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Delimiting baridine weevil evolution (Coleoptera: Curculionidae: Baridinae)

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Since the erection of the weevil subfamily Baridinae by Schönherr in 1836, no phylogenetic hypothesis using cladistic methods has been proposed for this extraordinarily diverse group. This study provides the first hypothesis for the evolution of Baridinae using phylogenetic methods, including 301 taxa and 113 morphological characters. Despite fairly well-resolved results, indicating paraphyly of nearly all of the currently recognized intrasubfamilial 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 and subsequent alteration of the current classification.

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ADDITIONAL KEYWORDS: character evolution – homoplasy – morphology – parsimony – phylogeny.

INTRODUCTION

Currently there are approximately 550 genera belonging to the subfamily Baridinae (Morimoto & Yoshihara, 1996), placed into nine tribes and 17 subtribes (Alonso-Zarazaga & 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 (1906–1909), Hustache (1938), Casey (1892, 1920, 1922), Bondar (1942, 1943a, b), Zherikhin & Gratshev (1995), and to a somewhat lesser extent Jekel (1865), Pascoe (1889), Voss (1958), Schönherr (1836), and LeConte & Horn (1876).

The subfamily was first erected by Schönherr (1836) through use of the subdivision *Baridides*. To date, Baridinae has changed in both name and rank several times. Casey (1922) divided Barinae (now Baridinae) 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, admitted that the limits amongst many of the tribes were indistinguishable, most likely because of his coarse examination of taxa and utilization of few characters.

Hustache's (1938) treatment divided Barinae into seven tribes (Table 1). LeConte & Horn (1876, 1883) regarded Baridinae as a tribe within Curculionidae, Barini, and divided the tribe into two groups, Barides and Centrini, based on the North American fauna. Much progress was made by Zherikhin & Egorov (1990) towards understanding higher-level relationships of Curculionidae. They recognized a much broader Baridinae *s.l.*, one containing five tribes, Baridini, Trigonocolini, Zygopini, Ceutorhynchini, and Orobitini. This division was based on the presence

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

Tribe	Subtribe
Ambatini Lacordaire, 1863	
Peridinetini Lacordaire, 1866	
Pantotelini Lacordaire, 1866	Pantotelina Lacordaire, 1866 Cyrionychina Casey, 1922
Optatini Champion, 1907	
Barini Lacordaire, 1866	Diorymerina Lacordaire, 1866 Coleomerina Casey, 1922 Coelonertina Casey, 1922 Eurhinina Lacordaire, 1866 Barina Schönherr, 1836
Centrinini Lacordaire, 1866	Centrinina Lacordaire, 1866 Madopterina Lacordaire, 1866 Apostasimerina Schönherr, 1836
Madarini Lacordaire, 1866	Lyterida Lacordaire, 1866 Leptoschoina Lacordaire, 1866 Eutoxina Champion, 1907 Madarina Lacordaire, 1866 Barymerina Lacordaire, 1866

Table 2. Current classification of Baridinae (*sensu* Alonso-Zarazaga & Lyal, 1999); authorship of Apostasimerina follows Prena (2009a)

Tribe	Subtribe
Ambatini Lacordaire, 1863	
Anopsilini Bondar, 1942	
Baridini Schönherr, 1836	Baridina Schönherr, 1836 Coelonertina Casey, 1922 Coleomerina Casey, 1922 Diorymerina Jekel, 1865 Eurhinina Lacordaire, 1866
Madarini Jekel, 1865	Madarina Jekel, 1865 Barymerina Lacordaire, 1866 Eutoxina Champion, 1908 Leptoschoinina Lacordaire, 1866 Tonesiina Alonso-Zarazaga & Lyal, 1999
Madopterini Lacordaire, 1866	Apostasimerina Schönherr, 1844 Madopterina Lacordaire, 1866 Thaliabaridina Bondar, 1943 Torcina Bondar, 1943 Zygobaridina Pierce, 1907
Nertinini Voss, 1954	
Optatini Champion, 1907	
Pantotelini Lacordaire, 1866	Cyrionychina Casey, 1922 Pantotelina Lacordaire, 1866
Peridinetini Lacordaire, 1866	

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 lateroventral margin of the elytron, and the fusion of the metepimeron and the metepisternum. In a slightly later publication, Zherikhin & Gratshev (1995) proposed a similar classification as had Zherikhin & Egorov (1990), but recognized Baridinae as a family, Barididae, and divided it into five subfamilies, Baridinae, Ceutorhynchinae, Trigonocolinae, Orobitinae, and Zygopinae. They also proposed Brachyceridae (including Dryophthoridae) 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 & Egorov (1990). Although many of the hind-wing synapomorphies, proposed by Zherikhin & Gratshev (1995), for Barididae are fairly precise, such as the cu-a (Cubital-Anal) 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 (radiomedial vein) in Baridinae *s.s.* (which can actually be present in a few genera). Oberprieler *et al.* (2007) followed the classification proposed by Zherikhin & Gratshev (1995), while also noting that this classification also brings together groups that share other features, such as the ascending metepisternum. These features certainly are informative of close relationships amongst the four groups mentioned above, and may be indicative of a larger cohesive groupingOberprieler *et al.* (2007) also mention, however, that none of the characters used by Zherikhin & Gratshev (1995), nor by any previous authors who have proposed classifications of baridine weevils, have been tested in a phylogenetic analysis. Thus if they do signify a broader grouping, without testing these and additional hypotheses of homology in a phylogenetic framework, the taxonomic ranks of these groups will continue to be debated and will remain controversial.

The current, most widely accepted classification of Baridinae is in the strict sense and is based on Alonso-Zarazaga & Lyal (1999). It largely follows the classification system of Hustache (1938), and divides a total of 546 genera into nine tribes (including 17 *incertae sedis* genera; Table 2). Despite the wide use of Alonso-Zarazaga & Lyal's system, though, more recent works have suggested additional tribes that should be recognized within the classification system of Baridinae (Prena 2009a, b).

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 (Zherikhin & Egorov, 1990; Zherikhin & Gratshev, 1995; Alonso-Zarazaga & Lyal, 1999; 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. As a result of 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.

This study follows a treatment of baridine morphology (Davis, 2009) that may serve as a reference, particularly for character terminology used heretofor; it more thoroughly explains the morphological characters used here and examines in detail other plausible, phylogenetically informative characters.

MATERIAL AND METHODS

Taxon sampling (Appendix 1)

Following Alonso-Zarazaga & Lyal (1999), species were sampled from each of the nine tribes and 16 of the 17 subtribes in Baridinae [taxa for Apostasimerina (tribe Madopterini) were not examined], with a total of 283 baridine species, representing 231 genera, included in the analysis (Table 1). A total of 29 species was sampled for the outgroup, consisting of 12 subfamilies outside of Baridinae. As a result of ambiguity in hypothesized sister-groups to Baridinae, a range of outgroups were included in an attempt to produce a stronger inference (Nixon & Carpenter 1993). The final analysis included a total of 301 taxa (Appendix 1). Outgroup selection was based on phylogenies produced by Marvaldi *et al.* (2002), and previous baridine classifications by Zherikhin & Egorov (1990), and Zherikhin & Gratshev (1995).

Taxa were borrowed from the following institutions:

USNM – National Museum of Natural History (United States National Museum), Smithsonian Institution, Washington, DC, 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 carried out 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 performed for those males.

For body dissections, specimens were first relaxed by soaking them in warm water for ~10–15 min, 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 glycerine, as digesting was not required for these parts. The remaining dissected parts were digested in a weak (~10%) KOH solution for 10–15 min, 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 eighth tergum. After dissections were completed, all parts were stored in glycerine.

Mouthpart dissection

Following dissection of the body, the head was digested further in 10% KOH for ~15–30 min, 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 maxillae 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 scanning electron microscopy (SEM) images were captured using a LEO 1550 FESEM (Field Emission Scanning Electron Microscope). 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 > 2× width (0); round, spherical – length 2× 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); dorsoventrally compressed (1)

In the lateral view, adult body shape can be wide or round (Figs 3, 4) or dorsoventrally 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 character 1, where the dorsal surface, including the pronotum, becomes 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 three conditions: the pronotum may be narrower than the elytra (Fig. 6), as viewed dorsally, 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, although 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 often produces 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, producing a small, smooth groove.

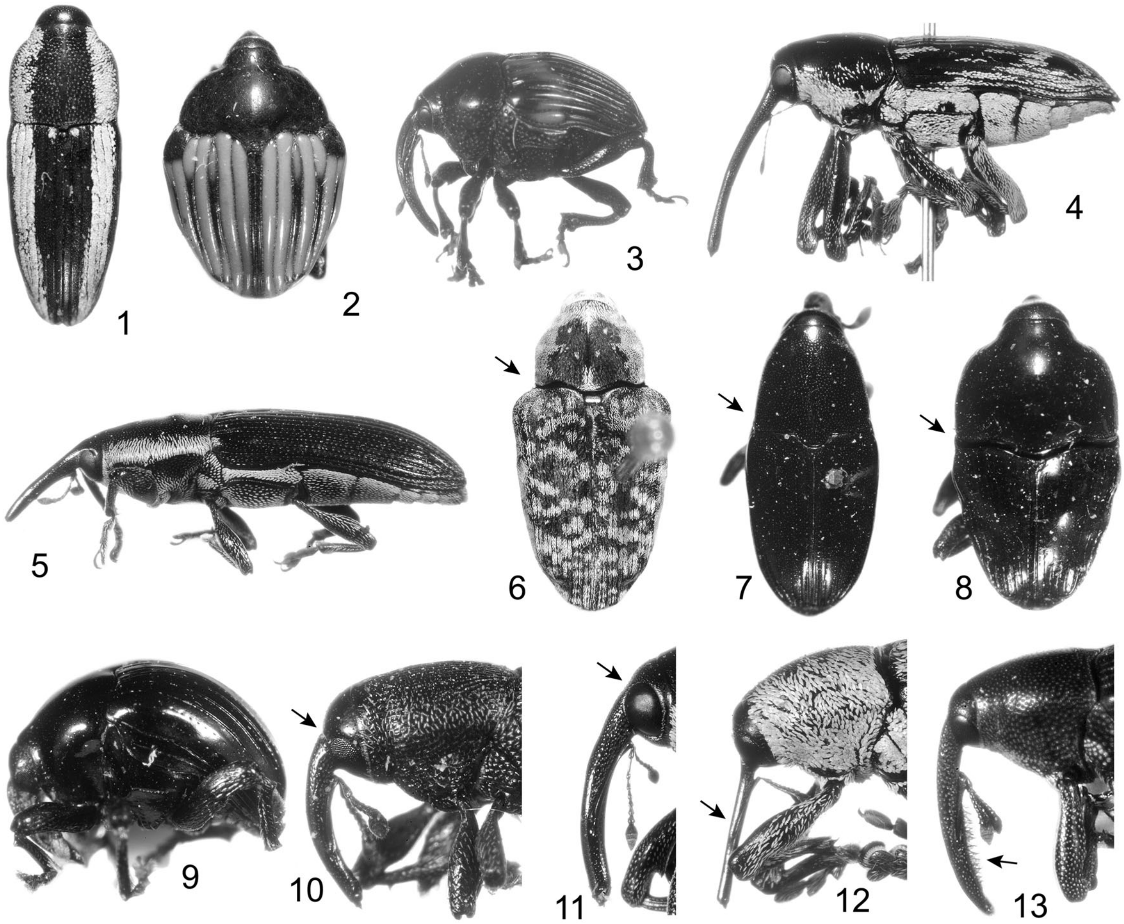
6. Rostrum, setae along ventral margin (males only):
Absent (0); present (1)

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

7. Rostrum, shape (lateral view):
Enlarged basally (0); width subequal along entire length (1); wide basally, gradually narrowing apically (2)

Although 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 medially, or entirely cylindrical and subequal throughout the length (Fig. 12).

8. Rostrum, shape (lateral view):
Robust, short (0); narrow, long (1)



Figures 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), showing narrower posterior region of the prothorax in comparison to elytral humeri; 7, *Loboderes citriventris* (dorsal view), showing relatively equal width of posterior region of the prothorax and elytral humeri, creating a smooth/flush junction; 8, *Madarellus laticollis* (dorsal view), showing a relatively larger posterior region of the prothorax in comparison to elytral humeri and also creating a smooth/flush junction; 9, *Prodinus* sp. (lateral view). 10–13, adult head and rostrum, lateral view. 10, *Centrinogyna strigata*, showing a small cleft at the rostrum-head junction; 11, *Pardisomus biplagiatus*, showing smooth rostrum-head junction; 12, *Strongylotes squamans*, showing cylindrical rostrum that is approximately equal in width along its length; 13, *Myctides imberbis*, showing elongate setae on apicoventral margin of male rostrum.

This character can be particularly ambiguous given the large amount of variation in rostrum lengths and widths. In general, a short rostrum is one that is much shorter than the longitudinal length of the pronotum, usually three-quarters to half of the length of the pronotum. Long generally applies to a rostrum that is equal in length to or longer than the pronotum.

9. Rostrum, curvature:

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

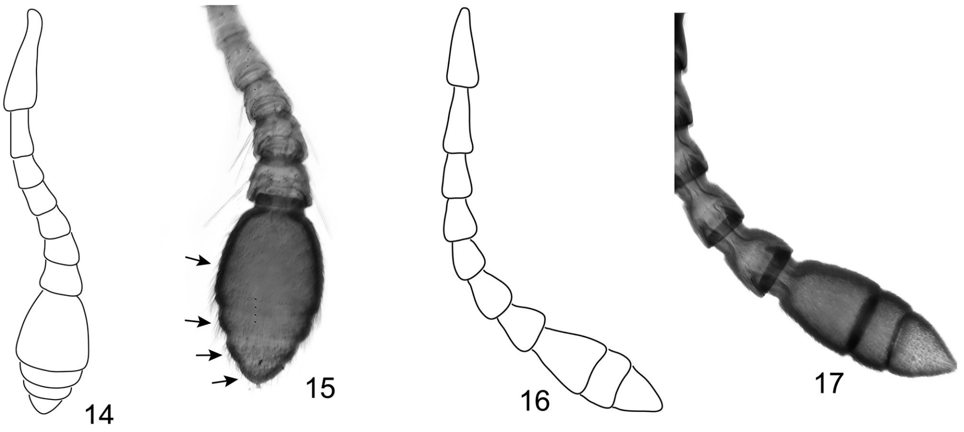
Characterizing the curvature of the rostrum can be quite difficult. No ambiguity is faced when the rostrum is straight or sublinear. The point at which the rostrum changes from being broadly curved to strongly curved is not usually obscure. Most genera possess a rostrum that is broadly curved. Rostra that are strongly curved often are not elongate or greater in length than the length of the pronotum, and the apex of the rostrum 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 at the middle usually allows for a small error range.



Figures 14–17. Antennae. 14–15, *Oligolochus bracatus*; 15, enlargement of apical end, showing three articles with third article annulated, giving the appearance of four articles; 16–17, *Camelodes leachii*; 17, enlargement of apical end.

Thus, antennae that 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:
Six (0); seven (1); three (2)

The number of funicular articles in Baridinae is always seven, whereas outgroups possess varying numbers.

12. Antenna, number of club articles:
Appearing as four (0); three (1)

The number of club articles in Baridinae appears to vary between three (Figs 16, 17) and four (Figs 14, 15), as in the outgroups; however, it is unsure if the apical 'fourth article' in Baridinae is the result of an annulated third article.

13. Antenna, club:
Round, globose, 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 three 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; in between these two states is the typical (normal) form of the baridine club, in which the articles typically are not compacted but are slightly longer. Only a few outgroups do 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, although not dependent, is the shape formed by the association of the funicle and club. Often, although not always, when the club articles are short and compact, the funicular articles may also be compact and relatively wide, approximately similar in width to the club, and form a smooth lateral margin 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 character 13, although it is useful in distinguishing clubs with short or long articles. A compact club is always composed of short articles (Fig. 14), and an elongate club is always composed of long articles; however, a 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 that 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 close to the eye and does not touch it, but in some taxa it actually meets the surface of the compound eye's anterior margin.

MOUTHPARTS

17. Mandibles, dentition:
Pseudomonodentate (molar region fused with primary incisor) (0); monodentate, with a small notch

separating the large incisor from the molar region (1); bidentate, with two large, apical teeth, and a molar region (2); tridentate, with three 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 monodentatation, one in which the mandible possesses a distinct incisor and molar region (monodentate) and the other (pseudomonodentate) in which the molar region is fused with the incisor (Fig. 23) and the dentation lost. Mandibles may also bear two (Fig. 21) or three incisors (Figs 18–20, 22). Only outgroups have mandibles that 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); incisors subequal (2)

Regarding incisor size, the primary incisor may be largest in both forms of monodentate mandibles (Fig. 23) and also 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 subjective 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 orientated linearly in mono-, bi-, or tridentate mandibles (Figs 22, 23). The primary incisor is always linear in monodentate 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 or row (Figs 24, 25), a dense, scattered grouping throughout the palpiger (Fig. 26), or a sparse, small grouping largely restricted to the apico-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 or row (Figs 29, 30) or randomly scattered, forming no specific orientation (Figs 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 centre of the frons (Fig. 33).

24. Compound eyes:
Elongate along anteroventral surface (0); round, large along anterior surface (1); teardrop-like, large along anterior surface (2); round, bulging along anteroventral surface (3); round along anteroventral 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 subcircular. Also in the outgroups, the eyes may be teardrop-shaped, in which the dorsal margin is more rounded and the ventral margin angled (Conoderinae), or round and bulging from the head (Ceutorhynchinae).

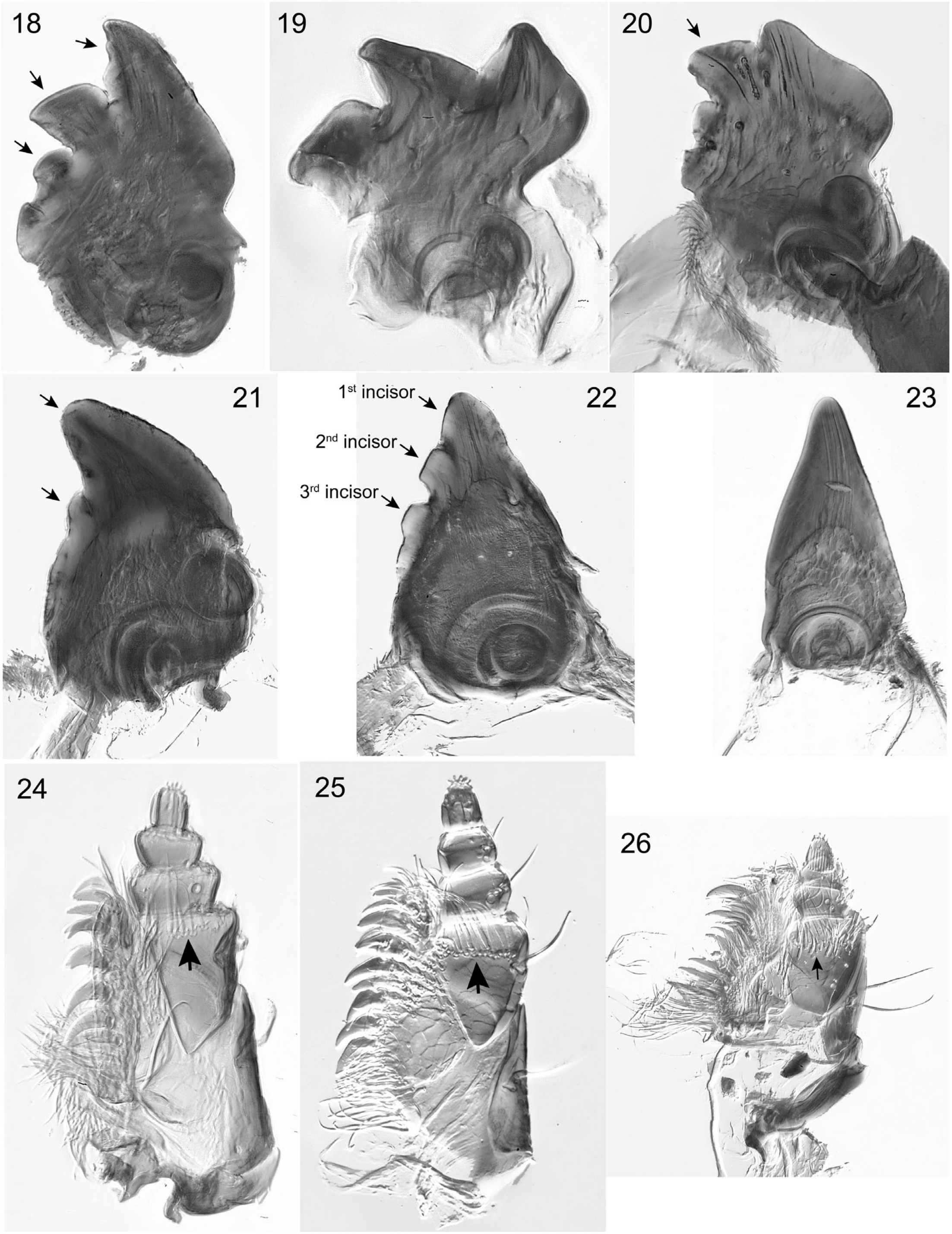
PROTHORAX

25. Prothorax:
Normal, proportional to abdomen (0); enlarged (1)

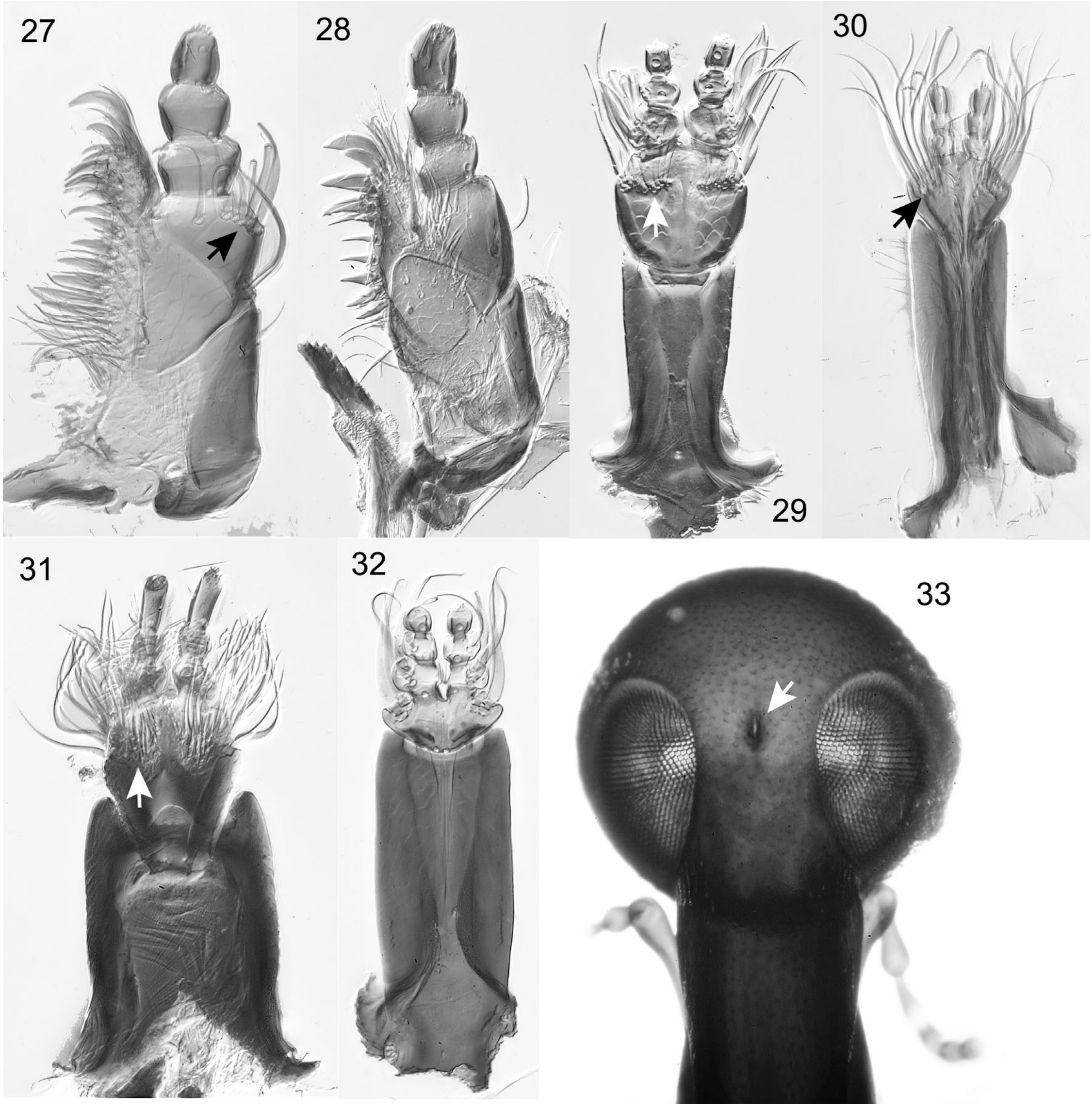
The prothorax may be proportional in size to the abdomen (and elytra), in which it often is smaller than the abdomen (Figs 6, 7), or it may be enlarged (Fig. 8).

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



Figures 18–26. Mouthparts. 18, *Oligolochus ornatus*, right mandible, showing tridentate mandible in which the first incisor is largest; 19, *Plocamus clavisetes*, right mandible, showing tridentate mandible in which all incisors are subequal in size; 20, *Eisonyx opaca*, right mandible, showing tridentate mandible in which the second incisor is largest; 21, *Parallelosomus amplitarsis*, right mandible, showing bidentate mandible in which the first incisor is largest; 22, *Torcus nigrinus*, right mandible, showing tridentate mandible in which the first incisor is largest; 23, *Coleomerus boliviensis*, right mandible, showing monodentate mandible produced by fusion of incisors and molar region; 24, *Oligolochus bracatus*, right maxilla, showing distinct row of setae near distal margin of palpiger; 25, *Anthinobaris* sp., right maxilla, showing distinct row of setae near distal margin of palpiger; 26, *Loboderes citriventris*, right maxilla, showing a rather scattered positioning of setae near distal margin of palpiger.

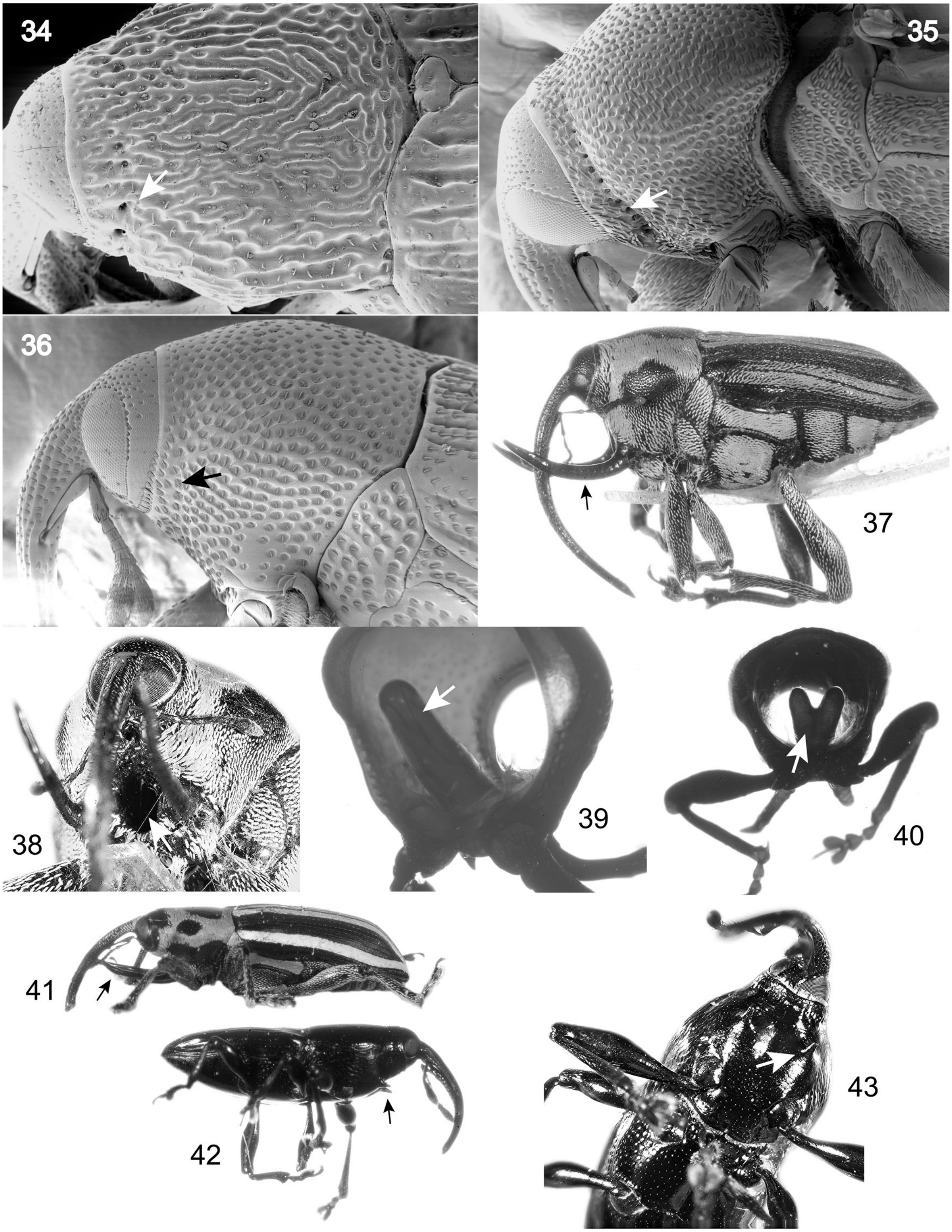


Figures 27–33. 27–32, mouthparts. 27, *Linogeraeus viduatus*, right maxilla, showing restricted patch of setae near distal margin of palpiger; 28, *Xystus ruficollis*, right maxilla, showing restricted patch of setae near distal margin of palpiger; 29, *Anthinobaris* sp., labium, showing distinct row of setae near distal margin of prementum; 30, *Linogeraeus viduatus*, labium, showing distinct row of setae near distal margin of prementum; 31, *Loboderes citriventris*, labium, showing rather scattered positioning of setae near distal margin of prementum; 32, *Microcholus punticollis*, labium, showing rather scattered positioning of setae near distal margin of prementum; 33, *Peridinetus irroratus*, head and rostrum (anterior aspect), showing foramen at centre of frons.

