



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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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, Sonnetini, 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 Centrinini, 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 Orbitini. 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

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, Oorbitinae, and Zygoninae. 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

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 Leptoschoina 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	

groups mentioned above, and may be indicative of a larger cohesive grouping. Oberprieler *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 heretofore; 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 $> 2\times$ width (0); round, spherical – length $2\times$ 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).

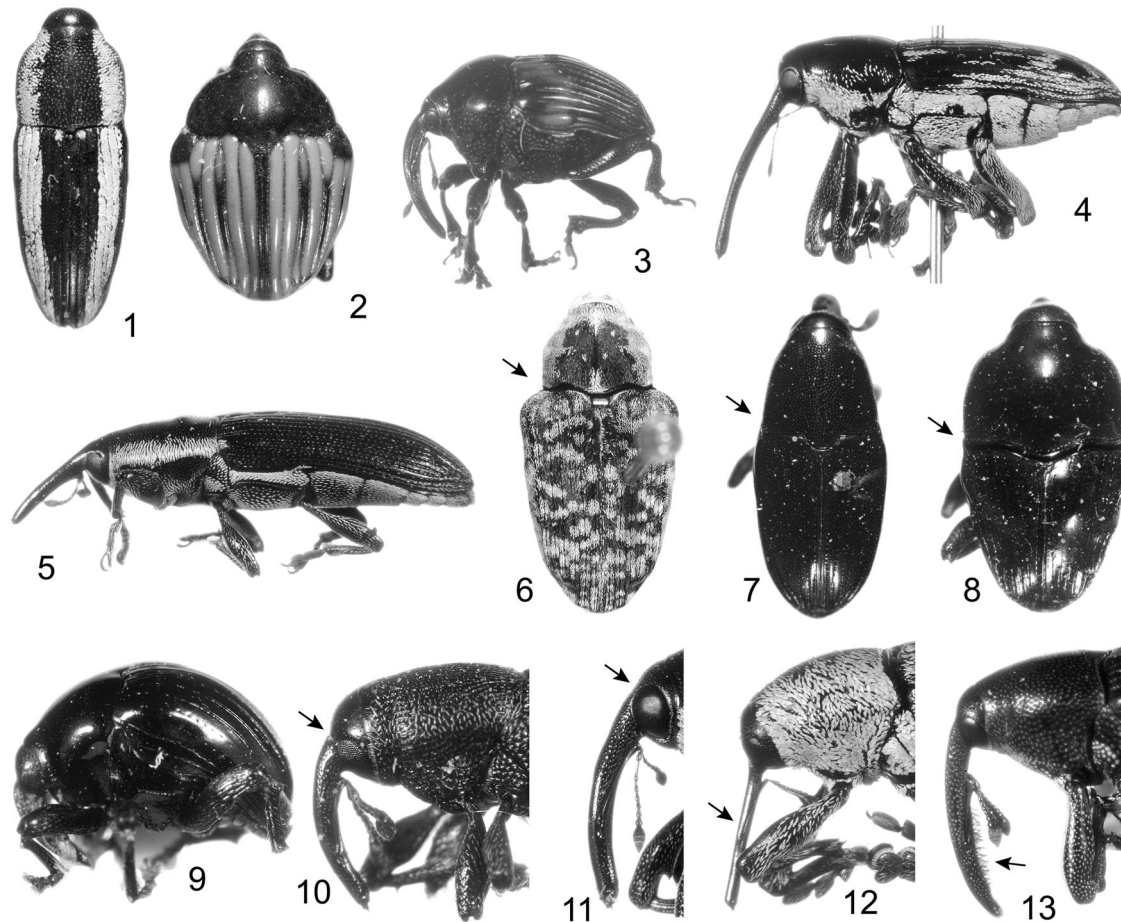
7. Rostrum, shape (lateral view):

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

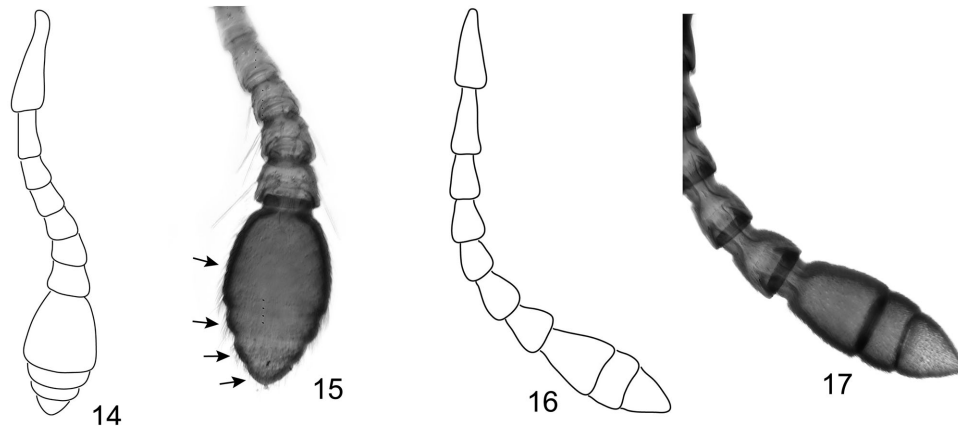
strongly curved is not usually obscure. Most genera possess a rostrum that is broadly curved. Rostra that are strongly curved often are not elongate or greater in length than the length of the pronotum, and the apex of the rostrum is recurved underneath the prosternum in habitus.

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 braccatus*; 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 monodentation, 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:

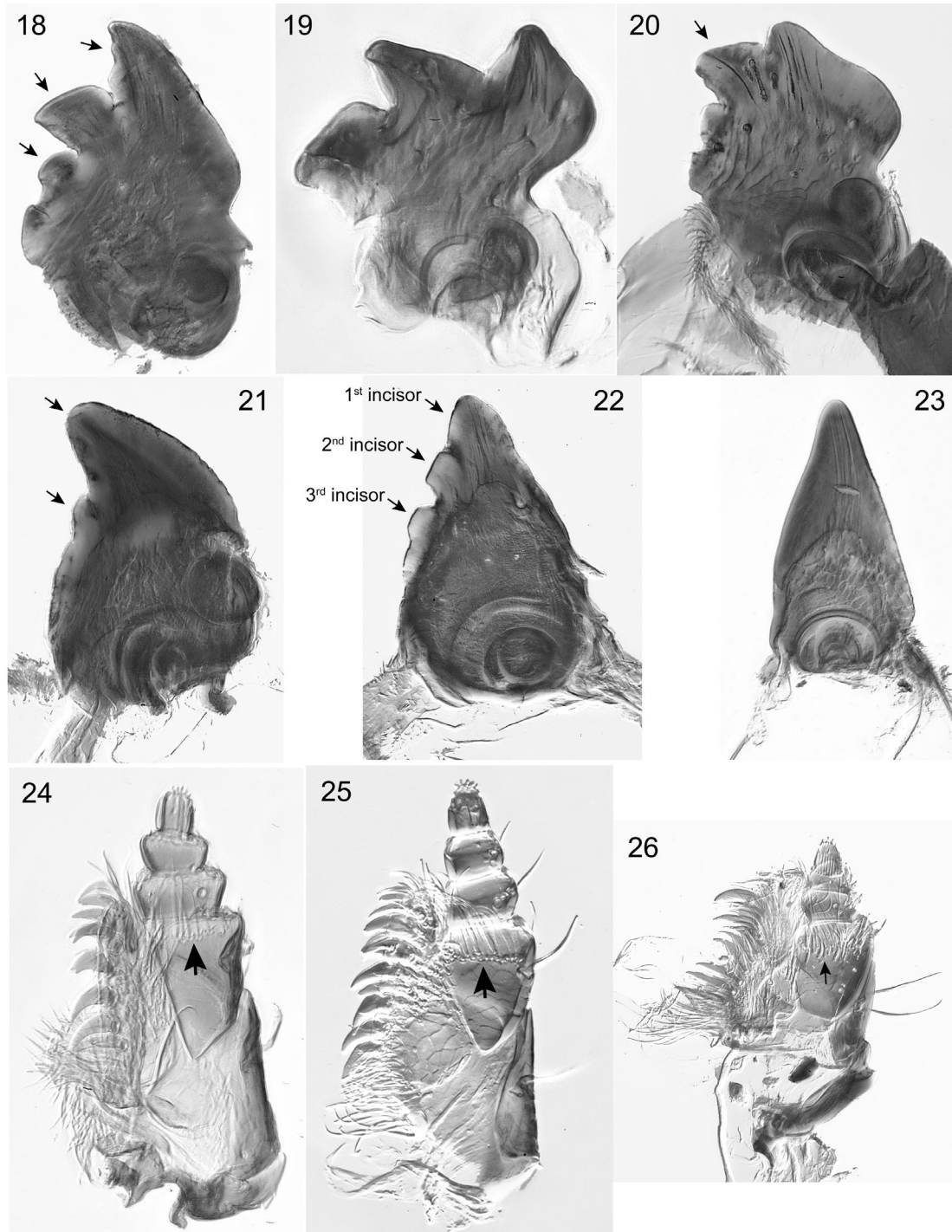
Normal, proportional to abdomen (0); enlarged (1)

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).

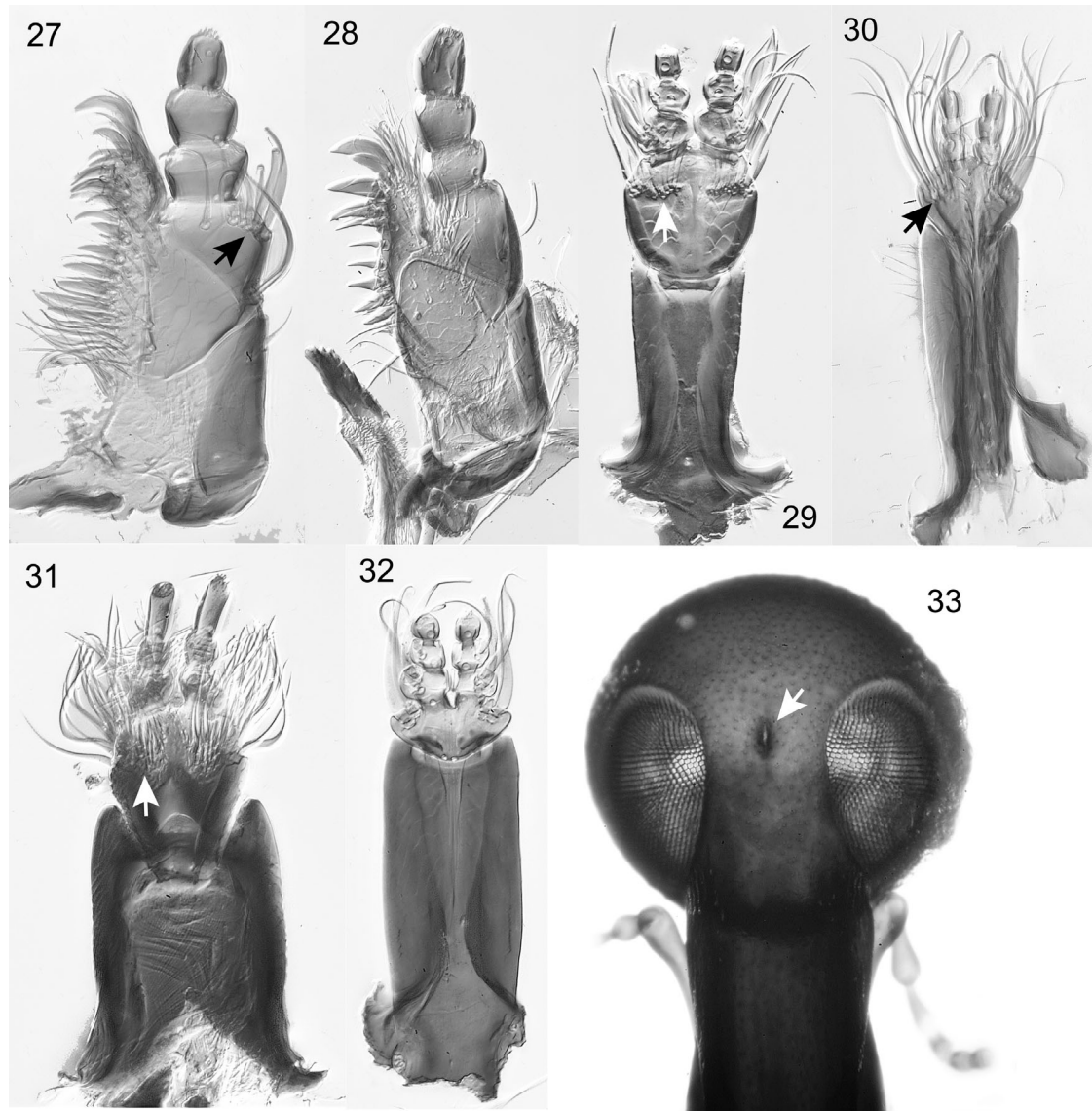
26. Thorax, pronotum – puncture collar near anterior margin:

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 bractus*, 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 punicollis*, 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.

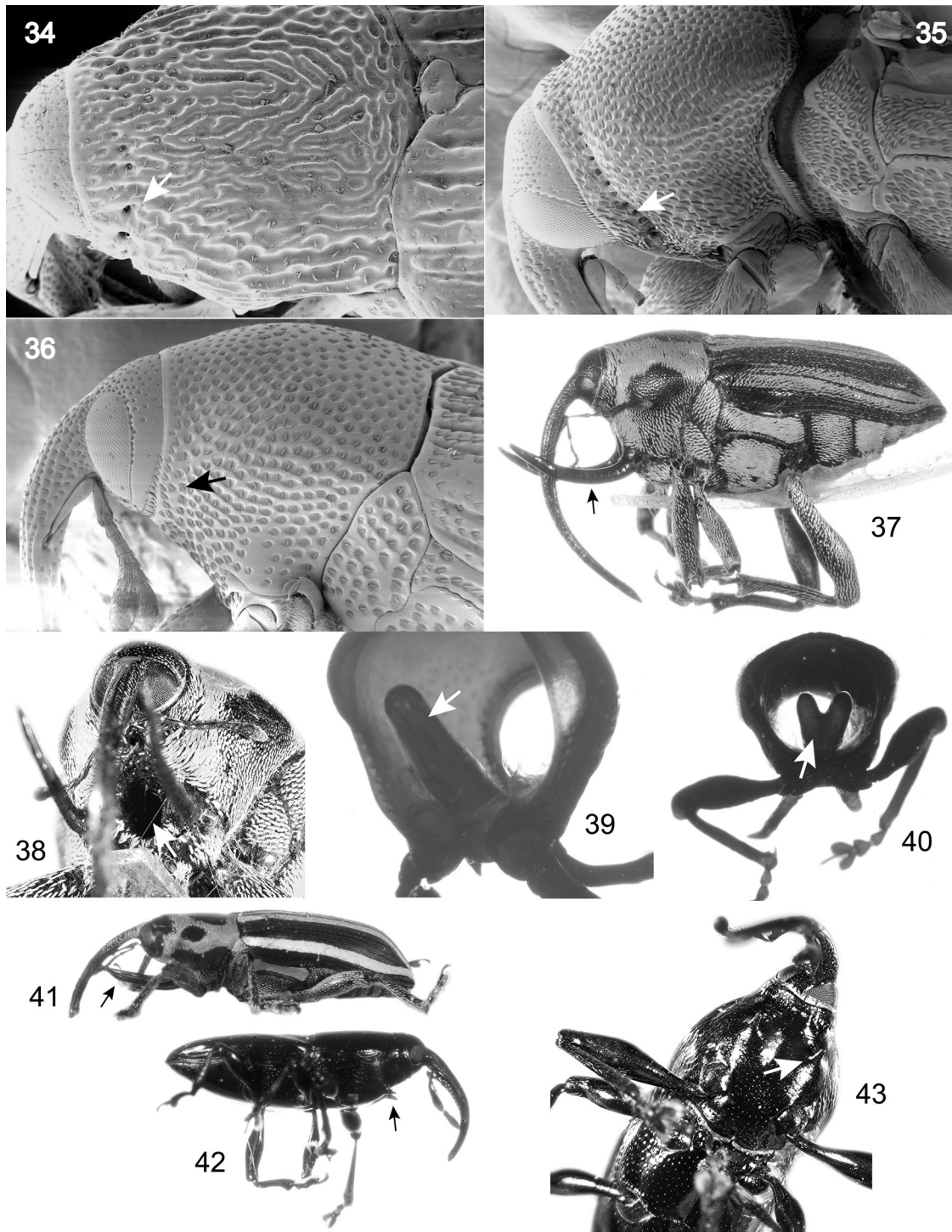
and deep (Figs 34, 35) or small and reduced in size and depth (Fig. 36). In a restricted number of baridines, but mostly in sister-groups, this puncture collar is often absent.

