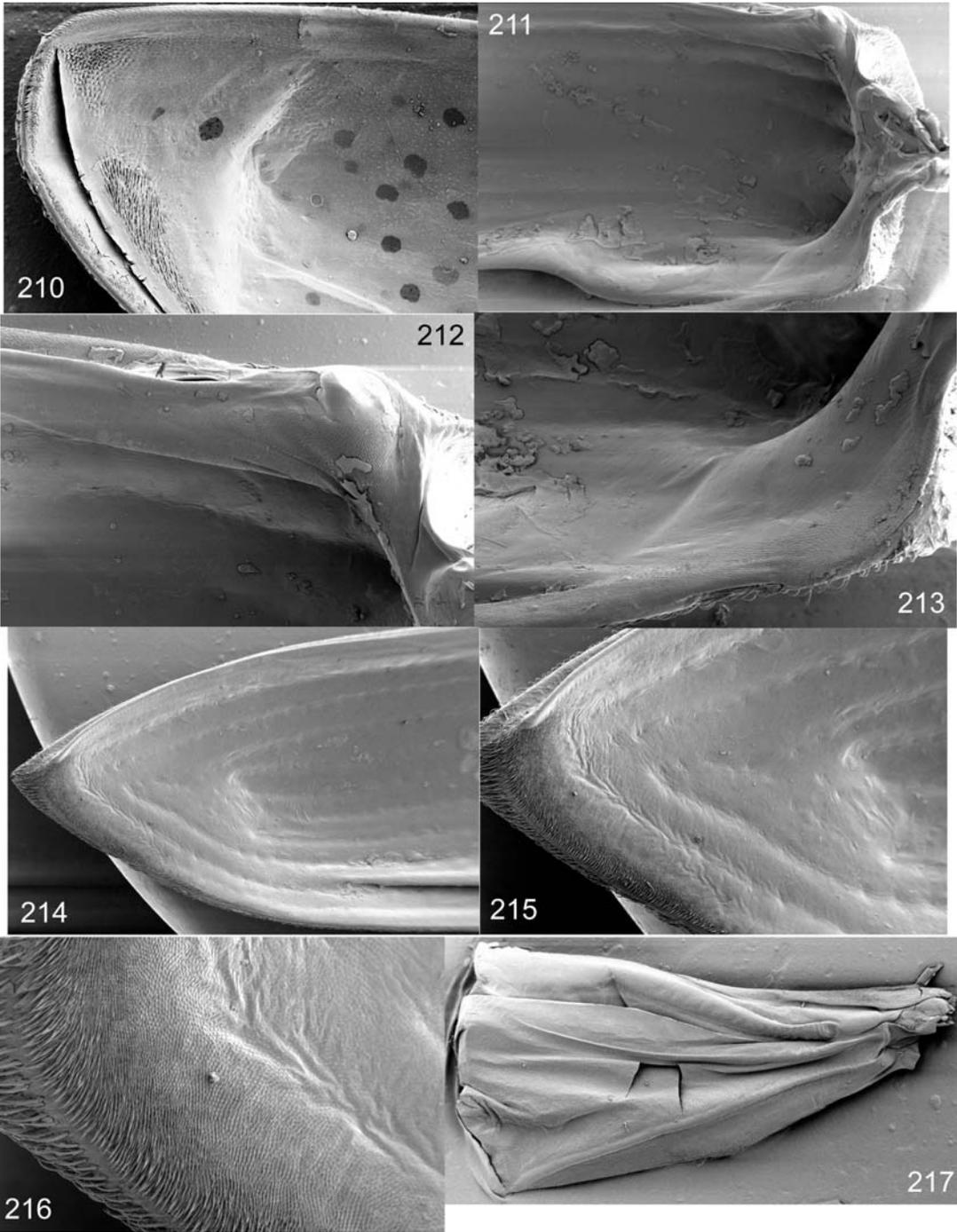


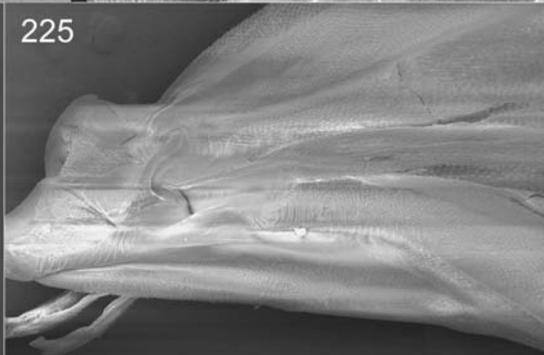
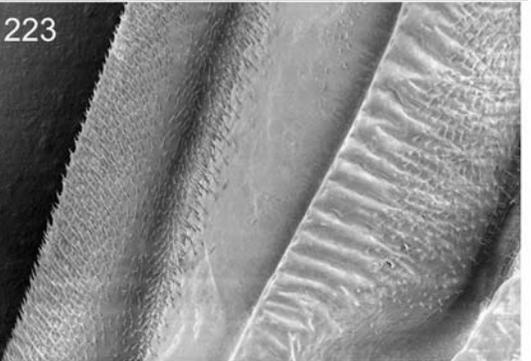