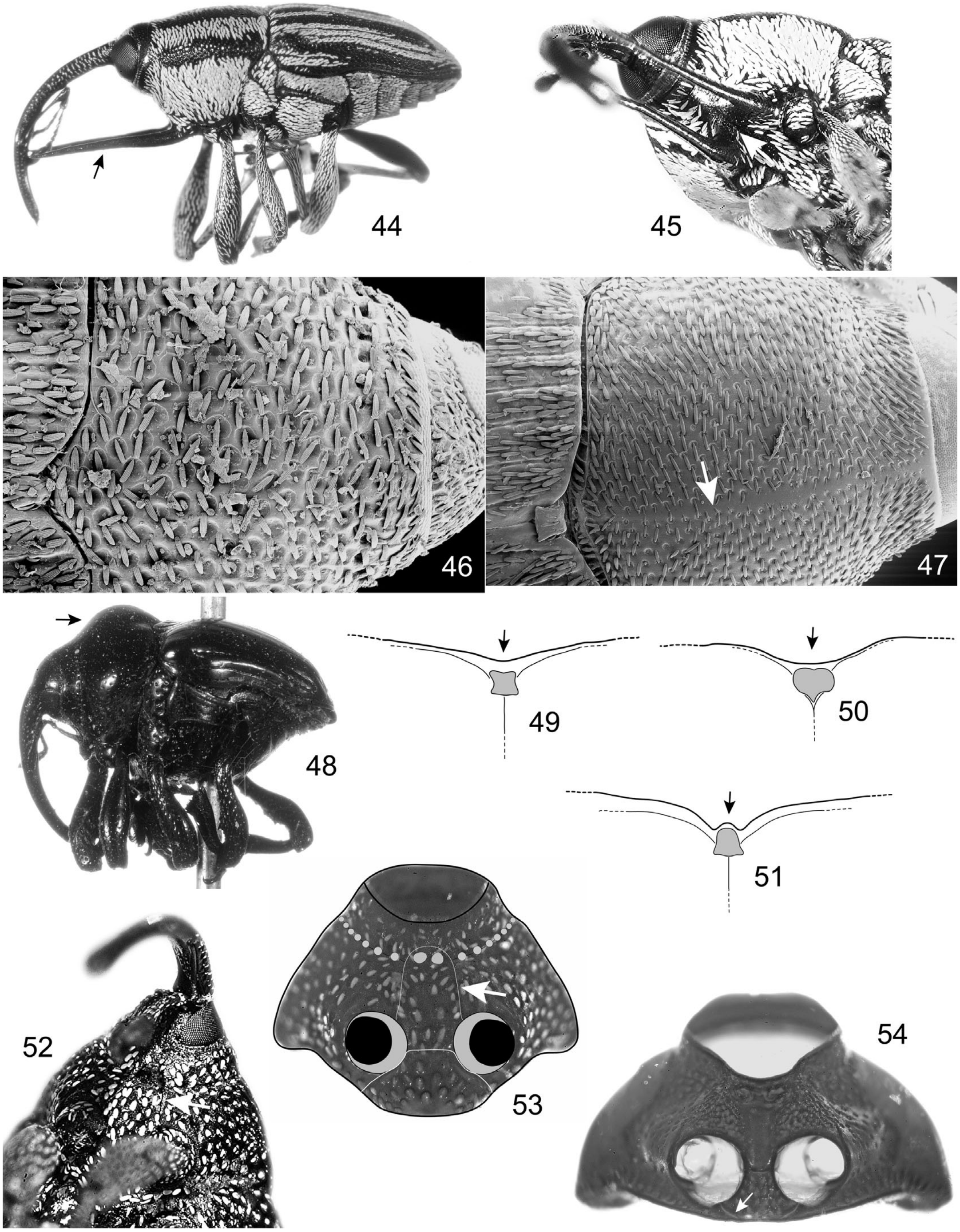
and deep (Figs 34, 35) or small and reduced in size and depth (Fig. 36). In a restricted number of baridines, but mostly in sister-groups, this puncture collar is often absent.

27. Thorax, prosternal horns in males:
Horns present, long, horn sheath simple and deep (0); horns absent (1); horns present, long, horn sheath bifurcate and deep (2); horns present, long, horn sheath shallow/absent (3); horns present, short, horn sheath shallow/absent (4); horns present, fused, and long, horn sheath simple and deep (5)

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



Figures 34–43. 34, *Pertorcus* sp., showing enlarged punctures along collar of prothorax and irregular longitudinal ridges on pronotum; 35, *Odontocorynus creperus*, showing enlarged punctures along collar of prothorax; 36, *Pachybaris porosa*, showing small punctures along collar of prothorax. 37–38, *Centrinus curvirostris*. 37, adult male (lateral view), showing elongate prosternal horns; 38, prosternum, showing horn sheath; 39, *Orissus meigenii*, showing simple horn sheath of male; 40, *Demoda vittata*, showing bifurcate horn sheath of male; 41, *Demoda vittata*, adult male (lateral view), showing elongate/well-developed prosternal horns; 42–43, *Eutoxus* sp.; 42, adult male (lateral view), showing short/weakly developed prosternal horns; 43, showing prosternal horns in ventral view and absence of horn sheath.



Figures 44–54. 44–45, *Geraeus lineellus*. 44, adult male (lateral view), showing elongate/well-developed prosternal horns; 45, prosternum, indicating absence of horn sheath; 46, *Catapastus squamirostris*, scanning electron micrograph (SEM) of pronotum without longitudinal smooth line; 47, *Trichodirabius longulus*, SEM of pronotum showing longitudinal smooth line; 48, *Vallius sulcatus*, adult lateral view, showing developed convexity on pronotum; 49–51, posterior margin of pronotum and mesoscutellum. 49, *Trichodirabius longulus*, showing fairly linear posterior margin of pronotum with only slight convexity; 50, *Pycnogeraeus modestus*, showing posterior margin of pronotum with broadly rounded convexity at middle; 51, *Pertorcus* sp., showing protrusion at posterior margin of pronotum with small notch for reception of mesoscutellum; 52–53, *Zygobaris nitens*. 52, prosternum (photograph), showing lateral carina along shallow ventral depression; 53, prosternum (illustration), showing lateral carina along shallow ventral depression; 54, *Xystus ruficollis*, prosternum (mesosternal process), indicating suture at sternellum-hypomeron junction.

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 that 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 or hump (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), although 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, broadly rounded protrusion in the middle (Fig. 50), which may also have a small concavity in the centre (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 that 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 a 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, a ventral-most pair of punctures may be particularly enlarged and deep (Figs 52, 53).

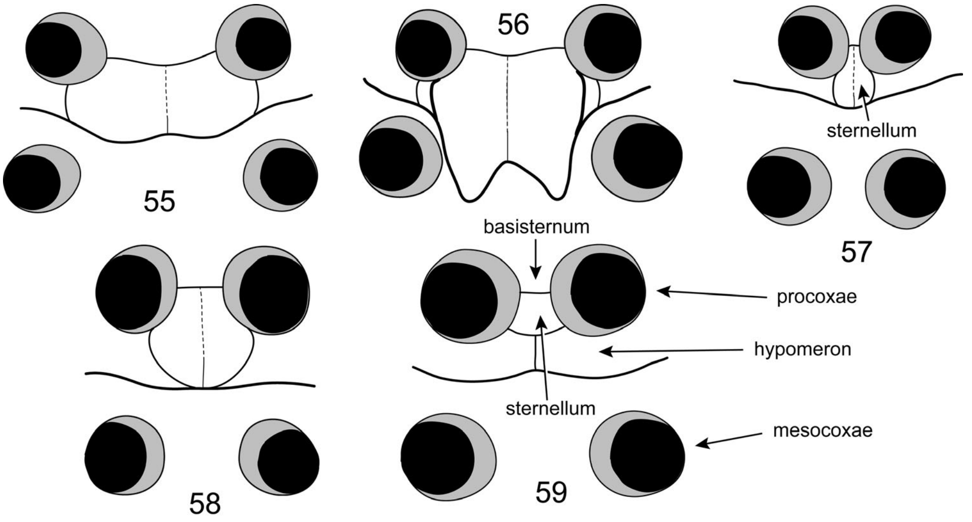
36. Thorax, prosternal process:
Posterior margin straight and formed by hypomeron (0); produced, truncate, posterior margin broadly rounded and formed by sternellum (1); produced, V-shaped, posterior margin formed by sternellum (2); posterior margin with slight concavity and formed by sternellum (3); posterior margin with small notch, truncate, and formed by hypomeron (4); posterior margin with obtuse point medially and formed by sternellum (5); posterior margin with slight concavity and formed by hypomeron (6)

The prosternal process (Figs 53–59) may be produced and truncate with the posterior margin broadly rounded (Fig. 53) or V-shaped (Fig. 56). In these developed and produced cases, the hypomeron is discontinuous, interrupted mesally by the sternellum, in which case the sternellum mostly forms the prosternal process. The prosternal process can also be rather weakly developed and relatively straight (Figs 54, 58), pointed (Fig. 57), with a small, median notch, or concave. The concave condition can be formed either by the hypomeron (Fig. 59) or extension of the sternellum (Fig. 55). In these weakly developed conditions, the hypomeron often forms the posterior margin of the prosternal process (Fig. 59), and the sternellum is often not produced and does not interrupt the hypomeron from joining mesally; however, the case in which the sternellum divides the hypomeron is common too in these conditions. Of course there are also many intermediate conditions.

COXAE

37. Procoxae, intercoxal distance:
Procoxae separated by < 1× diameter of coxa (0); procoxae separated by ~1× diameter of coxa (1); procoxae separated by > 1× diameter of coxa (2); procoxae touching (3)

38. Mesocoxae, intercoxal distance:
Mesocoxae separated by < 1× diameter of coxa (0); mesocoxae separated by ~1× diameter of coxa (1); mesocoxae separated by > 1× diameter of coxa (2)



Figures 55–59. Prosterna (prosternal process). 55, *Limnobaris calandriformis*, prosternal process formed by extension of the sternellum; 56, *Loboderes citriventris*, prosternal process formed by extension of the sternellum; 57, *Madopterus talpa*, posteromedial margin of prosternal process formed by sternellum and remainder of posterior margin formed by hypomeron; 58, *Parallelosomus amplitarsis*, posterior margin of prosternal process mostly formed by hypomeron, with sternellum just reaching posteromedial margin; 59, *Peridinetus cretaceus*, prosternal process formed by hypomeron.

39. Metacoxae, intercoxal distance:
Metacoxae separated by < 1× diameter of coxa (0); metacoxae separated by ~1× diameter of coxa (1); metacoxae separated by > 1× 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 possess this character.

41. Thorax, mesepimeron:
Not ascended (not visible dorsally) (0); ascended (visible dorsally) (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 (the latter state usually occurs when the derm is largely glabrous).

43. Thorax, sclerolepidia – shape:
Flat (digitate type), small (0); projecting (peg-like type), large (1); absent (2); feather-like, hair-like (plumose type) (3); multi-furcate (digitate type with ~eight digiti of unequal lengths), string-like (4)

Baridines only possess sclerolepidia of the digitate type (Fig. 60) and peg-like type (Fig. 61), whereas all types can be found in the outgroups (Lyal *et al.*, 2006).

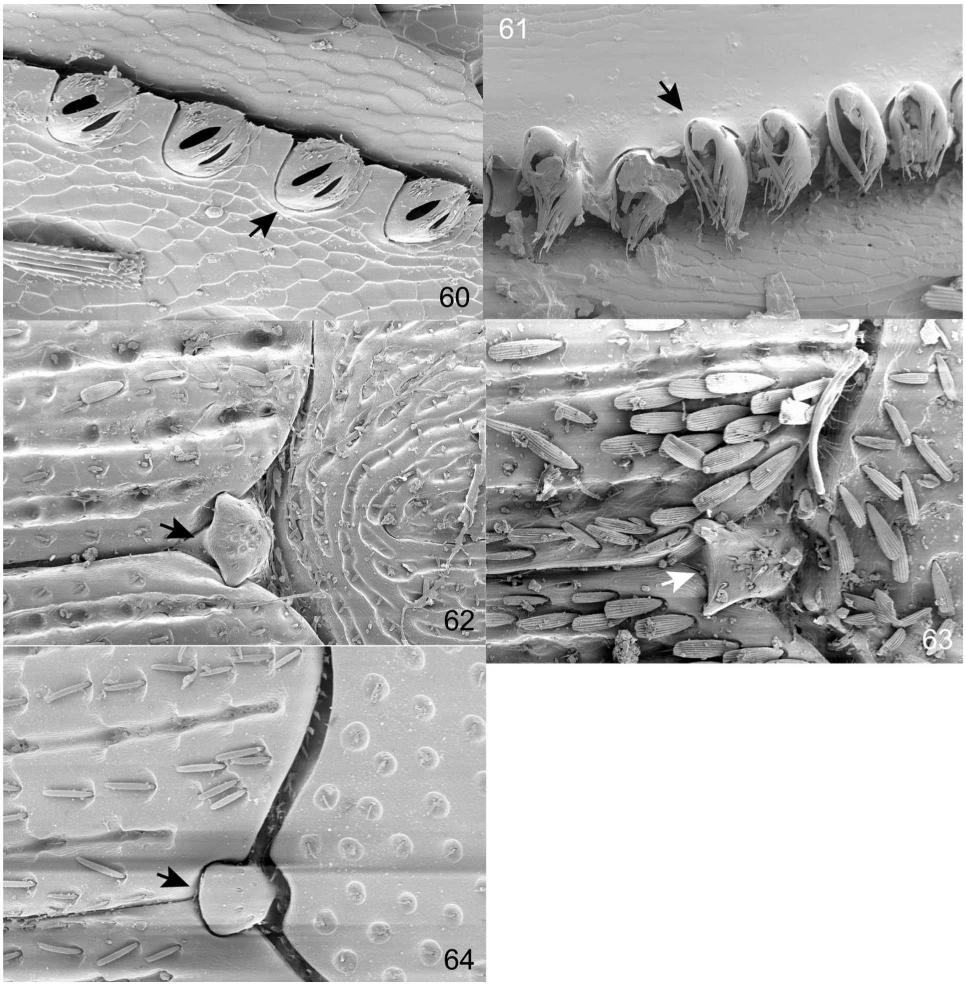
MESONOTUM

44. Mesonotum, mesoscutellum – 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 characterize and 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 and subjective.

45. Mesonotum, mesoscutellum – 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 subtlety appears sometimes between states. In general, the anterior margin may



Figures 60–64. 60, *Zygobarella zanthoxyli*, showing digitate sclerolepidia (scanning electron micrograph, SEM); 61, *Lydamis cinnamomeus*, showing peg-like sclerolepidia (SEM). 62–64, mesoscutella. 62, *Pertorcus* sp., showing posterior margin with central projecting; 63, *Pycnogeraeus striatirostris*, showing posterior margin with concavity; 64, *Pachybaris porosa*, showing rounded posterior margin.

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, truncate, no protrusion (2); quadrate protrusion (3)

Baridinae only possess states 0 and 1, where the posterior margin is triangular, having concave anterolateral margins. States 2 and 3 occur in sister-groups, such as Conoderinae and Ceutorhynchinae, 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 anterolateral margins of the mesonotum are broadly concave, the posterior margin forms an acute apex. When the anterolateral margins are more deeply concave, the posterior margin forms a more projecting, lobed apex.

47. Mesonotum – punctures on mesoscutum:
Only along anterior margin of mesoscutum (0); throughout mesoscutum (1); absent (2)

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

48. Mesonotum – posterior margin of mesoscutum:
With small notch/V-shape at posterior margin of longitudinal mesothoracic suture (0); no notch at posterior margin of longitudinal mesothoracic suture, posterior margin linear and smooth (1); no notch at

posterior margin of longitudinal mesothoracic suture, with two concavities on either side of suture along posterior margin of mesoscutum (2)

Along the posterior margin of the mesoscutum, a notch or small invagination may be present at the posterior apex of the longitudinal mesothoracic suture (Fig. 65). Alternatively, this notch may be absent, where the posterior margin of the mesoscutum is smooth and continuous (Fig. 66). Outgroup taxa tend to possess state 2.

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, ventral lobes absent (3)

The pair of lobes on the ventral margin of the prescutum (when viewing the metanotum anteriorly) may have a shallow concavity (Fig. 67) or a deep concavity that reaches the ventral 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, weakly developed (1); present, strongly 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), weakly developed (Figs 71, 74), or absent (Fig. 72).

51. Metanotum, scutellar groove – longitudinal crest:
Absent (0); present, weakly developed (1); present, strongly 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, although its presence is quite scattered across taxa. When present, it may be strongly developed and enlarged (Fig. 69, 72) or weakly developed 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 some outgroups is it found to be angular and 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 – posterolateral margin:
With acute, projecting lobe (0); without lobe, margin broadly rounded (1)

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

55. Metanotum, metascutellum – line reaching from metascutum to alacrista (metascutellar line):
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).

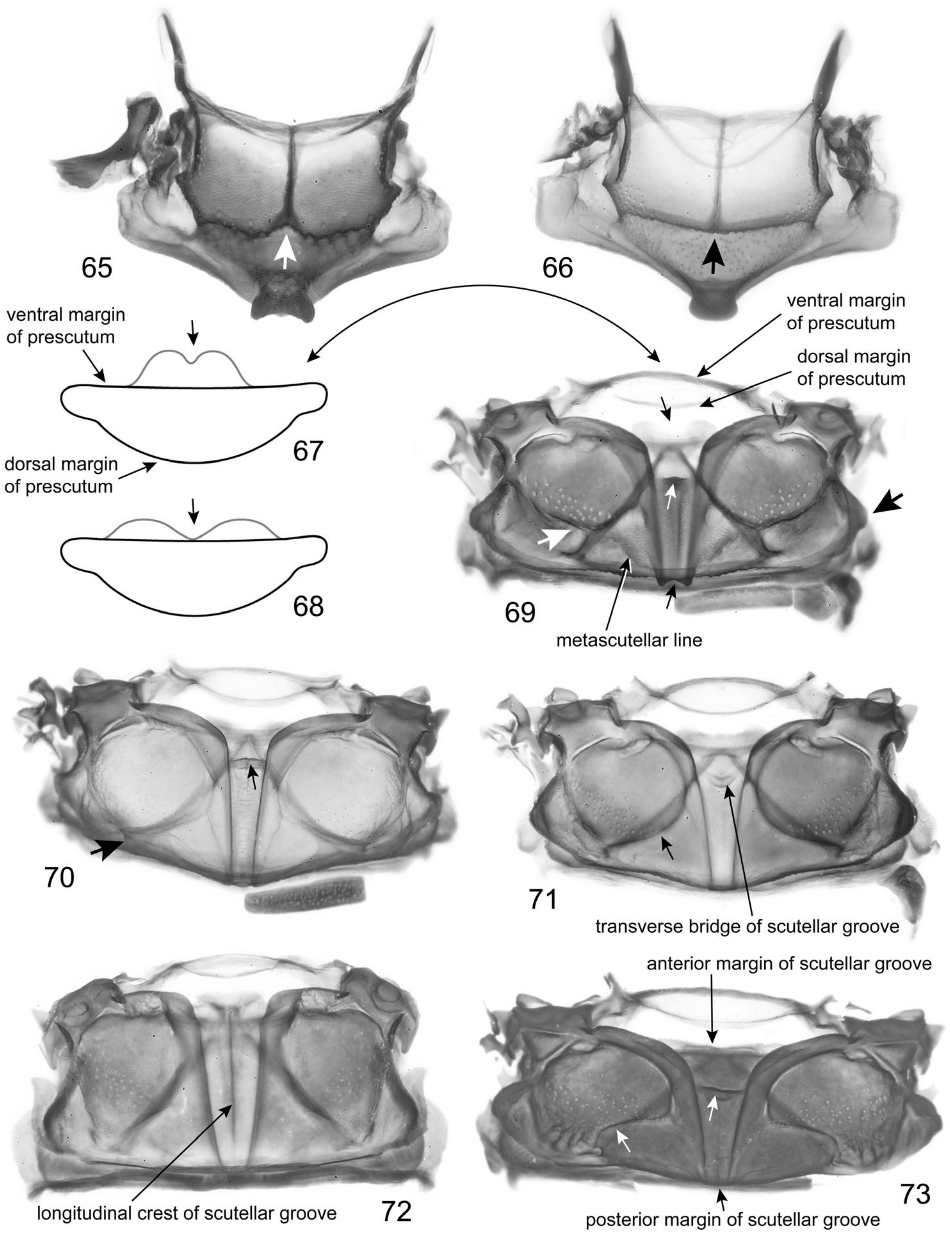
56. Metanotum, metascutum – posteromedial margin:
Straight, shallowly concave (0); concave (1); convex (2); quadrate (3)

In Baridinae, the posteromedial margin of the metascutum may be relatively straight (Fig. 72), concave (Figs 73, 74), or convex (Figs 69–71). A characteristic of many outgroup taxa (such as in Conoderinae and Ceutorhynchinae) is a quadrate shape of this margin.

57. Metanotum, metascutum – posterior margin:
With definite margin separating it from posterior margin of the metanotum (0); with indefinite margin, merging with posterior margin of metanotum (1)

In Baridinae, the metascutum may be well defined, with a distinct posterior margin separating it from the posterior of the metanotum and/or the metascutum is widely separate from the posterior margin of the metanotum (Fig. 69). Alternatively, the metascutum may have an indistinct margin, in which case 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)



Figures 65–73. 65, *Pycnogeraeus ochraceus*, mesoscutum with small notch at posterior apex of longitudinal mesothoracic suture; 66, *Garnia* sp., showing smooth/ linear posterior margin of mesoscutum (lacking notch); 67–68, generalized types of prescuta. 67, large pair of lobes along ventral margin of prescutum with shallow central concavity; 68, small pair of lobes along ventral margin of prescutum with central concavity reaching ventral margin. 69–73, metanota. 69, *Leptoschoinus fucatus*, indicating lobe at anterior margin of scutellar groove with central concavity, anterior of scutellar groove with developed bridge, posterior margin of scutellar groove developed, concave, and projecting beyond posterior margin of metanotum, posterolateral margins of metanotum with developed lobe/projection, metascutum that is widely separated from posterior margin of the metanotum, a rounded, convex posteromedial margins of the metascutum, and presence of metascutellar lines; 70, *Garnia* sp., indicating anterior of scutellar groove with developed bridge and posterior margin of the metascutum that is narrowly separated from posterior margin of the metanotum; 71, *Centrinus curvirostris*, showing weakly developed bridge at anterior of scutellar groove and rounded posteromedial margins of metascutum; 72, *Peridinetus irroratus*, showing well-developed longitudinal crest of the scutellar groove; 73, *Camelodes leachii*, showing relatively straight anterior and posterior margins of the scutellar groove, well-developed bridge at anterior of scutellar groove, and concave posteromedial margins of metascutum.

The metascutum may bear large (Fig. 69), small, or no 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), although 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 may become subjective.

METENDOSTERNITE

60. Metendosternite – longitudinal flange:
Long (0); short (1)

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

61. Metendosternite – metafurcal arm:
Bifurcate (0); simple (1)

62. Metendosternite – stalk:
Longitudinally elongate (0); quadrate (1); transversely elongate (2)

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

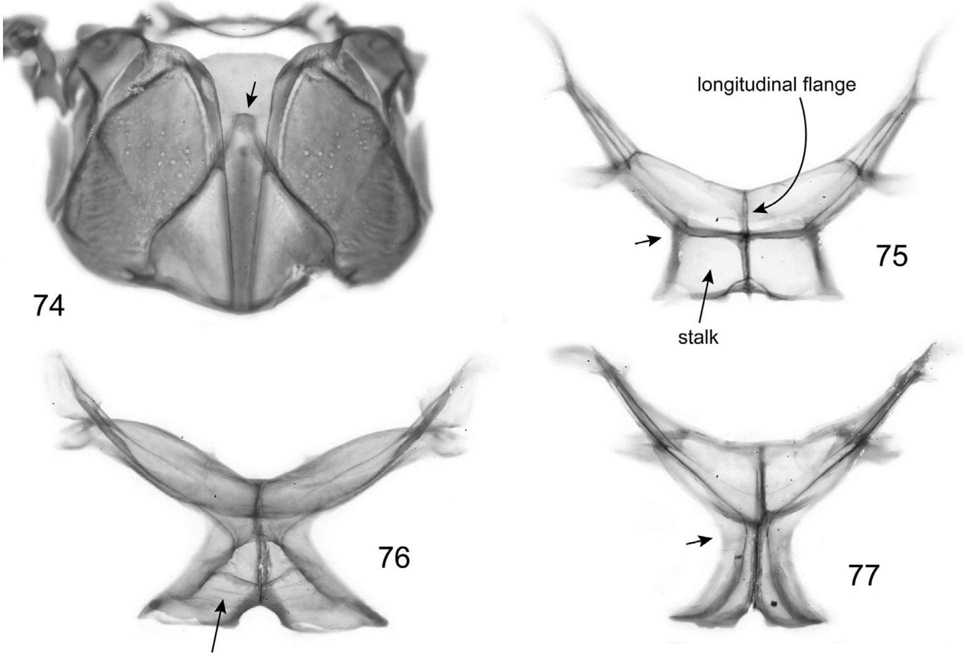
63. Metendosternite – anterior metafurcal tendons:
Closer to longitudinal suture (0); closer to metafurcal arm (1); in middle (2)

64. Metendosternite, shape:
Quadrate (transversely or longitudinally quadrate) (0); longitudinally elongate, stalk elongate and curved (1)

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

65. Metendosternite, hemiductus:
Developed, produced (0); weakly developed, small (1)

Most Baridinae possess a large, produced hemiductus (Figs 75–77), although a few, including many outgroup taxa, bear a small, weakly developed hemiductus.



Figures 74–77. 74, *Madopterus talpa*, metanotum, showing weakly developed bridge at anterior of scutellar groove; 75–77, metendosternite. 75, *Leptoschoinus fucatus*, showing relatively quadrate stalk; 76, *Pardisomus biplagiatus*, showing relatively short stalk; 77, *Madopterus talpa*, showing elongate, curved stalk.

LEGS

66. Thorax, legs – pre-tarsal ungues (claws):
Connate, parallel (0); separate, diverging (1); only one claw present (2); separate, with two large central teeth between ungues (3); separate, widely diverging (4)

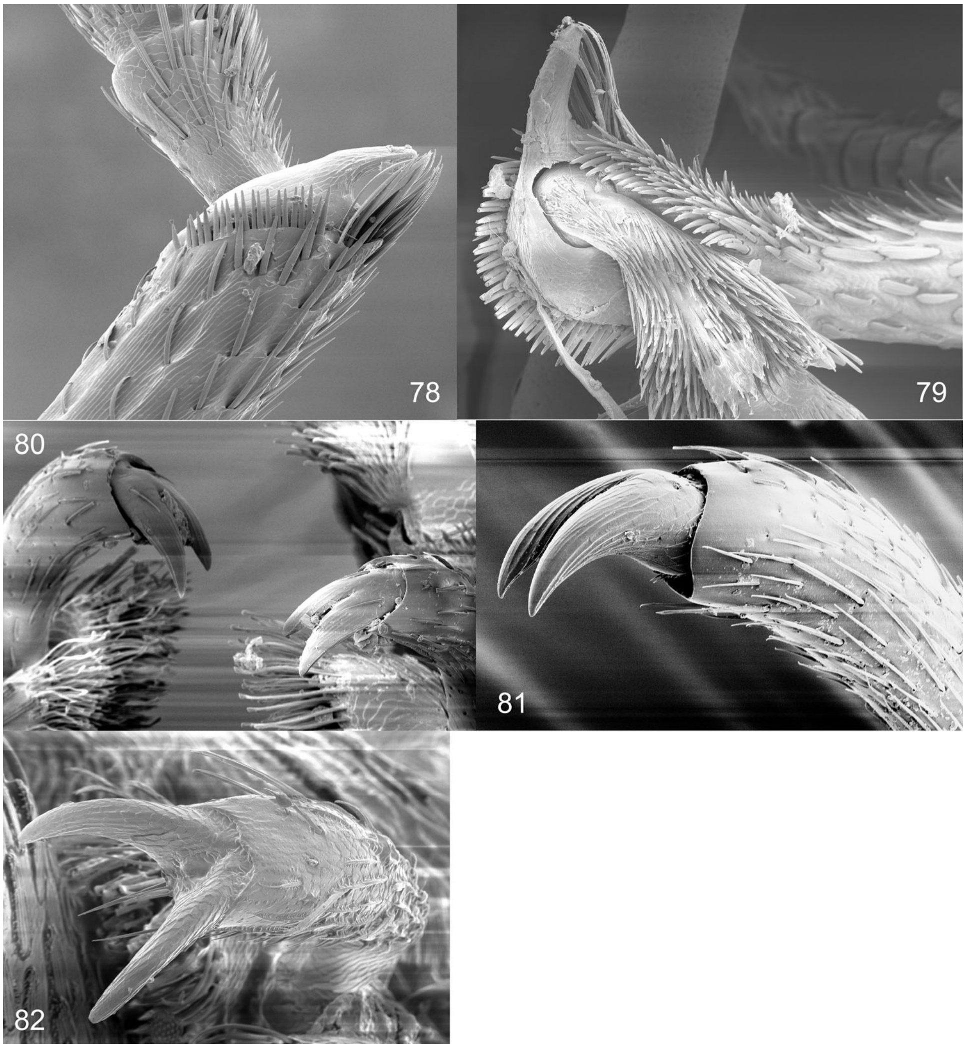
Most baridines possess connate (Figs 80, 81) or separate/diverging (Fig. 82) pre-tarsal ungues, although a few have widely diverging ungues with nearly 180° separating them or have only a single ungue. Only outgroup taxa (Conoderinae, Ceutorhynchinae) have ungues which bear central teeth.

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 weakly developed (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:
An uncus arising from the outer apical angle and a premucro from the inner angle (0); a large uncus at



Figures 78–82. 78, *Madarus bistrigellus*, apical tibial uncus; 79, *Demoda vittata*, apical tibial uncus; 80, *Zygobarella zanthoxyli*, connate pretarsal ungues; 81, *Anthinobaris* sp., connate pretarsal ungues; 82, *Baris* sp., diverging pretarsal ungues.

outer angle with outer angle setal tuft and premucro absent (1); an uncus at inner angle with a converging setal tuft at inner angle (2); an uncus near middle of apical margin or near inner angle and premucro on inner angle (3); apical margin bare, with no spines (4); many spines present (5); a large uncus at middle of apical margin and premucro absent (6)

Most baridines possess one large uncus at the inner apical angle (along with an adjacent tuft of elongate setae that are convergent with the uncus) (Figs 78, 79). As discussed by Thompson (1992), the subsequent migration of the uncus from the inner angle to the outer angle may represent a transformation series. In concordance with migration of the uncus, the proximal setose fringe also shifts, moving from the subapical angle and margin to the outer margin, eventually becoming absent in some taxa. Outgroups possess tibiae with a range of all of these states, as well as other spines in addition to the uncus and premucro.