27. Thorax, prosternal horns in males:

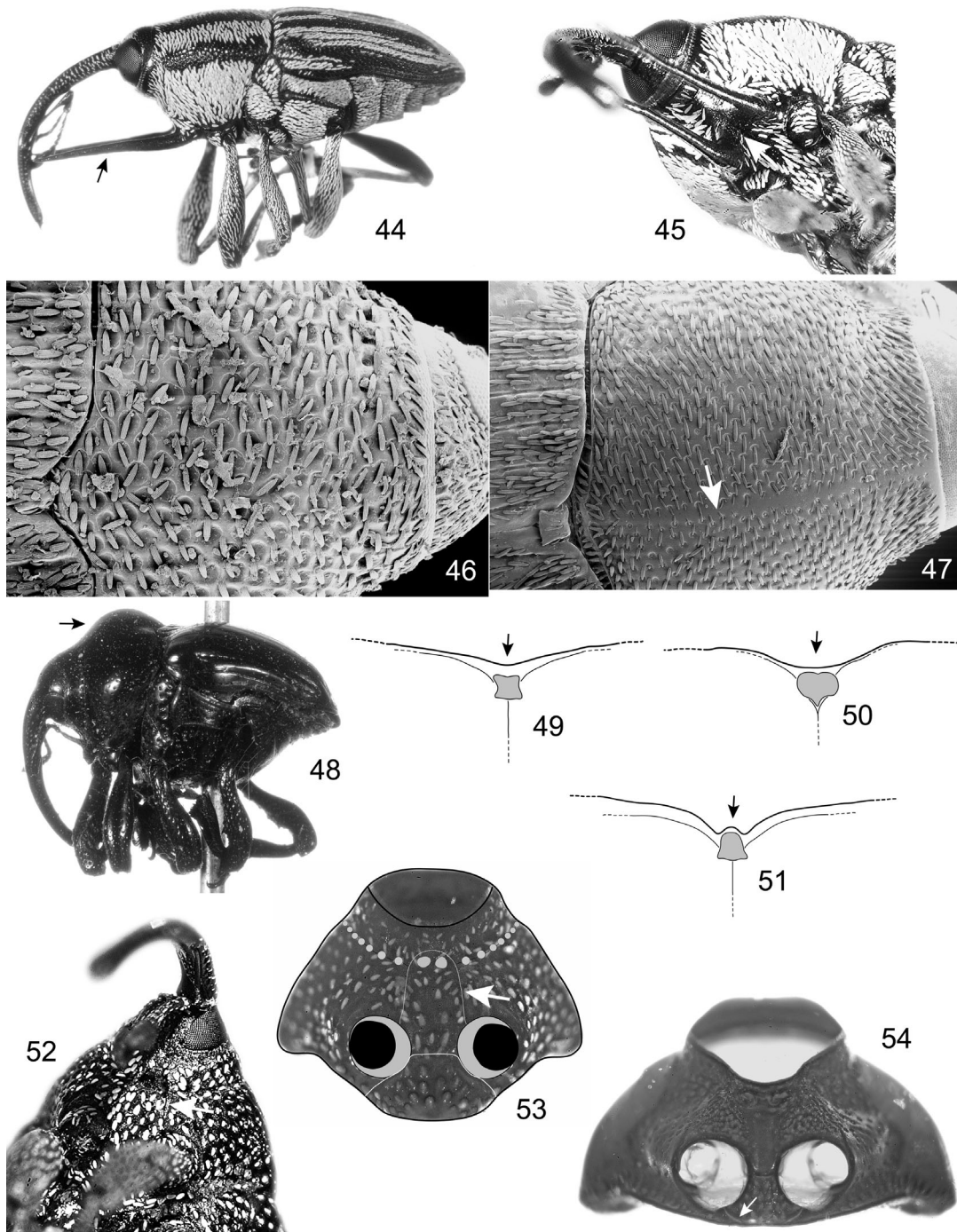
Horns present, long, horn sheath simple and deep (0); horns absent (1); horns present, long, horn sheath bifurcate and deep (2); horns present, long, horn sheath shallow/absent (3); horns present, short, horn

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 prosteral horns; 45, prosteral horn, 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, prosteral horn (photograph), showing lateral carina along shallow ventral depression; 53, prosteral horn (illustration), showing lateral carina along shallow ventral depression; 54, *Xystus ruficollis*, prosteral horn (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.

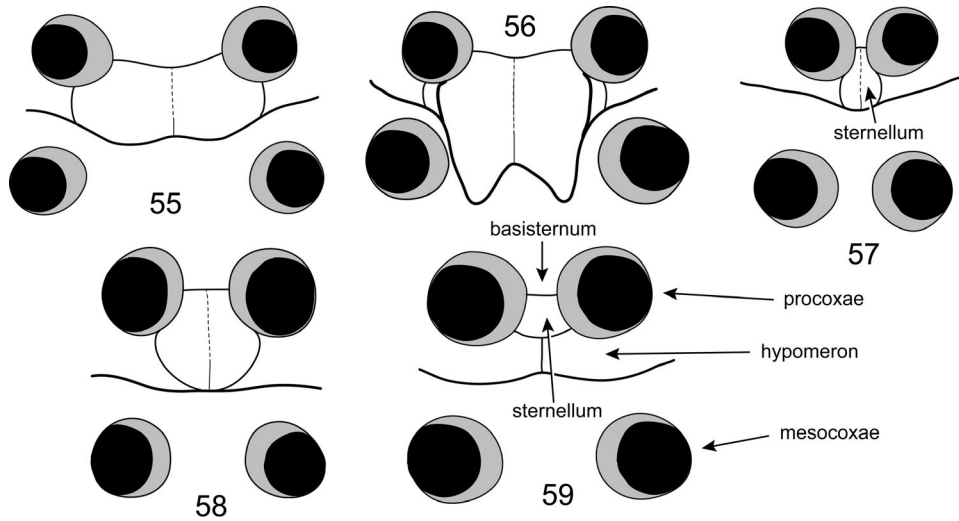
COXAE

37. *Procoxae, intercoxal distance:*

Procoxae separated by $< 1 \times$ diameter of coxa (0); procoxae separated by $\sim 1 \times$ diameter of coxa (1); procoxae separated by $> 1 \times$ diameter of coxa (2); procoxae touching (3)

38. *Mesocoxae, intercoxal distance:*

Mesocoxae separated by $< 1 \times$ diameter of coxa (0); mesocoxae separated by $\sim 1 \times$ diameter of coxa (1); mesocoxae separated by $> 1 \times$ diameter of coxa (2)



Figures 55–59. Prosterna (prosternal process). 55, *Limnobaris calandriiformis*, 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 $< 1\times$ diameter of coxa (0); metacoxae separated by $\sim 1\times$ diameter of coxa (1); metacoxae separated by $> 1\times$ 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 \sim 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:

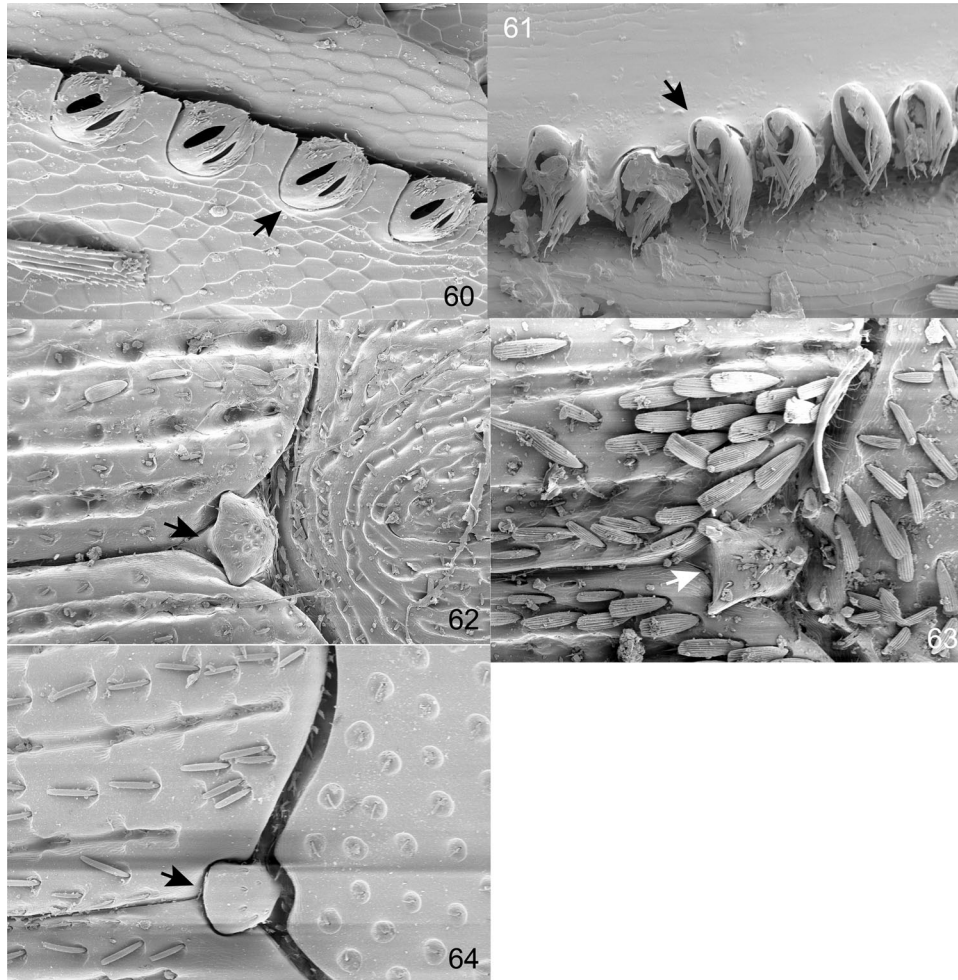
Round (0); heart-shaped, with a cleft at middle (1); concave (2); acute (3); quadrate (4); concave with central projection (5); round with central projection (6)

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, *Pycnogeræus 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.

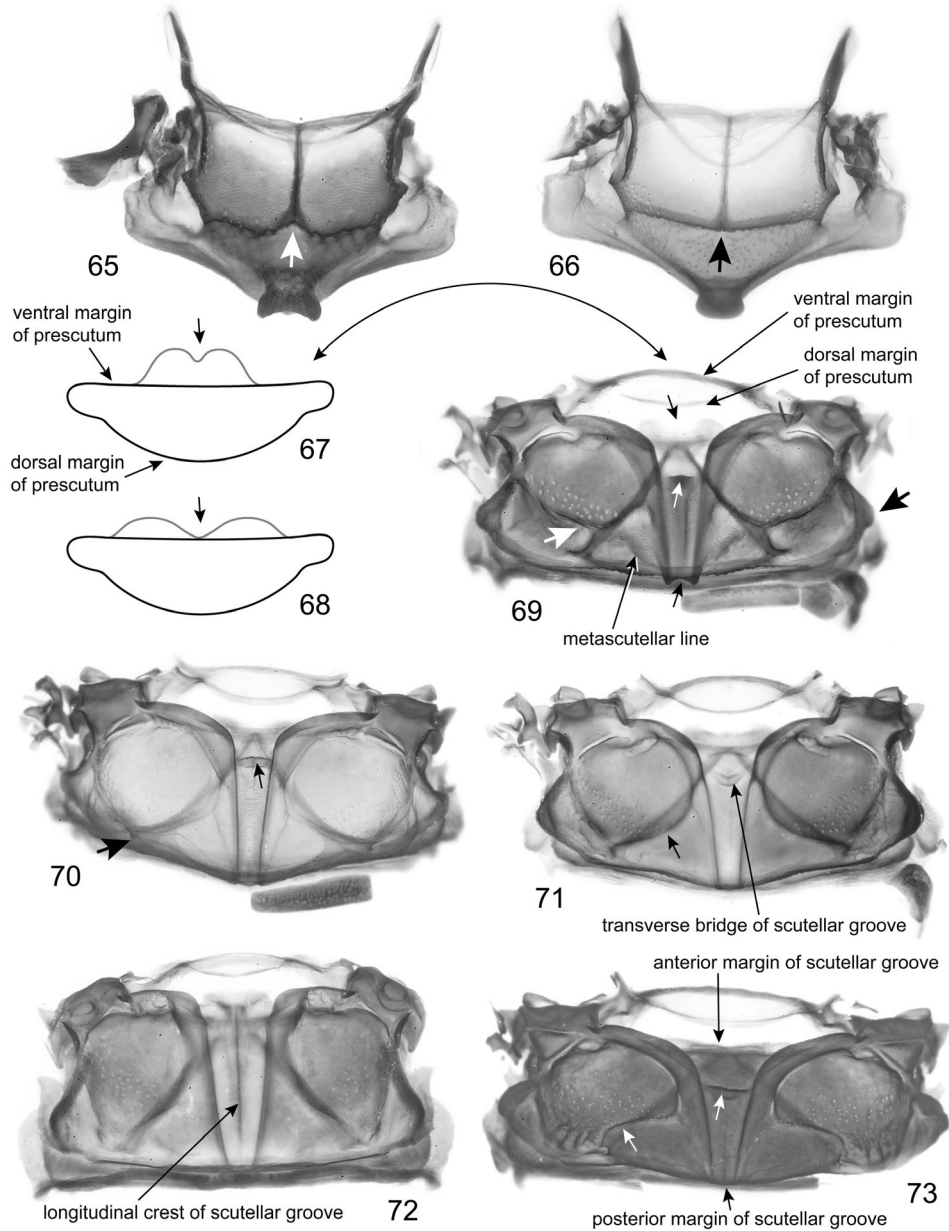
57. *Metanotum, metascutum – posterior margin:*

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*:

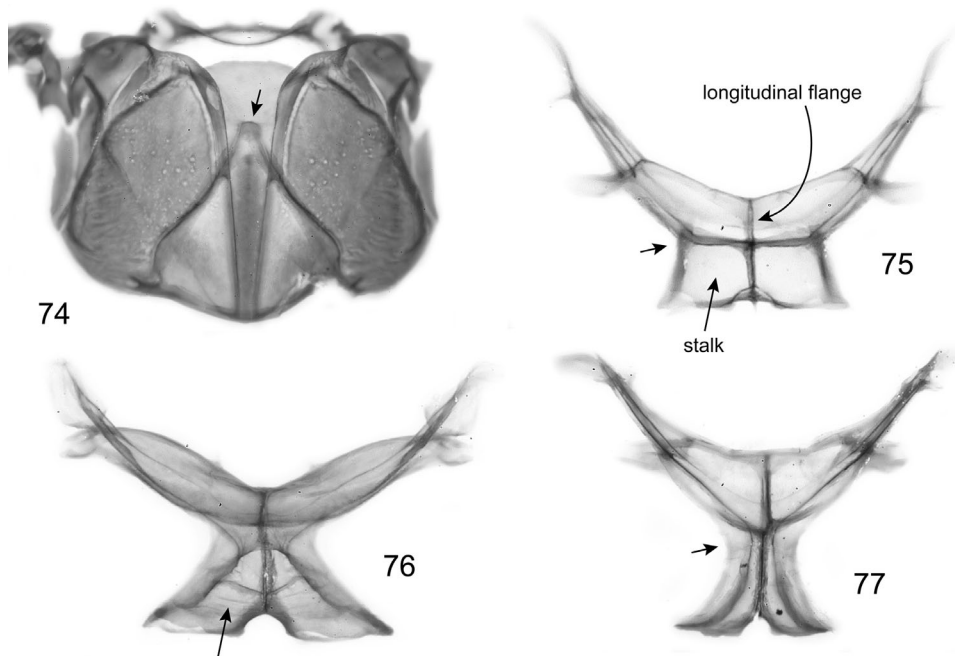
Quadrate (transversely or longitudinally quadrate) (0); longitudinally elongate, stalk elongate and curved (1)

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 out-group 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)

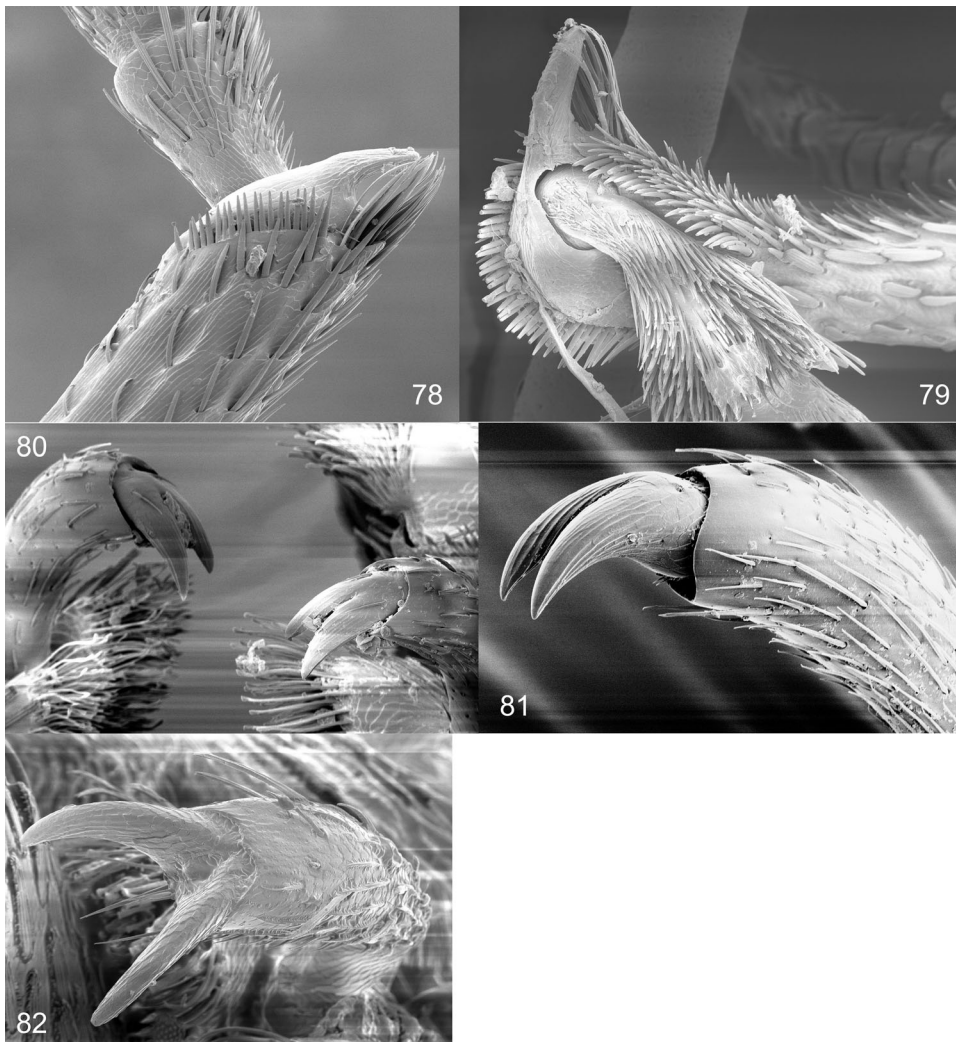
68. Thorax, legs – ventral surface of femora with depression for reception of tibia:

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.