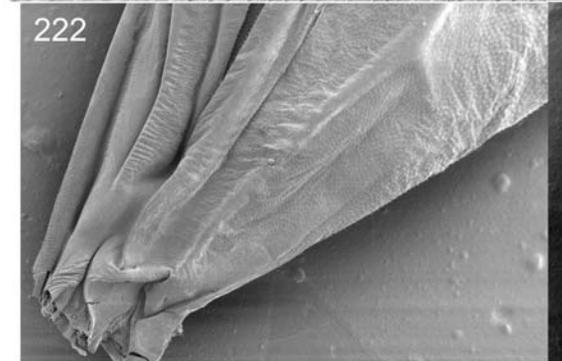
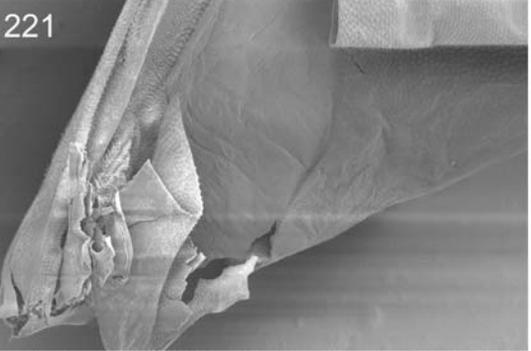
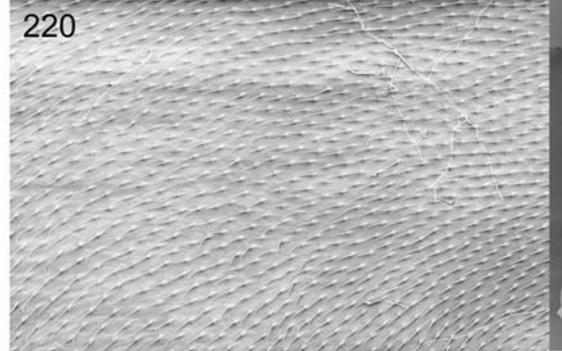
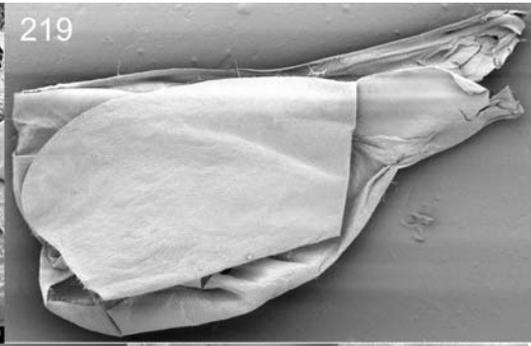


