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Phylogenetic analysis of Eurytominae (Chalcidoidea: Eurytomidae) based on morphological characters

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A phylogenetic study of the Eurytominae (Hymenoptera: Chalcidoidea) treating 178 taxa and based on 150 morphological characters is given. Several cladograms using the complete species sample, but obtained with different weightings, are presented. Local studies were also carried out to provide possible alternate topologies. The deep nodes of the trees were unstable and were never supported, but most of the superficial nodes were stable and robust. The results therefore provide support for a generic classification of the subfamily. The large genus *Eurytoma* – which includes about half of the described species of the subfamily – proved to be polyphyletic, and is redefined in a narrowed sense using putative synapomorphies. *Bruchophagus* and *Prodecatoma* were similarly redefined. The genera *Philolema* and *Aximopsis* are reconsidered and defined in a broader concept. A number of the species presently included in *Eurytoma* were transferred to these genera. Finally, 22 new generic synonymies are proposed and 33 species are transferred. The study also demonstrates that the Eurytomidae are polyphyletic. The results strongly support a sister-group relationship between the Heimbrinae and the Chalcididae. The Rileyinae consist of two groups of unrelated taxa. A redefinition of the subfamily in a more restricted sense is supported by our results. The remaining group, consisting of the traditional Rileyinae, is included in the subfamily Buresiinae. Considered in this way they comprise the genera *Buresium* and *Macrorileya*, the latter being a senior synonym of *Archirileya*. The Buresiinae appear as the sister group of the Eurytominae. We propose to restrict the family Eurytomidae to these two taxa. This sister-group relationship provides evidence to polarize the biological habits within Eurytominae. The common ancestor of Buresiinae is presumed to parasitize insects (mostly at the egg stage) living in grass stems. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, **151**, 441–510.

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The Eurytomidae is one of the largest families of the Chalcidoidea with 1457 nominal species in 83 genera (Noyes, 2006; modified by Gates, 2007; Gates, Metz & Schauff, 2006). The family is present and common in all zoogeographical regions. Eurytomids exhibit a wide range of biologies, but the majority of the larvae are endophytic: as seed eaters, gall formers, or as parasitoids of phytophagous insects. Most eurytomids are primary or secondary parasitoids, attacking eggs, larvae, or pupae of various arthropod groups (Diptera, Coleoptera, Hymenoptera, Lepidoptera, Orthoptera, and Araneae). The secondary parasitic eurytomids mostly attack Ichneumonoidea. Some genera include strictly phytophagous species: *Austrodecatoma*, *Ausystole*, *Cathilaria*, *Prodecatoma* (*s.s.*), *Risbecoma*, *Systole*, and *Tetramesa*; their larvae develop in the stems of wild grasses, including cereal crops, or in seeds of Umbelliferae, Leguminosae, Rosaceae, etc. Others are gall formers in the roots and twigs of several plants, e.g. *Aranedra* and *Foutsia* develop in Neotropical *Philodendron* spp. (Bouček, 1988; Noyes, 2002). However, it is difficult to assess the exact host–parasitoid relationships for most endophytic species. One fraction of Eurytomidae that are supposed to develop as parasitoids may well be inquilines. Various genera (*Sycophila*, *Ficomila*) reared from syconia of *Ficus* are actually inquilines in Epichrysomallinae galls. Moreover, some eurytomids, such as *Eurytoma pachyneuron* Girault, 1916 and *Eurytoma parva* Phil-

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*Corresponding author. E-mail: gerard.delvare@cirad.fr lips, 1918, are known to switch to phytophagy before and/or after consuming an insect host (Phillips, 1917; Phillips, 1927). Another interesting case of biological plasticity concerns species belonging to the *Eurytoma rosae* aggregate. In this group, adults are morphologically similar and impossible to segregate into morphospecies (Claridge & Askew, 1960). Their larvae, however, show different behaviour according to the species. Whereas larvae of *E. rosae* predate on the inquiline cynipids associated with *Rosa* spp., *Eurytoma brunniventris* larvae are associated with oaks and feed both on the gall-forming cynipid larvae and on the gall tissue. This short account points to the great diversity of the biology and the quick evolution of diet habits and feeding behaviour in related taxa.