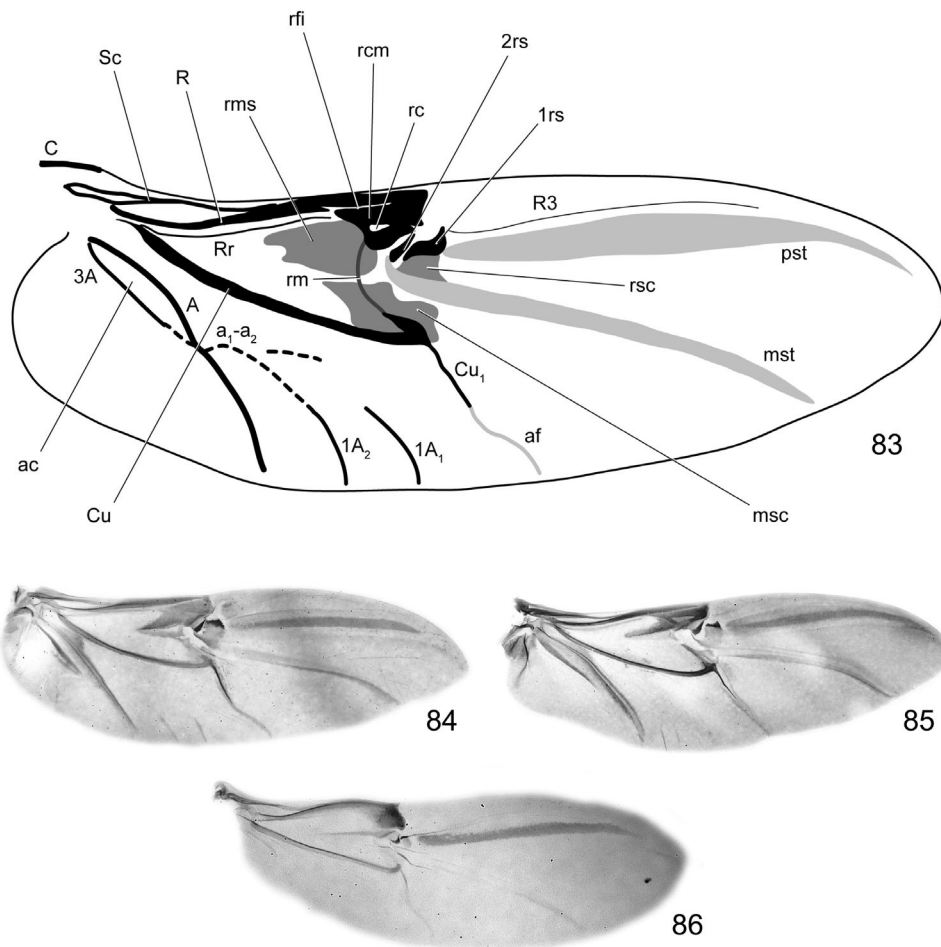
HIND WINGS (FIGS 83–86)

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, *Cyliandrocopturus 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)

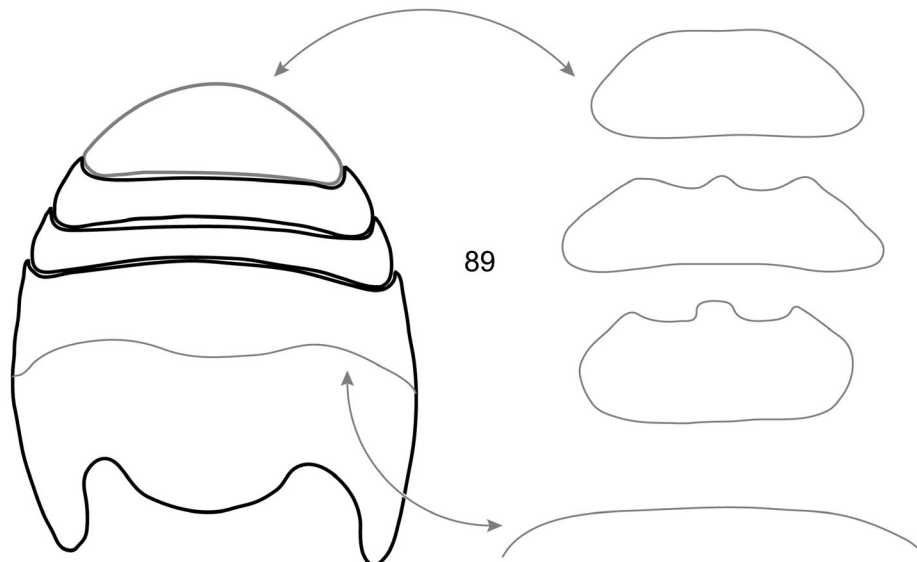
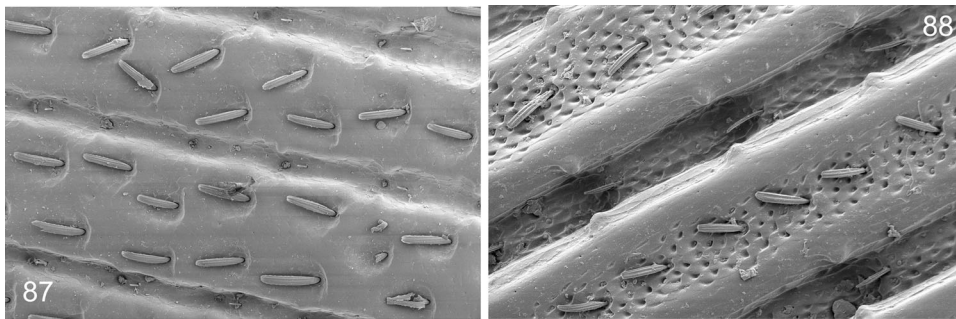
78. *Wing, venation – 3A* (3rd Anal):
 Absent (0); present, reduced (1); present, nearly con-
 nected with 4A (2); wing weakly developed/small or
 absent (3)

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 long-
 itudinal ridges that are absent of punctures. Punc-
 ture 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:*

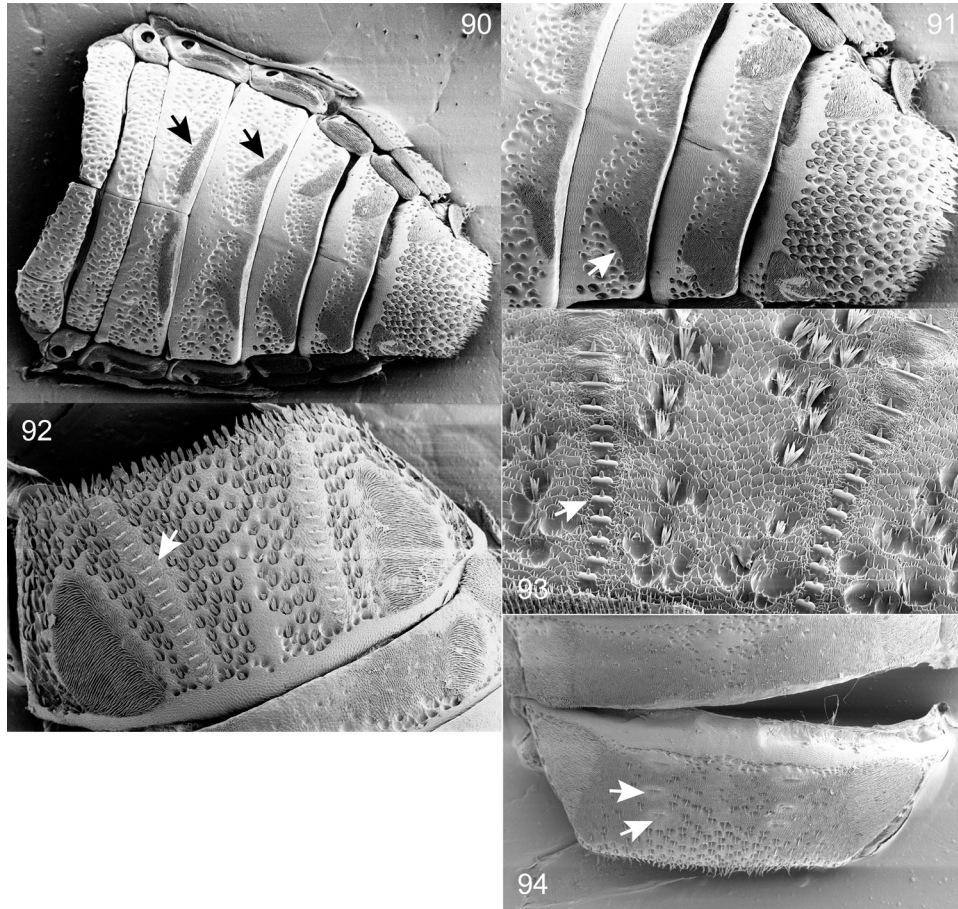
Fused (0); separated (1)

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, *Deipyryrus hirsutulius*, 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)

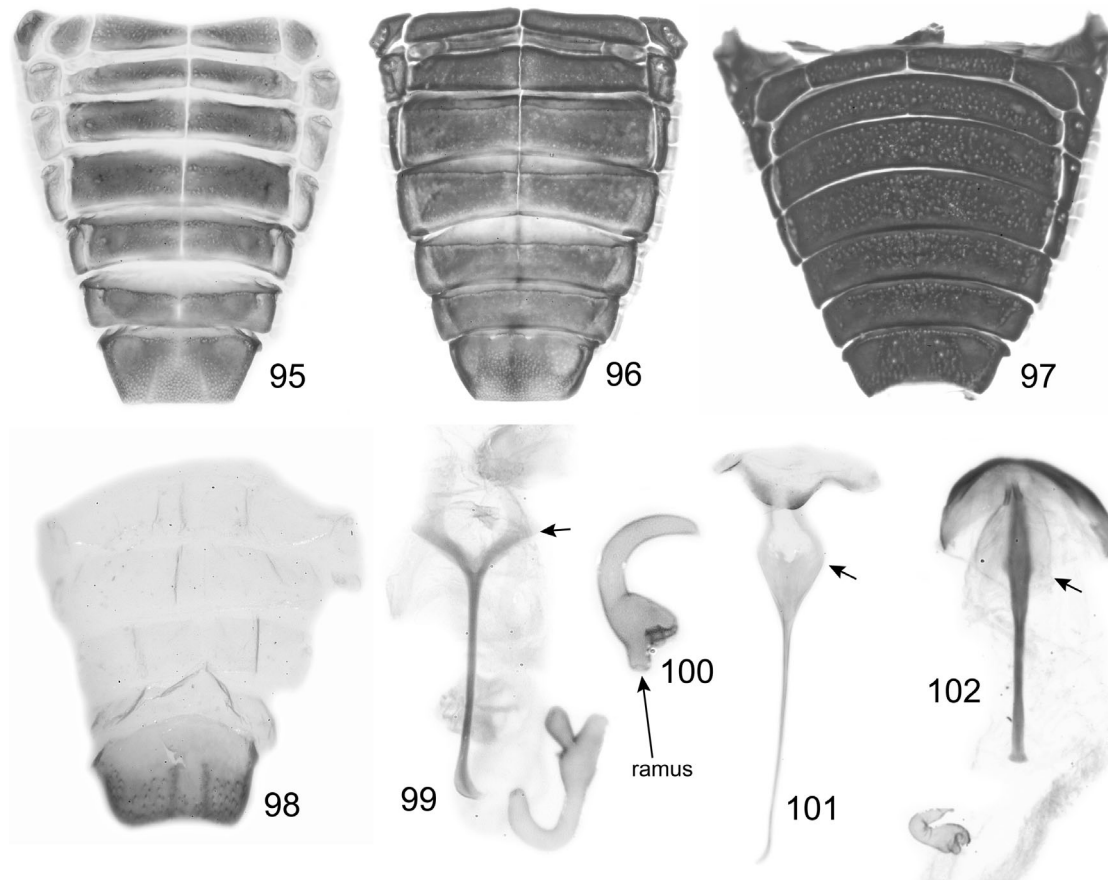
The spermatheca may have both ramus and collum present (with the ramus often developed and elongate) (Figs 99, 100) or the ramus may be weakly developed or absent.

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, *Strongylothes 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)

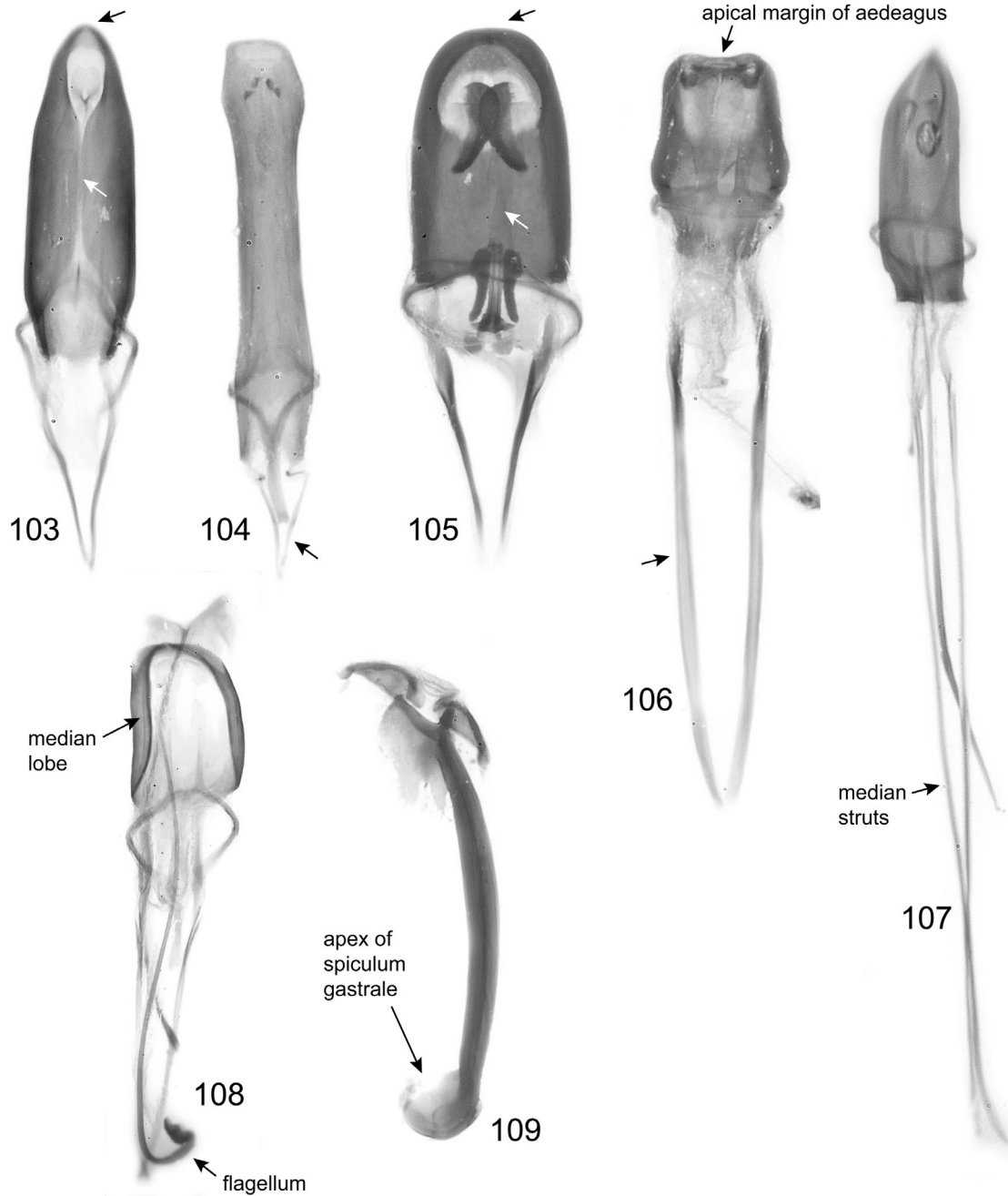
Most baridines possess a fairly wide central, lightly sclerotized area on the dorsal surface of the median lobe (Figs 106, 108), in which a thin area on the lateral sides of the median lobe is more heavily scler-

otized. 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 per-

formed 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 Orbitidinae, 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 & Donoghue, 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