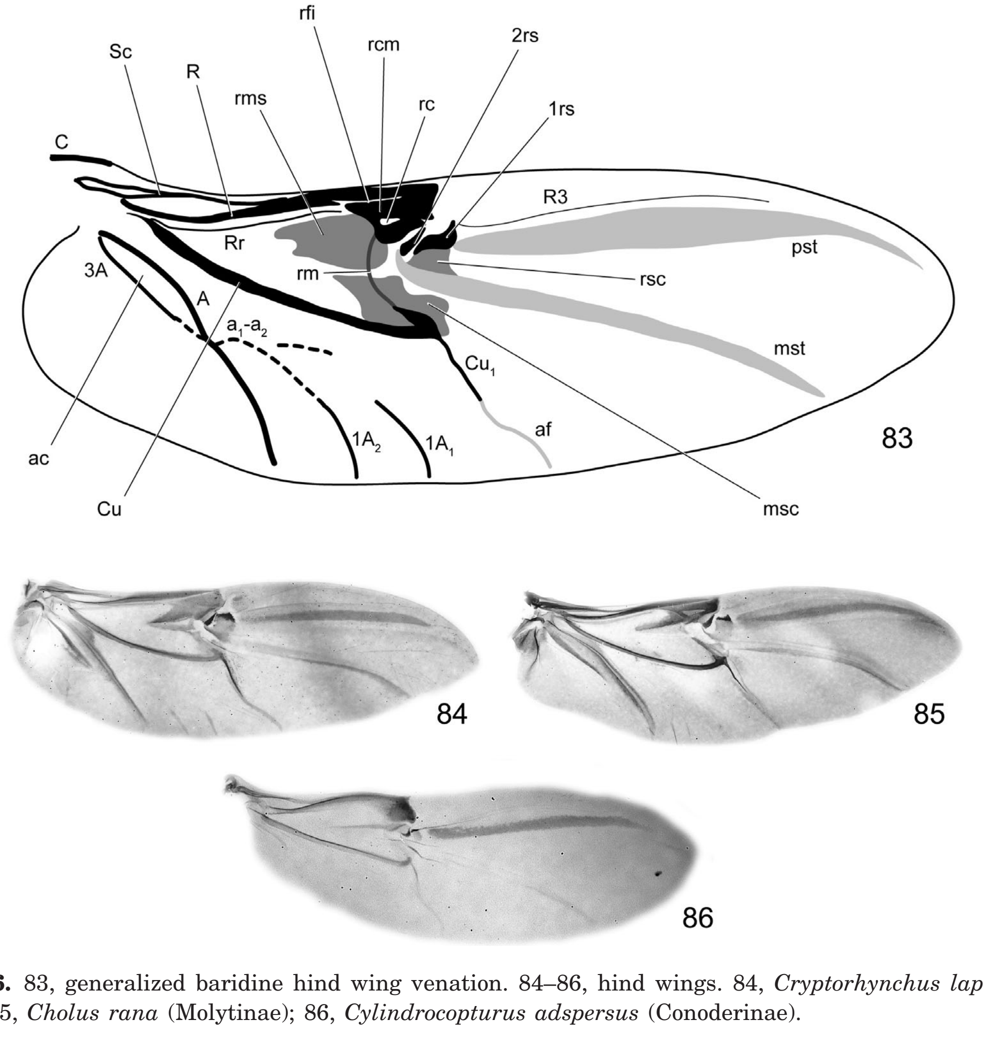
70. Tarsus, bilobed third tarsomere:
Small, reduced (fifth tarsomere usually elongate) (0); enlarged (fifth tarsomere usually normal size) (1); intermediate (2)

When the third tarsomere is small, the fifth tarsomere is usually also elongate, and when it is enlarged or expanded, the fifth tarsomere is usually 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 (3rd radial)*:*
Absent (0); present with dark vein (1); present with white stripe (2); wing weakly developed/small or absent (3)

72. Wing, venation – 2rs (2nd radial sclerite)*:*
Absent (0); present (1); wing weakly developed/small or absent (2)



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

73. Wing, venation – mst (medial stripe)*:*
Developed (0); reduced (1); wing weakly developed/small or absent (2); absent (3)

74. Wing, venation – rm (radiomedia)*:*
Absent (0); present (1); wing weakly developed/small or absent (2)

75. Wing, venation – 1A1 (1st Anal branch)*:*
Absent (0); present (1); wing weakly developed/small or absent (2)

76. Wing, venation – 1A2 (2nd Anal branch)*:*
Absent (0); present (1); wing weakly developed/small or absent (2)

77. Wing, venation – A (1st Anal)*:*
Absent (0); present (1); wing weakly developed/small or absent (2)

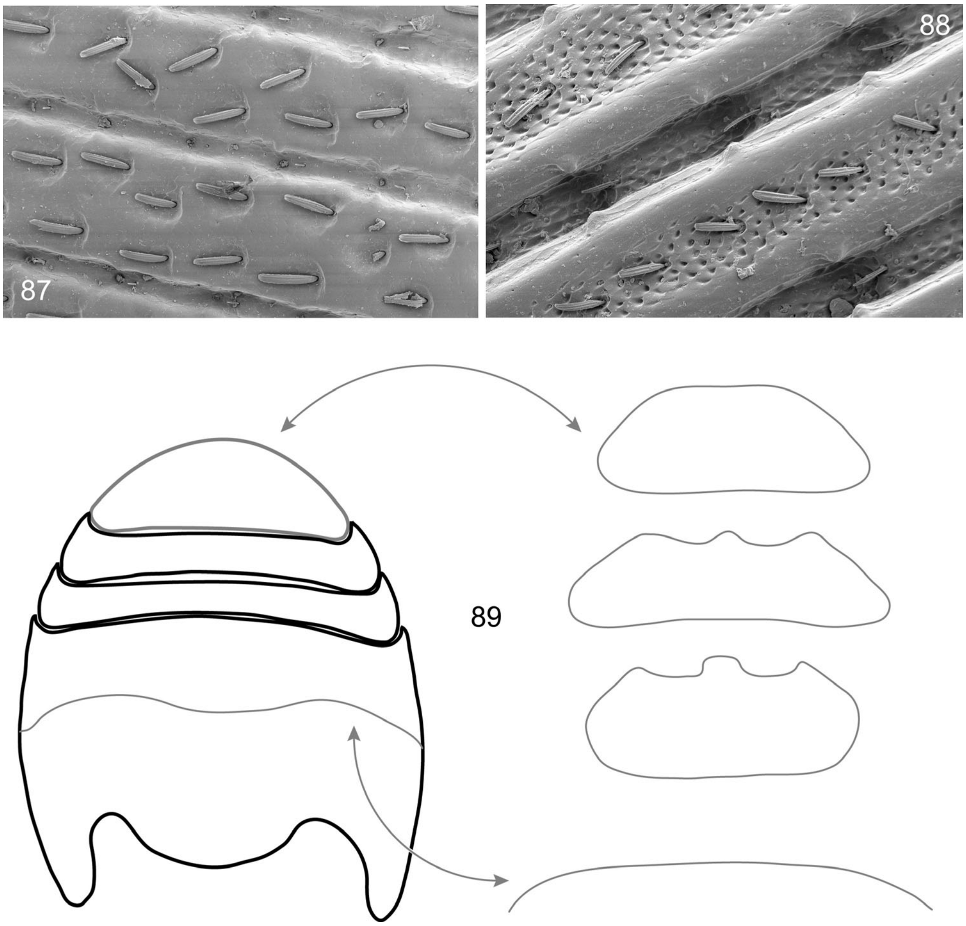
78. Wing, venation – 3A (3rd Anal)*:*
Absent (0); present, reduced (1); present, nearly connected with 4A (2); wing weakly developed/small or absent (3)

79. Wing, venation – Rr (radial recurrent vein)*:*
Absent (0); present (1); wing weakly developed/small or absent (2)

ELYTRA

80. Thorax, elytra – intervals:
With more than one row of punctures (0); one row of punctures (1); no punctures (2); ridges present (3)

The elytral intervals typically are either flattened, in which case they may be smooth, have punctures (each of which bear a scale), or have developed longitudinal ridges that are 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).



Figures 87–89. 87–88, elytra. 87, *Odontocorynus creperus*, showing intervals that have scattered punctures; 88, *Coleomerus boliviensis*, showing intervals with a single column of punctures; 89, *Idiostethus tubulatus*, ventrites, showing variation seen in the posterior margin of ventrites 1 and 5.

81. Thorax, elytra – hump (at apical area where many striae converge/elytral declivity):
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 case the lateral margins of both elytra join (or nearly meet) at their acute apices. This condition is often associated with complete enclosure of the pygidium by the elytra, although not always. The other condition, which is often 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 some 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), although 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 sometimes with a central lobed or quadrate 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 are usually present on the ventrites, they particularly may be present along the anterior margin of ventrite 5, or they may be absent, in which case 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 shrivelled *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)

90. Abdomen, pygidium (tergite 7) – plectra:
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 weak plectral development.

91. Abdomen, pygidium (tergite 7) – with longitudinal median carina/crest:
Absent (0); present (1)

When a longitudinal median carina 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)

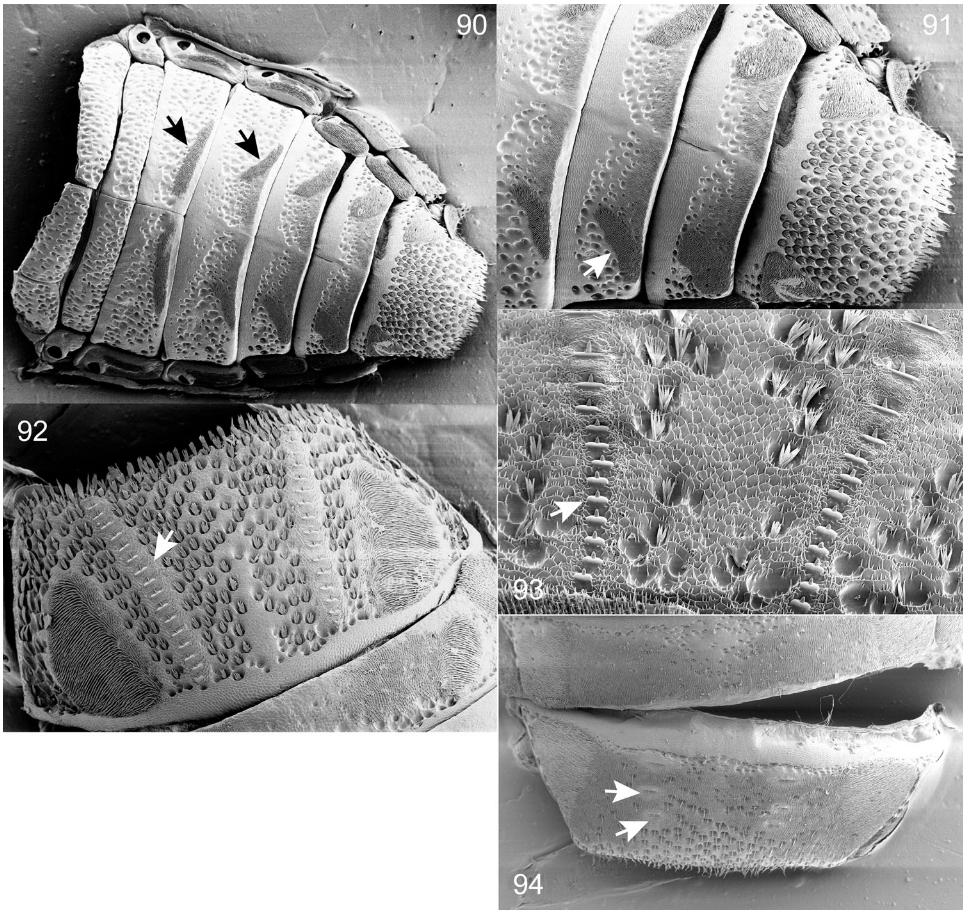
94. Abdomen, central tergite 3:
Fused (0); separated (1)

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, spiracular tergite 1:
Fused (0); separated (1)



Figures 90–94. 90–91, *Acythopeus* sp. 90, tergum and spiculate patches on the median sclerites; 91, enlargement of tergites 4–7; 92, *Pycnogeraeus modestus*, tergite 7, showing lines of dense plectra; 93, *Deipyrus hirsutulus*, plectra on tergite 7; 94, *Diastethus eurthinoides*, sparse plectra on tergite 7.

99. Abdomen, spiracular tergite 2:
Fused (0); separated (1)

100. Abdomen, spiracular tergite 3:
Fused (0); separated (1)

101. Abdomen, spiracular tergite 4:
Fused (0); separated (1)

102. Abdomen, spiracular tergite 5:
Fused (0); separated (1)

103. Abdomen, spiracular tergite 6:
Fused (0); separated (1)

104. Abdomen, tergites – lateral spiculate patches of central tergites (Figs 90, 91):
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)

Female genitalia

105. Female, eighth sternite – lateral margin:
With acute angle (0); with rounded angle (1)

The base of the female eighth sternite (before the apodeme) may have lateral margins that are quadrate and angular (Fig. 99) or rounded to not produced (Figs 101, 102).

106. Female, spermatheca:
With ramus and collum present (0); only collum present (ramus small or absent) (1)

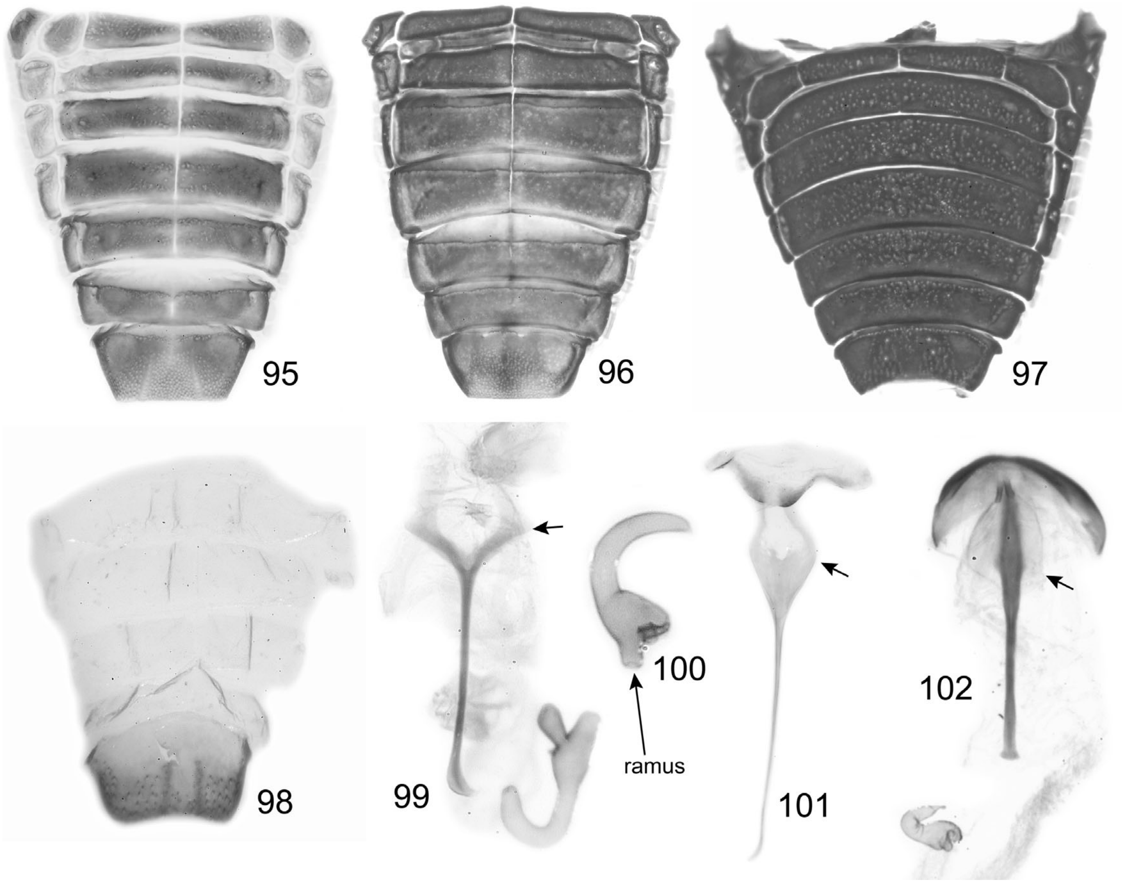
The spermatheca may have both ramus and collum present (with the ramus often developed and elongate) (Figs 99, 100) or the ramus may be weakly developed or absent.

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/apodemes:
Very short, weakly developed (0); approximately as long as aedeagus (1); longer than aedeagus, thin (2)



Figures 95–102. 95–98, terga. 95, *Centrinus curvirostris*; 96, *Peridinetus irroratus*; 97, *Xystus ruficollis*; 98, *Calandrinus grandicollis*. 99–102, female genitalia. 99, *Limnobaris* sp., spermatheca and sternite 8, showing angular lateral margin of basal part of sternite (not including the apodeme); 100, *Strongylotes squamans*, spermatheca, showing developed ramus; 101, *Parasomenes curvirostris*, sternite 8, showing rounded lateral margin of basal part of sternite; 102, *Zena* sp., spermatheca and sternite 8, showing lateral margin of basal part of sternite that is not produced/linear.

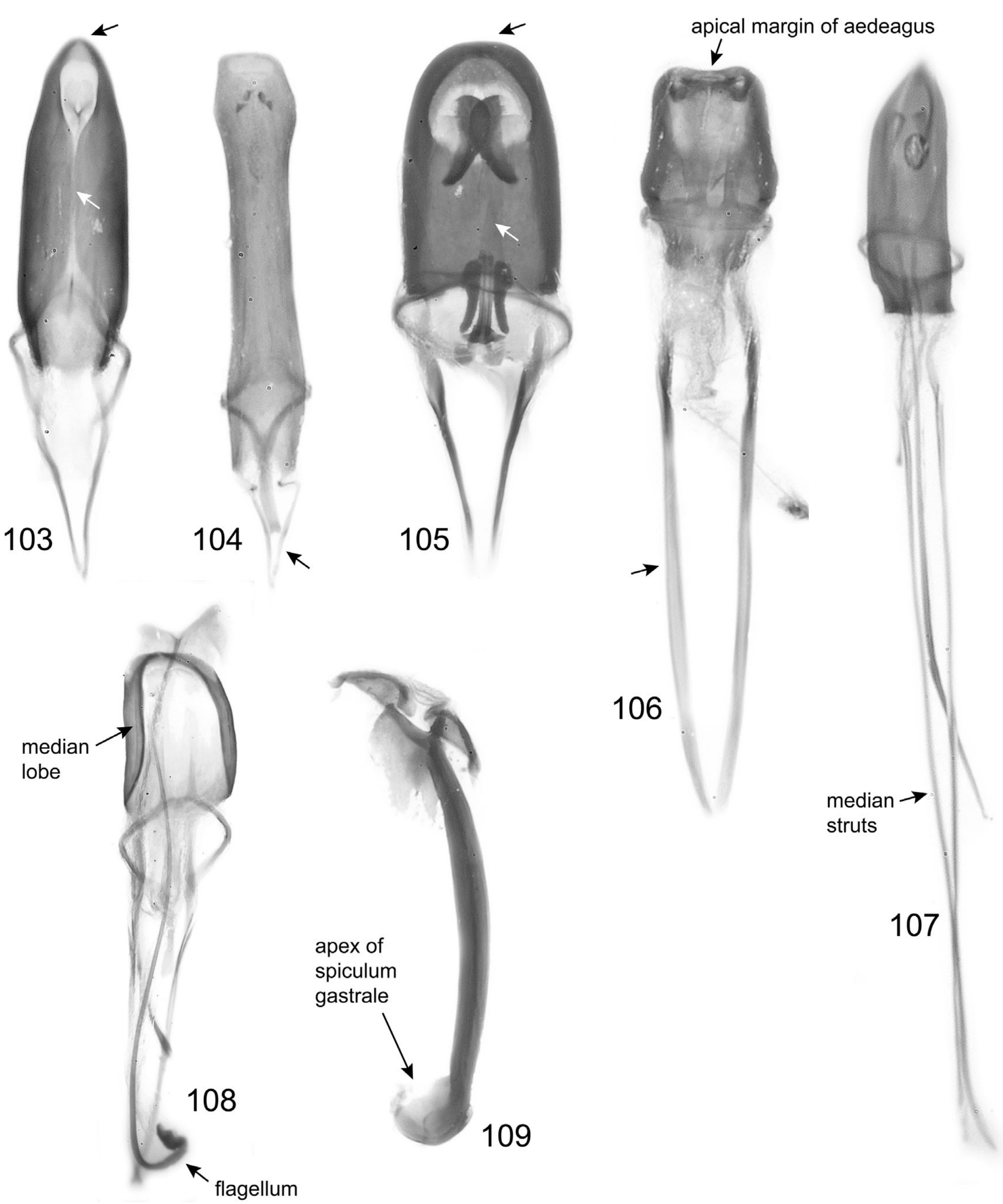
There is enormous variation in length in the median struts, most being approximately equal in length to the aedeagus (Figs 103, 105), although they may be weakly developed and short (Fig. 104) or several times longer than the aedeagus (Figs 106–108).

109. Male, aedeagus – sclerotization of dorsal surface and lateral margins of median lobe (pedon), as viewed dorsally:
Central, wide, lightly sclerotized area with thin lateral, strongly sclerotized areas (0); median lightly sclerotized area smaller, with lateral, strongly sclerotized areas wider (1); lateral strongly sclerotized areas nearly touching (2); entire dorsal surface of median lobe strongly sclerotized (3)

Most baridines possess a fairly wide central, lightly sclerotized area on the dorsal surface of the median lobe (Figs 106, 108), in which a thin area on the lateral sides of the median lobe is more heavily sclerotized. The lateral, heavily sclerotized areas of the median lobe may also be nearly touching (Fig. 103) or touching (Fig. 105), where the entire dorsal surface is uniformly heavily sclerotized. Somewhat intermediate between these are slightly wider lateral, heavily sclerotized areas, in which the central, lightly sclerotized area is slightly narrower but not to the extent to which the heavily sclerotized areas are nearly touching (Fig. 107). This intermediate state (1) may be difficult to distinguish from state 0.

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.



Figures 103–109. Male genitalia. 103–108, aedeagus. 103, *Stethobaroides nudiventris*, showing acute apical margin of the median lobe and the lateral, heavily sclerotized areas of the median lobe that are nearly touching; 104, *Barilepton filiforme*, showing aedeagus with short median struts; 105, *Garnia* sp., showing broadly rounded apical margin of the median lobe and the lateral, heavily sclerotized areas of the median lobe that are touching/fused; 106, *Pardisomus biplagiatus*, showing concave apical margin of the median lobe and aedeagus with long median struts; 107, *Solenosternus dividuus*, showing aedeagus with long median struts; 108, *Pteracanthus smidtii*, showing fairly wide central, lightly sclerotized area on the dorsal surface of the median lobe and internal flagellum; 109, *Stereobaris interpunctata*, showing spiculum gastrale with expanded apex.

111. Male, ninth sternite – apex of spiculum gastrale:
Subequal in width to remainder of apodeme (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 apodeme/manubrium:
Monofurcate, narrow (0); bifurcate (1); monofurcate, wide (2); absent (3); very reduced (4)

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

PHYLOGENETIC METHODS

Parsimony analyses with full taxon matrix

The full taxon matrix (FTM; Appendix 2), consisting of 113 characters and 301 taxa, was compiled in WinClada (Nixon, 1999b). Phylogenetic analyses were performed using NONA (Goloboff, 1999) and Tree analysis using New Technology (TNT; Goloboff *et al.*, 2003). In NONA, two strategies were used for ratchet runs (Nixon, 1999a) during tree exploration. One ran single ratchet sets for 4000 iterations while sampling 35–50 characters and holding one tree per iteration. The second style utilized multi-ratchet sets. One set of runs used two simultaneous threads and ten sequential ratchet runs, performing 200 iterations per run while sampling 35–45 characters and holding one tree per iteration. Another set of runs used two simultaneous threads and 20 sequential ratchet runs, performing 100 iterations per run while sampling 35 characters and holding one 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 1000 ratchet iterations, including 100 cycles of both TD and TF per iteration.

Reduced taxon matrix

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 nearly all subtribes [taxa for Apostasimerina (tribe Madopterini) were not examined], and all taxa with approximately 50% missing data (because of the inability to dissect type specimens) were removed from the dataset, which did not interfere with obtaining a reasonable sampling from each tribe and subtribe. All outgroup taxa in the full dataset were included in the reduced taxon matrix (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. 118), as a few of the major nodes collapsed in the strict consensus (Fig. 119).

Clade support analyses

Bootstrap analyses performed using TNT gave similar results to jackknife runs. As a result, and because previous studies have reported greater utility of jackknifing to bootstrapping in morphological studies (e.g. Hovenkamp, 2006), only jackknife values are reported here. Previous studies also have preferred bootstrapping over jackknifing because of the uncertainty in the percentage of characters (or taxa) to delete during replications (Soltis & Soltis, 2003). However, because bootstrapping assesses group support in a slightly different manner, by analysing re-sampled matrices of the same size, and jackknifing more directly assesses 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 1000 ratchet iterations, including 100 cycles of both TD and TF per iteration.

Bremer support values (Bremer, 1994) (both absolute and relative) were calculated in TNT; using the most-parsimonious (MP) trees obtained from the final TNT parsimony run, 10 000 suboptimal trees within 15 steps of the MP trees were searched for and retained.

Character tracing

Characters of interest and those supporting the monophyly of Baridinae *s.s.* were selected to trace their evolution on the resulting cladogram in WinClada. In addition, where indicated, those characters indicative of a possible broader grouping of Barididae (Zherikhin & Gratshev, 1995) were traced, namely character 51 (presence of a longitudinal crest on the scutellar groove of the metanotum, Fig. 126). In each case, tracing was performed under fast optimization (accelerated transformation, ACCTRAN), which favours character reversal over convergence. These characters include 41 (ascension of the mesepimeron, Fig. 125), 46 (posterior margin of mesonotum, Fig. 122), 54 (lateral margin of metanotum, Fig. 123), and 98 (fusion of lateral tergites, Fig. 124). Although not shared amongst all Baridinae, character 88 (tergite sclerotization) was also traced (Fig. 121).

RESULTS

Strict consensus trees

The duration of the FTM analysis in TNT was ~37 h using an Intel Duo Centrino processor, and the total number of rearrangements examined was 3 930 947 747 326. A strict consensus tree (Fig. 110) was calculated from 33 MP trees of length 4509 and consistency index (CI) = 5, retention index (RI) = 51. The length of the consensus tree was 4850 with CI = 4, RI = 48. The considerably longer length of the strict consensus is largely because of 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 are given in Figure 116, and jackknife values of 50 and greater are reported. Results of the continuous jackknife function (CJF) analyses for the FTM phylogeny are reported for topological congruence (Fig. 112) and conflict (Fig. 113). Characters and character states were mapped onto the branches of the strict consensus tree under fast optimization (Fig. 117).

The duration of the RTM analysis was considerably shorter, a mere ~1.6 h, and the total number of rearrangements examined was 135 442 242 201. A strict consensus tree was calculated from 110 most-parsimonious trees of length 2692 (Fig. 119). The length of the consensus tree was 2958 with CI = 7, RI = 44. The absolute and relative Bremer support values for each clade of the RTM tree are given in Figure 119, and jackknife values of 50 and greater are also reported. Results of the CJF analyses for the RTM phylogeny are also reported for topological congruence (Fig. 114) and conflict (Fig. 115). Similar to the strict consensus tree of the FTM analysis, characters and character states for the RTM analysis were mapped onto the branches of the strict consensus tree under fast optimization (Fig. 120).

According to the current classification of Alonso-Zarazaga & Lyal (1999), a monophyletic Baridinae was not recovered (Figs 110, 111). 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 Orobitidinae, followed by Conoderinae (although Conoderinae is divided in these results), Curculioninae, Molytinae, Cryptorhynchinae, and Ceutorhynchinae. The position of Conoderinae (as well as the other subfamilies previously mentioned) within the outgroup is considered uncertain in this study, and this result may be because of low taxon sampling or may also reflect instability in current 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 98 (Fig. 124), 99, and 100 share the same topological distribution, and character 101 is similar in distribution. Based on the results of this study, characters 41 (Fig. 125), 46 (Fig. 122), 54 (Fig. 123), and 98–100 appear to be indicative, and may be considered diagnostic, of a monophyletic Baridinae. Character 88 (Fig. 121) also is shared by most Baridinae. As some taxa in the outgroup that were previously included in Baridinae share some features with Baridinae (as defined here), such as the developed lobe on the lateral margin of the metanotum, their 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 because of the combination of high homoplasy and small ratio of characters to taxa, as well as missing data.

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 & Donaghue, 1989). This high level of homoplasy is also evident from the CJF analyses of both the FTM and RTM. Despite the implementation of thorough tree searches in TNT, the CJF plots suggest that stability of tree topology has not been achieved for the baridine phylogeny; even when the probability of character removal is low, dramatic changes are noticeable in the steep decline in tree congruence (Figs 112, 114) and the contrasting sudden increase in tree conflict (Figs 113, 115).

Although the morphology of nearly all body regions was studied, very few synapomorphies were hypothesized and even fewer appeared to withstand a phylogenetic test. Many factors are believed to have contributed to this phenomenon. Owing to its size, it is doubtful that the dataset is free of errors. Thus, it is possible that some phylogenetic noise was introduced through human error. Another contributing factor is primary homology assessment. As a result 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

110

Figure 110. Strict consensus tree of analysis of full taxon matrix – length 4850 steps (of 33 most-parsimonious trees of length 4509 steps) produced in TNT, with old classification, including tribes and subtribes, indicated.