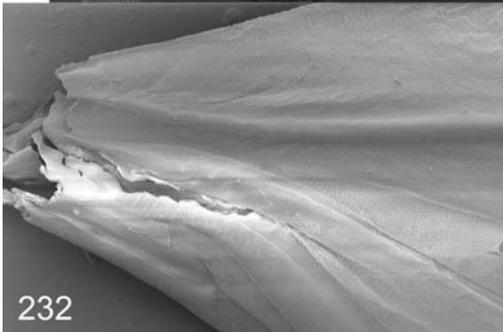
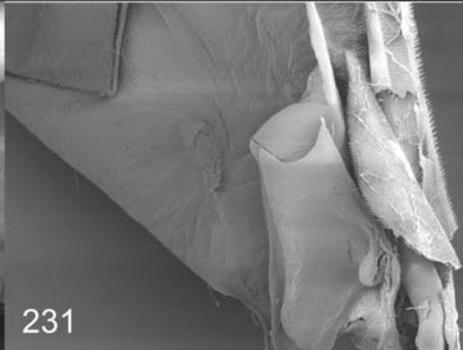
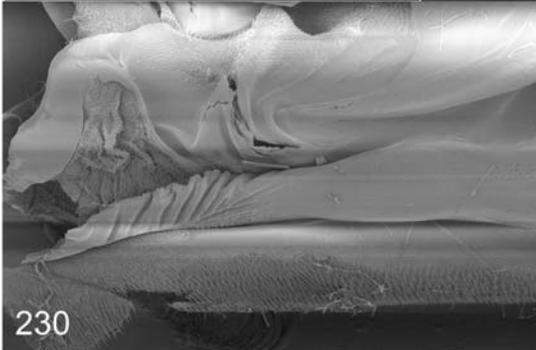
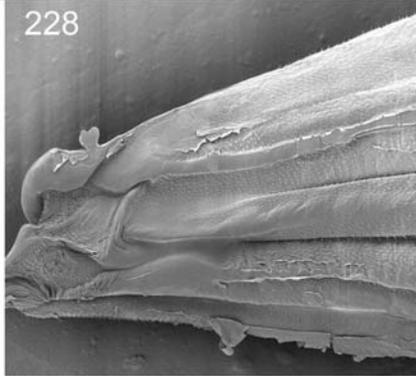
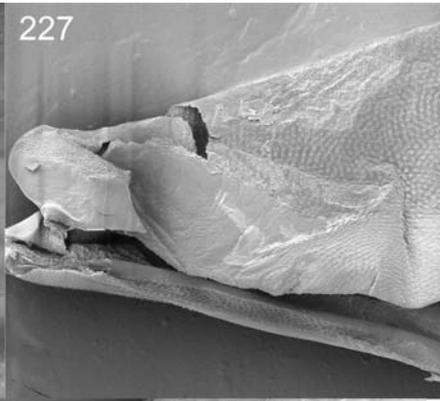
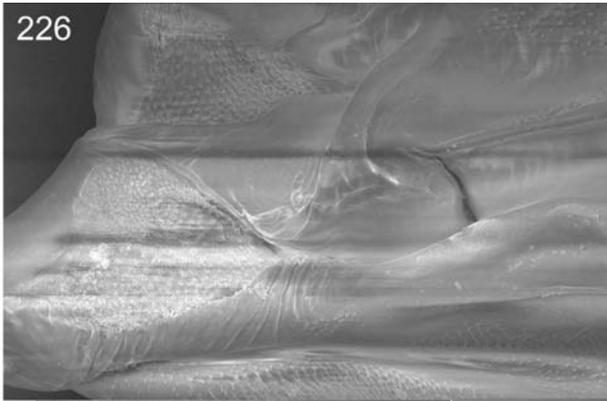