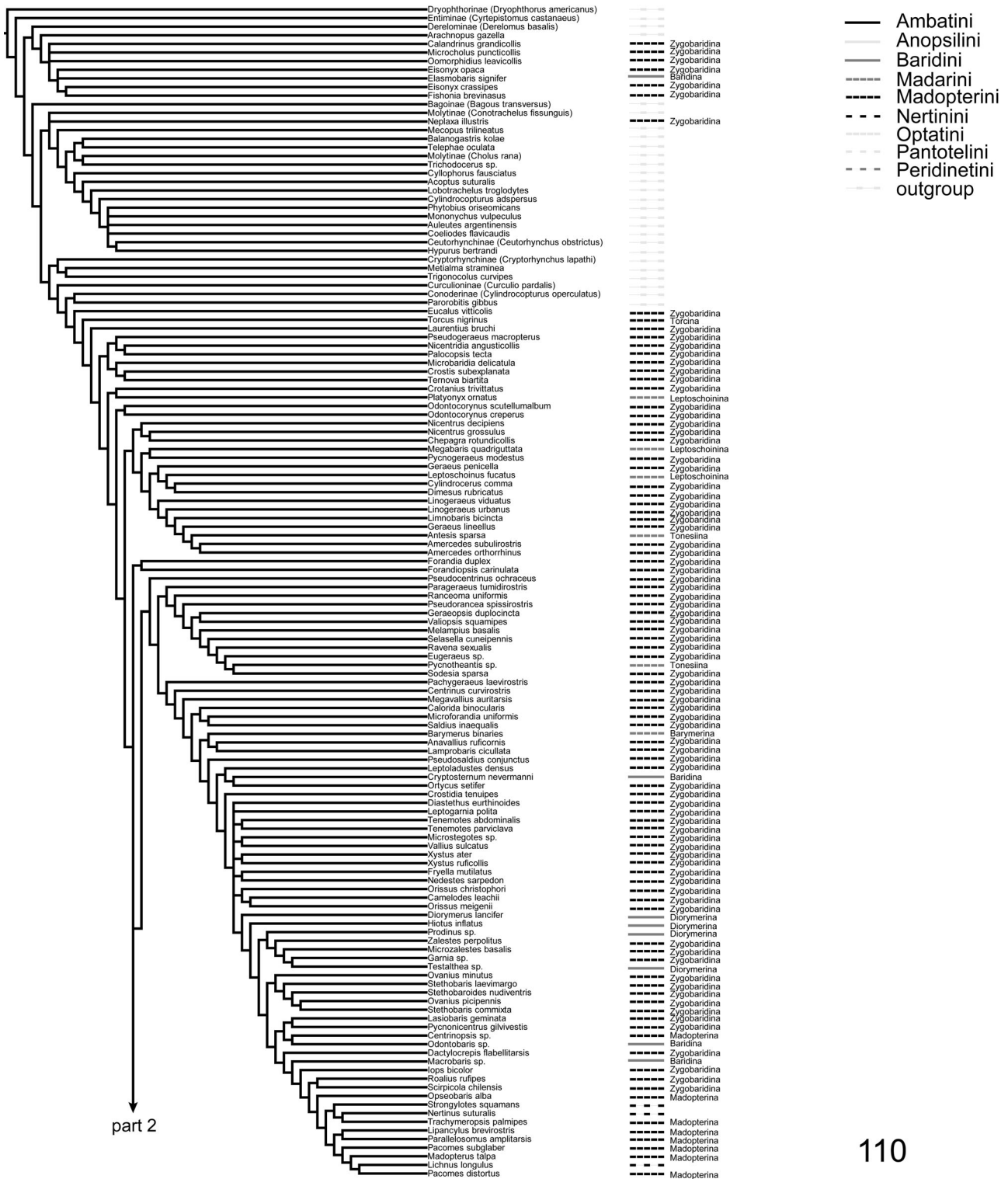


Figure 110. Strict consensus tree of analysis of full taxon matrix – length 4850 steps (of 33 most-parsimonious trees of length 4509 steps) produced in TNT, with old classification, including tribes and subtribes, indicated.

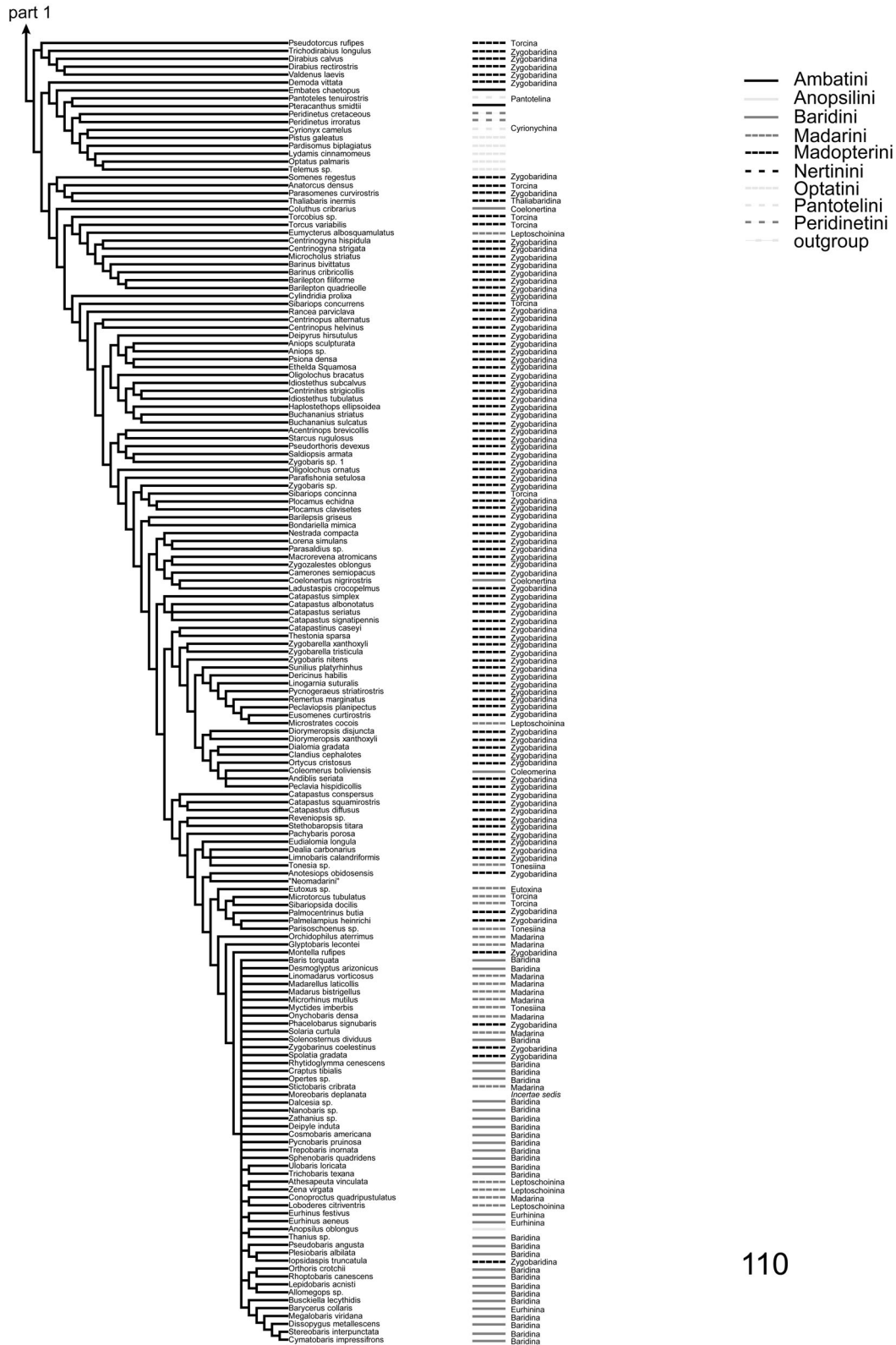
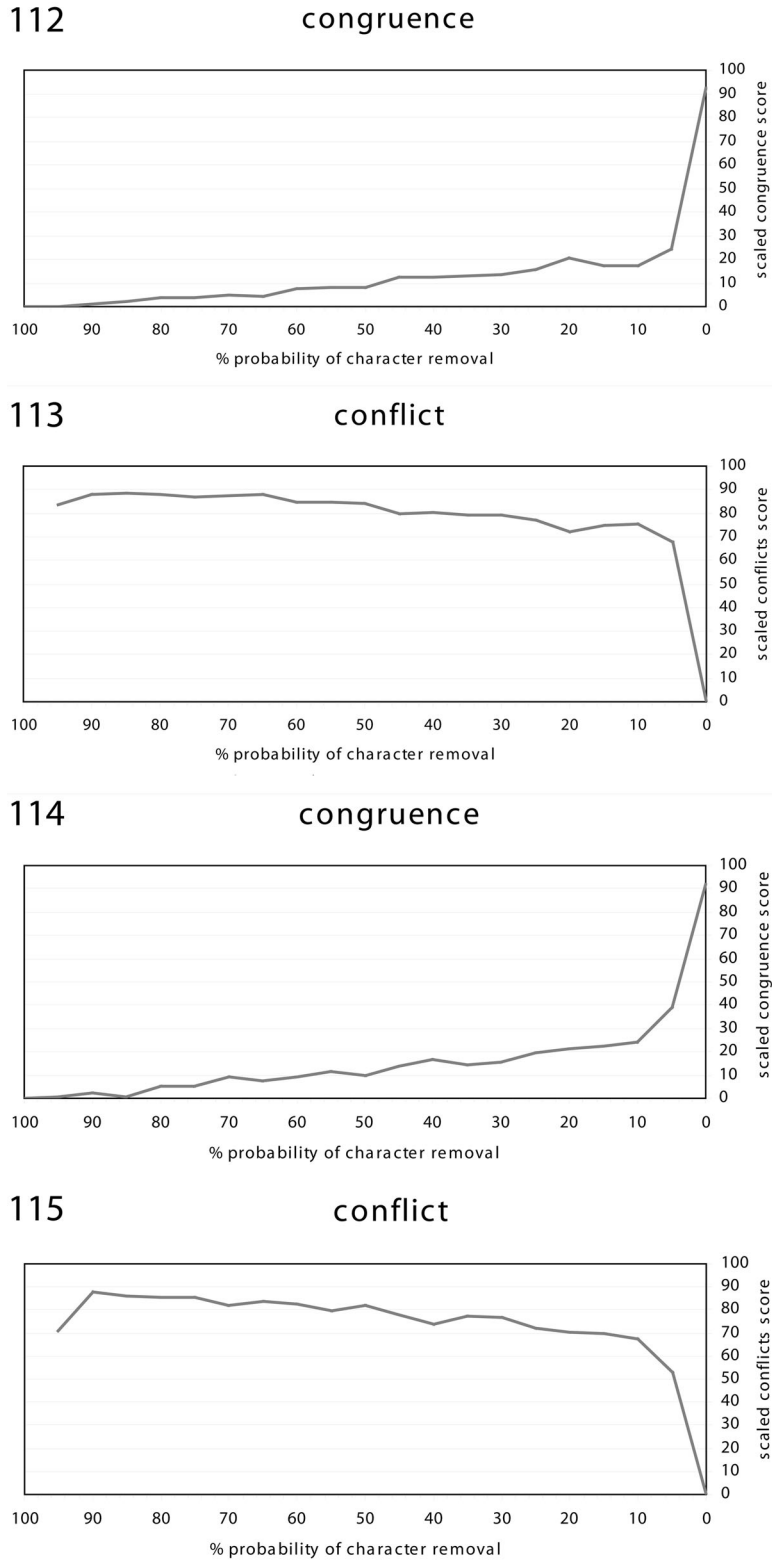


Figure 110. Continued



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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.



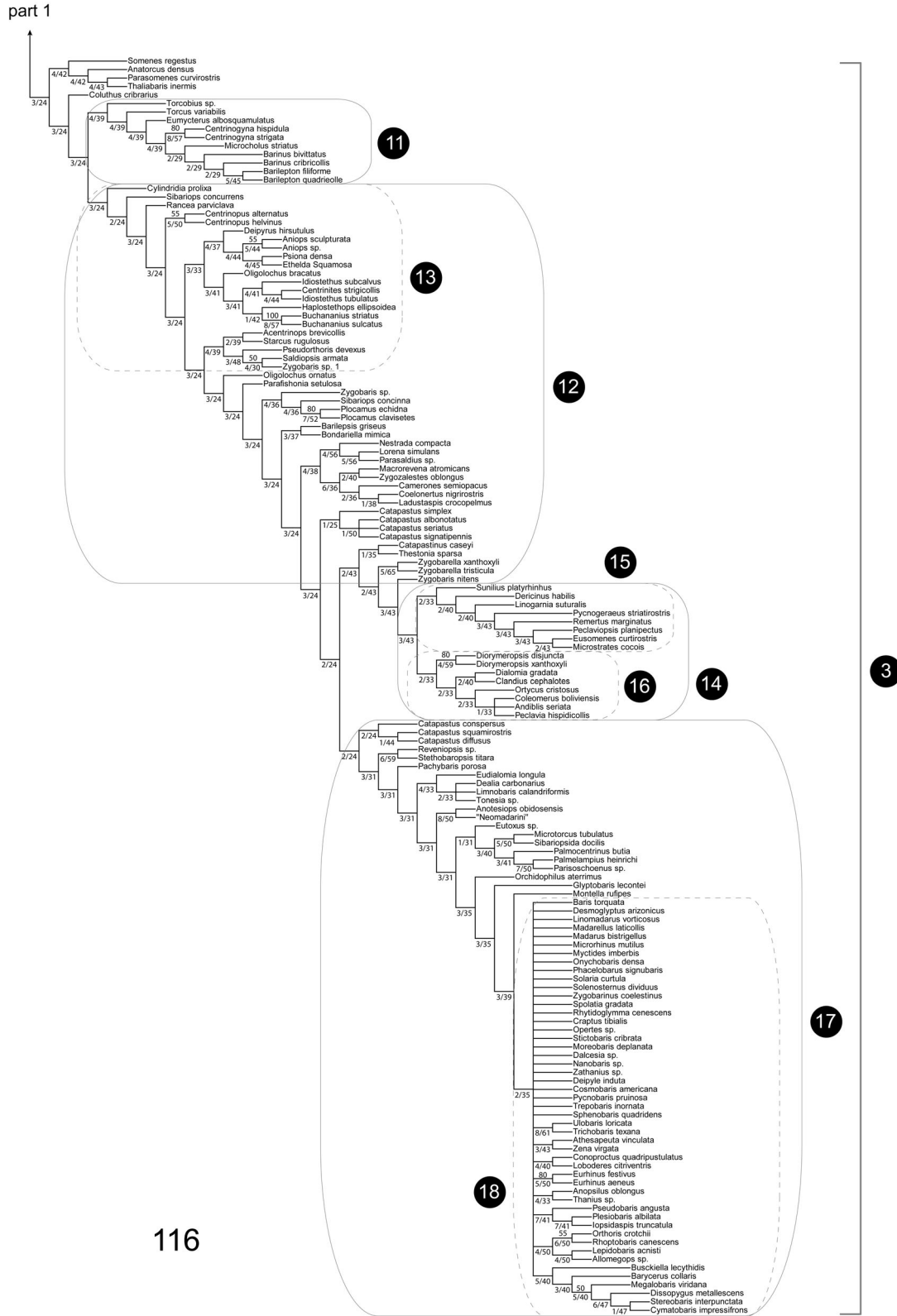
Figures 112–115. Continuous jackknife function plots. 112, tree congruence of full taxon matrix (FTM) trees as the probability of character removal changes; 113, tree conflict of FTM trees as the probability of character removal changes; 114, tree congruence of reduced taxon matrix (RTM) trees as the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



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Figure 116. Continued

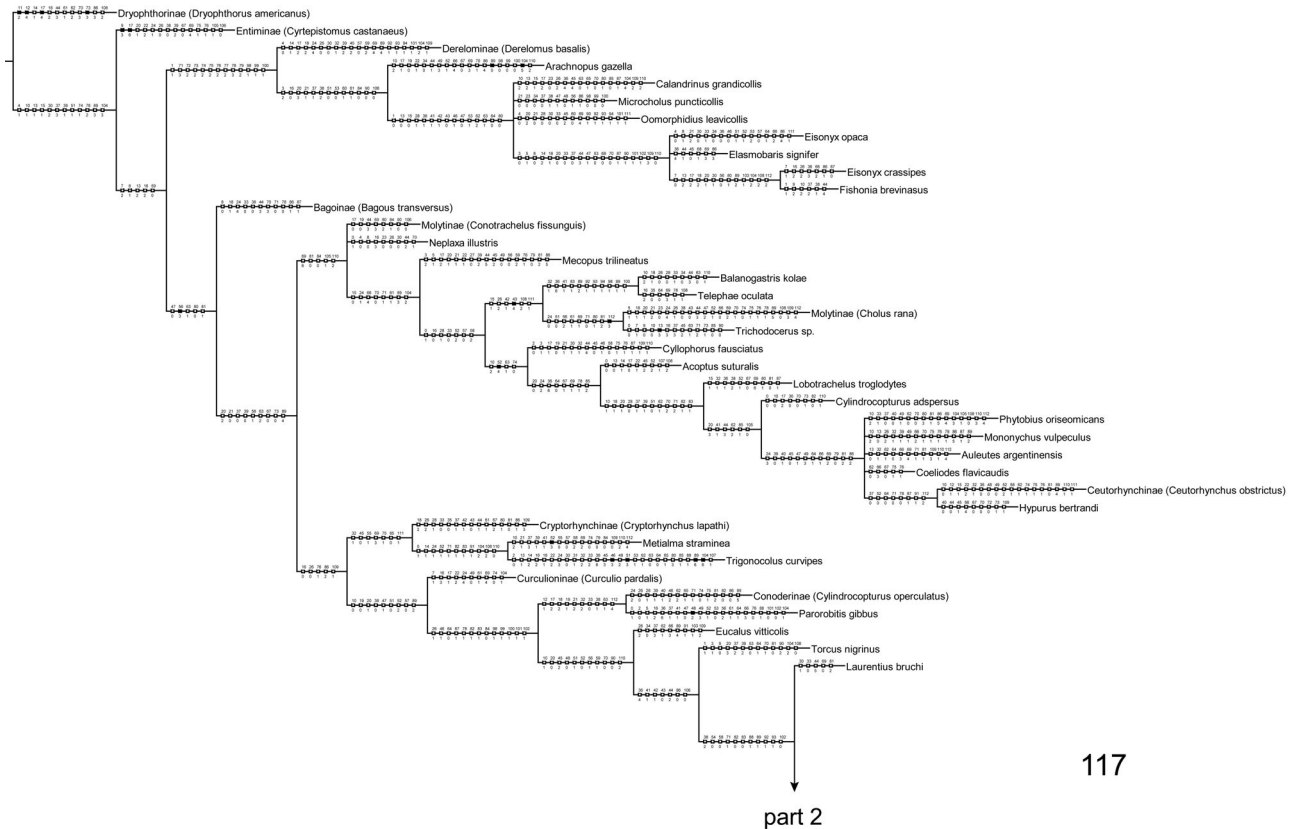


Figure 117. Strict consensus tree of analysis of full taxon matrix, with characters (below branches) and character states (above branches) mapped onto branches using WinClada's fast optimization (ACCTRAN).