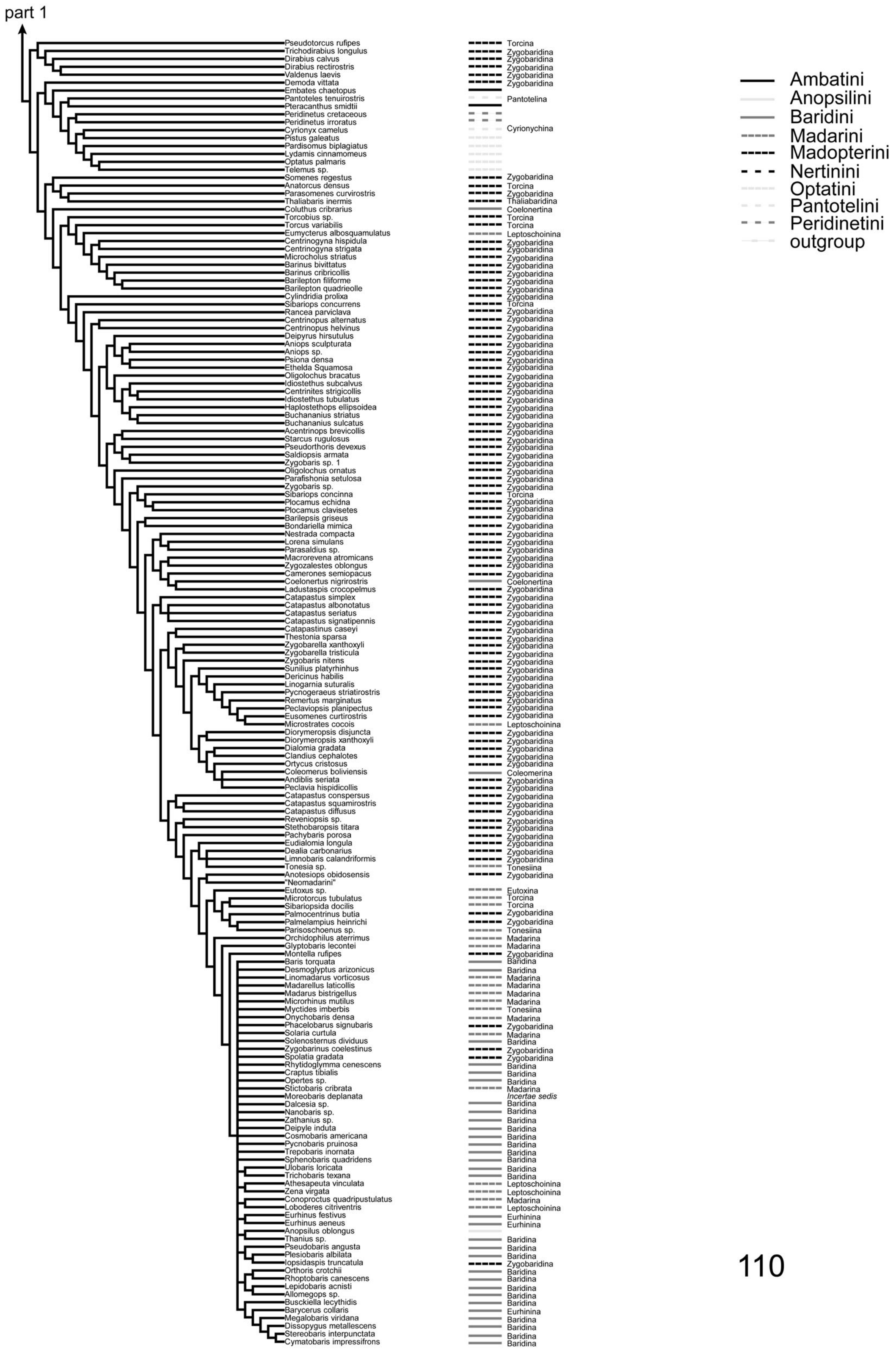


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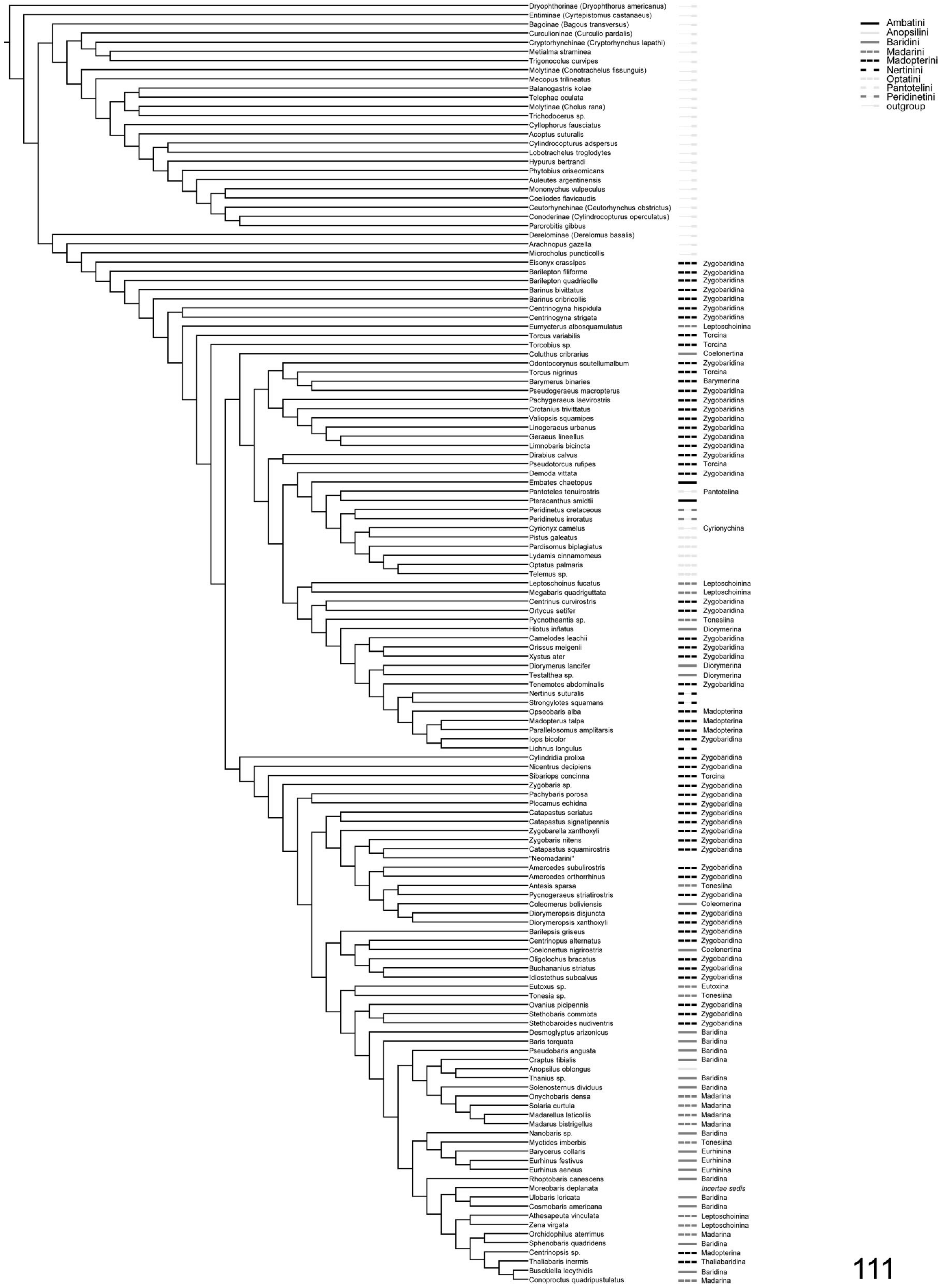
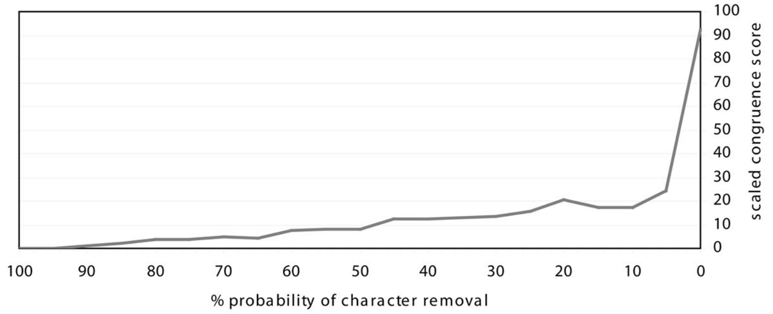
Figure 110. *Continued*



111

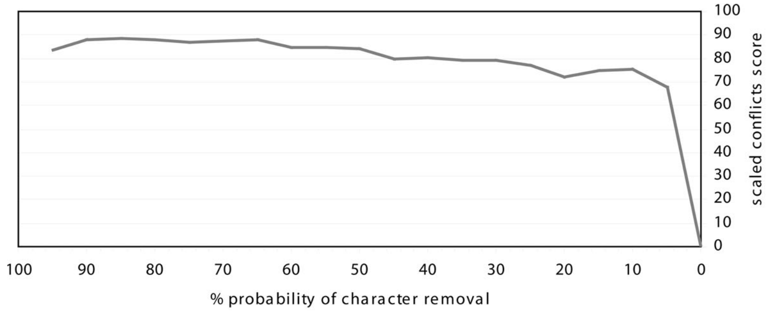
Figure 111. 1 of 110 most-parsimonious trees produced from analysis of the reduced taxon matrix – length 2692 steps, produced in TNT, with old classification, including tribes and subtribes, indicated.

112



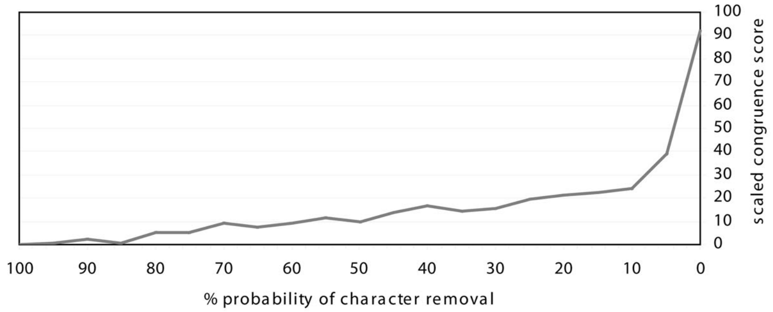
congruence

113



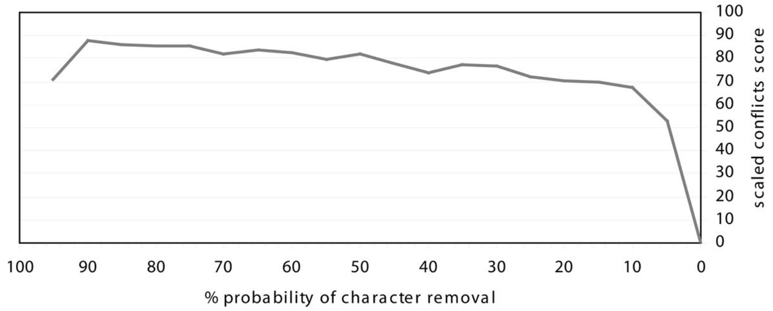
conflict

114



congruence

115



conflict

Figures 112–115. Continuous jackknife function plots. 112, tree congruence of full taxon matrix (FTM) trees as the probability of character removal changes; 113, tree conflict of FTM trees as the probability of character removal changes; 114, tree congruence of reduced taxon matrix (RTM) trees as the probability of character removal changes; 115, tree conflict of RTM trees as the probability of character removal changes.

Figure 116. Strict consensus tree of analysis of full taxon matrix, with suggested revised classification. Numbers above nodes indicate jackknife values, numbers below nodes indicate Bremer values (absolute Bremer/relative Bremer).

of homology, and the large degree of homoplasy may indicate that many character states that were hypothesized to be homologous are actually not. As a result of 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. Nonetheless, synapomorphies that are present in the majority of taxa can be defined for Baridinae *s.s*. The lateral margin of the metanotum is developed and projecting (character 54) in most

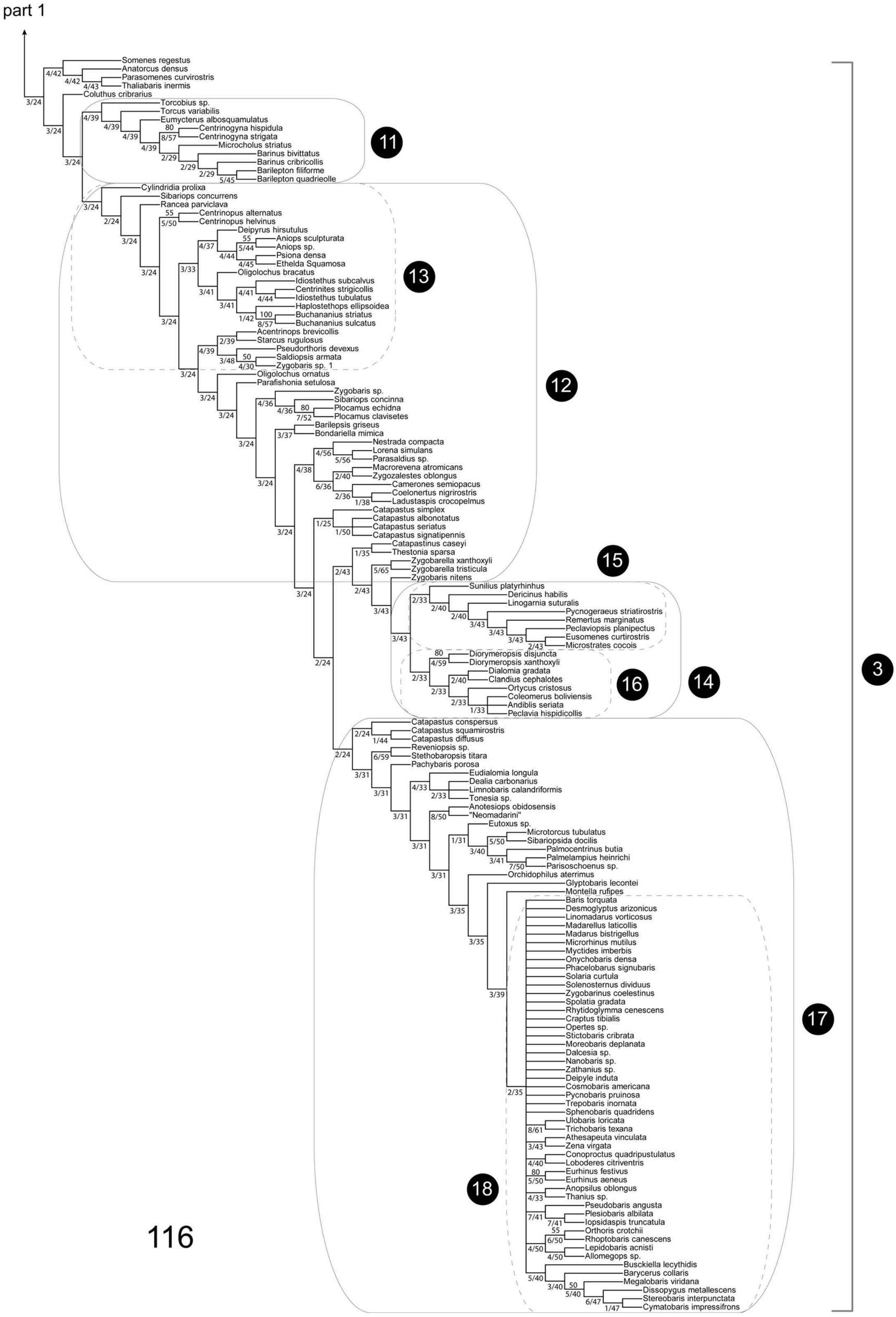
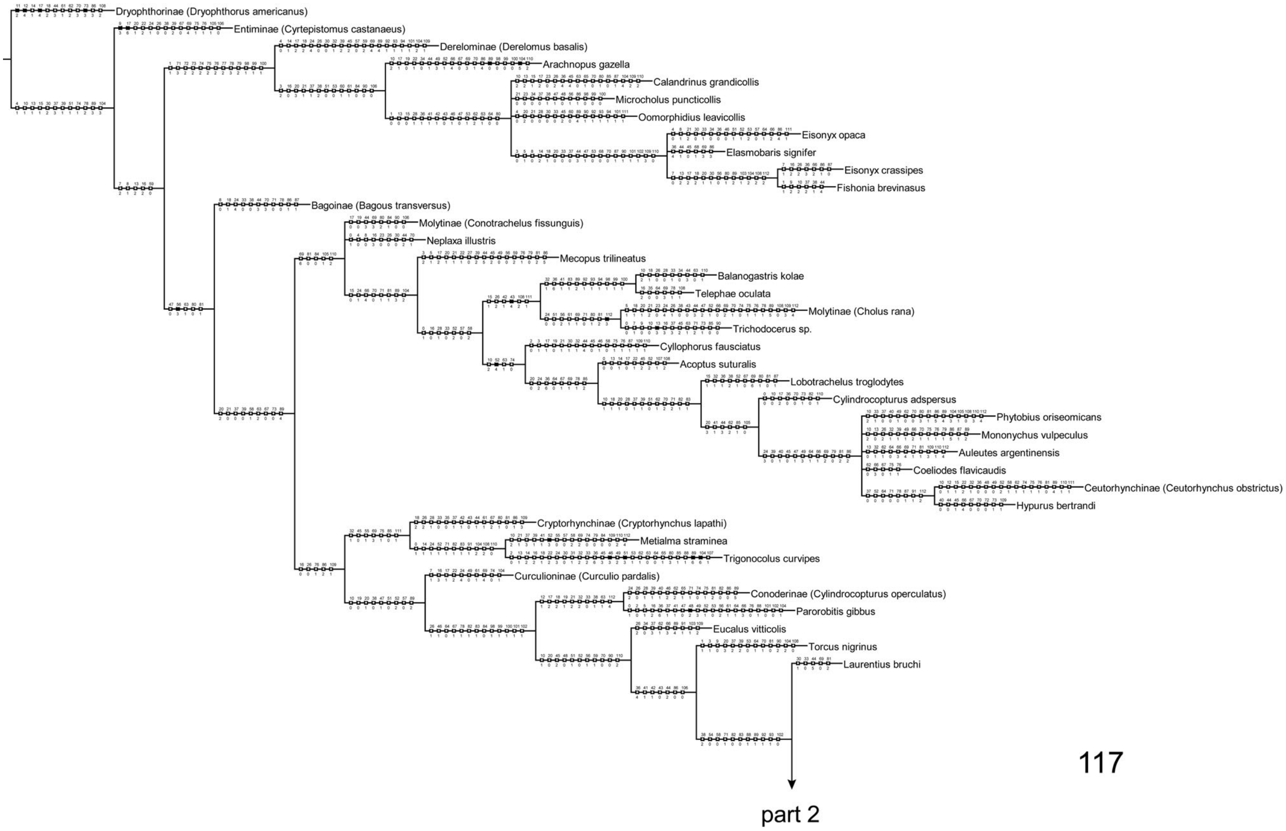


Figure 116. *Continued*



117

Figure 117. Strict consensus tree of analysis of full taxon matrix, with characters (below branches) and character states (above branches) mapped onto branches using WinClada's fast optimization (ACCTRAN).

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, whereas outgroups possess various forms of a reduced margin that does not form a projecting apex (Fig. 122). Although not included in the phylogenetic analysis, the strong submarginal fold on the lateroventral surface of the elytra does indeed appear to by a synapomorphy for the broader definition of Baridinae *s.l.*, albeit a homoplasious one. Also observed within nearly all of Baridinae *s.s.* as delimited here, but not included in the analysis, is the division of the first median sclerite of the tergum into four separate sclerites (Figs 95, 97). This feature appears to be a unique synapomorphy of this group and does not seem to be found in other Curculionidae.

COMPARISON OF COMPLETE MATRIX ANALYSIS TO RTM

As has been shown by numerous studies (e.g. Graybeal, 1998; Hillis, 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 FTM 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, not surprisingly, are fewer than those present in the FTM tree. The majority of clades shared in both the FTM 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. However, it also supports evidence suggesting that taxon composition, despite affecting the number of clades present in a phylogenetic tree, has little effect on overall topology (Miller & Hormiga, 2004). Thus, although greater taxon sampling is always desirable, and certainly is desired with baridines and weevils in general, more rigorous character examination is needed to help resolve baridine phylogeny. Also, although the FTM

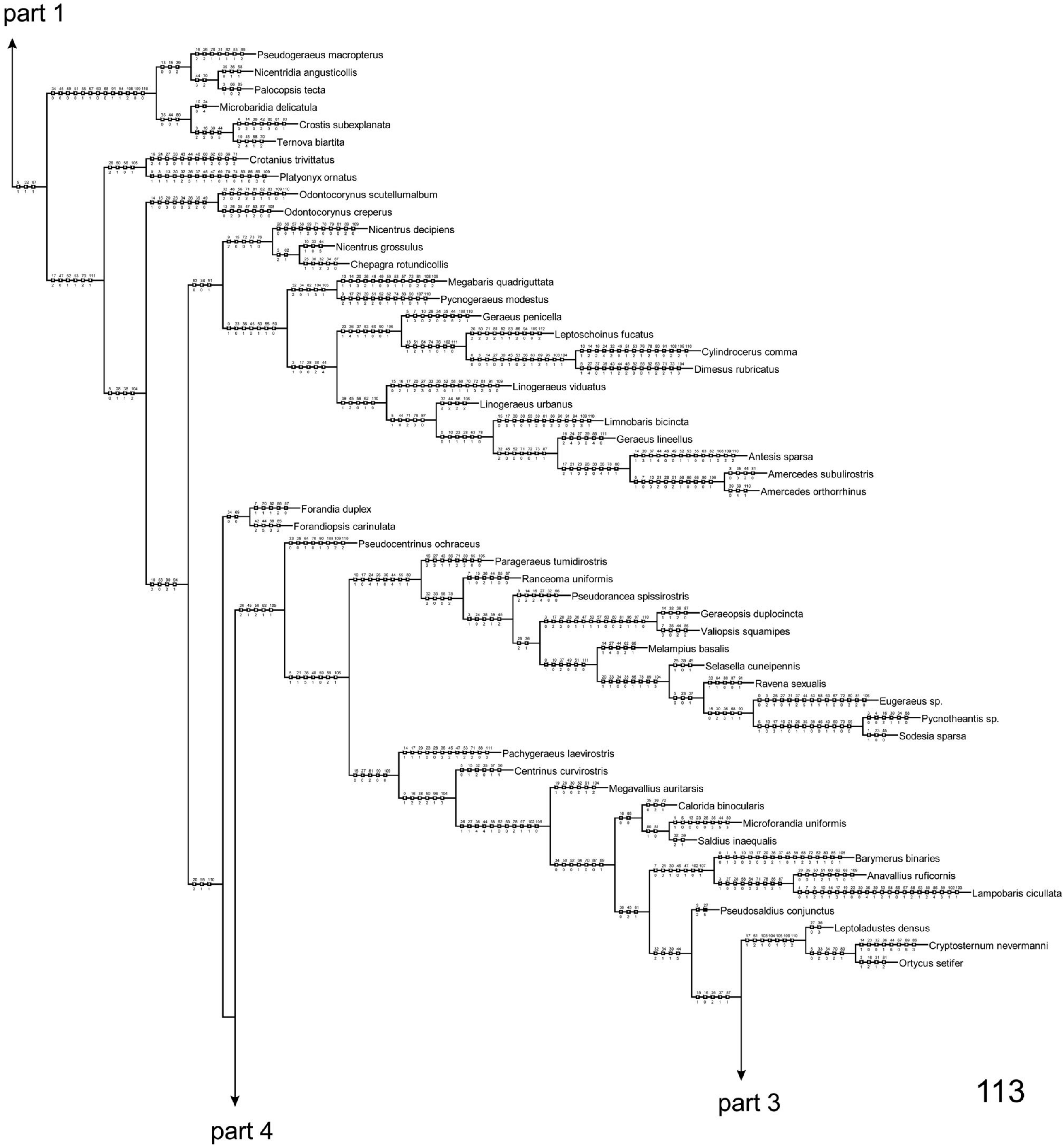


Figure 117. *Continued*

contained more than 50 taxa with approximately 60% missing data, the inclusion of these taxa appears not to have greatly affected topological accuracy (in comparing the strict consensus tree of the FTM analysis to that of the RTM analysis). These results support 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 are 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.

Figure 117. *Continued*

Implications for baridine classification

Despite the breadth of this study, in which only 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.

Although the characters suggestive of a larger grouping, Barididae, were examined and most were tested in the analysis, it remains uncertain whether this group should be formally recognized. Indeed this hypothesis has become more enticing through the results provided here, as those characters do appear to be relatively robust throughout the five subfamilies in Zherikhin & Gratshev (1995); however, until a larger and more thorough sampling of outgroup taxa is obtained, namely taxa within the other four subfamilies, Ceutorhynchinae, Trigonocolinae, Orobitidinae, and Conoderinae, this hypothesis should remain informal for the time being and the taxonomic rankings of these groups considered unresolved. The closest lineages to this larger grouping, in turn, are less clear.

As a result of this study, it is evident that the current classification for Baridinae *s.s.* 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. In addition, 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 FTM tree that are suggestive of a revised classification of Baridinae (Fig. 116), although 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 because of 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. By providing further refinement of characters and more rigorous studies of baridine phylogeny, these groupings may or may not represent true clades. The characters shared amongst the indicated paraphyletic groupings are also not only strictly present within those taxa and may be present within adjacent taxa

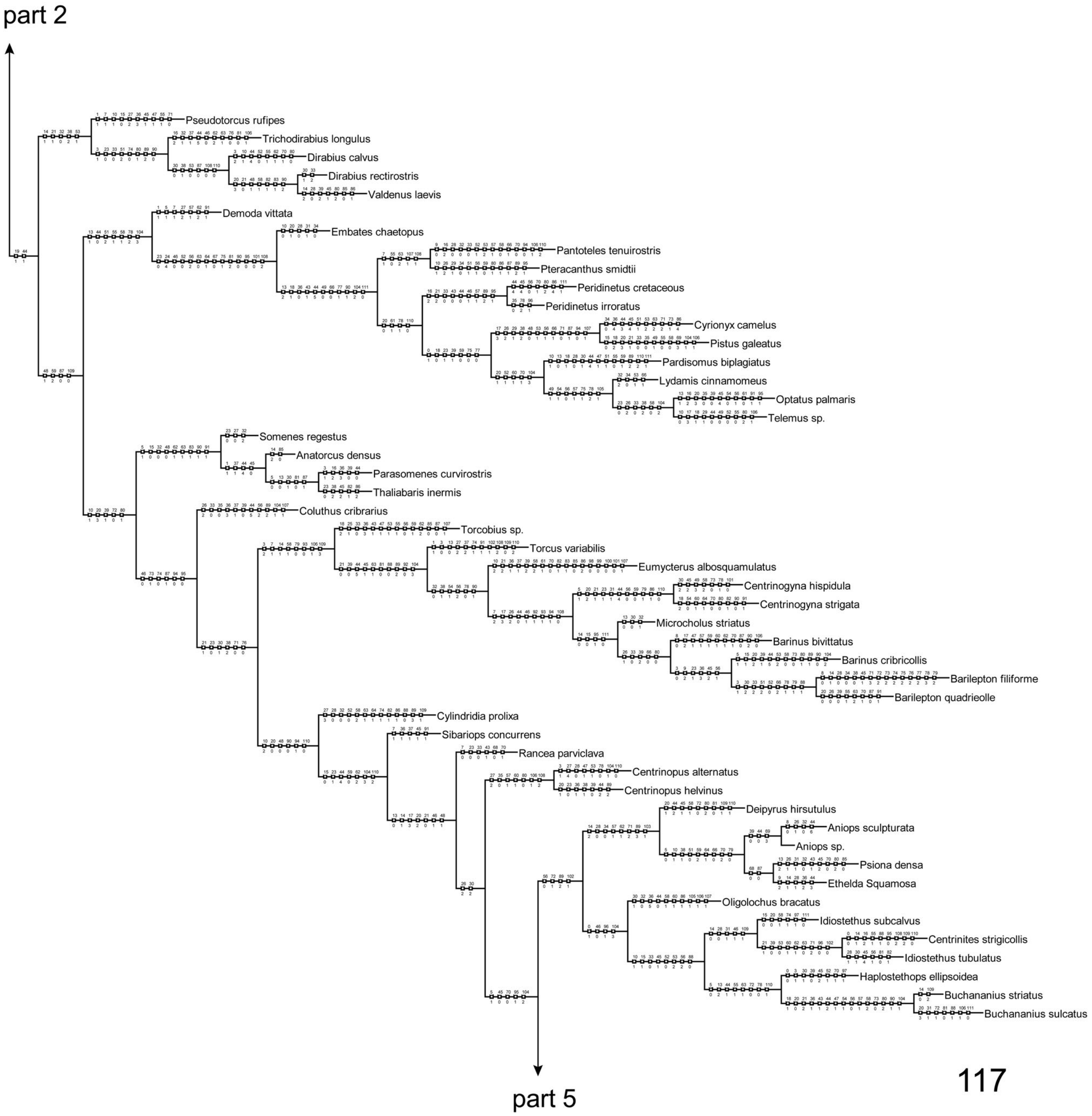


Figure 117. *Continued*

as well. The characters that only provide significant structure to groups (and clades) (i.e. are possessed by a majority of the taxa) are mentioned below. Although most groups 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 follows 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