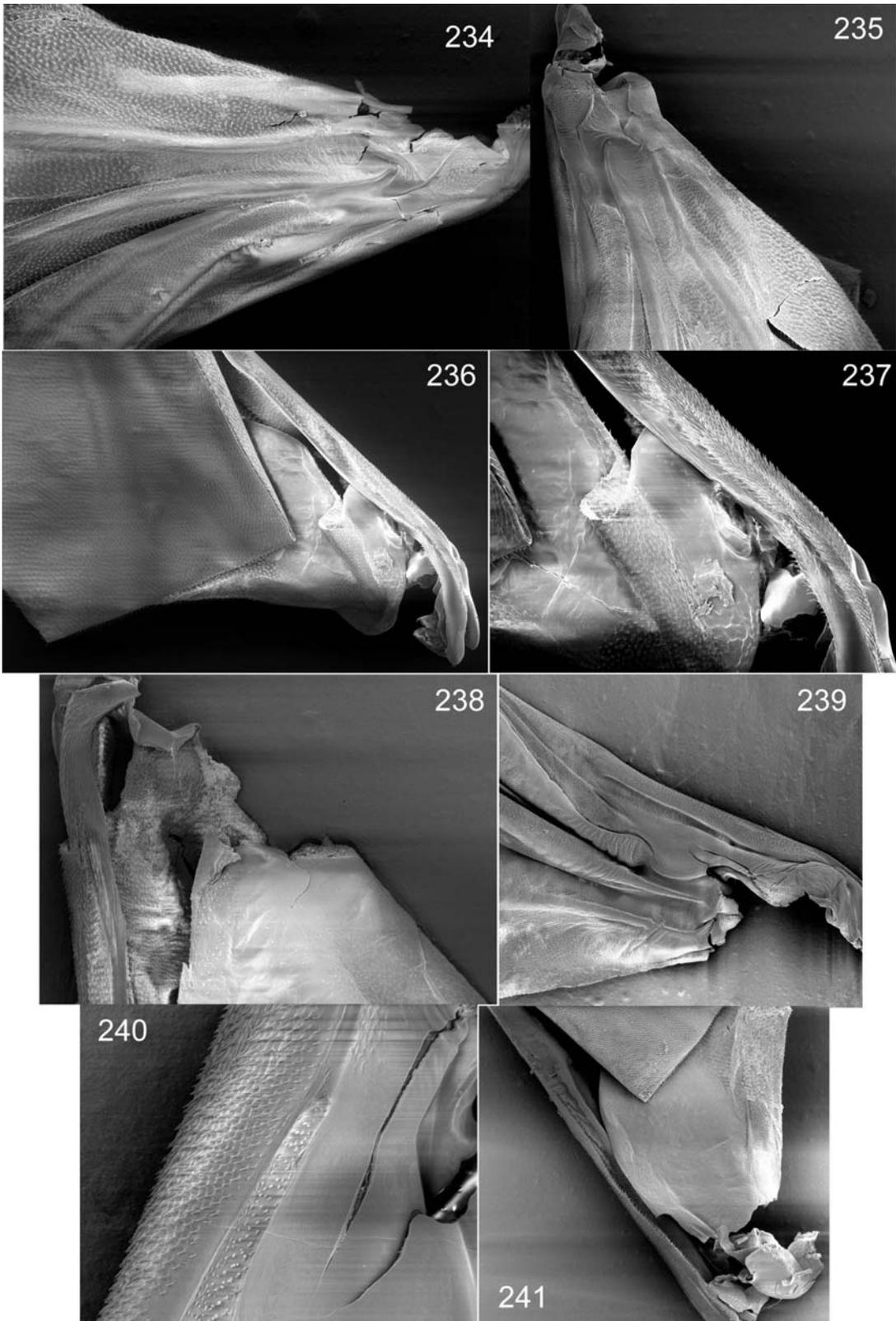


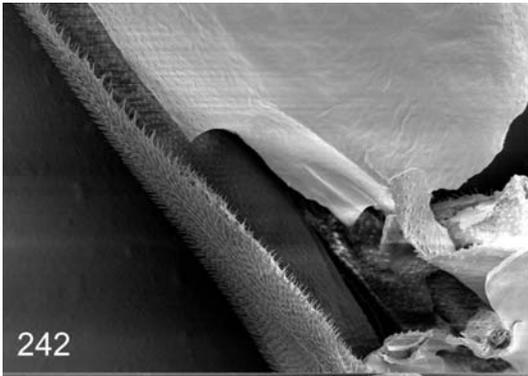








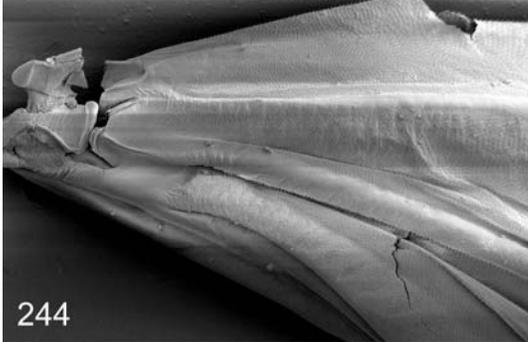




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## **Chapter VI: Mites associated with pro-thoracic horn cavities in baridine weevils (Coleoptera: Curculionidae)**

### **Abstract**

Mite (Acari) phoresy has been fairly well documented in insects and is known to occur in a number of beetle groups. While conducting a phylogenetic analysis of the weevil subfamily Baridinae, mites were found to be associated with the horn sheaths of a number of genera which also possess pro-sternal horns. While mites are commonly found associated with beetles, they have not been documented thus far in weevils. This association is briefly characterized and illustrated.