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 be 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.

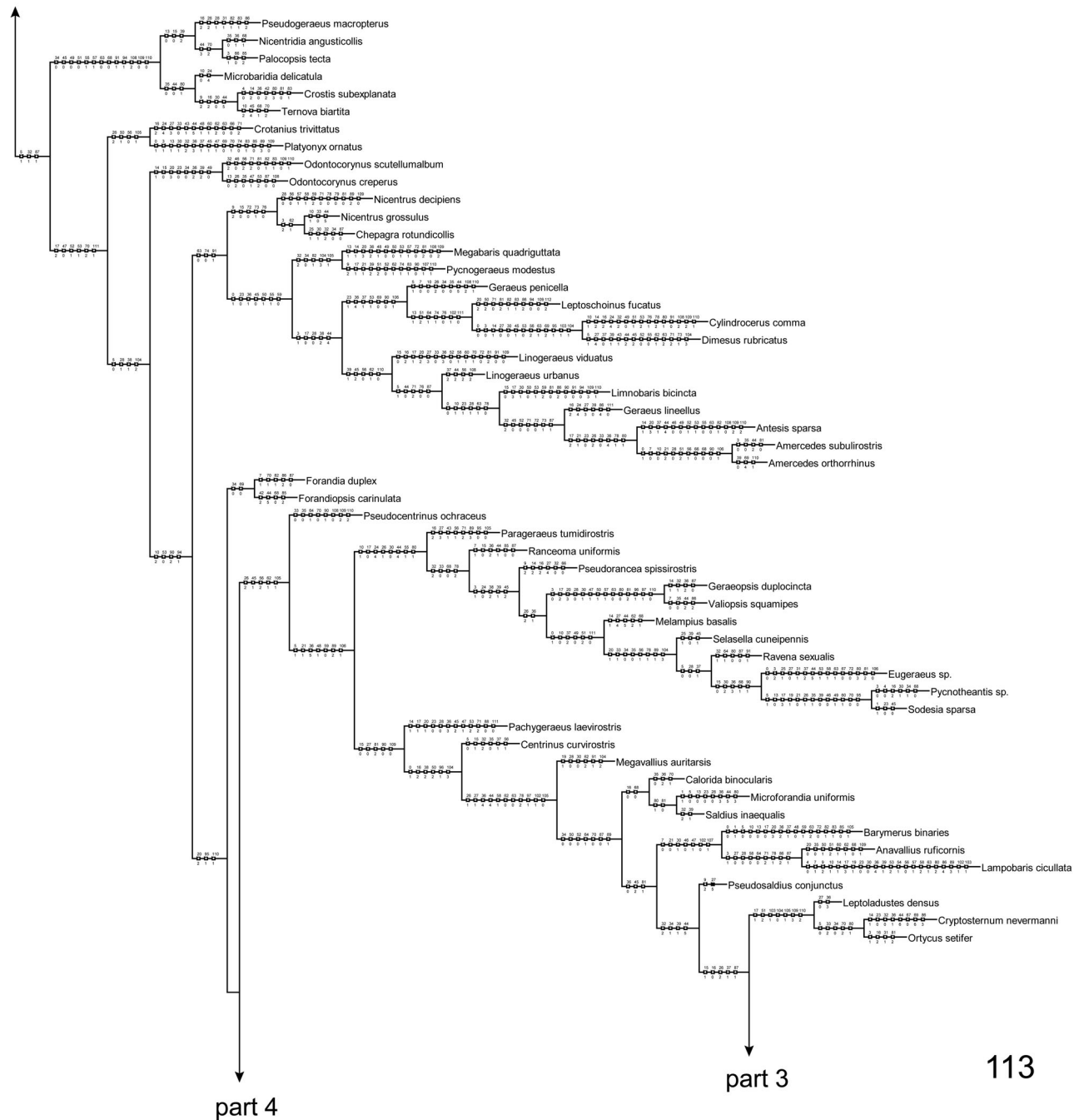
COMPARISON OF COMPLETE MATRIX ANALYSIS TO RTM

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

part 1



113

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.

part 2

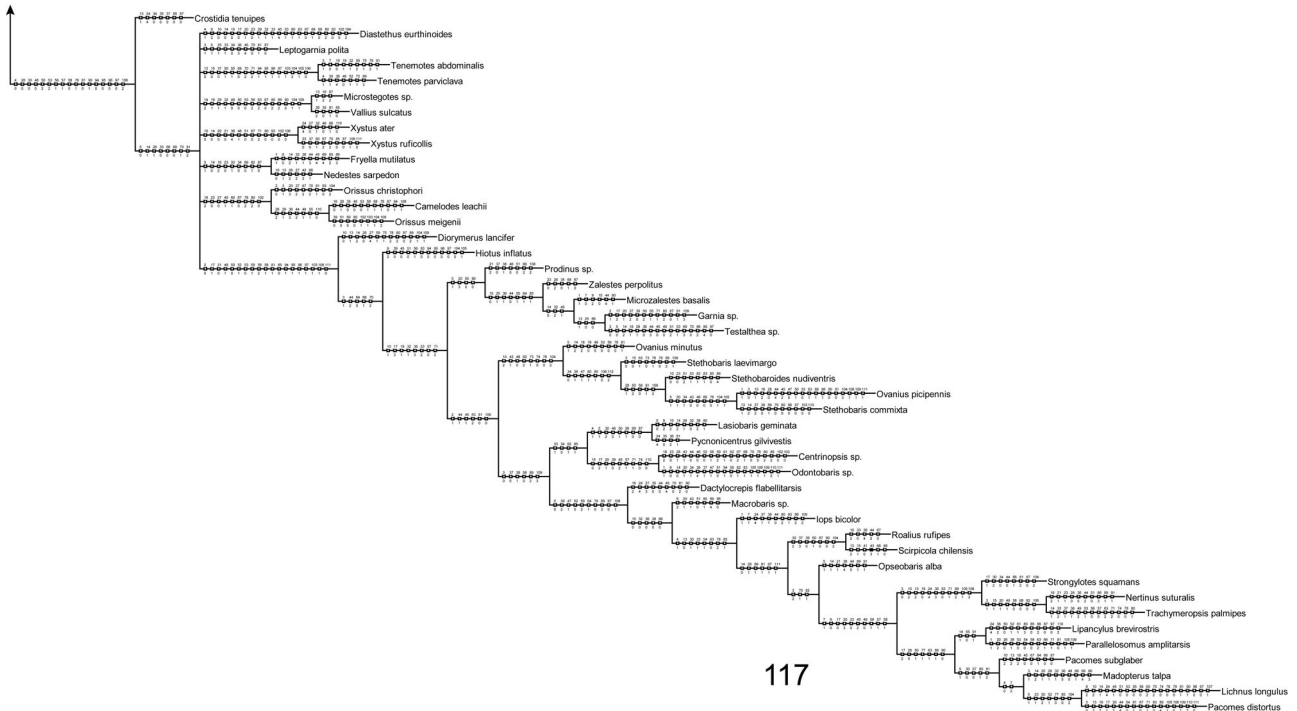


Figure 117. Continued

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, Orobittidinae, 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

part 2

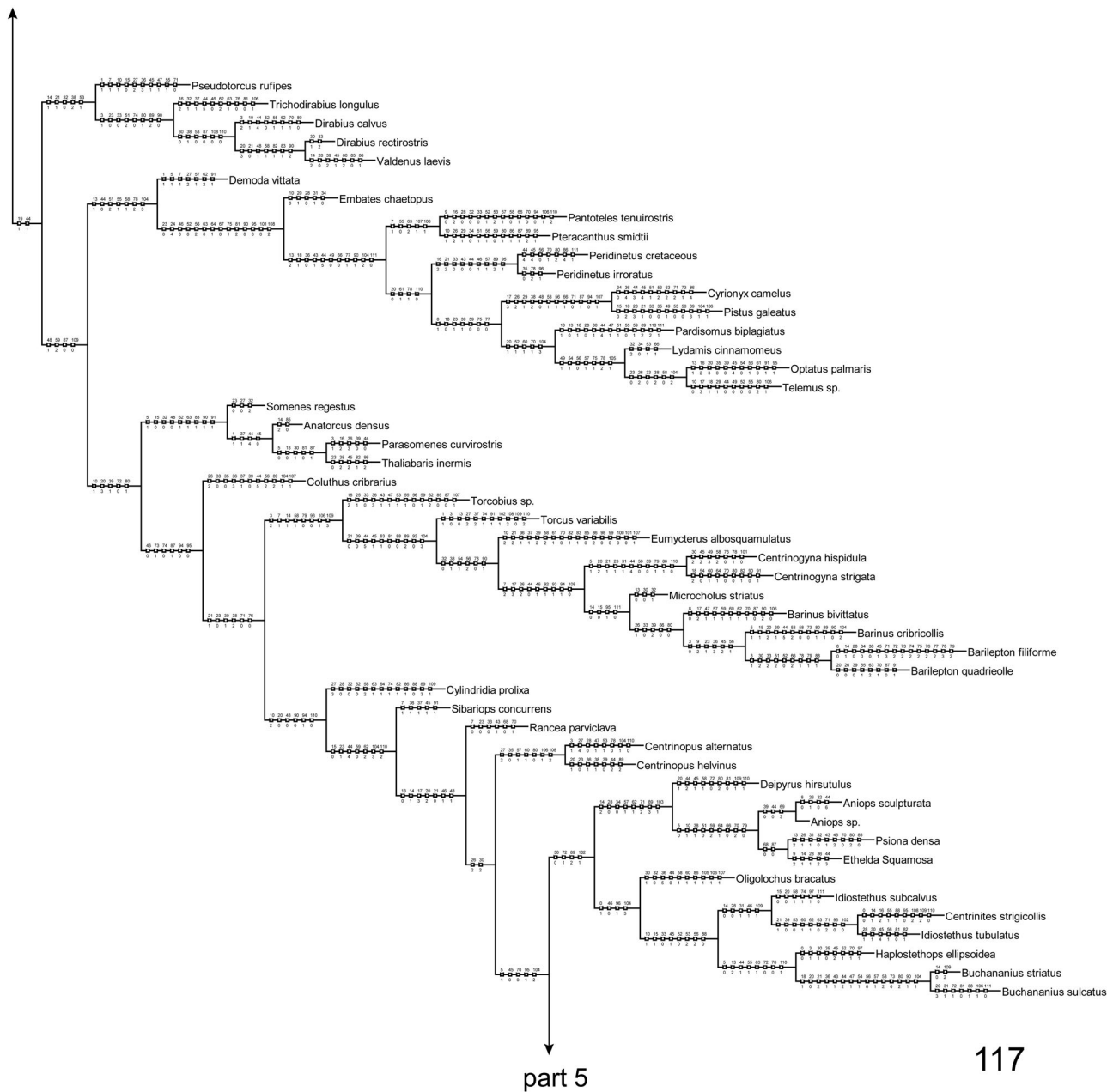
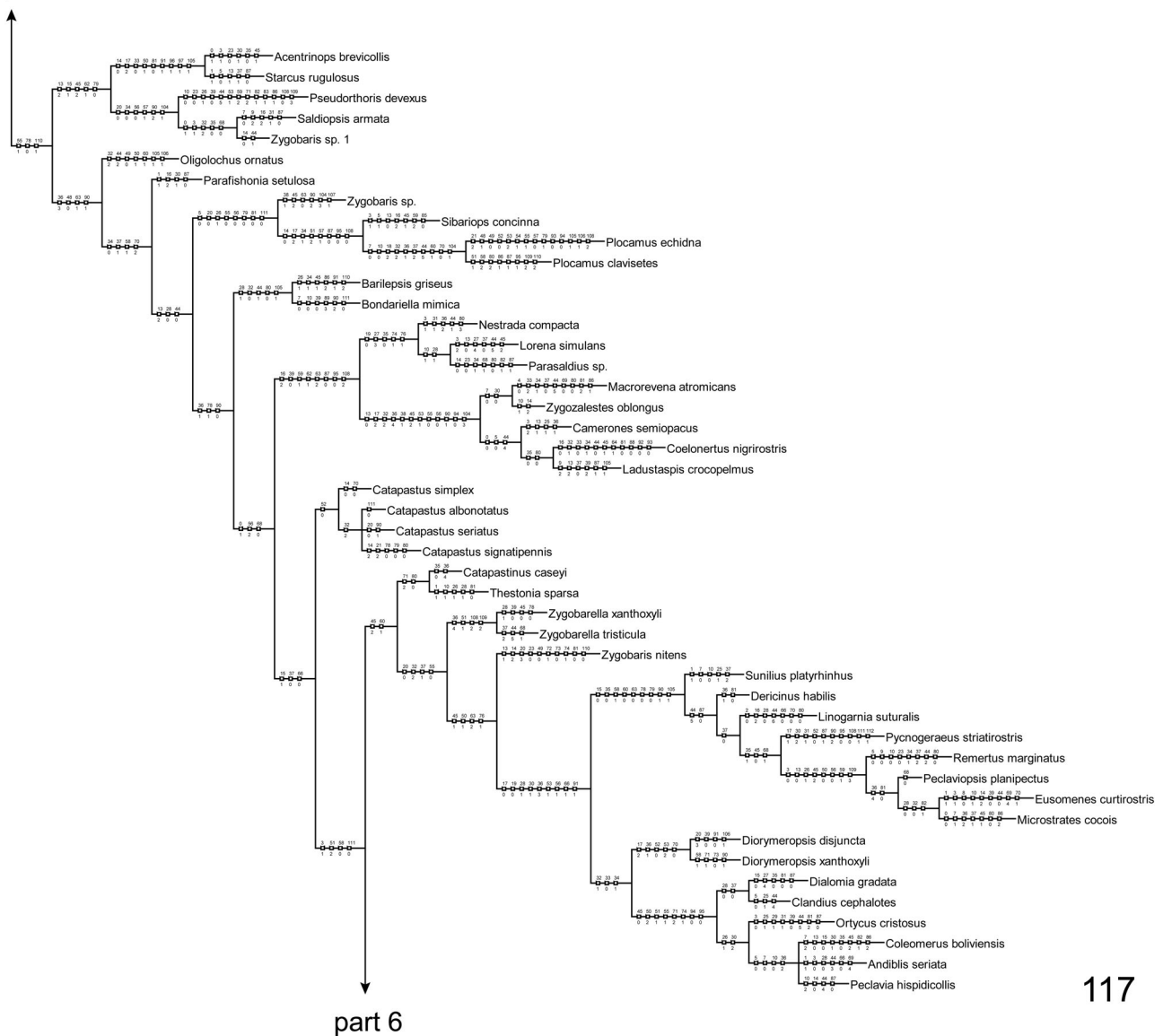


Figure 117. Continued

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

part 4



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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