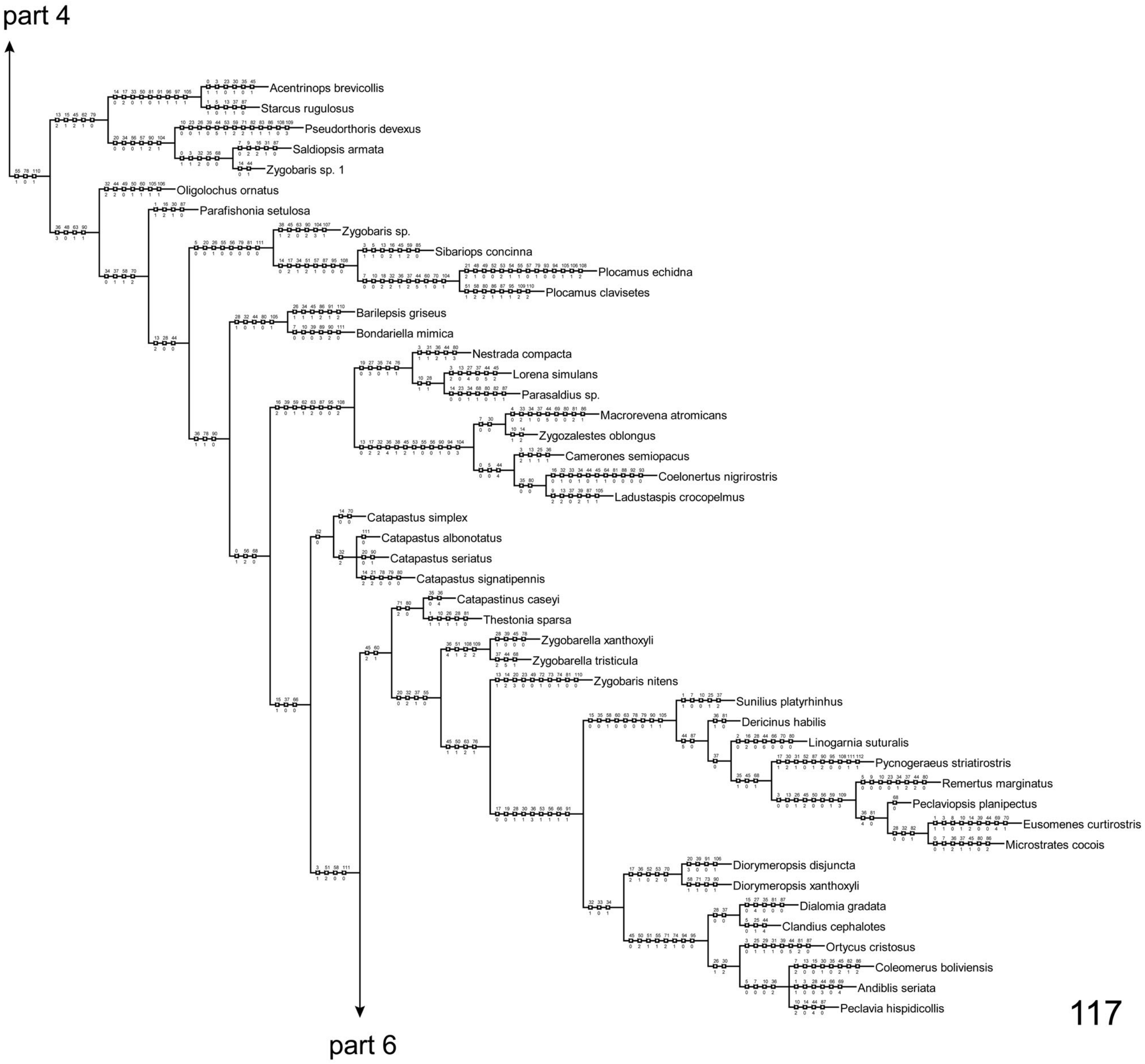
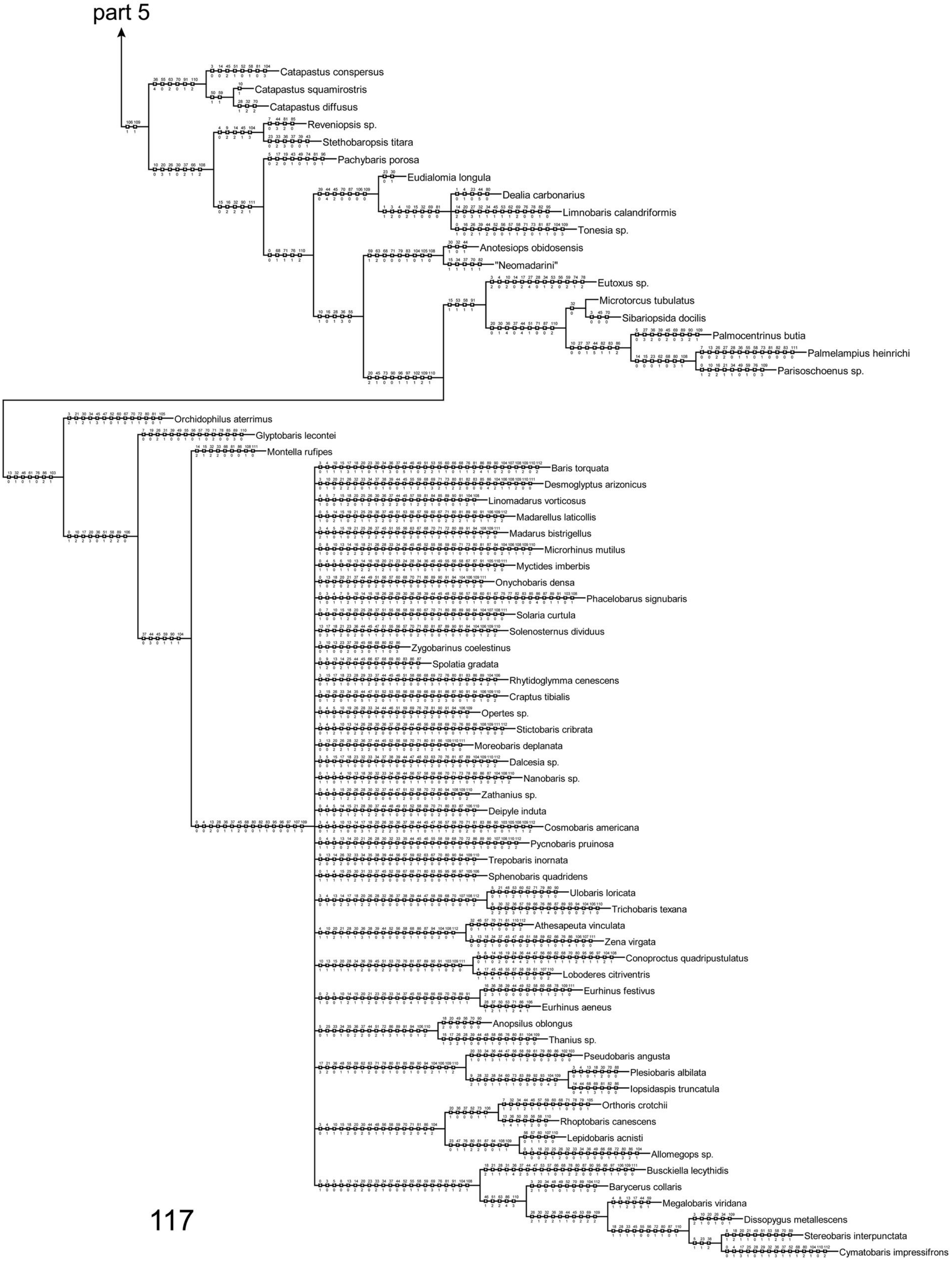


Figure 117. *Continued*

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. 118). As with the FTM, characters were optimized using accelerated transformation in WinClada. The topology of the RTM tree and the corresponding characters supporting the groups are similar to the FTM tree; however, it is clear that some groups are missing and are different in taxon composition because of 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



117

Figure 117. *Continued*

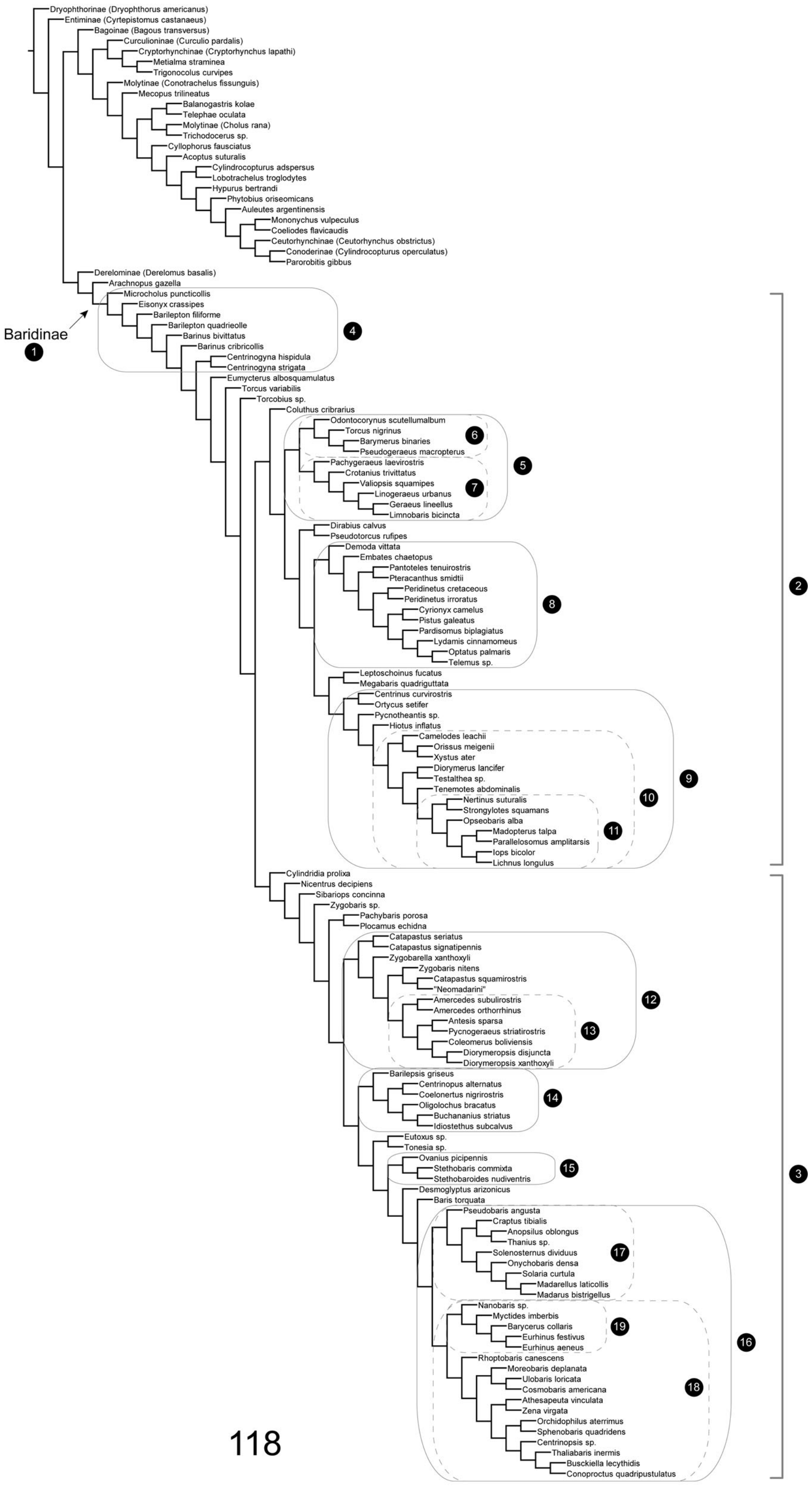
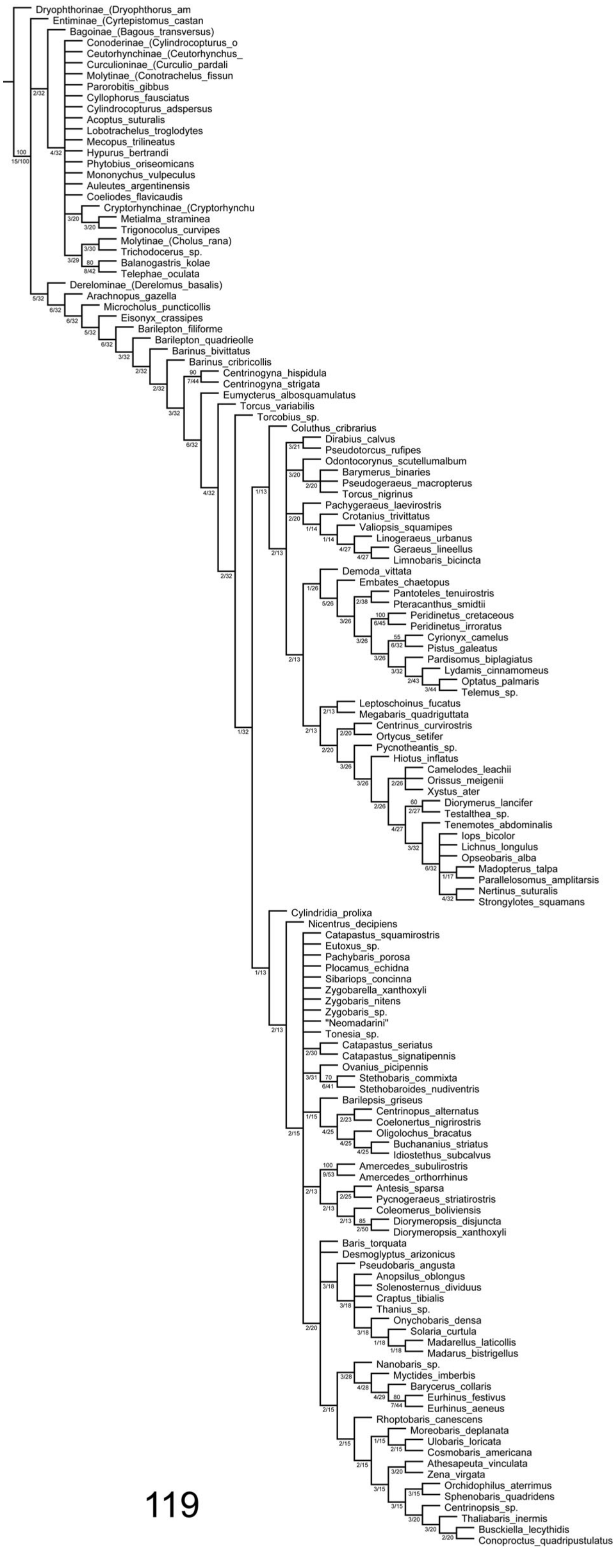


Figure 118. 1 of 110 most-parsimonious trees produced from analysis of the reduced taxon matrix, with suggested revised classification.



119

Figure 119. Strict consensus tree from analysis of reduced taxon matrix – length 2958 steps (of 110 most-parsimonious trees of length 2692). Numbers above nodes indicate jackknife values, numbers below nodes indicate Bremer values (absolute Bremer/relative Bremer).

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 some incongruence in results obtained from analyses of both the FTM (Fig. 116) and the RTM (Fig. 118), the strict consensus tree of the FTM analysis is the first hypothesis for baridine evolution, and thus is believed to represent the basis of an improved hypothesis of baridine classification over previously proposed non-cladistic treatments. Given the data, the RTM analysis produced a strict consensus tree (Fig. 119) with similar topology to that of the FTM. Regardless of the high amount of homoplasy, several characters support clades and suggest groupings that are present in the analyses of both the FTM and the RTM. Although jackknife values and Bremer support values are 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.

EVOLUTION OF PRO-STERNAL HORNS IN BARIDINAE

As mentioned in the character discussion above and in the review of baridine morphology in Davis (2009), in Baridinae, including a few genera in closely related subfamilies (Conoderinae), males have evolved horns on the prosternum that function in male–male combat, although other functions may be likely. These horns vary in development amongst males of different sizes (the smaller males possessing smaller horns) and vary in morphological structure (Figs 37, 41–45). Many species possessing horns, although not all (Figs 43, 45), also possess a horn sheath (Figs 38–40). Few studies have examined the evolution of beetle horns using phylogenies. Those that have (e.g. Emlen *et al.*, 2005) did so with scarab beetles (Scarabaeidae), which possess dorsal horns on the pro-notum.

In contrast to previous studies involving baridines that possess relatively long horns and elongate horn sheaths, a great diversity of horns and horn sheaths

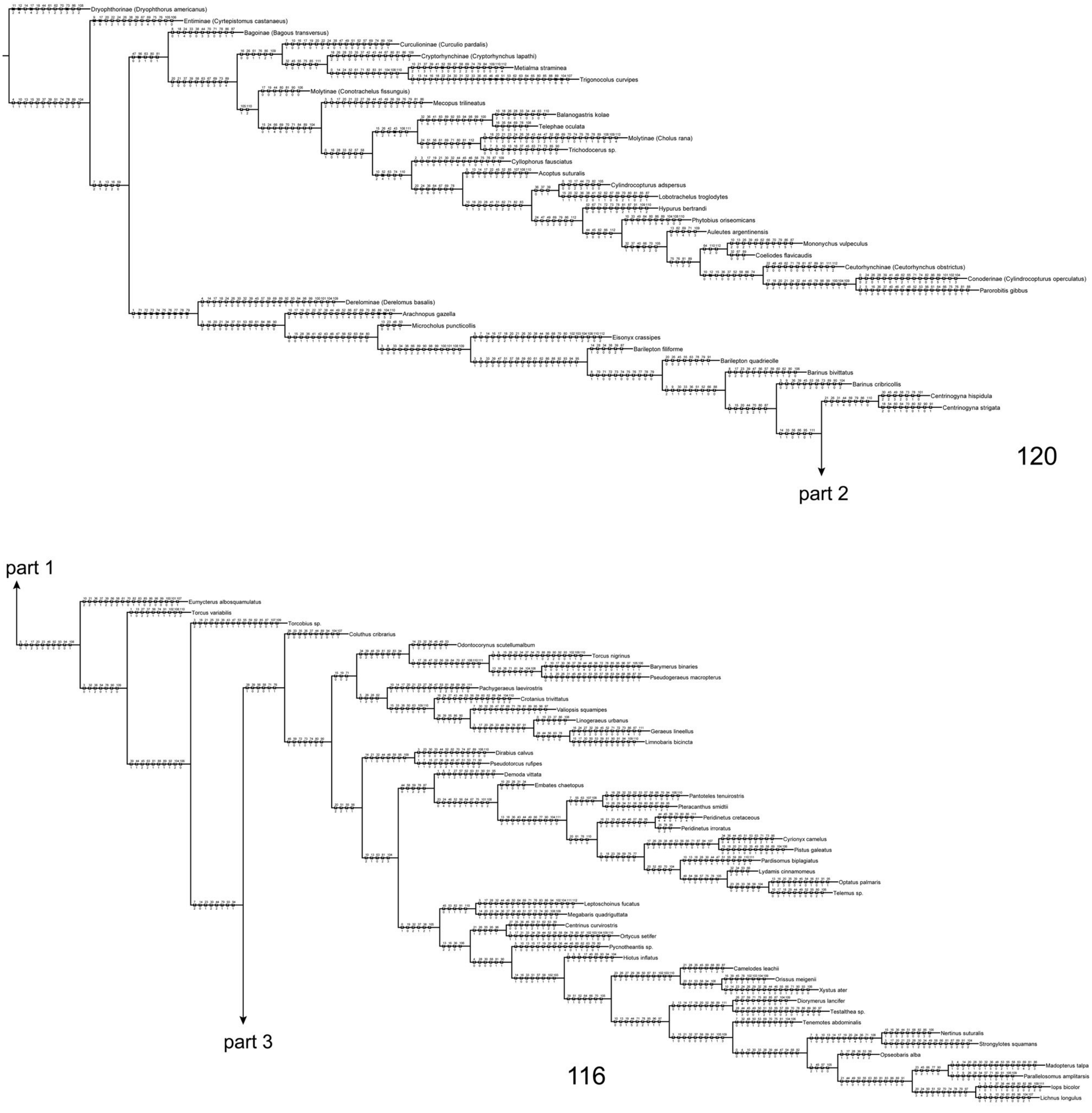


Figure 120. 1 of 110 most-parsimonious trees produced from analysis of the reduced taxon matrix, with characters (below branches) and character states (above branches) mapped onto branches using WinClada's fast optimization (ACCTRAN).

have evolved multiple times throughout the subfamily (Fig. 127). As the phylogenetic results hypothesize, the five general types of horns have evolved multiple times. Although it is possible that all ancestral baridines possessed horns and they 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 intergeneric morphological differences seen in the horns. These differences may also be a result of behavioural differences. The behaviour of only a few species has been studied, and in a large number of taxa it is

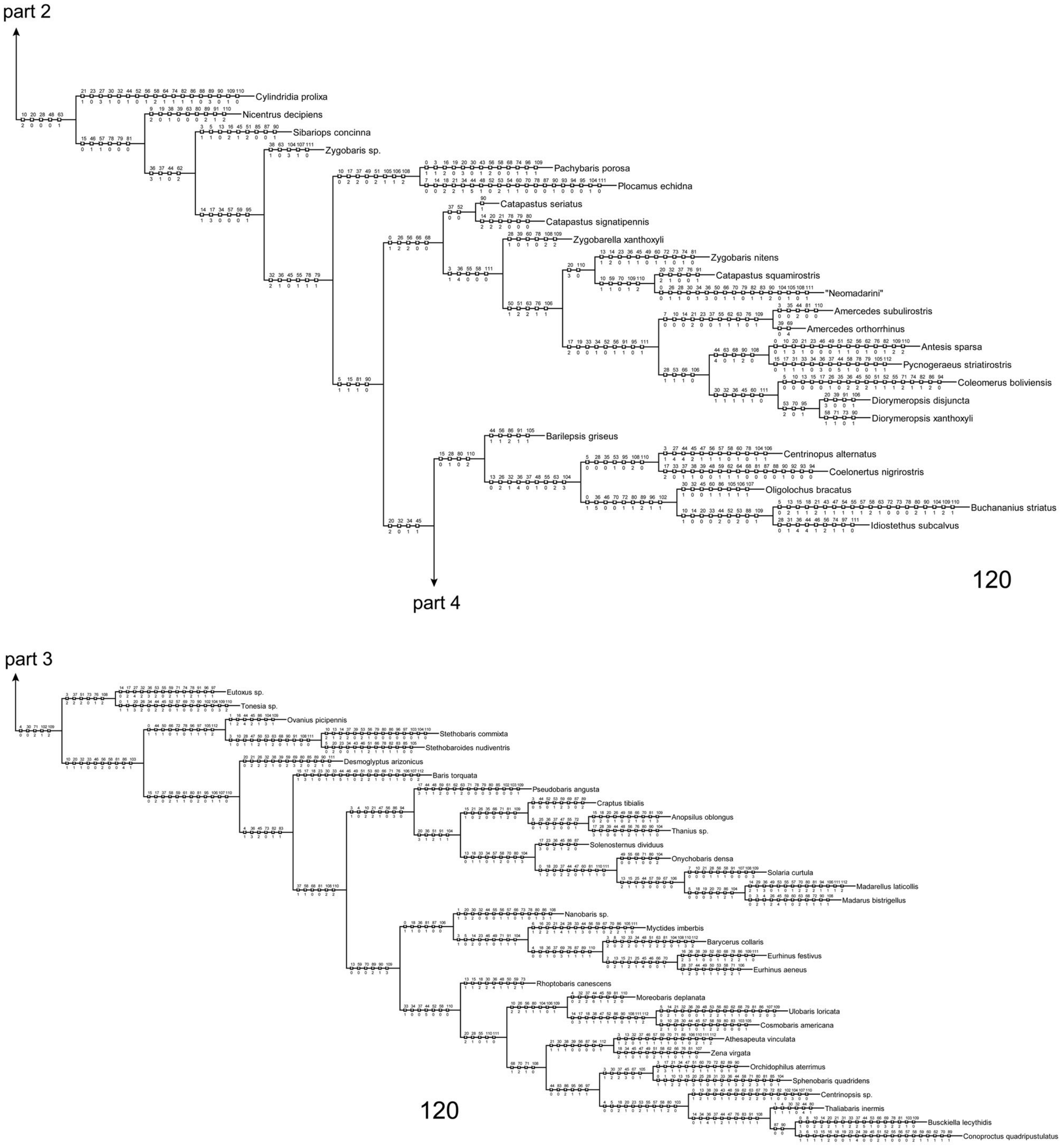
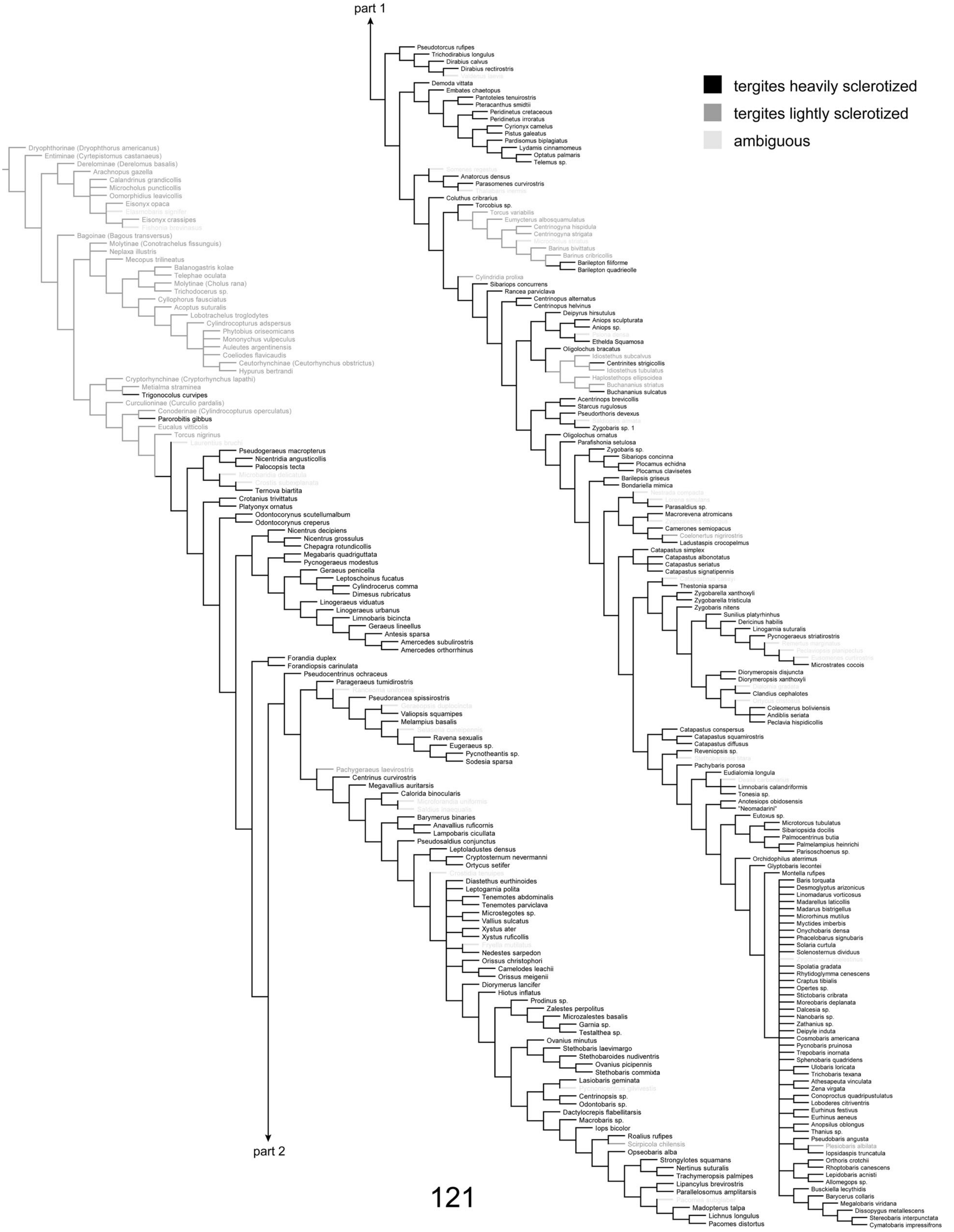


Figure 120. *Continued*

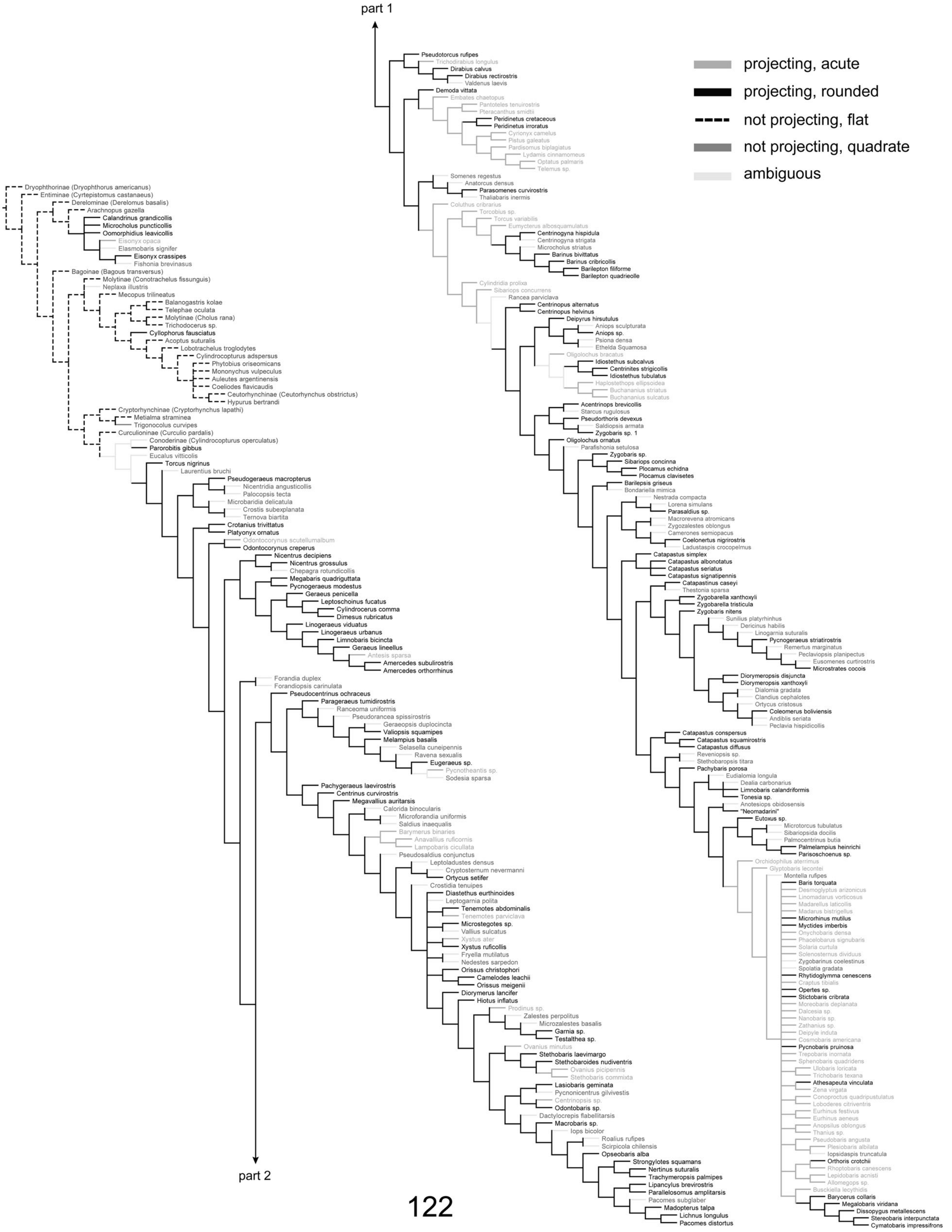
possible that these horns play an insignificant role in male–male aggression (Eberhard & Garcia, 2000; Eberhard *et al.*, 2000).

Correlation between the presence of the different types of horns and the presence of plectra (sound-producing stridulatory structures) on the seventh tergite of the abdomen was also examined, as it is known that the presence of both are strongly associated with the display of aggressive behaviour in males. These characters were mapped onto the strict consensus tree and adjacently aligned (Fig. 127). As apparent from the aligned trees, the presence of horns



121

Figure 121. Character 88 (sclerotization of tergites) mapped onto strict consensus tree of full taxon matrix analysis.



122

Figure 122. Character 46 (posterior margin of mesonotum), supporting monophyly of Baridinae, mapped onto strict consensus tree of full taxon matrix analysis.