**Keywords:** Acari, horn sheath, phoretic, parasite host.

### **Introduction**

Mites have been found associated with a number of insect orders, including Hymenoptera most notably various groups of solitary and social bees (Engel 1996; Klimov *et al.* 2007; Michener 2000) and Formicidae (Eickwort 1990), Lepidoptera, Odonata (Andrés and Cordero 1998), Diptera, and Coleoptera (Silphidae, Curculionidae, Tenebrionidae, Staphylinidae, Scarabaeidae, Chrysomelidae, Carabidae, Lucanidae, Cerambycidae, Passalidae, Elateridae) among others (OConnor 1982). The list of insect-mite associations is slightly less among the more common associations with mites in Mesostigmata, and a comprehensive review can

be found in Hunter and Rosario (1988). Some mites have also been utilized as biological control agents towards other mites as well as towards some insect pests (McMurtry and Croft 1997). In Curculionidae, mites in Podapolipidae (Actinedida) have been recorded on the genus *Hylobius* (Molytinae; Thomas *et al.* 1967). Mesostigmatan mites have also been recorded to occur on extant weevils in Dryophthoridae, as well as on extinct dryophthorids (Davis and Engel 2006). It is assumed that mites are phoretic on weevils, as no documented cases of mutualism or parasitism with or on weevils exist to date. However, it is peculiar to note that many dryophthorids, both extant and extinct, appear to be found associated with similar mesostigmatan mites, those disc-like and flattened, indicating a long history of association with a restricted group of mites. Furthermore, the mites usually are found attached to the legs, often the hind legs.

It appears that no mites have been recorded to occur on weevils in the subfamily Baridinae, although this shortfall has likely been the result of a lack of researchers in this group. Through examination of 231 baridine genera (see Chapter 1) during a phylogenetic analysis, several baridine genera were noted to bear mites in their horn sheaths. Herein, mites of the suborder Mesostigmata are described to occur in the acarinarium/prothoracic cavity (horn sheath) of the baridine weevils *Camelodes leachii*, *Xystus ater*, *Orissus meigenii*, *Linonotus regalis*, *Linonotus distinctus*, *Nedestes sarpedon*, *Pseudosaldius conjunctus*, *Parasaldius longipes*, *Parasaldius sedulus*, *Dactylocrepis pinnatitarsis tubifera*, *Dimesus thoracicus*, *Nestrada inflatula*, and *Stegotes honestus*.

## **Materials and methods**

A few mites were removed from the weevil specimen and heated in KOH for approximately 10 minutes. The mites were subsequently mounted on a glass slide in Euparal mounting medium for digital photography. Digital photographs were blended using the montage software Combine Z, and SEM images were captured using a LEO 1550 FESEM.

## **Description of baridine-mite association**

Approximately 10 mite specimens (Figs. 7-16) were found attached to the cuticle of the concavity located between the prothoracic horns of the weevil specimens (Figs. 1-6). Many genera within Baridinae possess elongate horns projecting anteriorly, protruding from the prothorax ventrally, just anterior to the procoxae (Figs. 1-2). Many also possess a deep concavity (the horn sheath) between the pair of horns, although some only bear a shallow depression. It is in the horn sheath where the mites were found. Three to four mites were positioned near the rim of the concavity, while the remainder were attached along the bottom at the terminal end of the sheath (situated deep inside of the pronotum).

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### **Figure captions**

**Figs. 1-6.** Adult photos (ventral view), showing mites in horn sheaths. 1-3, *Camelodes leachii*; 4-5, *Orissus meigenii*; 6, *Xystus ater*.

**Figs. 7-10.** Photos of mites. 7-8, dorsal view; 9, enlargement of anterior region; 10, enlargement of posterior region.

**Figs. 11-16.** SEM's. 11, ventral view; 12, dorsal view; 13, enlargement of posterior region; 14, enlargement of anterior region; 15, dorsal view; 16, enlargement of posterior region and dorsal setae.