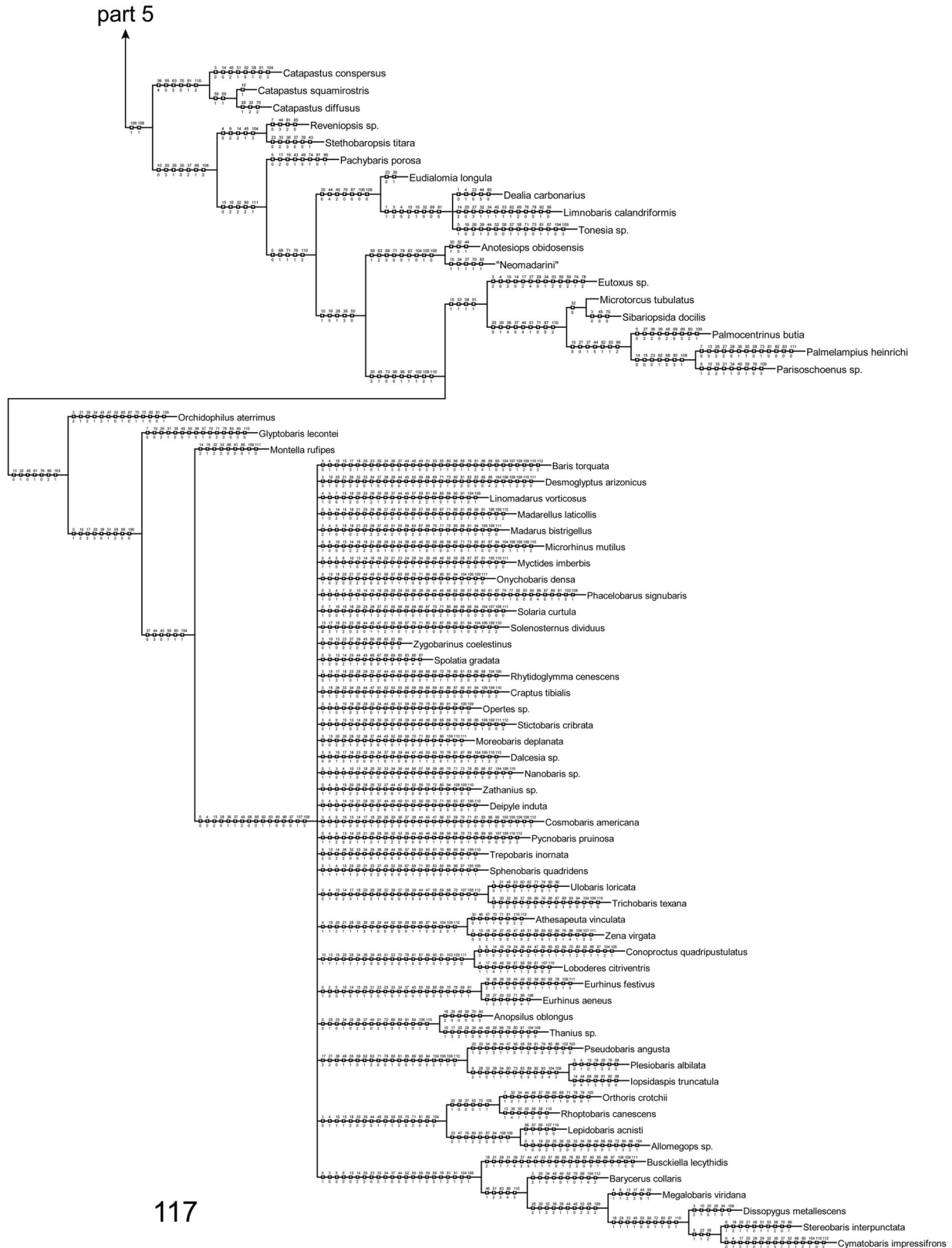
Group 2: 62, 72, 73, 74, 75

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



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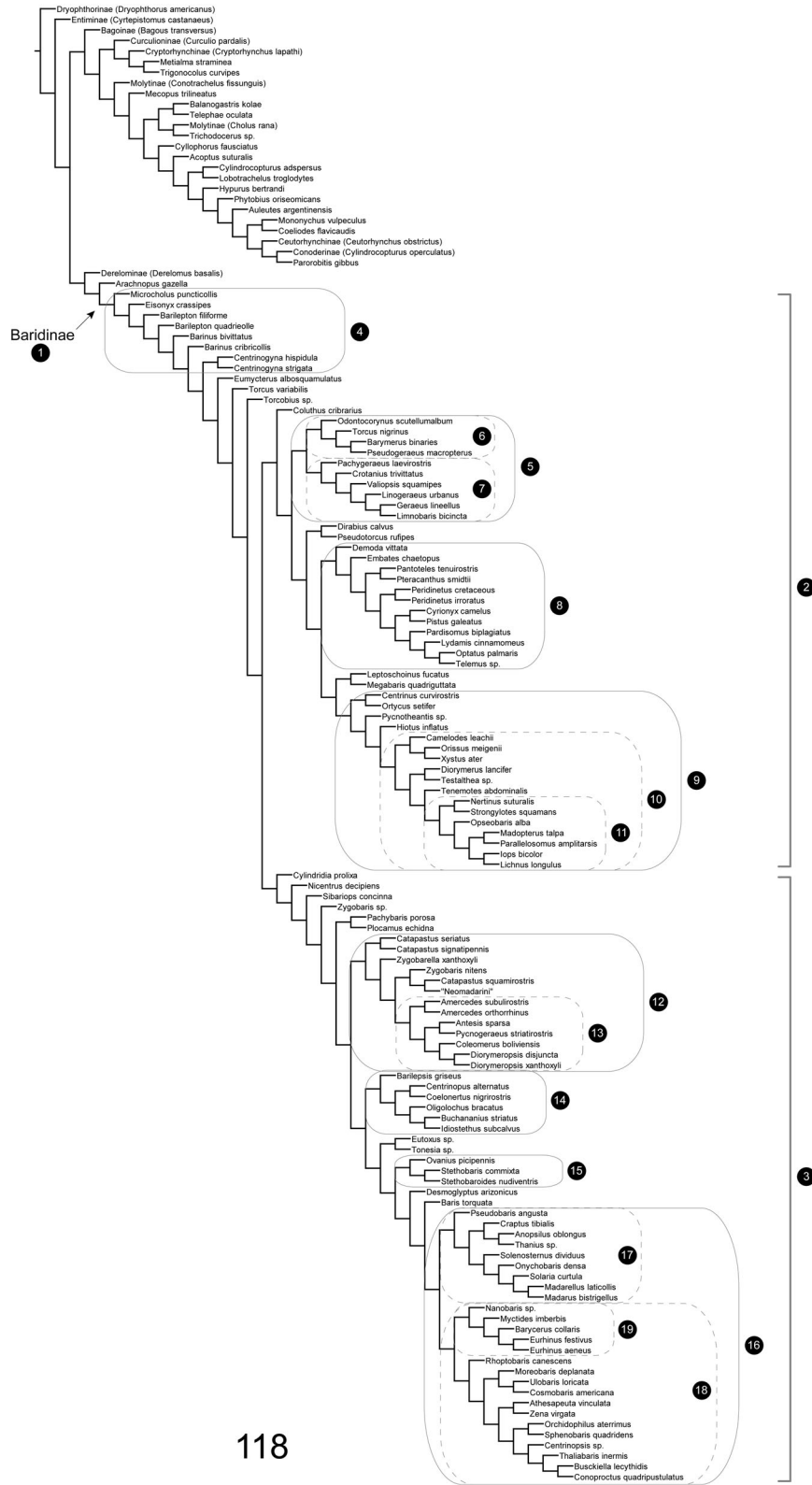


Figure 118. 1 of 110 most-parsimonious trees produced from analysis of the reduced taxon matrix, with suggested revised classification.



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

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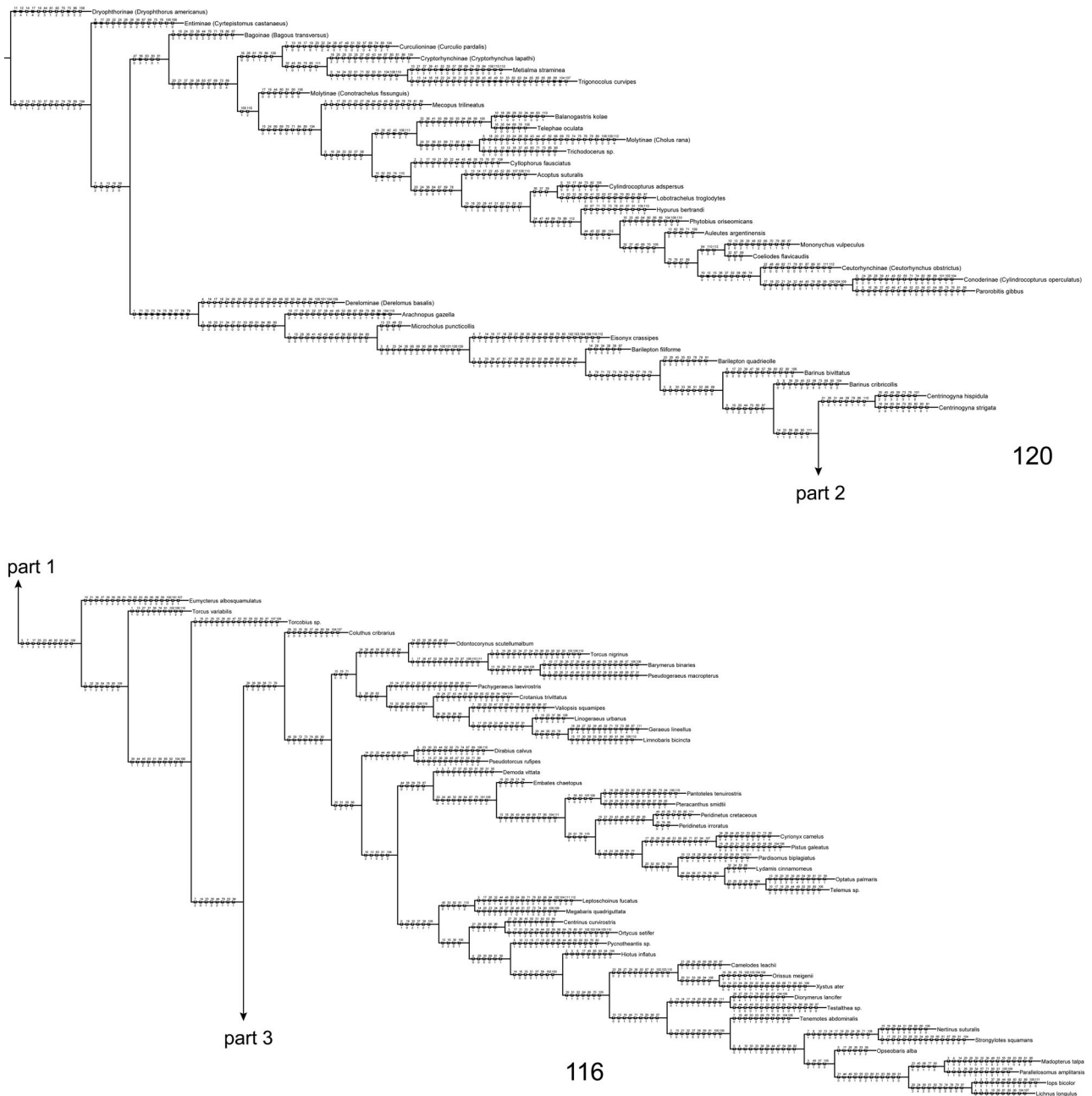
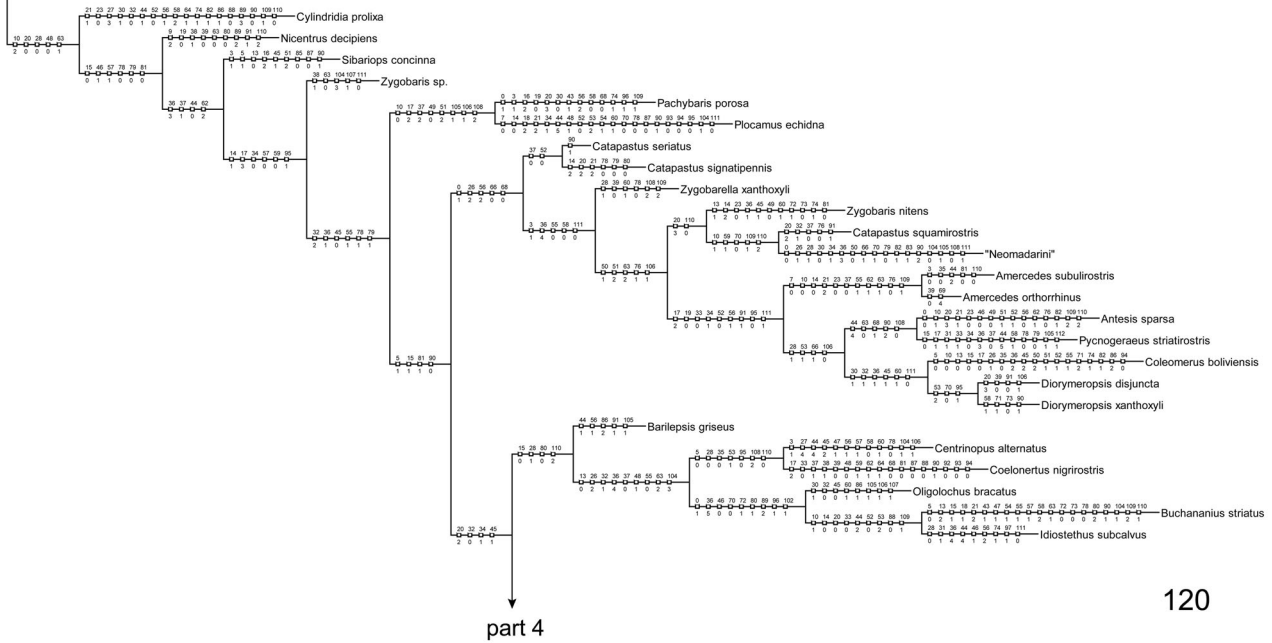


Figure 120. 1 of 110 most-parsimonious trees produced from analysis of the reduced taxon matrix, with characters (below branches) and character states (above branches) mapped onto branches using WinClada's fast optimization (ACCTRAN).

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

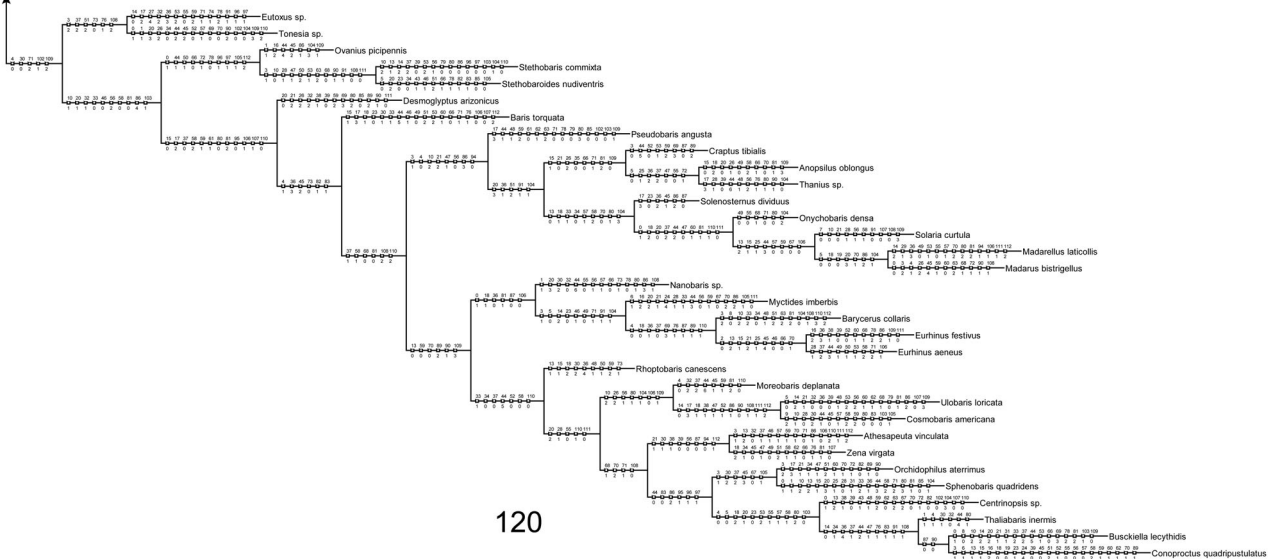
part 2



120

part 4

part 3



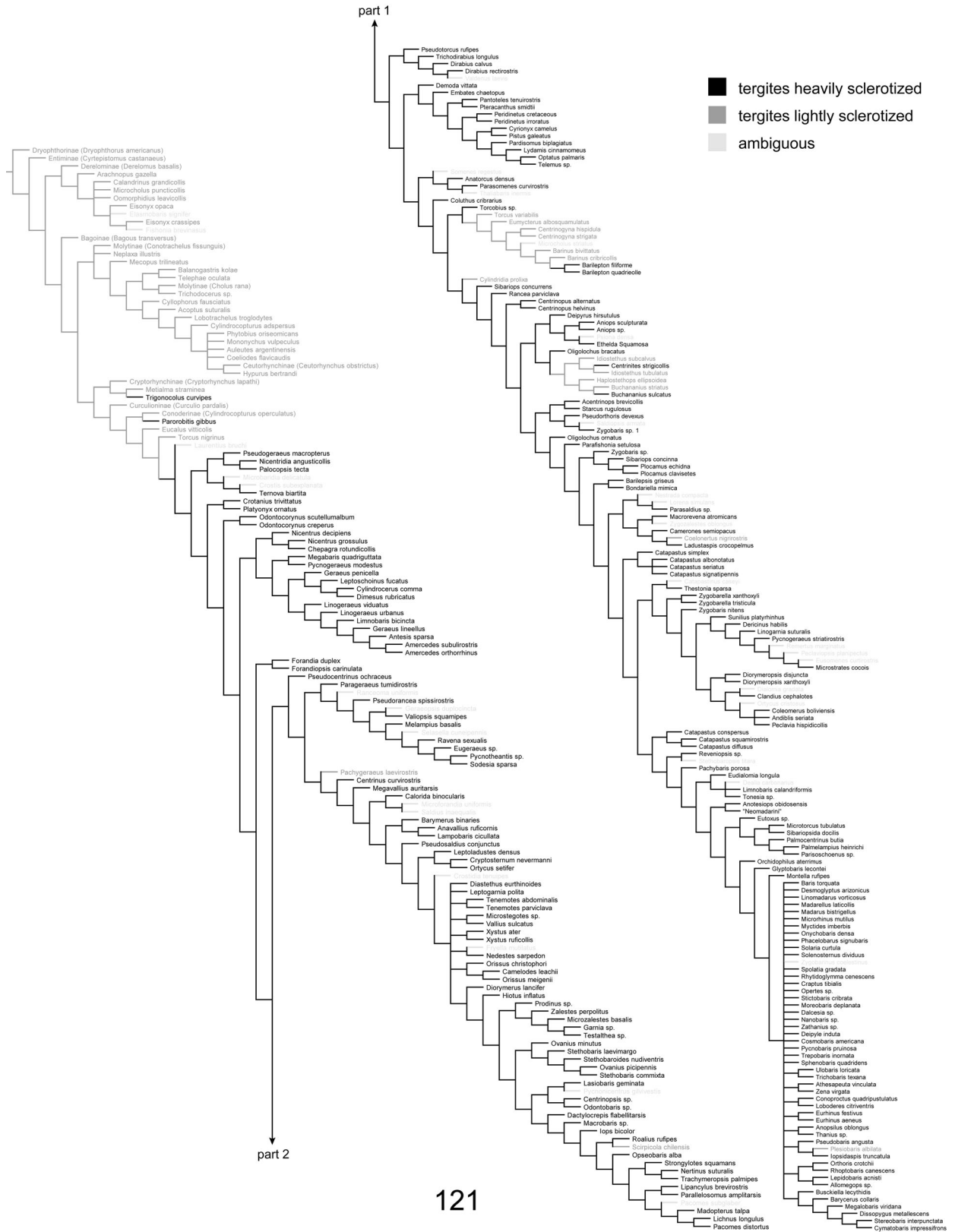
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Figure 120. Continued