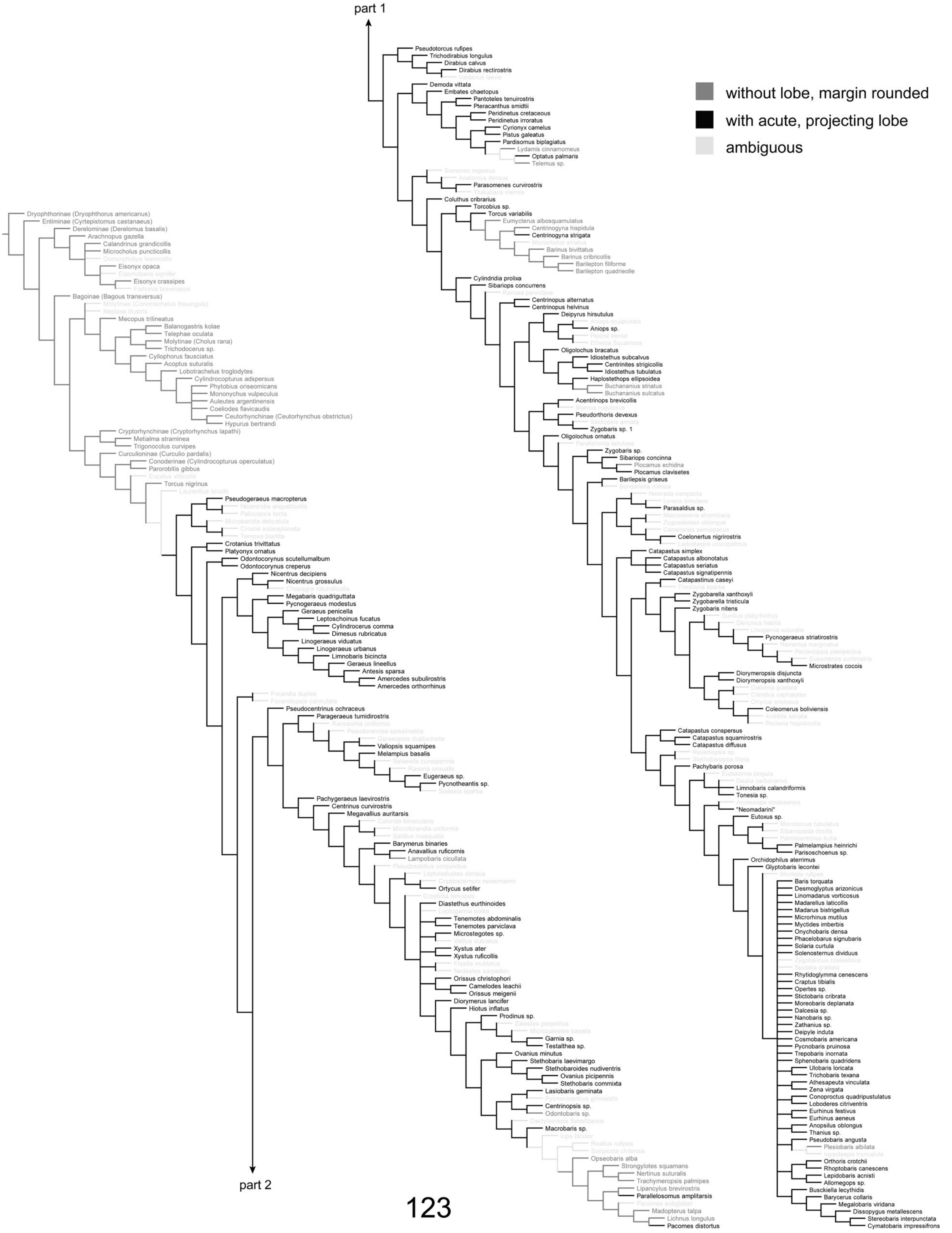
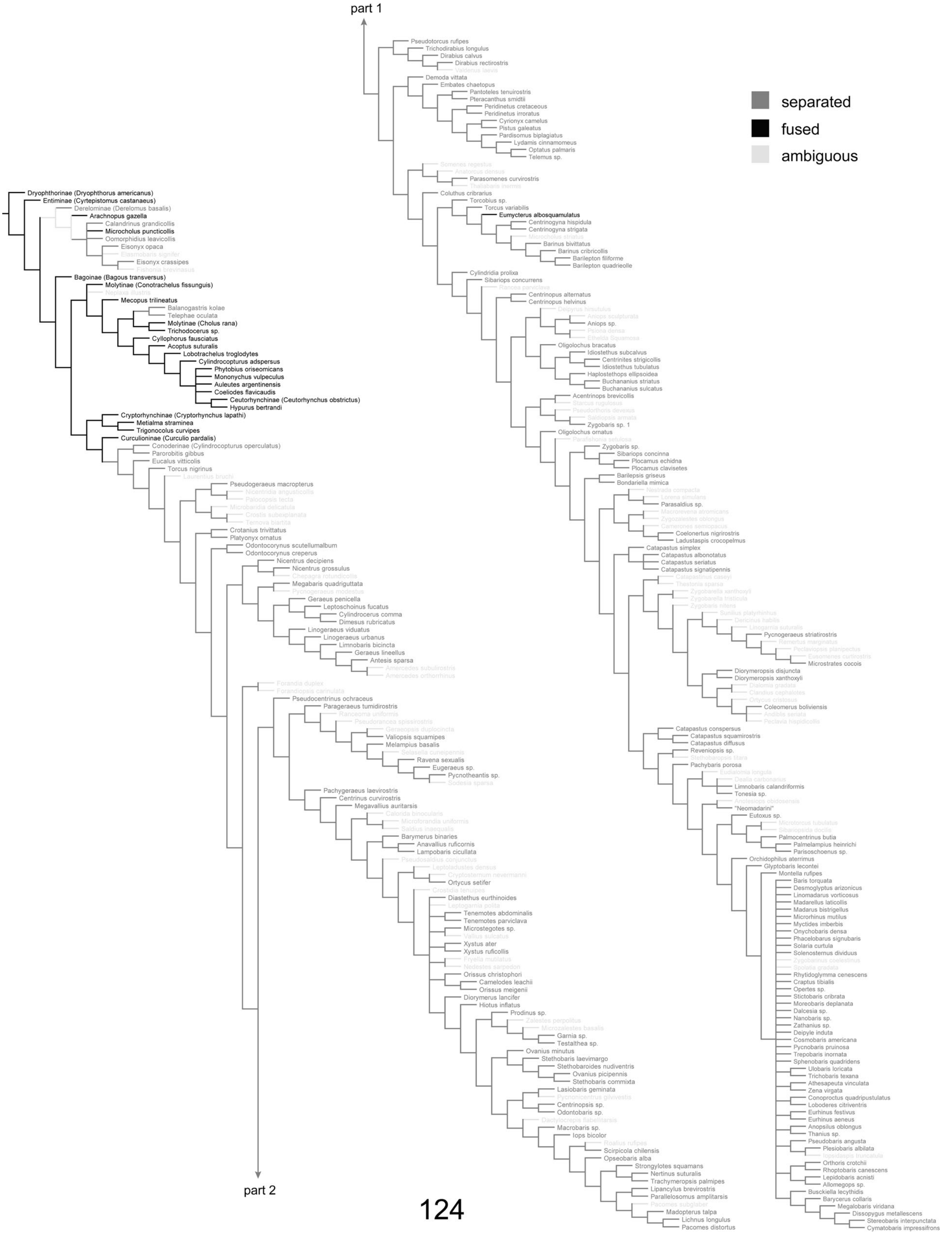


Figure 123. Character 54 (lateral margin of metanotum), supporting monophyly of Baridinae, mapped onto strict consensus tree of full taxon matrix analysis.



124

Figure 124. Character 98 (abdominal lateral tergite), supporting monophyly of Baridinae, mapped onto strict consensus tree of full taxon matrix analysis.

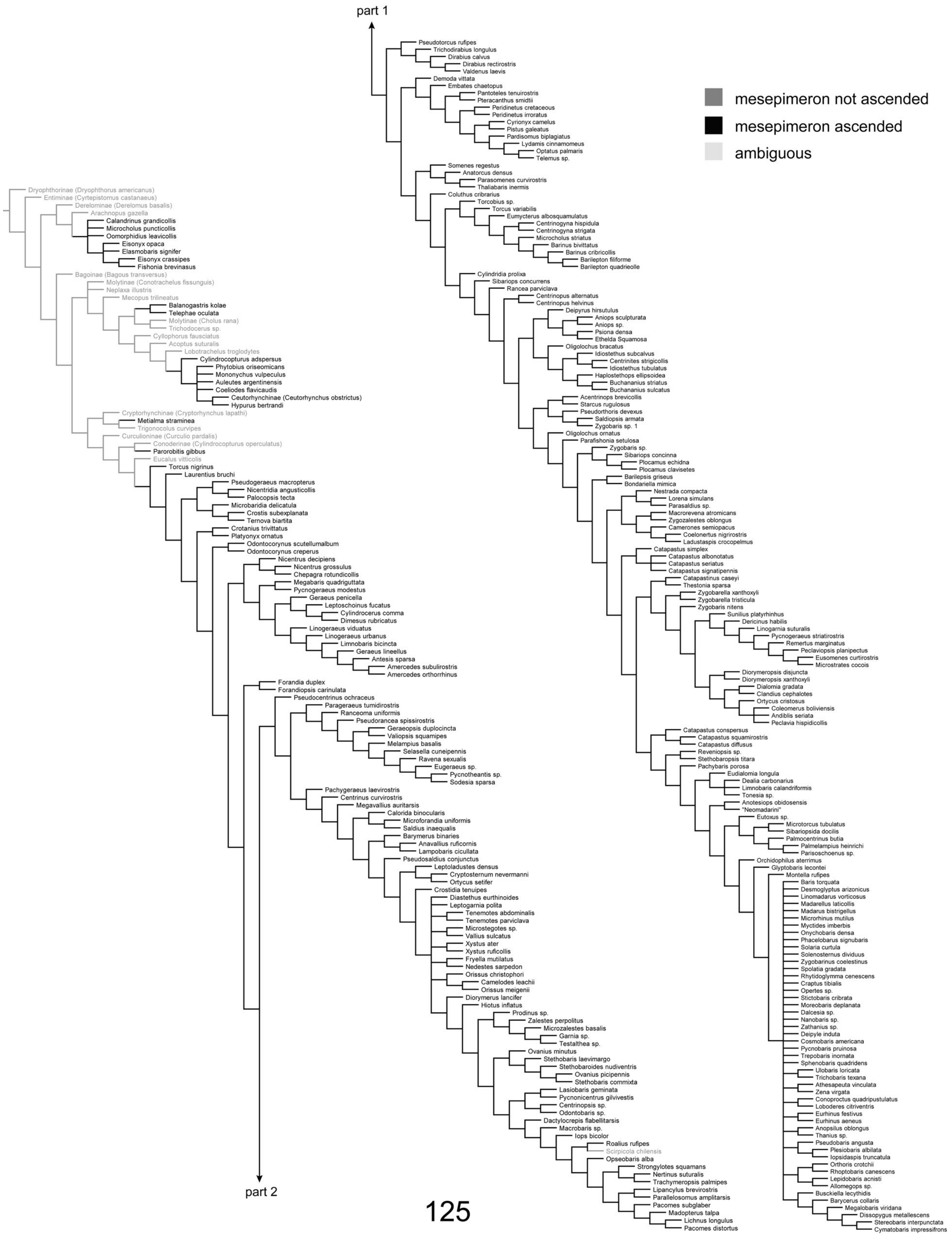
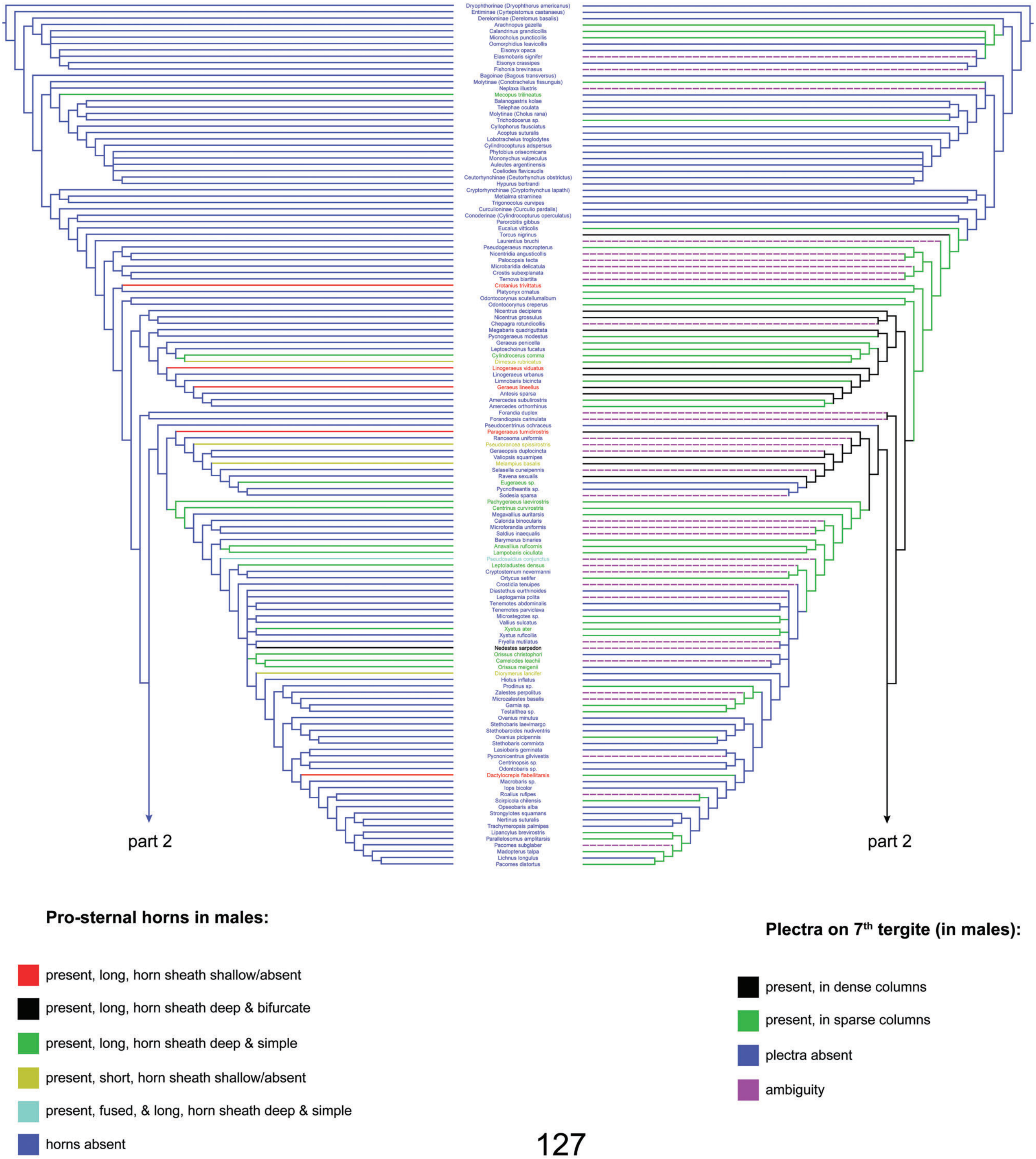


Figure 125. Character 41 (mesepimeron), supporting monophyly of Baridinae, mapped onto strict consensus tree of full taxon matrix analysis.

126

Figure 126. Character 51 (longitudinal crest on scutellar groove of metanotum), supporting monophyly of Baridinae and possibly suggestive of a more inclusive grouping, Barididae (Zherikhin & Gratshev, 1995), mapped onto strict consensus tree of full taxon matrix analysis.



127

Figure 127. Strict consensus tree of full taxon matrix analysis, with horn evolution mapped onto the left phylogeny and plectral evolution mapped onto the right phylogeny.

strongly correlates with the presence of plectra. In addition, the taxa that possess horns that 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 (because of the reduced form of the

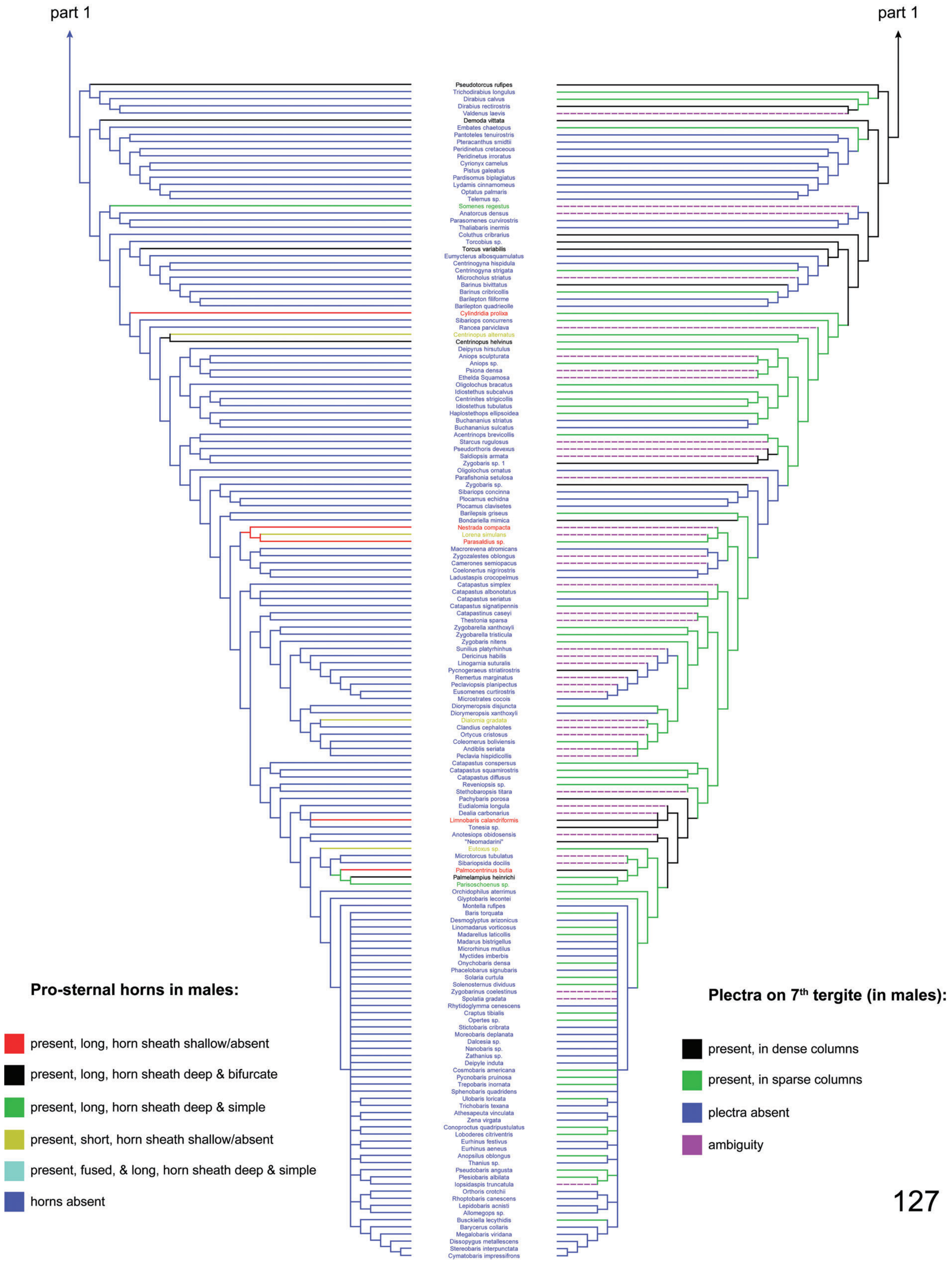


Figure 127. *Continued*

plectra and file) or produce very different sounds to species that 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 to the species that possess the reduced form of plectra.

As there are many more baridine (and non-baridine) genera believed to possess horns than were examined in this study, the historical accuracy of the phylogeny and evolutionary history of the horns presented here is uncertain. Future research to 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 prosternal horns in weevils.

BIOGEOGRAPHY OF BARIDINAE

From examination of the mapping of the biogeographical zones onto the strict consensus tree (Fig. 128), no specific distribution or dispersal patterns are visible. Approximately 75% of the known baridine genera are found in the Neotropics. As relatively few Old World taxa were included in this study, it is difficult to interpret any biogeographical patterns. In order to assess biogeographical patterns within Baridinae definitively, denser sampling is needed of Old World taxa.

HOST PLANT UTILIZATION

As host-plant records are available for extremely few baridine genera, no definitive trends in host plant evolution are evident. In addition, because many baridines are known to oviposit in different plants than those they feed on, examining patterns of host-plant evolution is not straightforward. It is believed that the superfamily Curculionoidea originated sometime during the early to middle Jurassic (Grimaldi & Engel, 2005), with the Curculionidae appearing during the middle Cretaceous (Farrell, 1998; McKenna *et al.*, 2009). 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 might exist to explain host-plant patterns in Baridinae, one that requires much more biological data to address than are presently known or available.

FINAL THOUGHTS AND FUTURE DIRECTIONS IN BARIDINE PHYLOGENETICS

A high amount of homoplasy in phylogenies with large numbers of taxa that are produced from morphological data can be expected and may not be cause for much concern. As homology is a *post hoc* assessment, those characters that turn out not to be homologous on a phylogeny are homoplasies (Wake, 1999). Thus, homoplasies not only give structure to trees as synapomorphies do, but 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 & 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 & Huelsenbeck, 1992). Thus, separating the amount of homoplasy that is the result of noise and that which is the result of 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 assess further the quality of the data, future work on baridine phylogenetics should include implementation of phylogenetic models and tests for judging the quality of phylogenetic information in character data, such as examination of the distributions of tree-length skewness (Huelsenbeck, 1991). Given the results from analyses of the FTM and the RTM, the data from this study appear to be consistent (Hillis, 1995), in that addition of more data from the RTM to the FTM resulted in similar phylogenies.

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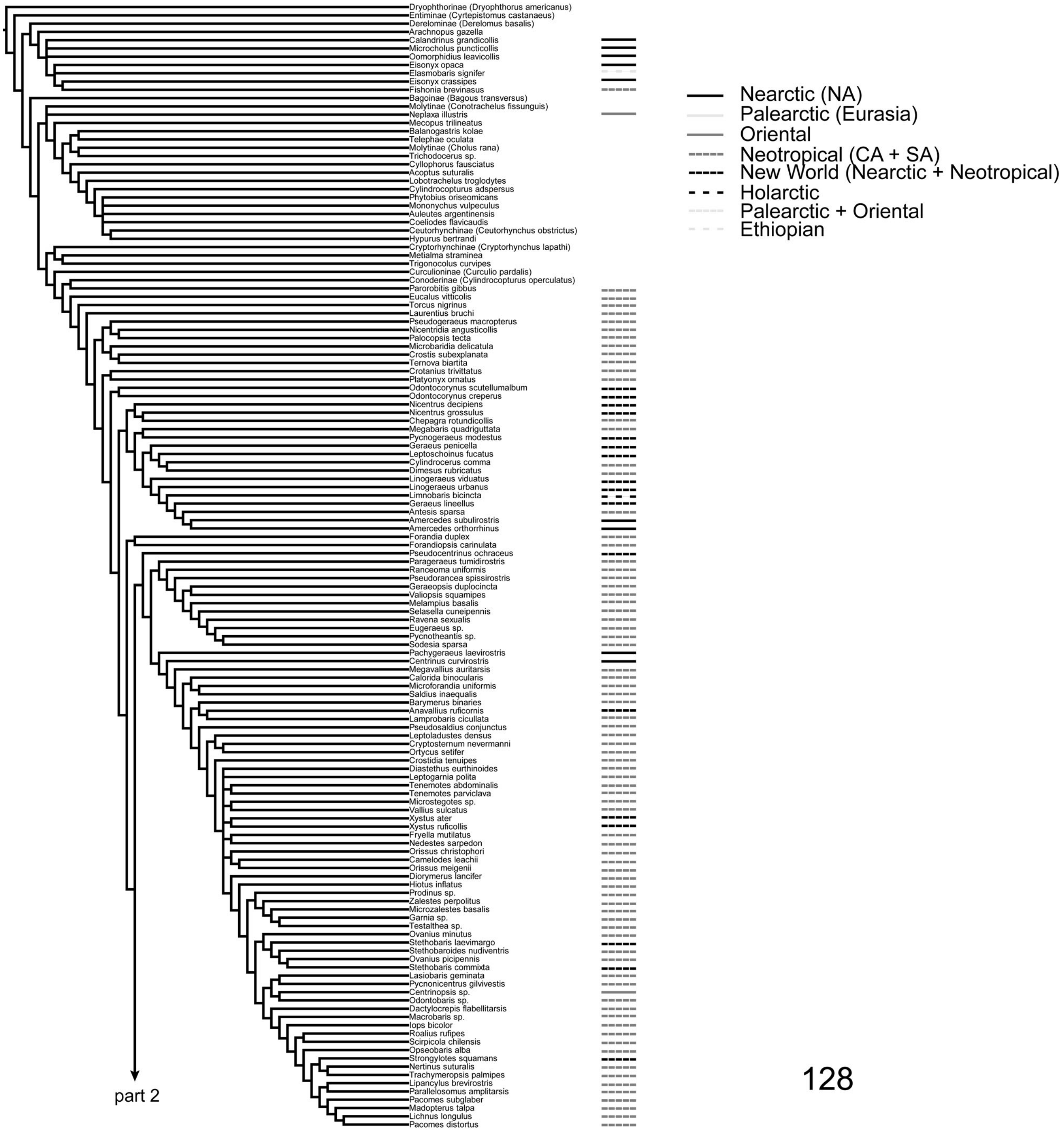

Figure 128. Biogeographical regions mapped onto strict consensus tree of full taxon matrix analysis.

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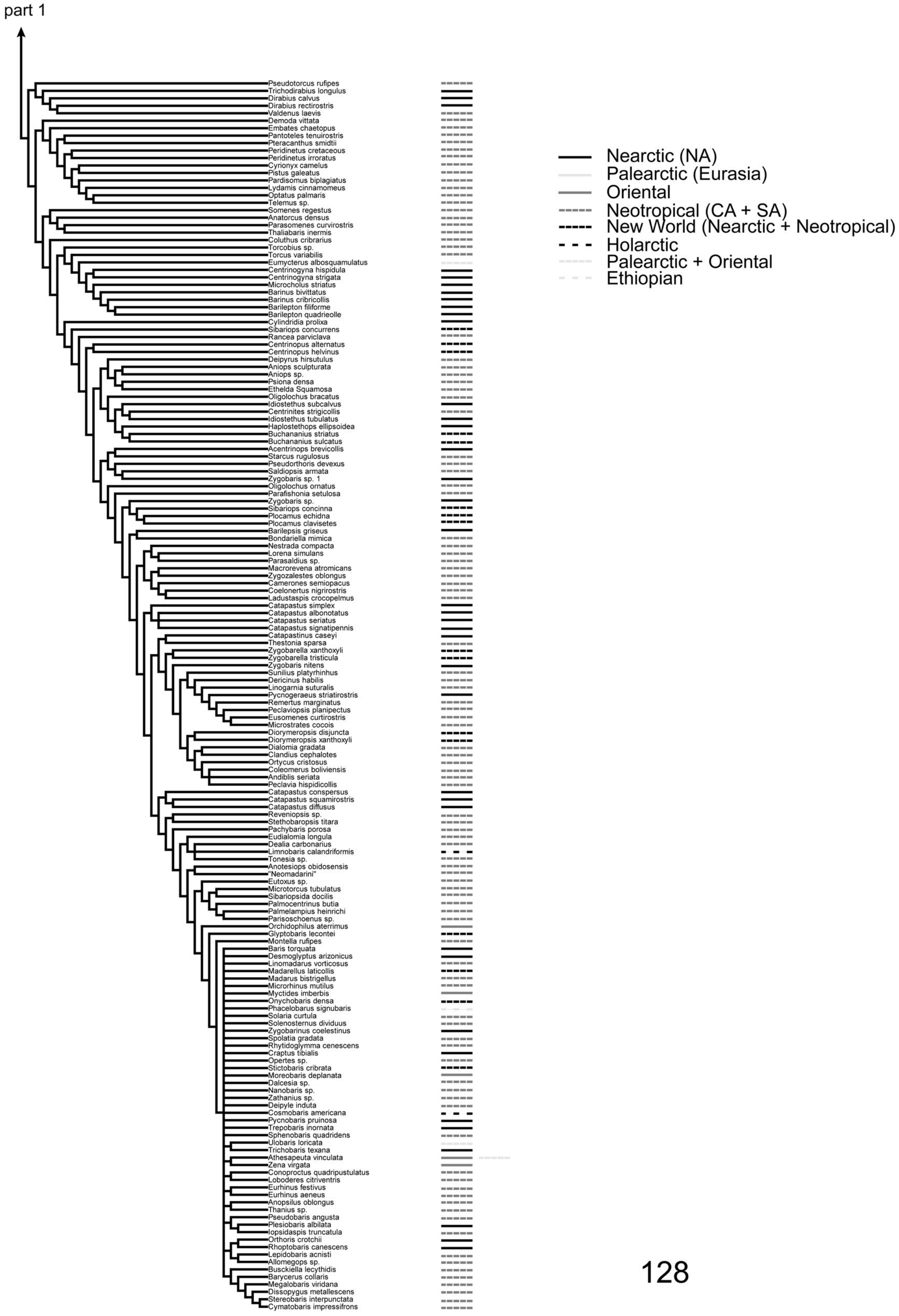

Figure 128. *Continued*

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APPENDIX 1

Taxa examined. Classification follows that of Alonso-Zarazaga & Lyal (1999).

Subfamily (family)	Tribe	Subtribe	Taxon
Bagoinae			*Bagous transversus* LeConte, 1876
Cossoninae	Cossonini		*Cossonus impressifrons* Boheman, 1838
Curculioninae	Curculionini	Curculionina	*Curculio pardalis* (Chittenden, 1908)
	Derelomini		*Derelomus basalis* Blatchley & Leng, 1916
Hylesininae (Scolytidae)	Hylastini		*Hylurgops planirostris* Wood & Bright, 1992
Orobitidinae			*Parorobitis gibbus* Korotyaev, Konstantinov, & O'Brien, 2000
Conoderinae	Arachnopodini		*Arachnobas gazella* Boisduval, 1835
	Coryssomerini		*Metialma signifera* Pascoe, 1871
	Coryssopodini		*Cyllophorus fasciatus* Faust, 1886
	Lechriopini		*Acoptus suturalis* LeConte, 1876
	Lobotrachelini		*Lobotrachelus troglodytes* (Desbrochers des Loges, 1891)
	Mecopini		*Mecopus trilineatus* Rosenschoeld, 1838
	Menemachini		*Balanogastris kolae* (Desbrochers des Loges, 1895)
	Menemachini		*Telephae oculatus* (Say, 1824)
	Trichodocerini		*Trichodocerus* Chevrolat, 1879 sp.
	Zygopini		*Cylindrocopturus adspersus* (LeConte, 1876)
	Zygopini		*Cylindrocopturus operculatus* (Say, 1824)
Molytinae	Cholini		*Cholus rana* Schönherr, 1825
	Conotrachelini		*Conotrachelus fissunguis* LeConte, 1876
	Trigonocolini		*Trigonocolus curvipes* Klima, 1935
Entiminae	Cyphicerini	Cyphicerina	*Cyrtepistomus castaneus* (Roelofs, 1873)
Dryophthorinae (Dryophthoridae)			*Dryophthorus americanus* Bedel, 1885
Cryptorhynchinae	Cryptorhynchini	Cryptorhynchina	*Cryptorhynchus lapathi* (Linnaeus, 1758)
Ceutorhynchinae	Ceutorhynchini		*Ceutorhynchus obstrictus* (Marsham, 1802)
	Ceutorhynchini		*Coeliodes flavicaudis* Boheman, 1844
	Cnemogonini		*Auleutes bosqi* Hustache, 1939
	Hypurini		*Hypurus bertrandi* (Perris, 1852)
	Mononychini		*Mononychus vulpeculus* (Fabricius, 1801)
	Phytobiini		*Phytobius griseomicans* Schwarz, 1892

APPENDIX 1 *Continued*

Subfamily (family)	Tribe	Subtribe	Taxon
Baridinae	Ambatini		*Ambates chaetopus* Champion, 1909
	Ambatini		*Pteracanthus smidtii* Dejean, 1835
	Anopsilini		*Anopsilus oblongus* Boheman, 1844
	Baridini	Baridina	*Allomegops* Hustache, 1951a, b sp.
	Baridini	Baridina	*Baris torquata* Hustache, 1938
	Baridini	Baridina	*Busckiella lecythidis* (Champion, 1909)
	Baridini	Baridina	*Cosmobaris americana* Casey, 1920
	Baridini	Baridina	*Craptus tibialis* Casey, 1922
	Baridini	Baridina	*Cryptosternum nevermanni* Heller, 1936
	Baridini	Baridina	*Cymatobaris impressifrons* Casey, 1922
	Baridini	Baridina	*Dalcesia* Casey, 1922 sp.
	Baridini	Baridina	*Deipyle induta* Champion, 1909
	Baridini	Baridina	*Desmoglyptus arizonicus* Casey, 1920
	Baridini	Baridina	*Dissopygus metallescens* (Boheman, 1836)
	Baridini	Baridina	*Elasmobaris signifer* Reitter, 1895
	Baridini	Baridina	*Lepidobaris acnisti* Champion, 1909
	Baridini	Baridina	*Macrobaris* Champion, 1909 sp.
	Baridini	Baridina	*Megalobaris viridana* (Boheman, 1836)
	Baridini	Baridina	*Nanobaris* Champion, 1909 sp.
	Baridini	Baridina	*Odontobaris* Champion, 1909 sp.
	Baridini	Baridina	*Opertes* Casey, 1922 sp.
	Baridini	Baridina	*Orthoris crotchii* LeConte, 1876
	Baridini	Baridina	*Plesiobaris albilata* (LeConte, 1876)
	Baridini	Baridina	*Pseudobaris angustula* LeConte, 1876
	Baridini	Baridina	*Pycnobaris pruinosa* Casey, 1892
	Baridini	Baridina	*Rhoptobaris canescens* LeConte, 1876
	Baridini	Baridina	*Rhytidoglymma aenescens* Faust, 1896
	Baridini	Baridina	*Solenosternus dividuus* (Champion, 1909)
	Baridini	Baridina	*Sphenobaris quadridens* Champion, 1909
	Baridini	Baridina	*Stereobaris interpunctata* Casey, 1922
	Baridini	Baridina	*Thanius* Casey, 1922 sp.
	Baridini	Baridina	*Trepobaris inornata* Champion, 1909
	Baridini	Baridina	*Trichobaris texana* LeConte, 1876
	Baridini	Baridina	*Ulobaris loricata* Reitter, 1895
	Baridini	Baridina	*Zathanius* Casey, 1922 sp.
	Baridini	Coelonertina	*Coelonertus nigrirostris* Solari & Solari, 1906
	Baridini	Coelonertina	*Coluthus cribrarius* Champion, 1908
	Baridini	Coleomerina	*Coleomerus boliviensis* Hustache, 1949
	Baridini	Diorymerina	*Diorymerus lancifer* Guerin-Meneville, 1839
	Baridini	Diorymerina	*Hiotus inflatus* Casey, 1922
	Baridini	Diorymerina	*Prodinus* Casey, 1922 sp.
	Baridini	Diorymerina	*Testalthea* Casey, 1922 sp.
	Baridini	Eurhinina	*Barycerus collaris* Gyllenhal, 1836
	Baridini	Eurhinina	*Eurhinus festivus* (Fabricius, 1792)
	Baridini	Eurhinina	*Eurhinus aeneus* Schönherr, 1844
	Madarini	Barymerina	*Barymerus binarius* Hustache, 1938
	Madarini	Eutoxina	*Eutoxus* Schönherr, 1844 sp.
	Madarini	Leptoschoinina	*Acythopeus* Pascoe, 1874 sp.
	Madarini	Leptoschoinina	*Athesapeuta vinculata* Faust, 1894
	Madarini	Leptoschoinina	*Eumycterus albosquamulatus* Boheman, 1838
	Madarini	Leptoschoinina	*Loboderes citriventris* Hustache, 1938
	Madarini	Leptoschoinina	*Megabaris quadriguttata* (Klug, 1829)
	Madarini	Leptoschoinina	*Microstrates cocois* Bondar, 1941
	Madarini	Leptoschoinina	*Platyonyx ornatus* Schönherr, 1826
	Madarini	Leptoschoinina	*Zena virgata* Hustache, 1938
	Madarini	Madarina	*Conoproctus quadripustulatus* Fabricius, 1801
	Madarini	Madarina	*Glyptobaris lecontei* Champion, 1909

APPENDIX 1 *Continued*

Subfamily (family)	Tribe	Subtribe	Taxon
	Madarini	Madarina	*Linomadarus vorticosus* Casey, 1922
	Madarini	Madarina	*Madarellus ebenus* Hustache, 1938
	Madarini	Madarina	*Madarus bistrigellus* Boheman, 1844
	Madarini	Madarina	*Microrhinus mutilus* (Boheman, 1844)
	Madarini	Madarina	*Onychobaris densa* LeConte, 1876
	Madarini	Madarina	*Orchidophilus aterrimus* (Waterhouse, 1874)
	Madarini	Madarina	*Solaria curtula* Champion, 1908
	Madarini	Madarina	*Stictobaris cribrata* (LeConte, 1876)
	Madarini	Madarina	*Neomadarus* Hustache, 1938 sp.
	Madarini	Tonesiina	*Antesis sparsa* (Klug, 1829)
	Madarini	Tonesiina	*Myctides imberbis* Lea, 1906
	Madarini	Tonesiina	*Parisoschoenus* Faust, 1896 sp.
	Madarini	Tonesiina	*Pycnotheantis* Casey, 1922 sp.
	Madarini	Tonesiina	*Tonesia* Casey, 1922 sp.
	Madopterini	Madopterina	*Centrinopsis* Roelofs, 1875 sp.
	Madopterini	Madopterina	*Lipancylus brevirostris* (Casey, 1922)
	Madopterini	Madopterina	*Madopterus talpa* Schönherr, 1833
	Madopterini	Madopterina	*Opseobaris alba* Bondar, 1942
	Madopterini	Madopterina	*Pacomes distortus* Casey, 1922
	Madopterini	Madopterina	*Pacomes subglaber* Casey, 1922
	Madopterini	Madopterina	*Parallelosomus amplitarsis* (Casey, 1922)
	Madopterini	Madopterina	*Trachymeropsis palmipes* Champion, 1907
	Madopterini	Thaliabaridina	*Thaliabaris inermis* Marshall, 1952
	Madopterini	Torcina	*Anatorcus densus* Casey, 1922
	Madopterini	Torcina	*Microtorcus tubulatus* Casey, 1922
	Madopterini	Torcina	*Pseudotorcus rufipes* Hustache, 1949
	Madopterini	Torcina	*Sibariops concinnus* (LeConte, 1876)
	Madopterini	Torcina	*Sibariops concurrens* (Casey, 1892)
	Madopterini	Torcina	*Sibariopsida docilis* Casey, 1922
	Madopterini	Torcina	*Torcobius* Casey, 1922 sp.
	Madopterini	Torcina	*Torcus nigrinus* Hustache, 1939
	Madopterini	Torcina	*Torcus variabilis* Hustache, 1939
	Madopterini	Zygobaridina	*Acentrinops brevicollis* Casey, 1920
	Madopterini	Zygobaridina	*Amercedes subulirostris* Casey, 1893
	Madopterini	Zygobaridina	*Amercedes orthorrhinus* Champion, 1909
	Madopterini	Zygobaridina	*Anavallius ruficornis* Casey, 1922
	Madopterini	Zygobaridina	*Andiblis seriata* Casey, 1922
	Madopterini	Zygobaridina	*Aniops sculpturatus* Casey, 1922
	Madopterini	Zygobaridina	*Aniops* Casey, 1922 sp.
	Madopterini	Zygobaridina	*Anotesiops obidosensis* Casey, 1922
	Madopterini	Zygobaridina	*Barilepis grisea* (LeConte, 1876)
	Madopterini	Zygobaridina	*Barilepton filiforme* LeConte, 1876
	Madopterini	Zygobaridina	*Barilepton quadricolle* LeConte, 1876
	Madopterini	Zygobaridina	*Barinus bivittatus* (LeConte, 1878)
	Madopterini	Zygobaridina	*Barinus cribricollis* (LeConte, 1876)
	Madopterini	Zygobaridina	*Bondariella mimica* Hustache & Bondar, 1942
	Madopterini	Zygobaridina	*Buchananius striatus* (LeConte, 1876)
	Madopterini	Zygobaridina	*Buchananius sulcatus* (LeConte, 1876)
	Madopterini	Zygobaridina	*Calandrinus grandicollis* LeConte, 1876)
	Madopterini	Zygobaridina	*Calorida binocularis* Casey, 1922
	Madopterini	Zygobaridina	*Camelodes leachii* (Kirby, 1819)
	Madopterini	Zygobaridina	*Camerones semiopacus* Casey, 1922
	Madopterini	Zygobaridina	*Catapastinus caseyi* Champion, 1909
	Madopterini	Zygobaridina	*Catapastus conspersus* Casey, 1892
	Madopterini	Zygobaridina	*Catapastus squamirostris* Casey, 1920
	Madopterini	Zygobaridina	*Catapastus albonotatus* Linell, 1897
	Madopterini	Zygobaridina	*Catapastus diffusus* Casey, 1892

APPENDIX 1 *Continued*

Subfamily (family)	Tribe	Subtribe	Taxon
	Madopterini	Zygobaridina	*Catapastus seriatus* Casey, 1920
	Madopterini	Zygobaridina	*Catapastus signatipennis* Linell, 1897
	Madopterini	Zygobaridina	*Catapastus simplex* Casey, 1920
	Madopterini	Zygobaridina	*Centrinites strigicollis* Casey, 1892
	Madopterini	Zygobaridina	*Centrinogyna hispidula* Casey, 1920
	Madopterini	Zygobaridina	*Centrinogyna strigata* Casey, 1892
	Madopterini	Zygobaridina	*Centrinopus alternatus* Casey, 1892
	Madopterini	Zygobaridina	*Centrinopus helvinus* Casey, 1892
	Madopterini	Zygobaridina	*Centrinus curvirostris* Boheman, 1844
	Madopterini	Zygobaridina	*Chepagra rotundicollis* Casey, 1922
	Madopterini	Zygobaridina	*Clandius cephalotes* Casey, 1922
	Madopterini	Zygobaridina	*Crostidia tenuipes* Casey, 1922
	Madopterini	Zygobaridina	*Crostis subexplanata* Casey, 1922
	Madopterini	Zygobaridina	*Crotanius trivittatus* Champion, 1908
	Madopterini	Zygobaridina	*Cylindridia prolixa* (LeConte, 1876)
	Madopterini	Zygobaridina	*Cylindrocerus comma* Boheman, 1844
	Madopterini	Zygobaridina	*Dactylocrepis flabellitarsis* Boheman, 1844
	Madopterini	Zygobaridina	*Dealia carbonaria* Hustache, 1938
	Madopterini	Zygobaridina	*Deipyrus hirsutulus* Champion, 1908
	Madopterini	Zygobaridina	*Demoda vittata* Casey, 1922
	Madopterini	Zygobaridina	*Dericinus habilis* Casey, 1922
	Madopterini	Zygobaridina	*Dialomia gradata* Casey, 1922
	Madopterini	Zygobaridina	*Diastethus eurhinoides* Champion, 1907
	Madopterini	Zygobaridina	*Dimesus rubricatus* (Hustache, 1939)
	Madopterini	Zygobaridina	*Diorymeropsis disjuncta* Champion, 1908
	Madopterini	Zygobaridina	*Diorymeropsis xanthoxyli* (Linell, 1897)
	Madopterini	Zygobaridina	*Dirabius calvus* Casey, 1920
	Madopterini	Zygobaridina	*Dirabius rectirostris* (LeConte, 1876)
	Madopterini	Zygobaridina	*Eisonyx crassipes* LeConte, 1880
	Madopterini	Zygobaridina	*Eisonyx opacus* Casey, 1893
	Madopterini	Zygobaridina	*Ethelda squamosa* Casey, 1922
	Madopterini	Zygobaridina	*Eucalus vitticollis* (Blanchard, 1851)
	Madopterini	Zygobaridina	*Eudialomia longula* Casey, 1922
	Madopterini	Zygobaridina	*Eugeraeus* Champion, 1908 sp.
	Madopterini	Zygobaridina	*Eusomenes curtirostris* Casey, 1922
	Madopterini	Zygobaridina	*Fishonia brevinasus* Casey, 1922
	Madopterini	Zygobaridina	*Forandia duplex* Casey, 1922
	Madopterini	Zygobaridina	*Forandiopsis carinulata* Casey, 1922
	Madopterini	Zygobaridina	*Fryella quadrituberculata* Hustache, 1929
	Madopterini	Zygobaridina	*Garnia* Casey, 1922 sp.
	Madopterini	Zygobaridina	*Geraeopsis duplocincta* Champion, 1908
	Madopterini	Zygobaridina	*Geraeus lineellus* Casey, 1892
	Madopterini	Zygobaridina	*Geraeus penicillus* (Herbst, 1797)
	Madopterini	Zygobaridina	*Haplostethops ellipsoideus* Casey, 1920
	Madopterini	Zygobaridina	*Idiostethus subcalvus* (LeConte, 1878)
	Madopterini	Zygobaridina	*Idiostethus tubulatus* (Say, 1831)
	Madopterini	Zygobaridina	*Iops bicolor* Hustache, 1939
	Madopterini	Zygobaridina	*Iopsidaspis truncatula* Casey, 1922
	Madopterini	Zygobaridina	*Ladustaspis crocopelma* Boheman, 1844
	Madopterini	Zygobaridina	*Lamprobaris cucullata* Champion, 1908
	Madopterini	Zygobaridina	*Lasiobaris geminata* Champion, 1908
	Madopterini	Zygobaridina	*Laurentius bruchi* (Hustache, 1949)
	Madopterini	Zygobaridina	*Leptogarnia polita* Casey, 1922
	Madopterini	Zygobaridina	*Leptoladustes densus* Casey, 1922
	Madopterini	Zygobaridina	*Leptoschoinus fucatus* (Klug, 1829)
	Madopterini	Zygobaridina	*Limnobaris bicincta* Champion, 1908
	Madopterini	Zygobaridina	*Limnobaris calandriformis* Champion, 1908

APPENDIX 1 *Continued*

Subfamily (family)	Tribe	Subtribe	Taxon
	Madopterini	Zygobaridina	*Linogarnia suturalis* Casey, 1922
	Madopterini	Zygobaridina	*Linogeraeus urbanus* (Boheman, 1859)
	Madopterini	Zygobaridina	*Linogeraeus viduatus* (Hustache, 1949)
	Madopterini	Zygobaridina	*Lorena simulans* Casey, 1922
	Madopterini	Zygobaridina	*Macrorevena atromicans* Casey, 1922
	Madopterini	Zygobaridina	*Megavallius auritarsis* Casey, 1922
	Madopterini	Zygobaridina	*Melampius basalis* (Hustache, 1950)
	Madopterini	Zygobaridina	*Microbaridia delicatula* Casey, 1922
	Madopterini	Zygobaridina	*Microcholus puncticollis* LeConte, 1876
	Madopterini	Zygobaridina	*Microcholus striatus* LeConte, 1876
	Madopterini	Zygobaridina	*Microforandia uniformis* Casey, 1922
	Madopterini	Zygobaridina	*Microstegotes* Casey, 1922 sp.
	Madopterini	Zygobaridina	*Microzalestes basalis* Casey, 1922
	Madopterini	Zygobaridina	*Montella rufipes* Bondar, 1948
	Madopterini	Zygobaridina	*Nedestes sarpedon* Casey, 1922
	Madopterini	Zygobaridina	*Neplaxa illustris* Casey, 1922
	Madopterini	Zygobaridina	*Nestrada compacta* Casey, 1922
	Madopterini	Zygobaridina	*Nicentridia angusticollis* Casey, 1922
	Madopterini	Zygobaridina	*Nicentrus decipiens* Casey, 1892
	Madopterini	Zygobaridina	*Nicentrus grossulus* Casey, 1893
	Madopterini	Zygobaridina	*Odontocorynus scutellumalbum* (Say, 1831)
	Madopterini	Zygobaridina	*Odontocorynus creperus* Boheman, 1844
	Madopterini	Zygobaridina	*Oligolochus bracatus* (Casey, 1892)
	Madopterini	Zygobaridina	*Oligolochus ornatus* (Casey, 1920)
	Madopterini	Zygobaridina	*Oomorphidius laevicollis* (LeConte, 1876)
	Madopterini	Zygobaridina	*Orissus meigeni* Pascoe, 1889
	Madopterini	Zygobaridina	*Orissus christophori* Hustache, 1938
	Madopterini	Zygobaridina	*Ortycus cristosus* Casey, 1922
	Madopterini	Zygobaridina	*Ortycus setifer* (Boheman, 1844)
	Madopterini	Zygobaridina	*Ovanius picipennis* Hustache, 1938
	Madopterini	Zygobaridina	*Ovanius minutus* Hustache, 1949
	Madopterini	Zygobaridina	*Pachybaris porosa* LeConte, 1876
	Madopterini	Zygobaridina	*Pachygeraeus laevirostris* Casey, 1920
	Madopterini	Zygobaridina	*Palmelampius heinrichi* O'Brien & Kovarik, 2000
	Madopterini	Zygobaridina	*Palmocentrinus butia* Bondar, 1949
	Madopterini	Zygobaridina	*Palocopsis tecta* Casey, 1922
	Madopterini	Zygobaridina	*Parafishonia setulosa* Casey, 1922
	Madopterini	Zygobaridina	*Parageraeus tumidirostris* Casey, 1920
	Madopterini	Zygobaridina	*Parasaldius* Casey, 1922 sp.
	Madopterini	Zygobaridina	*Parasomenes curvirostris* Hustache, 1939
	Madopterini	Zygobaridina	*Peclavia hispidicollis* Casey, 1922
	Madopterini	Zygobaridina	*Peclaviopsis planipectus* Casey, 1922
	Madopterini	Zygobaridina	*Phacelobarus singularis* Gyllenhal, 1844
	Madopterini	Zygobaridina	*Plocamus echidna* (LeConte, 1876)
	Madopterini	Zygobaridina	*Plocamus clavisetis* Champion, 1908
	Madopterini	Zygobaridina	*Pseudocentrinus ochraceus* (Boheman, 1844)
	Madopterini	Zygobaridina	*Pseudogeraeus macropterus* Champion, 1908
	Madopterini	Zygobaridina	*Pseudorancea armata* Boheman, 1844
	Madopterini	Zygobaridina	*Pseudorthoris devexus* Champion, 1908
	Madopterini	Zygobaridina	*Pseudosaldius conjunctus* Casey, 1922
	Madopterini	Zygobaridina	*Psiona densa* Casey, 1922
	Madopterini	Zygobaridina	*Pycnogeraeus modestus* Casey, 1920
	Madopterini	Zygobaridina	*Pycnogeraeus striatirostris* Casey, 1920
	Madopterini	Zygobaridina	*Pycnonicentrus gilvivestis* Casey, 1922
	Madopterini	Zygobaridina	*Rancea parviclava* Casey, 1922
	Madopterini	Zygobaridina	*Ranceoma uniformis* Casey, 1922
	Madopterini	Zygobaridina	*Remertus marginatus* Casey, 1922

APPENDIX 1 *Continued*

Subfamily (family)	Tribe	Subtribe	Taxon
	Madopterini	Zygobaridina	*Revena rubiginosa* Boheman, 1836
	Madopterini	Zygobaridina	*Reveniopsis* Casey, 1922 sp.
	Madopterini	Zygobaridina	*Roalius rufipes* Casey, 1922
	Madopterini	Zygobaridina	*Saldiopsis armata* Casey, 1922
	Madopterini	Zygobaridina	*Saldius inaequalis* Casey, 1922
	Madopterini	Zygobaridina	*Scirpicola chilensis* (Blanchard, 1851)
	Madopterini	Zygobaridina	*Selasella cuneipennis* Casey, 1922
	Madopterini	Zygobaridina	*Sodesia sparsa* Casey, 1922
	Madopterini	Zygobaridina	*Somenes spinifer* Casey, 1922
	Madopterini	Zygobaridina	*Spolatia gradata* Casey, 1922
	Madopterini	Zygobaridina	*Starcus rugulosus* Casey, 1922
	Madopterini	Zygobaridina	*Stethobaris commixta* Blatchley & Leng, 1916
	Madopterini	Zygobaridina	*Stethobaris laevimargo* (Champion, 1916)
	Madopterini	Zygobaridina	*Stethobaroides nudiventris* Champion, 1907
	Madopterini	Zygobaridina	*Sunilius platyrhinus* Casey, 1922
	Madopterini	Zygobaridina	*Tenemotes abdominalis* Casey, 1922
	Madopterini	Zygobaridina	*Tenemotes parviclava* Casey, 1922
	Madopterini	Zygobaridina	*Ternova bipartita* Casey, 1922
	Madopterini	Zygobaridina	*Thestonia sparsa* Casey, 1922
	Madopterini	Zygobaridina	*Trichodirabius longulus* Casey, 1920
	Madopterini	Zygobaridina	*Valdenus laevis* Casey, 1922
	Madopterini	Zygobaridina	*Valliopsis squamipes* Casey, 1922
	Madopterini	Zygobaridina	*Vallius sulcatus* Hustache, 1938
	Madopterini	Zygobaridina	*Xystus ater* (Boheman, 1844)
	Madopterini	Zygobaridina	*Xystus arnoldi* (Kirby, 1819)
	Madopterini	Zygobaridina	*Zalestes perpolitus* Casey, 1922
	Madopterini	Zygobaridina	*Zygobarella xanthoxyli* Casey, 1920
	Madopterini	Zygobaridina	*Zygobarella tristicula* Casey, 1920
	Madopterini	Zygobaridina	*Zygobarinus coelestinus* Blatchley & Leng, 1916
	Madopterini	Zygobaridina	*Zygobaris* LeConte, 1876 sp. 2
	Madopterini	Zygobaridina	*Zygobaris nitens* LeConte, 1876
	Madopterini	Zygobaridina	*Zygobaris* LeConte, 1876 sp. 1
	Madopterini	Zygobaridina	*Zygozalestes oblongus* Casey, 1922
	Nertinini		*Lichnus longulus* Hustache, 1938
	Nertinini		*Nertinus suturalis* (Boheman, 1844)
	Nertinini		*Strongylotes squamans* Boheman, 1844
	Optatini		*Lydamis cinnamomeus* Champion, 1907
	Optatini		*Optatus palmaris* Champion, 1907
	Optatini		*Pardisomus biplagiatus* (Desbrochers des Loges, 1906)
	Optatini		*Pistus galeatus* (Boheman, 1844)
	Optatini		*Telemus* Pascoe, 1889 sp.
	Pantotelini	Cyrionychina	*Cyrionyx camelus* Champion, 1907
	Pantotelini	Pantotelina	*Pantoteles tenuirostris* Boheman, 1845
	Peridinetini		*Peridinetus cretaceus* Pascoe, 1880
	Peridinetini		*Peridinetus irroratus* Schönherr, 1837
	Incertae sedis		*Moreobaris deplanata* (Roelofs, 1875)

APPENDIX 2

Character matrix – characters 0–36. * = [0,4]; $ = [0,1]; & = [2,3].

	0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100 105 110
Dryophthorus americanus	001000010102401014210201001100000111001000023122110002102122012010111232130000012000113002100000000000002?1020100
Bagous transversus	00101002011002012311020140110020001103010002312011010210312000011011123011100001010011110310000000000000301??????
Cylindrocopturus operculatus	00101002110012010221120120011020201100111002012111002210301000210111122110011011020101000510000000111110301??????
Ceutorhynchus obstrictus	101010021100120103113021301100201011001011023021000022103010001100111220101110000011012104110000000000002??010112
Curculio pardalis	001010011100020131001021400100200111000000020121100022103010010210101422100010210100112002100000000000001??011100
Cholus rana	101011021110020103111200401110200011000000103122110012102020010210001210100110111200010005100000000000002??003214
Cyrtepistomus castanaeus	00101001031001011601122110010020011103020002012211010210212200001010142211111021200011000310000000000000310??????
Derelomus basalis	01100002111002112221020140010000111103120002022211010210202200001011142322222232200011000410111000111100201011100
Cryptorhynchus lapathi	00101002111002010321200100211020101001100010102011010211311001021012132210111021100010100400000000000000301013110
Conotrachelus fissunguis	001010021110020120002001001100200111*0100002312?????????????00021010132210100021200011000400000000000000310010200
Acentrinops brevicollis	10111102112002010201200000211010101040210110411011111001100000120011120001000000100001011101111111111100210??????
Amercedes subulirostris	10101100110002010200020000210020201040210110201001120001100000110001022001000011100001011?01?????????????01011010
Amercedes orthorrhinus	10111100110002010200020000210020201140200110001001120001100000110001042001000011110001011?01?????????????01011110
Anavallius ruficornis	10111100112002002200000010010001011000020011042011112000020001010001102021010101101000121110011111111100301111110
Anopsilus oblongus	0011000211200210022100010111000010102221011002000002100000210121001102011000001101110131110111000011111101123210
Antesis sparsa	00111102111002110200310000211020201141210110400000111100000000100011122001000011111001011121111000111100200002210
Athesapeuta vinculata	00111102111002100201210100111010010131100110521001010000010101210011121000000011001101101210110000111111200103212
Barilepsis griseus	00101102112002100301200100111020011111210110111001011001101000210011122001000011010001211101111100111100210010210
Barilepton filiforme	00111002021002100301300100110020020130020110011011020010101200010021122322222232000001011210111100111100301003100
Barilepton quadrieolle	00111002121002000301000100011020021130100110021011020011101200020021121001000011000001001211111100111100301003100
Barinus bivittatus	00121002011002000201300000111010001140120110011110110102111101100011210010000000000001000220111100111100300003100
Barinus cribricollis	00101102121002010301200100111010001130110110521011011210100200010001122000000000100001010100111100111100201003100
Baris torquata	0010110211100211031110000011001$11113021011052100002120120211121000112210000101102110141110011100011111200012012
Barymerus binaries	01101000110000002000300100111010110121200110420101010000201100021011120100101021011100001100111111111100311??????
Buchananius striatus	1010100211100201031102010021102010111021011121011101021101200021001112000000000121000101021011111011111010001211
Buchananius sulcatus	10101002111002110311320100211021101110210111210111010211012000210011120010000001200001011210111110111110101010100
Busckiella lecythidis	10100002012000200221210000111001121142210110520101010101211001210001132100001021221101201201111111111111201110100
Calandrinus grandicollis	0012100211200201020131000021102001114121011004101?00?110?1??11200111120322222232100000010300000000111000400012200
Camelodes leachii	1010000211200211020021000020110020103121011020101121000111101000100012111010101122000100 11?0111000111100 3??010010
Catapastinus caseyi	101111021120021103012001002100201100402101100210010210012000102100010222010000110100?????????????????????00??????
Catapastus conspersus	10101102112002010301200100210020110140210110021001010000201000220001020?????????100001011101111100111100301011200
Catapastus squamirostris	10111102111002110301200100210020110140210110001001121000200100220001020001000011110001011101111100111100201011200
Catapastus albonotatus	10101102112002110301200100210020210110210110001001010001201000210001022?????????110001011100111100111100200010100
Catapastus diffusus	1011110211200211 0?????0100211020210140210110001001121000200100 22??01022?????????110001011101111100111100201011200
Catapastus seriatus	10101102112002110301000100210020210110210110001001010001201000210001022001000011110001011110111100111100200010110
Catapastus signatipennis	10101102112002210301220100210020210110210110001001010001201000210001022001000000010001011100111100111100200010110
Catapastus simplex	1010110211200201 0?????0100210020110110210110001001010001201000 21??01020?????????11000101 11??1111001111002000 10110
Centrinites strigicollis	00101102111000112301210100210021101140200110411011010001200010100011120211000011110001011200111000111100300022010
Centrinogyna hispidula	0012110211100211030121010021102101114010011042101301101000200001001112200000001110000111021011100011100030??????
Centrinogyna strigata	0012110211100211032121010021101101114010011041???101100000101001101112000100000100100111020111100011110030 1003010
Centrinopsis sp.	10100002111002100221100000111000110130100111020011010201211201020012120110000011200001211210111111111100301003000
Centrinopus alternatus	00111002112000100301200100240020111040210110421111011100110010220011122001000001010001011100111000111100101020010
Centrinopus helvinus	00101002112000100301100000221020111010100110221011011000110010220011122001000011010001011200111000111100301020210
Centrinus curvirostris	1010100211200201220021010020102021105120011021101121100010000012001112211010101102000101120011110111100311010110
Coelonertus nigrirostris	00101002112000100201200100210020101041100110011001011100001100121011022001000011000001000110000000111100300??????
Coleomerus boliviensis	10111002110000100000000100111010101021210110021001211101100010220011022201101011111001211101110000111100200010100