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



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



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

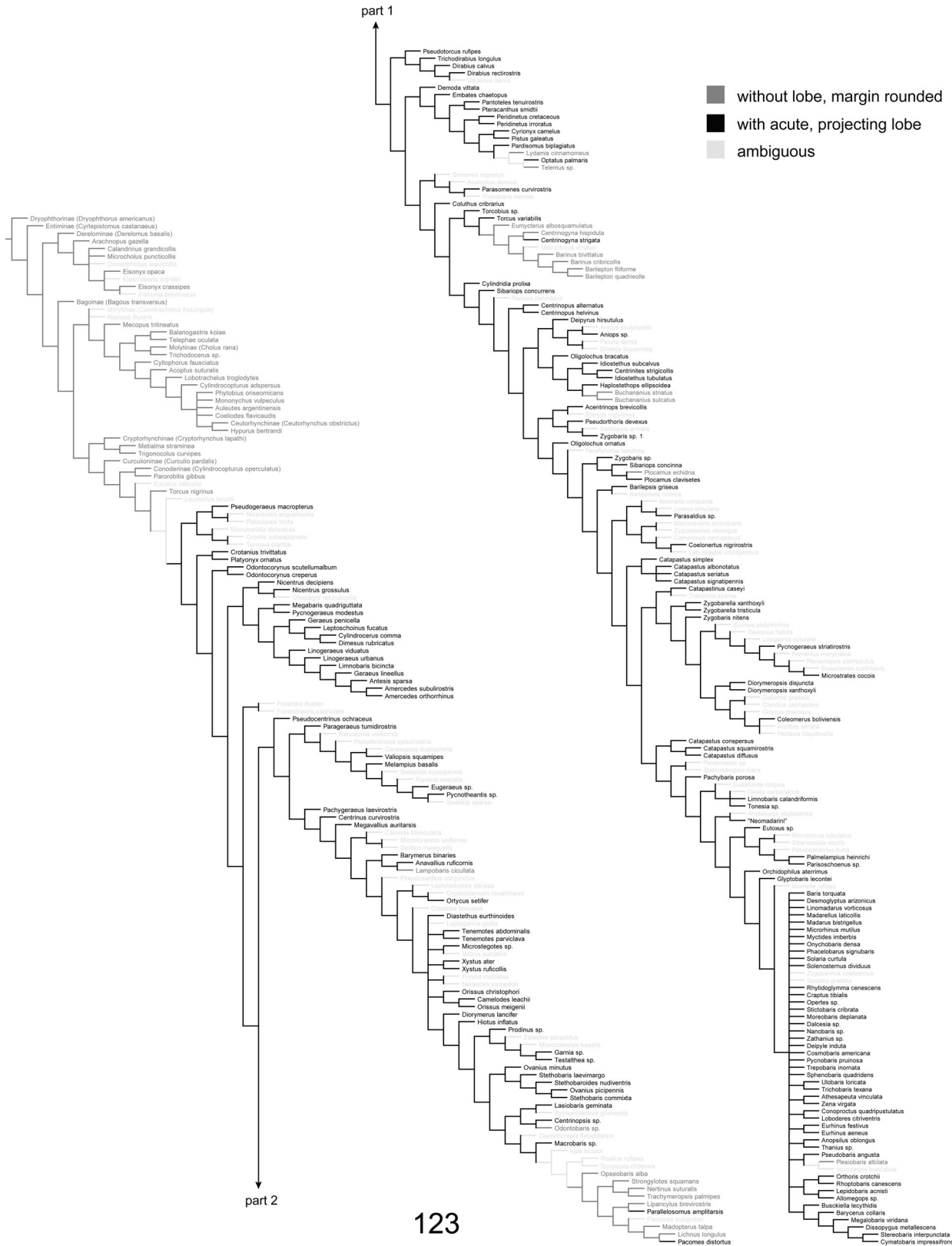


Figure 123. Character 54 (lateral margin of metanotum), supporting monophyly of Baridinae, mapped onto strict consensus tree of full taxon matrix analysis.

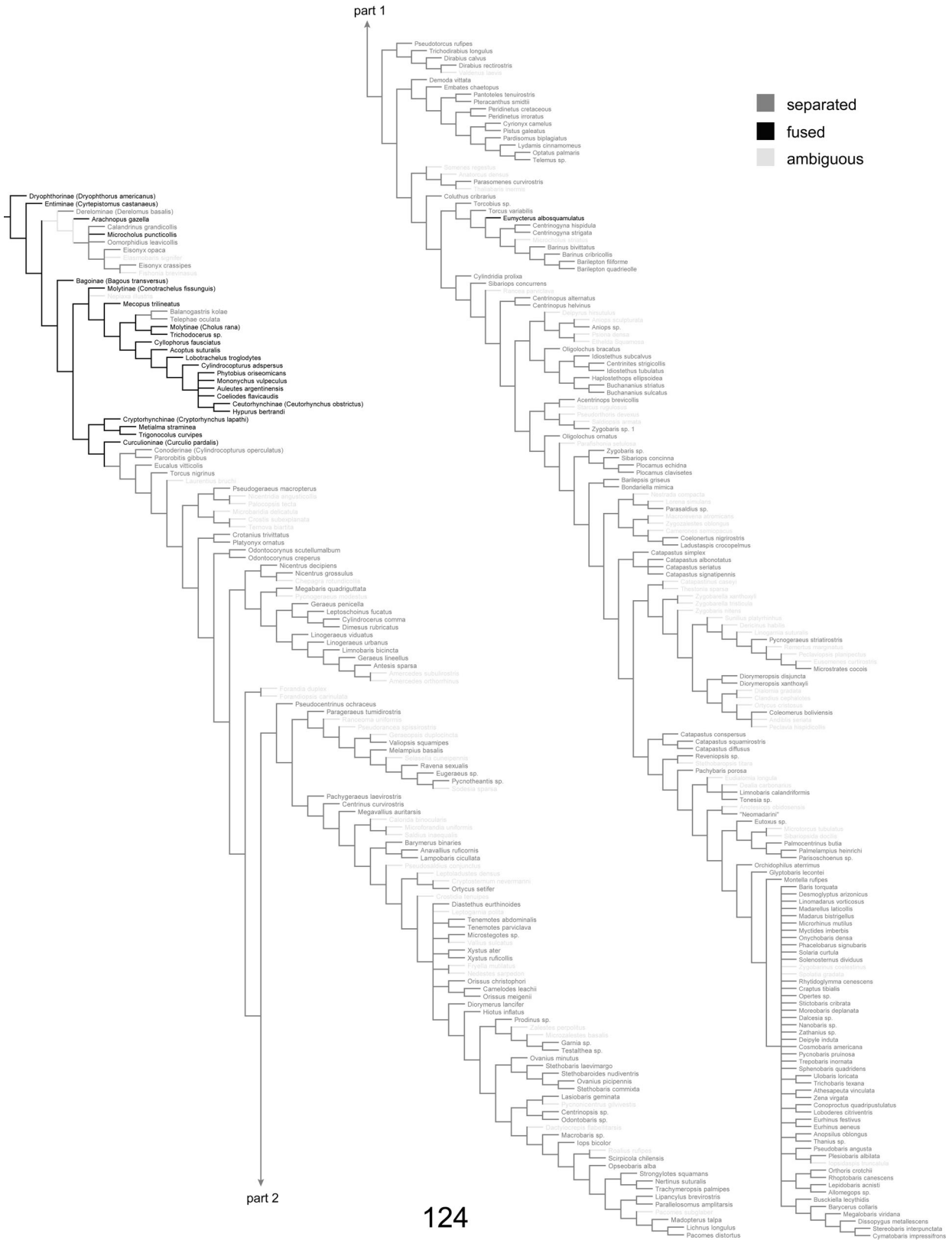
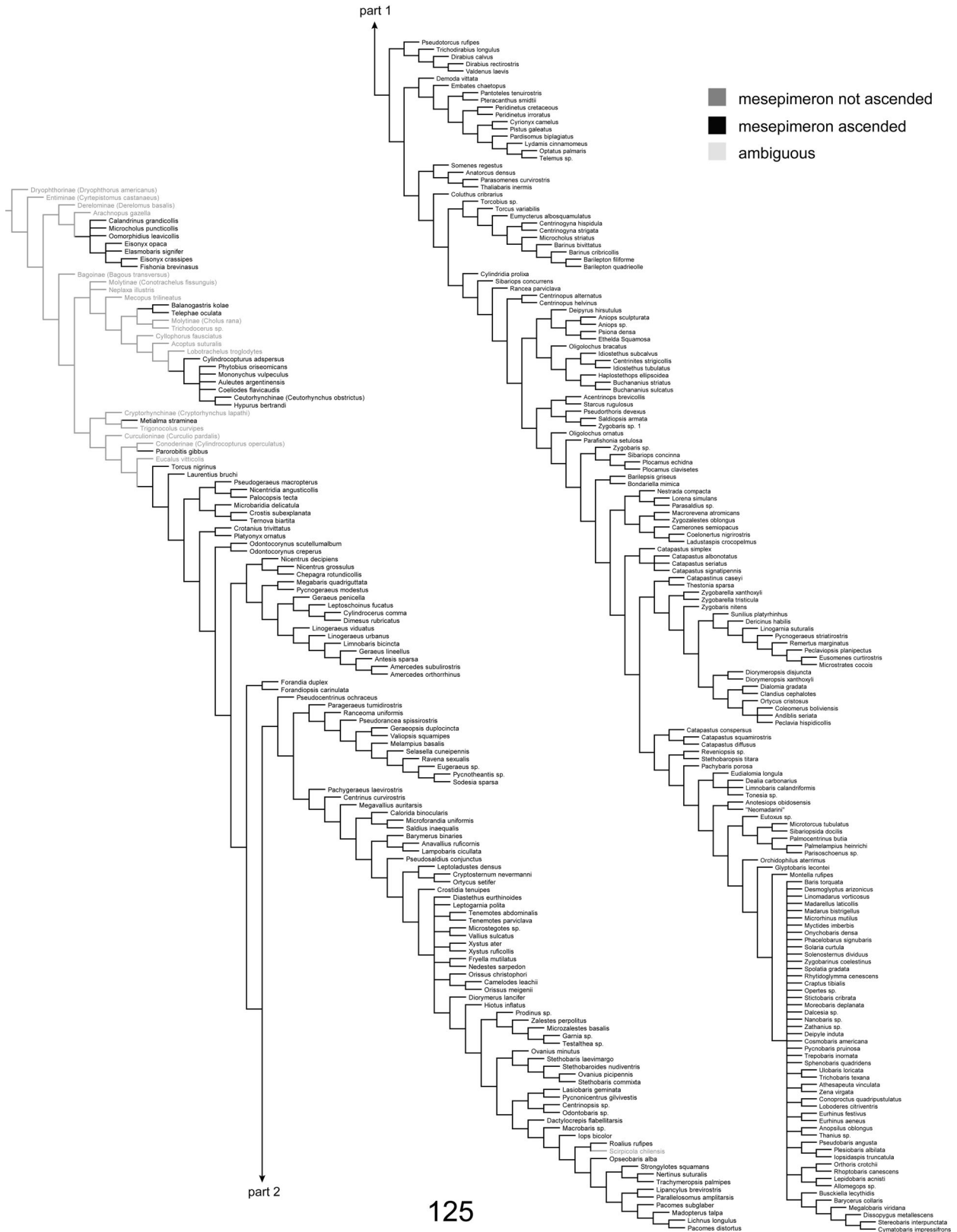


Figure 124. Character 98 (abdominal lateral tergite), supporting monophyly of Baridinae, mapped onto strict consensus tree of full taxon matrix analysis.



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

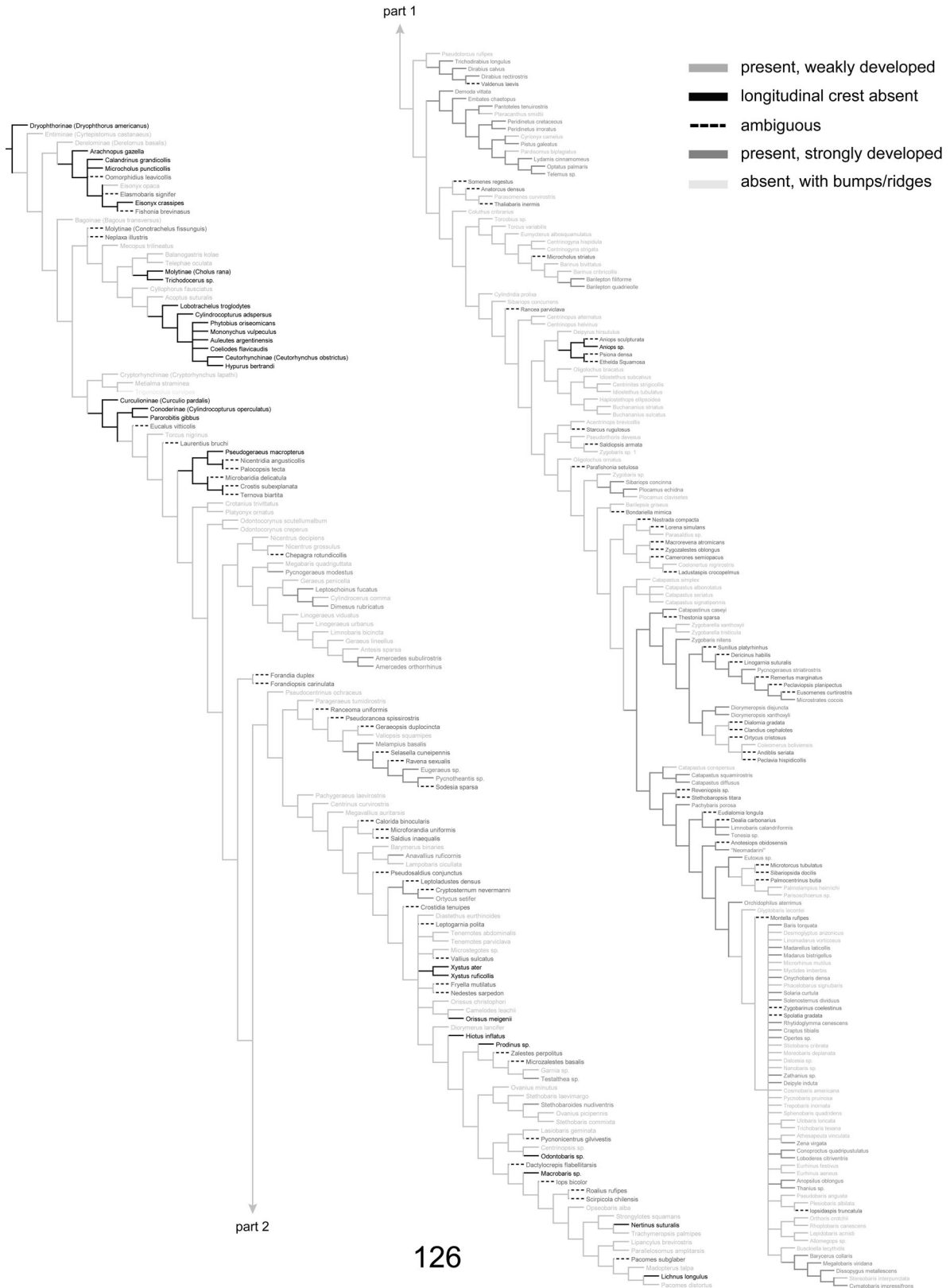
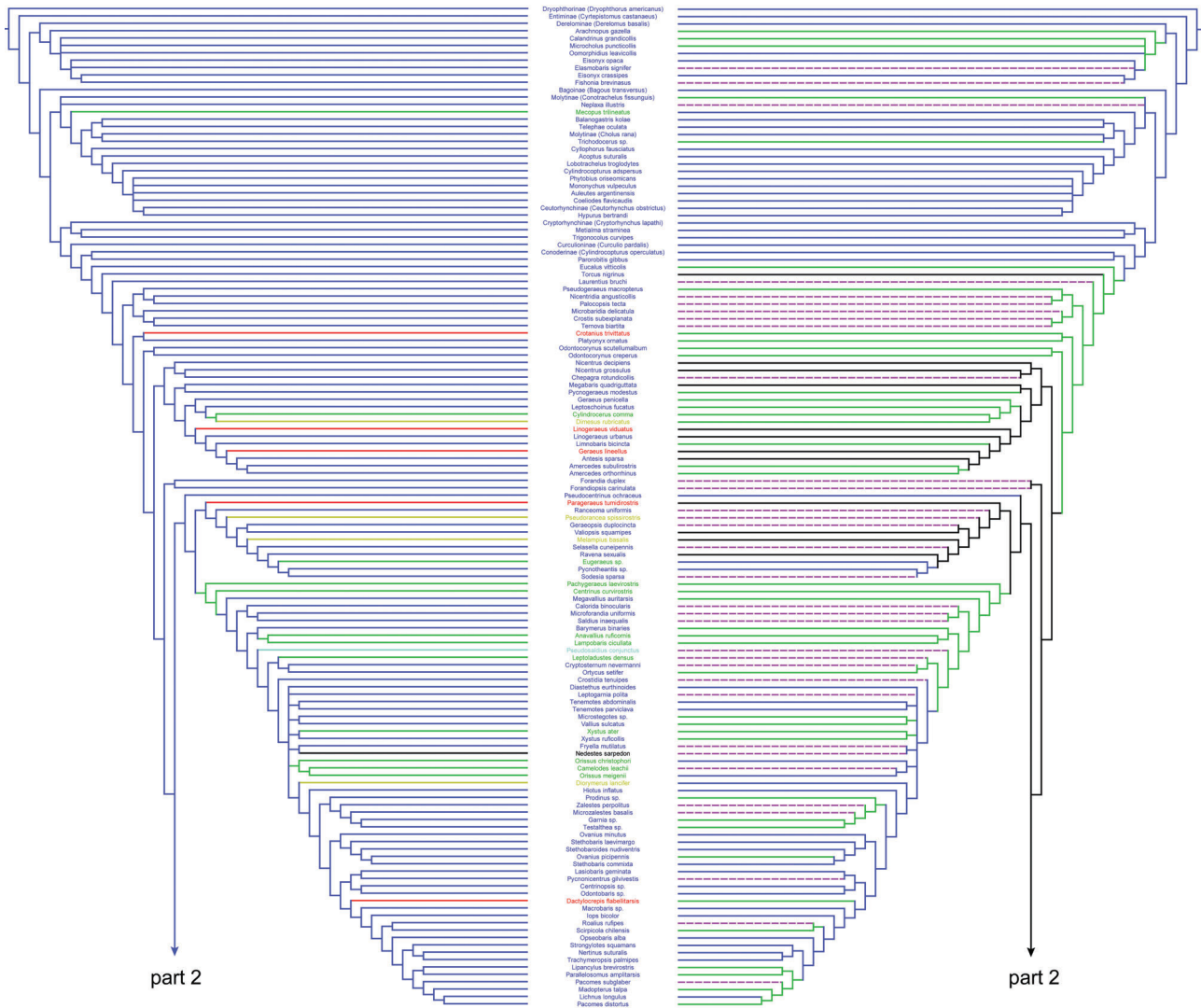