Conoproctus quadripustulatus	00110012111001012200100140111000111141200110200101021200002111110011121100001011201101201101111111111111102??11&100
Crostidia tenuipes	10100102112001010?????014021000021000021011052????????????????????11120??????????00000000??????????????????????????
Crotanius trivittatus	00101102111002012?????0140230020101140200111521011111100000110200001122210101011010001011100110000111100 3??011210
Cylindridia prolixa	0010100211200201020101000013001001114021011012000101000010220001101112200110001111100111030011100011110020?011010
Cylindrocerus comma	00101002111001212000000140100000211141200110411000111201200000011011122110101021110001011100111100111111101022100
Cyrionyx camelus	1010100211200201030100014021112011014021011134000001020110100102101012221110101102000141111011000011100020012000 0
Dactylocrepis flabellitarsis	00100002111002112?????014013000010103012011004????????????????????11020??????????020000011?00??????????????????????
Dealia carbonarius	00121102112002112?????000011000001011220011052????????????????????11100??????????00000100??????????????????????????
Deipyrus hirsutulus	00101102112000200301100100210020110140210110211011011000011000120011120201000011200001011?00?????????????????011110
Demoda vittata	011011011120010102012001001210201111401001100210110210011112002200111221101010210100010011211111001111003??010110
Desmoglyptus arizonicus	0010010211100210020102010021000020111010011001000101100120220121001113220100001122000041121011100011111120111200 0
Dialomia gradata	10111102112002100?????010024001010103021011000????????????????????11022??????????10000100??????????????????????????
Diastethus eurthinoides	10101002120002000000110000110100111101210110541001210100110010011000101110101011220001011110100000111100201020110
Dimesus rubricatus	00101102112001110000000100140000111140210111221001120000200000121011122211100011010001011101111100111111301011200
Diorymeropsis disjuncta	10111102112002110200300100211010101111200110011001120200100010220011020001001011110001011100111100111100201??????
Diorymeropsis xanthoxyli	101111021120021102000001002110101011112101100110011202001010102200110201000001011110001011111111110011111 00200??????
Diorymerus lancifer	10000002110001210?????0100040000201101210110521011011001211100001001021110111021210000000121011111111111111??011100
Dirabius calvus	0012100211100211020121000011100000114010011042100102000110010012001112111000101101000100120011110011110020000101 0
Dirabius rectirostris	0011100211200211020130000011101002114010011012101102100010110002001112211000101111110100122011110011110020000101 0
Dissopygus metallescens	101200020110002002110000001110102101201101101110010202000010012200110221100010111211014012111111000111111200111 10
Eisonyx crassipes	0010110101100220222111010021101000113021011031111100001001201121002102032222223210000110021000000011111120?023002
Eisonyx opaca	0010010211100020031102010011100001010021011031011101121020201121102102032222223200000141031000000011111030001301 0
Elasmobaris signifer	00101102011000200?????010011102000114021011010??????????????????0011130??????????00000131??????????????????????????
Embates chaetopus	0010100211000101020110004011002111014010011002001102000120120000101012211011102102000100110011100011100030002011 0
Eugeraeus sp.	0012100211000200000011010120002121003221011052101002110110100011001012210010101132000101111011110011110031 0??????
Eumycterus albosquamulatus	001210011120021102013200001110100111111201105100110110102022010100111200010000000101100210?100000000000000???1131?0
Eurhinus festivus	1001000211100221220112000111000010113010011004000001000120101121000113110000102101110121111111110001111111 00121100
Eurhinus aeneus	1001000211100221020112000111100010111221011034000111110120200121000103120000010110111014111111110001111111 01123110
Eusomenes curtirostris	11111102011000200?????010011001001014020011002????????????????????11141??????????10100100??????????????????????????
Eutoxus sp.	00120102112002010201200100140000211132210110011001021200001200021001112210010102111000101110111111111111102??022110
Fishonia brevinasus	01101100022002200?????010011101000111211011041????????????????????11020??????????10000101??????????????????????????
Fryella mutilatus	11100102012002212?????000011000011011121011034????????????????????01041??????????22100130???0??????????????????????
Garnia sp.	10110102110001010201100100110000201112200110011011211201201000001001022110101011210001001101111111111111113??013100
Geraeopsis duplocincta	00101102111002110?????010021001010112021011042????????????????????11022??????????02000100??????????????????????????
Geraeus lineellus	0011110211100201200000014013102021111020011000100111000100000011001112200100000101000141112111100011110020001100 0
Geraeus penicella	1011110011000201000000010021002011004120011050100111110110000000001110211000101101000101110111100011110020102111 0
Glyptobaris lecontei	101111001120001002003001002110011101022001100100000110010120012100111202000000001110000211300111111111111200022010
Haplostethops ellipsoidea	0011100211100211030120010021101010114020011012001101120120000021001112100100000111000101020011111111111110300??????
Idiostethus subcalvus	101011021110000003010001002100211011402101104110110102002010002200111200111000111100010102001111111111111030001120 0
Idiostethus tubulatus	101011021110000103012101002110111011402001104410110100001000???0011120211000011101001010200111100111100300011210
Iops bicolor	01101001111000100?????014011001001110112011001????????????????????1001022??????????2001012113101111101111113??012100
Ladustaspis crocopelmus	00101002122002102?????010021002021004012011042????????????????????0011022??????????010001011110110000111100310??????
Lamprobaris cicullata	101101011210021023012000001000001101402101104201110?????????????0011022??????????0100010111101100001111113??110110
Lasiobaris geminata	00101102122002210301200100111020010130210110111001111201100000120011002210101011100001001210111111111111113??003100
Laurentius bruchi	00101002111002010?????010011001000114020011052????????????????????11100??????????02000100??????????????????????????
Lepidobaris acnisti	0010110211100211022100000011002011011121011052011101100001121121001102020000010112211014012101100001111112001101 0
Leptoschoinus fucatus	101110021120010100002001001100201111412001104010012211011000000010111020101000110211012111011100001111102??010202
Lichnus longulus	0012010212200010020130014011000001110002011011111020101010020002100112221000100011110011131011110011111120111311 0
Limnobaris bicincta	001111021110020003000001001110101111102101100210010111010002001100111222100000010000012011001100001111002??013110
Limnobaris calandriformis	0112010211200221230100010013000011111220011041100102110120000011001112010100000110100100112011100011110020002021 0
Linogeraeus urbanus	1011110211200201000000000011002011111221011022100111100120000010001112221000001101000100112111100011110020002101 0

APPENDIX 2 *Continued*

	0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100 105 110
Linogeraeus viduatus	10111002112002002100200000130020101130210110421001110001001010100011121100001011020001011120111000111100200010010
Linomadarus vorticosus	00111000112002110221000101210010110132210110200001011000212201210011022100000011021110211101111000111111200113110
Lipancylus brevirostris	00121001101000100201300040110010011120020110121110011210111201001001121210101121311100201301111110111111301013210
Loboderes citriventris	0011110211100111010110010011100011112120011034001102120121120021001102010000101100110120110111100011111 01??022200
Lorena simulans	10121102111000102?????010024102011001020011052????????????????????11022?????????11000100?????????????????????????
Lydamis cinnamomeus	1010100211200201020110014011102021010011011152001102111101101100101012111011102102000100111011100011100031?020000
Macrobaris sp.	00100002121002100301100100110000001100020111111111000201200200021001022210101001100000011410111100111111301013100
Macrorevena atromicans	10100100112000102?????010021000022114010011052????????????????????11002?????????020001101?10?????????????????????
Madarellus laticollis	10110002112002210200320101110100110132210110320000021100012011210010022200000011221101211101111000111111101122112
Madarus bistrigellus	00121002112002110200320101210000110112210110340001021001002101220010121210000011111101211111110000111111100112100
Madopterus talpa	00110002111000200201100000111000111150020110121100110211101200001011141210101121121101311300111111111111301013110
Megabaris quadriguttata	10101002112001110200300000111020210120100110201010011101110000000011122100001011021001011121111000111100310002210
Megavallius auritarsis	10101102112002002201210100110000111140200110411011211000201000200011122110101021020001011201111111111110201??????
Melampius basalis	1011110211000211000021010024100020111221011052101002100120000022001112211010102111000101122011110011110 02??011100
Microbaridia delicatula	00101102110002010?????014011002011004020011000????????????????????11020?????????1100?????????????????????????????
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Microcholus striatus	00121002111000000?????000021100011114010011001??????????????????0011122?????????10000101?????????????????????????
Microforandia uniformis	11101002112000000?????000011002011013020011051????????????????????11020?????????30000100?????????????????????????
Microrhinus mutilus	10110102010000202221320100011000101101210110311001010001002011210011022001000011101101201210110000111111201111210
Microstegotes sp.	1010000211200121220121010011010010110121011052100001000021000002100202111010101122000101120011000011111 01??021110
Microstrates cocois	00101101112000100?????0100110010010121210110511001021100001100200011122?????????001001201111111100111100210013100
Myctides imberbis	1011101211100020221121004011100011110121011032100001100100110121001002210000001101110120121111100011111111?123200
Nertinus suturalis	00111001102002012000110140110010011150020110221111000011110200001001021110101021010001311111111111111111310023110
Nestrada compacta	10111102112002102?????010023002111002120011010????????????????????11022?????????31000100?????????????????????????
Nicentrus decipiens	001010021220020002000?0100110020111140100110221001011000011200000011122001000000000001011221111000111100200010210
Nicentrus grossulus	0012100212100200020000010011102010114010011052100101100010010010001112210100001101000101112111100011110 02??011210
Odontobaris sp.	111000021010020002011?0100110010111141100110121111001210210000120011022110001011001101011210111111111111311011210
Odontocorynus scutellumalbum	00101002111002100200300000111020210120120110220000011100200100020011122210101011001101011100110000111100200010110
Odontocorynus creperus	00101002111000100200300000211020110020120110221100011200100100020011122110101011010001001100110000111100200001210
Oligolochus bracatus	10101102112000100301200100211010011150210110000011011000001010220011120011000011110001111200111110111110311110210
Oligolochus ornatus	00101102112000100301200100211020211130210110201000111001100010210011120001000001110001011110111100111100211??????
Onychobaris densa	10110102112000100221020100110000110112210110220000021000012111210011120000000001101110131110111000011111201122100
Oomorphidius leavicollis	0012000211100000030120010011000000111121011002101???????????01210011122322222223200001000410111000111100300010110
Opseobaris alba	00121102111000100301210100111010011140020110011111010211200200001001121210101021011001011111111111111111301013110
Optatus palmaris	10101002112001012201300040211020101000200111540011021001110010001000121110111021020001001111111100111000210??????
Orchidophilus aterrimus	00121102111000100301210100111020111132210110030101020000200011210010121110000011000001211100111111111111211??????
Orissus meigenii	10100002112002112?????0000200100201131200110211011200201110000001000021110101021020001011110110000111111101022010
Orissus christophori	10010002112002112200310000100000201102210110511001210200110010001002022110101021210001011110100000111100201020110
Orthoris crotchii	00101101111002110221100100110020211100210110221011010000111111210011120001000000001101411210111000111111211123110
Ortycus cristosus	1010110211200?????????010111112110113120011050?????????????????????1022?????????12000100?????????????????????????
Ovanius picipennis	11100102111002112301100100110000101111210110420001111001200000210001122211000001100001111100111111111111310011112
Ovanius minutus	10110102112002210320200100110000101131210111110001011001001000220011022211000001010000011110111111111111201000100
Pachybaris porosa	1011100211000210220030010011000021011221011100100002100120000021001102200110001110000101112011111011110 02??021110
Pachygeraeus laevirostris	0010110211200210010011000020002011113010011022111101120020000012001112221010101102000101020011110011110 02??010100
Pacomes subglaber	00121001112002002?????000011000001110002011010????????????????????00121?????????12111100?????????????????????????
Palmelampius heinrichi	0011110011000000030100000022001021011121011051100101110120000011001102200100101130000120110111111111111102??012200
Pantoteles tenuirostris	00101001102002012?????0040110020001100100111520010021200210200021010120?????????020001001110110000111000201110200
Parageraeus tumidirostris	00101102111002012000210140131000111150100111411011011001100000120011122210101011110001011320111000111100201??????
Parallelosomus amplitarsis	01121001101000100201200000010010011100120110121110110000110200021011121110101121001101111301111111111111311011110
Parasaldius sp.	1010110211100200230020000023102011101120011000100101100120110012001112200110101101100101110011100011110 02??020110
Parasomenes curvirostris	01111002111000002201300100111010011131100110001001011000100200110011122100101011100101011111111100111100200??????

Pardisomus biplagiatus	10101002111000010211100140110010111100110111420110011000201111001000121110101011020001001210111000111000300020210
Parisoschoenus sp.	10111102112002002301010000101010211141210110511000011100201100110011022000000011311101201101111111111110201013210
Peclaviopsis planipectus	10101102112000100?????010011101021014021011052????????????????????11022?????????10000100?????????????????????????
Peridinetus cretaceous	00101002112002012211020040111020101100100110441010020001011201001000121110111111220001401210111100111000200020010
Peridinetus irroratus	0010100211200201221102004011102010100010011002101002000121120100100012211011112102000100121011111011100002??020000
Phacelobarus signubaris	101011011210022102113001002111201101311001101000110100000111102100100221000101110100004011111110001111101??113110
Pistus galeatus	10101002112002000321310140211120101000210111520001020100100001001010132010101011020001011110110000111000101120000
Platyonyx ornatus	10111102111001010200000100210010211131200110211101111100000100020011101110001011010100011300110000111100310010210
Plesiobaris albilata	00101102122000100311320100111020010101110110320011011011202011120011020001000001101000210500000000111111401122210
Plocamus echidna	00101000110002000221020100110020211112210110501010020211001010210011120001000001100001001110100000111100111020100
Plocamus clavisetes	00101000110002000221000100110020211112210110501001011000012010210011120001000000200001111110111100111100100002200
Prodinus sp.	10010102111002110301320100110000101130110110220011001200201000000011022210101011010000211100111111111111301020100
Pseudobaris angusta	0011010211200210030112010011000010113121011012011101100100120012001102200000000030110031110011000011110002??121210
Pseudocentrinus ochraceus	00101002112002010200200100211020101040100110211001011000200100121011120110101011010001011110111100111100210002210
Pseudogeraeus macropterus	00101102111000002300000100211021110140220110201100000201110100000001102011010101101110211101111000111100300020000
Pseudorthoris devexus	00101102110002110301000000111020110140200110521011011101010200120011120201000000111101111??????????????????003110
Pseudotorcus rufipes	01101001111002100201210100121020011130200110111101011101100100020011122010101011010001011120111100111100200011110
Psiona densa	00101002111002200?????010011002101014011011142????????????????????01020?????????21000000?????????????????????????
Pteracanthus smidtii	00101001111002010211200040211120110100100111520010010000101000021000122110111121120001111210111100111000200110100
Pycnogeraeus modestus	10101002122002010100010000111020210110120110201001120001100000100011122110101011011101011?01???????????????111110
Pycnogeraeus striatirostris	10111102112002100100000100211021210130210110501001120100101000200011122001001000110001011121111000111100210000111
Pycnonicentrus gilvivestis	10101102111002110?????014011002011002011011011????????????????????11002?????????0100?????????????????????????????
Pycnotheantis sp.	10100102110000002301100100110010211131200110420011021001100010120011020110101011110001011110111000111100311??????
Ranceoma uniformis	00101101111002000?????014011100020112010011011????????????????????11022?????????11000000?????????????????????????
Remertus marginatus	101010021000001000????000011101021113221011022????????????????????11122?????????01000100?????????????????????????
Ravena sexualis	10111002110002010?????010021000011001121011042??????????????????1011022?????????0100010011211111001111003??011100
Reveniopsis sp.	10110100120002210?????010011000011011221011031??????????????????0011022?????????1200000111001111001111003??021100
Rhoptobaris canescens	00101102111001110221100100110020110140210110520011110001200201210011020201000011001101411210111000111111201123010
Saldiopsis armata	10111100122002112?????010021102121004021011042????????????????????11020?????????11000100?????????????????????????
Saldius inaequalis	10101102112002000?????010011102021014021011041????????????????????11020?????????10000100?????????????????????????
Selasella cuneipennis	10111102110002010?????010121100021001220011041????????????????????11022?????????11000101?????????????????????????
Sibariops concinna	0011110211200000220100010011002011113121011001100102100001120021001112200100000010000001110111100011110020 0??????
Sibariops concurrens	0010100111200200020101010011101011111121011041000101100010000022001112200100001111000101110111100011110030 0??????
Solaria curtula	10110100110002110221000101111000110112210110320001021001101011210010020200000011111013111001100001111111300003100
Solenosternus dividuus	00110102112000100311320000110000110121210110010101021001012101210011020200000011101101201101110000111111301122210
Somenes regestus	00101102111002000?????000010102021114011011012????????????????????11122?????????11010100?????????????????????????
Stereobaris interpunctata	10100102112000200221110100211010211120210110111000010100002001220011020110001011121101401111111000111111200112110
Stethobaris commixta	10110102112001210301100100111000101112200110110101211201100000220001022211000000000000101111111100111110110002002
Stethobaris laevimargo	101000021120021003012?0100110000100111210111111101011201201000210011022210001010100001011210111111111111200010102
Stethobaroides nudiventris	1011000211000211030120000011100010011121011111110122110120000022001102221100001110110041111111111111111120?002102
Stethobaropsis titara	10110102120002210??????00011000012013020011101????????????????????11022?????????11000101?????????????????????????
Strongylotes squamans	0010100110200200010030004011102001013002011002111001001111120000101112111010102102100100121011111111111121 1??????
Telemus sp.	1010100211000201031110004021112010110021011102001002001001001100100012111011102122000100111011100011100021 1??????
Tenemotes abdominalis	1011000011000010020121010011000010110021011052100111020111020000100100221011102102000101111111111111111121 0??????
Tenemotes parviclava	101010021120001002002?010011001020114021011052000111120111000000100100221110101102000101131011111111111111 21???????
Thaliabaris inermis	01101002111000000?????000011101001114121011042??????????????????0011122?????????10110121??11?????????????????????
Torcobius sp.	001210011110021102213100011110101011302101111201110111010011002200111220010000101100000011201000001111002??113110

APPENDIX 2 *Continued*

	0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100 105 110
Torcus nigrinus	01111002101002010300300100110020011142020110221101010010101100021011121210101011001101000220000000111102??001200
Torcus variabilis	01101001111000110201300000121010111142200110510011011000101200010011122001100010100001010221000000111110301020210
Trachymeropsis palmipes	0011100110200211000010004011101002113112011012111201011100020002100102121000100111000101121011111111111310??????
Trichodirabius longulus	0011100211200211220121000011102010114120011052000102110010010021001112211000001110000101120011110011110020101111 0
Valdenus laevis	0011100211200221 0?????00001100000001140120110 11????????????????????11122??????????2111001 0??????????????????????????
Valiopsis squamipes	0010110011100201020 03?010021001020101021011022111111100121000010001102211010102102000121112201111111111002??011010
Vallius sulcatus	1010000211200221 0?????0100210100101001210110 52????????????????????00021?????????210000011?00?????????????????????
Xystus ater	10100002110002010200000140100000101141210110520011200200110000001010021210101011020001011100100000111100300020010
Xystus ruficollis	101000021100020102000000000110000201140210110521011200200110010001002022210101011020000001100100000111 1003??010100
Zena virgata	0010110211100010022121010011101011113010011050010002000000100111000112210000101101110140121011000011111120100310 1
Zygobarella xanthoxyli	1011110211200211030100010021102021014120011000100101100020001021000102200100000111000 1011?00???????????????00022100
Zygobarella tristicula	1011110211200211030100010021002021014221011052100101100020001021000112200100001111000 1011?00???????????????00022100
Zygobarinus coelestinus	001001021110001 00?????0000110000110112200110 33????????????????????0001122??????????11010131??????????????????????????
Zygobaris sp. 1	101111021120020103010001002110202100402101101210110110010100001200110200010000001100010111201111001111001000101 10
Zygobaris nitens	1011110211200121030130000021002021011121011001100012100020001022000102201010101110000101 1?00????????????????010000
Zygobaris sp.	00101002112002100301000100110020110131110110021001011000001000200011122001000000100001011120111100111100300110100
Zygozalestes oblongus	10101100111000202?????0100210000210141100110 02????????????????????11022??????????11000100??????????????????????????
Anatorcus densus	0110110211100220 0??????1001110200111 41??011040????????????????????11122??????????110100001??????????????????????????
Andiblis seriata	111010001100021 10??????1001100201011 21??011030????????????????????01042??????????11000 1011??????????????????????????
Aniops sculpturata	001010020110002 00??????1001100200101 40??011060????????????????????01132??????????11000 1011??????????????????????????
Anotesiops obidosensis	001111021110021 00??????1001110100101 32??011010????????????????????11022??????????11010 1011??????????????????????????
Calorida binocularis	101011021120020 00??????1001110201100 20??011041????????????????????11021??????????02000 1001??????????????????????????
Camerones semiopacus	001210021120011 02??????1012100202101 11??011042????????????????????11022??????????11000 1001??????????????????????????
Chepagra rotundicollis	00121002122 00??00??????1011110102101 40??011022????????????????????11122??????????01000 1001??????????????????????????
Clandius cephalotes	101110021120021 10??????1012100101011 30??011040????????????????????11022??????????11000 1011??????????????????????????
Crostis subexplanata	001001021210022 12??????1001100001100 00??012050????????????????????11020??????????30010 101??????????????????????????
Dericinus habilis	101111021120021 00??????1002110102100 11??011051????????????????????11022??????????10000 1001??????????????????????????
Ethelda Squamosa	001010021210001 00??????1002110201101 20??011030????????????????????01022??????????11000 1001??????????????????????????
Eudialomia longula	001111021100021 02??????0001100102101 12??011042????????????????????11120??????????11000 1001??????????????????????????
Forandia duplex	001010011120020 10??????1001110201101 40??011022????????????????????11101??????????01100 1201??????????????????????????
Forandiopsis carinulata	001010021120020 10??????1001110201101 40??012052????????????????????11002??????????01000 2011??????????????????????????
Iopsidaspis truncatula	001101021220020 00?0????1001110000101 01??011042????????????????????11132??????????11000 011??????????????????????????
Leptogarnia polita	101101021120021 10?0????1011100002101 31??011054????????????????????01020??????????01000 1001??????????????????????????
Leptoladustes densus	101011021120020 10??????1002010202111 31??011052????????????????????11120??????????01000 1011??????????????????????????
Linogarnia suturalis	100111021120021 02?0????1002100102100 30??011061????????????????????01020??????????01000 1001??????????????????????????
Microtorcus tubulatus	001111021110021 10?0????1001110100101 40??011041????????????????????11122??????????11000 1001??????????????????????????
Microzalestes basalis	110101001200020 00??????1011100002011 11??011041????????????????????11022??????????11000 1011??????????????????????????
Nedestes sarpedon	101001021100010 12??????0002200002101 01??012052????????????????????11001??????????02100 1001??????????????????????????
Neplaxa illustris	101000020110020 13??????0000100000111 00??000221????????????????????10161??????????00000 1000??????????????????????????
Nicentridia angusticollis	001011021110000 00??????1001100201100 10??011030????????????????????11122??????????01000 1011??????????????????????????
Palocopsis tecta	001111021110000 00??????1001100201101 40??011030????????????????????01022??????????01000 2011??????????????????????????
Parafishonia setulosa	011011021120001 02??????1002110101101 31??011040????????????????????11122??????????11000 1001??????????????????????????
Peclavia hispidicollis	101110001120020 10??????1001110201011 21??011040????????????????????11022??????????11000 1001??????????????????????????
Pseudorancea spissirostris	001111021210022 12??????1001410000011 50??011042????????????????????01022??????????11000 1011??????????????????????????
Pseudosaldius conjunctus	101011021220020 02??????1001510202111 00??011052????????????????????11120??????????01000 1001??????????????????????????
Rancea parviclava	001010001120001 00??????0001110101011 40??011142????????????????????11021??????????11000 1011??????????????????????????
Roalius rufipes	0010100211200 0?00??????10?1110200011 43??011021????????????????????00122??????????01000 1001??????????????????????????

Sibariopsida docilis	00101102111002110?0????100111010010140??011040????????????????????11120?????????110001001????????????????????????
Sodesia sparsa	11111102110000000??????00011002021013 1??011040????????????????????11120?????????110001011????????????????????????
Spolatia gradata	10110102122000200??????101110000110111??011010????????????????????00132?????????111001401????????????????????????
Starcus rugulosus	01101002112001?10??????10?211020101141??011042????????????????????11120?????????100001001????????????????????????
Sunilius platyrhinhus	11111100110002100??????101211010210032??011001????????????????????11022?????????110001011????????????????????????
Ternova biartita	00101102122002012??????100110000110040??011054????????????????????11122?????????110001011????????????????????????
Thestonia sparsa	11111102111002110??????100111020110110??011002????????????????????01022?????????000001011????????????????????????
Zalestes perpolitus	10010102110002110??????001210000101011??011002????????????????????11122?????????010001001????????????????????????
Cymatobaris impressifrons	00101102012000200311200101210110111131210110111001021200001001220011122110001011221101401211111000111111100112012
Pacomes distortus	00100102111002002101200100110000011100020110421110211201101201001000121110101021121000111400111111111111210011200
Megalobaris viridana	10101002112002200301200000210010221120110110601001020201201101220011022100001011021101411211111000111111200112310
Rhytidoglymma cenescens	00100102112002110311300000111100120112210110611001021000200101210001132110001011121001311410111000111111201??????
Craptus tibialis	00100102112002110201300100210000101011210110520101020101001201210001032100000011021101301201110000111111101120210
Testalthea sp.	10000002110001210311300100111000201101210110301010121100201000001001030210101011010001211400111110111111301010100
Barycerus collaris	10120002012000200201100000110000120110210110021010021001201001220011030100001011021101411111111000111111000113312
Opertes sp.	10111002111002100200300100211000101111210110621001021000202001210011032100001021021101211201110000111111101120110
Stictobaris cribrata	00101102121000200201300100211020110100100110221001011000101101210011100100001011111101311210111000111111100110102
Moreobaris deplanata	00100102112000100201200100211000210132210110610001010000100101210011020200000011121101411210111000111111100121000
Ulobaris loricata	00101002112000200311210100211000010100100110520111011200200011110011120200000010111101211200111000111111100013112
Neomadarus sp.	00111102111002110301300100111000211131210110001001021000200100220011021001001010111101011120111100111100011001210
Trichobaris texana	00101102122000200311200100211020210130100110520101011000210201210001120100001011011101401310100000111111201013012
Dalcesia sp.	00100002112002110311300000110000001110100110620211011100202101220011020100001011021101201110111000111111200121212
Nanobaris sp.	11101102111000100211300100110020001101210110620001011000111001210001020201000001111101301210111000111111200113210
Zathanius sp.	10111102122002110201200100211020010110210110620101020000200101210011020110000011311101211210110000111111100110210
Allomegops sp.	101010021110021102012000012100200011312101105201100110001012012100011202100010113211012012101100001111111??111110
Deipyle induta	10111002112002210201320100111020110112210110620010020000201001210011020200000011311001201210111000111111101123210
Cosmobaris americana	00101102121000000311200100210020110130110110100101011000112201210011020200000011001001111200111000111110110111112
Thanius sp.	00110002112002110301300101211000101022200110620011021000201101210001022110001011121101311111110000111111110??120210
Cryptosternum nevermanni	10101002112002110?????000021102002011121011062???????????????????010162?????????110001311????????????????????????
Pycnobaris pruinosa	10111102122000200201110100211020220011210110501001011001201001210011120110000011011101311100111000111111100003212
Tonesia sp.	111201021120021103013001002100000101122101102210010200010110002100111002000010111100010111201111001111000??023210
Trepobaris inornata	00110102122000200201300100210000001011100110620001011000012201120010020100000011111101211200110000111111100121210
Hiotus inflatus	10010002122002110100200100110000201101200110201011001001111000000110221101010110100000111101000001111110 11??????
Sphenobaris quadridens	11111102112002110201300101110021120112210110330001010000202001210010122200000011311000211210111111111111111??????
Coluthus cribrarius	00101002111002010201300100211020101031100110520011011000200200020011122101001011110001011220110000111100 1??110110
Aniops sp.	00101002111000200301200100210020110140100110001011001000010200121001132211000010110001011300111100111111200010210
Montella rufipes	10111102112000210??????10011100022010021011030??????????????012?0001122?????????1000010112101111111111111??012100
Palmocentrinus butia	00111002110002110??????10013101021012120011052??????????????0?2?0011102?????????1111012013211111111111102??021210
Bondariella mimica	00101100110002100??????10021102001011120011010??????????????0?2?0011122?????????0100010113201111001111002??010100
Eucalus vitticolis	00101002111002010??????10021002001010300000202??????????????0?1?0031120?????????011101200401000000111111301012200
Scirpicola chilensis	00101002111002010??????10011102001110300001311??????????????1?0?1011122?????????010001000300111111111111201013110
Ortycus setifer	10111002112002012100210100211021220101210110521011020000201000001011122110101021120001011100111111111111011013210
Parorobitis gibbus	10001102110012012??????100110020201161100102011023001010201001011031122210100011011101201210000000111 0001??011104
Arachnopus gazella	01121002112002010100311100110020010101210002112213001010212011001040131322222232200001400000000000000000 5??010200
Cyllophorus fausciatus	10011002112002000100210110111010101100100002401011014210300000011040160110011021010001010310000000000000 2??011100
Metialma straminea	10101002112002110301210110010020111103110102002011013210302000021010122110011020011100200411000000000000201020214
Balanogastris kolae	10101002112002010311200110010020110160100114312011012210302000001040160110100021010101000210111000111000211020110
Telephae oculata	10101002111002012301200110211020101060100114012011012210302000020040130110100011010101000210111000111000 2??010210
Cylindrocopturus adspersus	00101002110002000211300120110020001101110102312011004210302000210041110211000011010101000310000000000000201010100

APPENDIX 2 *Continued*

	0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100 105 110
Acoptus suturalis	00101002112000100001001120111020001160100002022011012210302000010041110110000011010002000310000000000000211120200
Lobotrachelus troglodytes	1010100211100201031110012011002010111121000201201100121030200011004016221000001111102010310000000000000211??????
Mecopus trilineatus	00121102111002002201111110100020011100120002522010010210011200021040160110101020020001500310000000000000211010200
Trigonocolus curvipes	10001002111001212311202130010001221160100002033012031111311000100110132110111021311111201611000000000000601121010
Hypurus bertrandi	1010100211100200031130013011002000116010010201211300021030200021004012000100000002110121031100000000000002??011202
Phytobius oriseomicans	10101002112002000311300130110020011160100102302111004210302000011011120210000010311101500410000000000000311000304
Mononychus vulpeculus	10101002112000000311300130210020101161111102302111004210302000211021121210011011021101510210000000000000201010200
Auleutes argentinensis	10101002111000000311300130110020101161101102302113004210302000110031142110000010011101200310000000000000201013104
Coeliodes flavicaudis	10101002111002000311300130110020001161101102302113004210302000011030122210011010021101200310000000000000201010200
Trichodocerus sp.	00101001100003013301200100211020001103100014022011002210202001011040110211100021120000000300000000000000211020213