Figure 126. Character 51 (longitudinal crest on scutellar groove of metanotum), supporting monophyly of Baridinae and possibly suggestive of a more inclusive grouping, Barididae (Zherikhin & Gratshev, 1995), mapped onto strict consensus tree of full taxon matrix analysis.

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Pro-sternal horns in males:

- present, long, horn sheath shallow/absent
- present, long, horn sheath deep & bifurcate
- present, long, horn sheath deep & simple
- present, short, horn sheath shallow/absent
- present, fused, & long, horn sheath deep & simple
- horns absent

Plectra on 7th tergite (in males):

- present, in dense columns
- present, in sparse columns
- plectra absent
- ambiguity

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

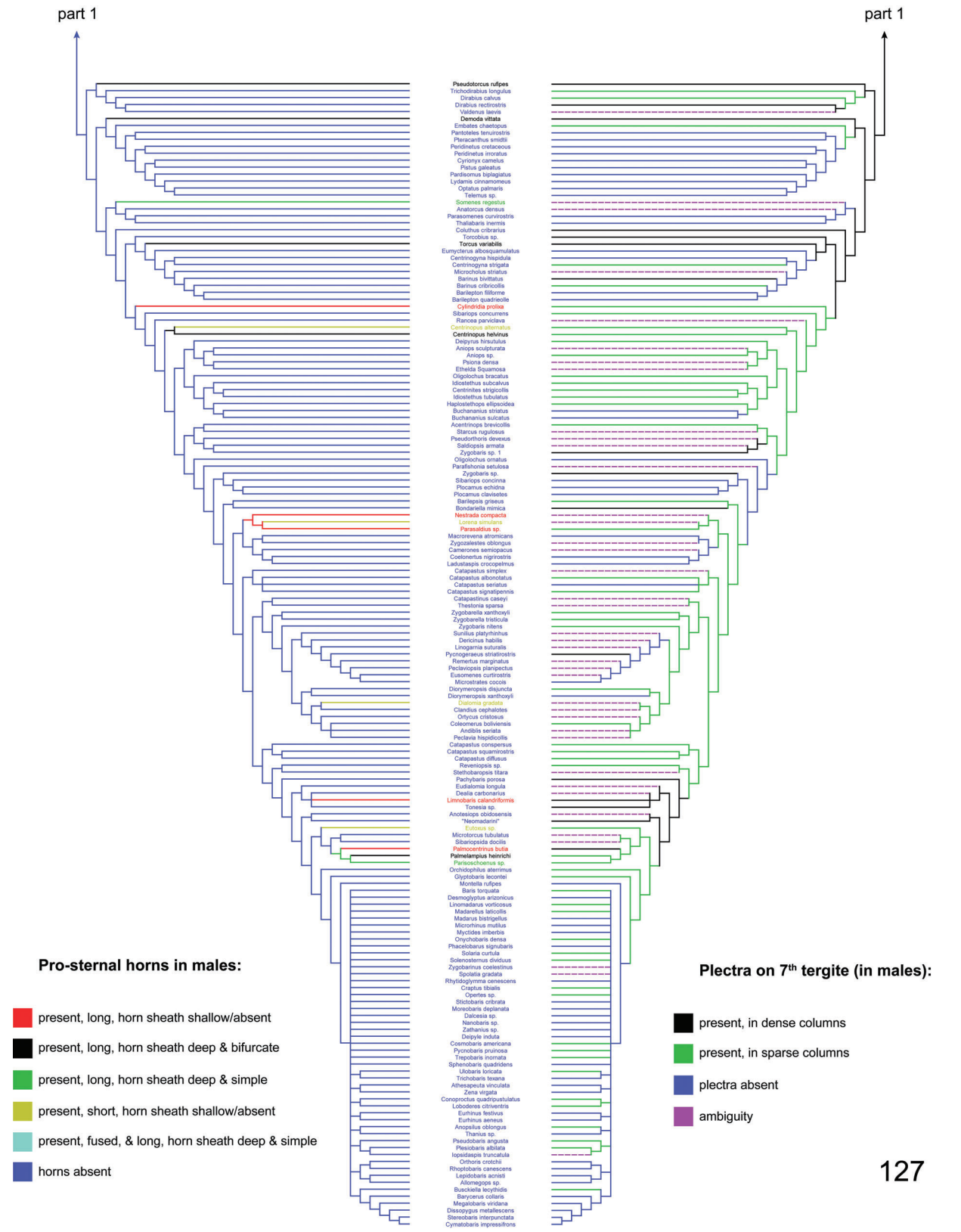


Figure 127. Continued

pectra 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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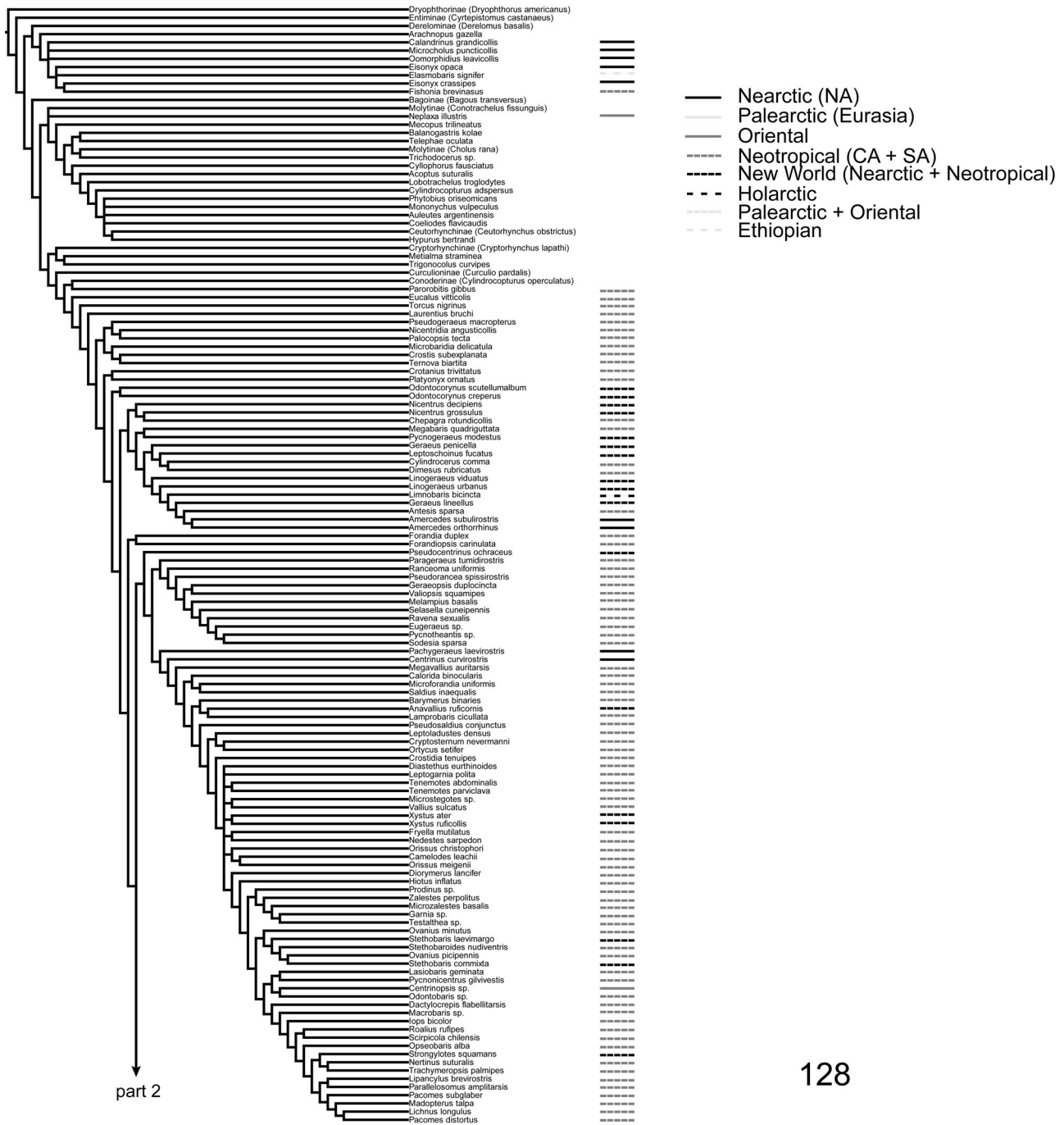


Figure 128. Biogeographical regions mapped onto strict consensus tree of full taxon matrix analysis.

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

APPENDIX 1 *Continued*

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

APPENDIX 1 *Continued*

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

APPENDIX 1 *Continued*

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

APPENDIX 1 *Continued*

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

APPENDIX 1 *Continued*

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

APPENDIX 2

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

Table with columns for species names and characters 0-110. Species include Dryophthorus americanus, Bagous transversus, Cyliandrocypturus operculatus, Ceutorhynchus obstrictus, Curculio pardalis, Choltus rana, Cyrtopistopus castaneae, Derelomus basalis, Cryptorhynchus lapathi, Conotrachelus fissunguis, Acentrinops brevicollis, Amercedes subulirostris, Amercedes orthorhinus, Anavallius ruficornis, Anopsilus oblongus, Athesis sparsa, Athesapelta vinculata, Barilepsis griseus, Barilepton filiforme, Barilepton quadrieolle, Barinus bivittatus, Barinus cribricollis, Baris torquata, Barymerus binaries, Buchananius striatus, Buchananius sulcatus, Busckella lecythidis, Calandrinus grandicollis, Camelodes leachii, Catapastinus caseyi, Catapastus conspersus, Catapastus squamirostris, Catapastus albonotatus, Catapastus seriatus, Catapastus signatipennis, Catapastus simplex, Centrinops strigicollis, Centrinognyna hispida, Centrinognyna strigata, Centrinopsis sp., Centrinopus alternatus, Centrinopus helveticus, Centrinus curvirostris, Coelonertus nigrirostris, Colcomerus boliviensis.

Conoproctus quadripustulatus
Crostidia tenuipes
Crotanion trivittatus
Cylindridia prolaxa
Cylindrocerus comma
Cyrtomyx camelus
Dactylocrepis flabellitarsis
Declia carbonaria
Deipyrrus hirsutus
Demodia vittata
Desmoglyptus arizonicus
Dialomia gradata
Diastethus curthinoides
Dimesus rubricatus
Diorymeropsis disjuncta
Diorymeropsis xanthoxyli
Diorymerus lancifer
Dirabius cabus
Dirabius rectirostris
Dissopygus metalllescens
Eisonyx crassipes
Eisonyx opaca
Elasmobaris signifer
Embates chaetopus
Eugereus sp.
Eumycterus albosquamulatus
Eurhinus festivus
Eurhinus aeneus
Eusomenes curtirostris
Eutoxia sp.
Fishonia brevinasus
Fryella mutilatus
Garnia sp.
Geracopsis duplocincta
Geracrus lineatus
Geracrus penicella
Glyptobaris lecontei
Haplotehops ellipsoidea
Idiostethus subcalvus
Idiostethus tubulatus
Iops bicolor
Ladustaspis crocopolimus
Lamprobaris cicutata
Lasiobaris geminata
Laurentius bruchi
Lepidobaris acristi
Leptoschoinus fucatus
Leptus longulus
Linnobaris bicincta
Linnobaris calandriformis
Lingeraeus urbanus

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	
<i>Toreus nigrinus</i>																								
<i>Torus variabilis</i>																								
<i>Trachymereopsis palmipes</i>																								
<i>Trichodirabus longulus</i>																								
<i>Valdenus laevis</i>																								
<i>Vallopsis squamipes</i>																								
<i>Vallius sulcatus</i>																								
<i>Xystus ater</i>																								
<i>Xystus ruficollis</i>																								
<i>Zena virgata</i>																								
<i>Zygobarella xanthoxyl</i>																								
<i>Zygobarella tristicula</i>																								
<i>Zygarinus coelestinus</i>																								
<i>Zygarinus</i> sp. 1																								
<i>Zygarinus nitens</i>																								
<i>Zygarinus</i> sp.																								
<i>Zygozales</i> oblongus																								
<i>Anatorcus densus</i>																								
<i>Andiblis seriata</i>																								
<i>Aniops sculpturata</i>																								
<i>Anioteopsis obidosens</i>																								
<i>Calorida binocularis</i>																								
<i>Camerones semiopacus</i>																								
<i>Chepagra rotundicollis</i>																								
<i>Clandius cephalotes</i>																								
<i>Derivinus habilis</i>																								
<i>Eithelda Squamosa</i>																								
<i>Eudaltomia longula</i>																								
<i>Forandia duplex</i>																								
<i>Forandiopsis carinulata</i>																								
<i>Iopsidaspis truncatula</i>																								
<i>Leptogarnia polita</i>																								
<i>Leptodastetes densus</i>																								
<i>Linogarnia suturalis</i>																								
<i>Microtorus tubulatus</i>																								
<i>Microzales basalis</i>																								
<i>Nedestes sarpedon</i>																								
<i>Neplaxa illustris</i>																								
<i>Nicentridia angusticollis</i>																								
<i>Palocopsis tecta</i>																								
<i>Paraflshonia setulosa</i>																								
<i>Plectranca hispidoicollis</i>																								
<i>Pseudoranca spissirostris</i>																								
<i>Pseudosalidius conjunctus</i>																								
<i>Raneca parviclava</i>																								
<i>Roatus rufipes</i>																								

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			
<i>Acoptus suturalis</i>	001010021120001000010011201110200011601000020220211012210302000010041110110000011010002000310000000000000211120200																									
<i>Lobotrachelus troglodytes</i>	101010021110020103111001201100201011112100020120110012103020001100401622100000111011020103100000000000002111102000																									
<i>Mecopus trilineatus</i>	0012110211002002201111101000200111001200022010010210011200011200021040160110101020200015003100000000000000002111010200																									
<i>Trigonocolus curvipes</i>	1000100211001212311202130010001221160100002033012031111311000100110132110111021311111201611000000000000000000601121010																									
<i>Hypurus bertrandi</i>	101010021100200031130013011002001160100102012113000210302000210040120001000000021101210311000000000002??0111202																									
<i>Phytobius oriseomicans</i>	101010021120020003113001301100200116010010230211100421030200001101112021000001031110150041000000000000003110000304																									
<i>Mononychus vulpeculus</i>	10101002112000000311300130210020101611111023021110042103020002110211210011010211015102100000000000000000201010200																									
<i>Auleutes argentinensis</i>	101010021110000000311300130110020101611011023021130042103020001100311421100000100111012003100000000000000000201013104																									
<i>Coeliodes flavicaudis</i>	101010021100200003113001301100200011611011023021130042103020000110301222100110100211012003100000000000000000201010200																									
<i>Trichodocerus</i> sp.	00101001100000030133012001002110200011031000140220110022102020010110401102111000211200000003000000000000000000211020213																									