Because of their diversified biology Eurytomidae also have contrasting economic importance. Most seed eaters of cultivated plants (*Bruchophagus*, *Systole*, *Eurytoma* of the *amygdali* group, etc.) are pest insects; however, some phytophagous species can be used for biological control as they feed on weeds or invasive plants (Burks, 1958; Simmonds, 1980). A biological control program using *Tetramesa romana* (Walker, 1873), a gall-stem eurytomid wasp, is presently being developed to slow the expansion of the invading *Arundo donax* L., 1753 (Poaceae) in southern USA (A. Kirk, pers. comm.). Finally, some beneficial Eurytomidae are used as biological control agents, e.g. *Eurytoma oryzivora* Delvare, 1988, which is a parasitoid of the stem borer *Maliarpha separatella* Ragonot, 1888 (Pyralidae) in tropical Africa (Delvare, 1988; Polaszek, 1998).

Abundantly trapped in biodiversity surveys (Noyes, 1989) and easily reared from various plant structures, Eurytomidae seem to have an underestimated ecological importance. Their high diversity [more than 25 000 species if the estimations provided by Noyes (2000) and Heraty & Gates (2004) for the Chalcidoidea as a whole are correct], their relatively homogeneous habitus, the presence of complexes of cryptic species, and the lack of recent and reliable taxonomic revisions, combine to prevent reliable specific identification. As a result most published biological data are doubtful.

The Eurytomidae have a quite distinct habitus among the other Chalcidoidea, and were recognized as a discrete group by Walker as early as 1832. Walker (1832) included four genera in the family: *Eurytoma*, *Decatoma, Isosoma*, and *Systole*. Ashmead (1904) described 23 new genera and erected the tribes Aximini, Eurytomini, Isosomini, Rileyini, and Decatomini, which were accepted by Bugbee (1936). These tribes were raised to subfamily rank (Ferrière, 1950) and maintained by Nikol'skaya (1952), Claridge (1961b), and Peck (1963). Burks (1971, 1979) added three new subfamilies (Heimbrinae, Prodecatominae, and Philoleminae) without any diagnoses. According to Gates (2007) the proposed names do not satisfy the criteria for availability set in Article 13 (ICZN, 1999). Finally, Zerova (1988) used Ashmead's system, but placed *Buresium* in a separate subfamily, the Buresiinae. Subba Rao (1978) broke away from Ashmead's classification, and recognized only two subfamilies (Rileyinae and Eurytominae). Stage & Snelling (1986), revising the Heimbrinae, added them to Subba Rao's classification and proposed the first classification based on a comparative morphological analysis. This classification was followed by Bouček (1988), in his monography of the Australasian chalcidoid fauna, DiGiulio (1997), and finally Noyes (2002), in his database of World Chalcidoidea. Gates (2007) tabulated the systems of classification previously used by different authors. He also synonymized the Buresiinae with the Eurytominae and revised the Rileyinae, which were defined more narrowly, i.e. the genera *Archirileya*, *Buresium*, and *Macrorileya* were excluded and transferred to Eurytominae.

Consequently, two systems of classification conflict: either Eurytominae are split into five subtaxa, following Ashmead (1904), or are kept undivided as proposed by Stage & Snelling (1986). Zerova (1988) carried out a character analysis and postulated ground-plan features for Eurytomidae, but she neither described how she polarized the characters nor distinguished between primitive and derived states in order tto define eurytomid taxa.

The generic classification is poorly supported. Furthermore, over one half of the species are described in the genus *Eurytoma* and, conversely, 42 genera are monospecific (Figs 1, 2). Generic distinctiveness is rarely clear despite recent attempts to improve our knowledge (e.g. Burks, 1971; Bouček, 1988; Narendran, 1994; Zerova, 1995). Indeed autopomorphies can be postulated for the monospecific genera, but the largest genera are not based on shared derived characters. As Burks (1971) wrote: 'Many species are

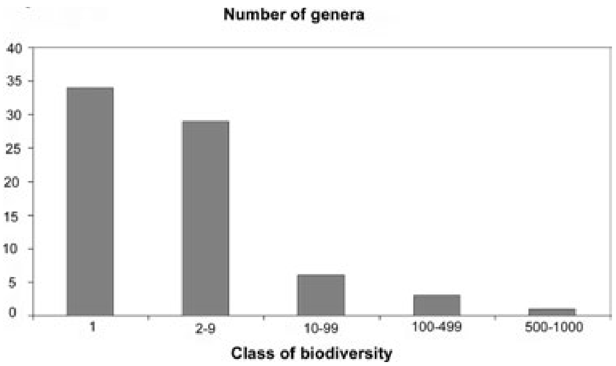

Figure 1. Described species of Eurytomidae: classes of biodiversity (number of species described within each genus) according to genus. Data from Noyes (2002).

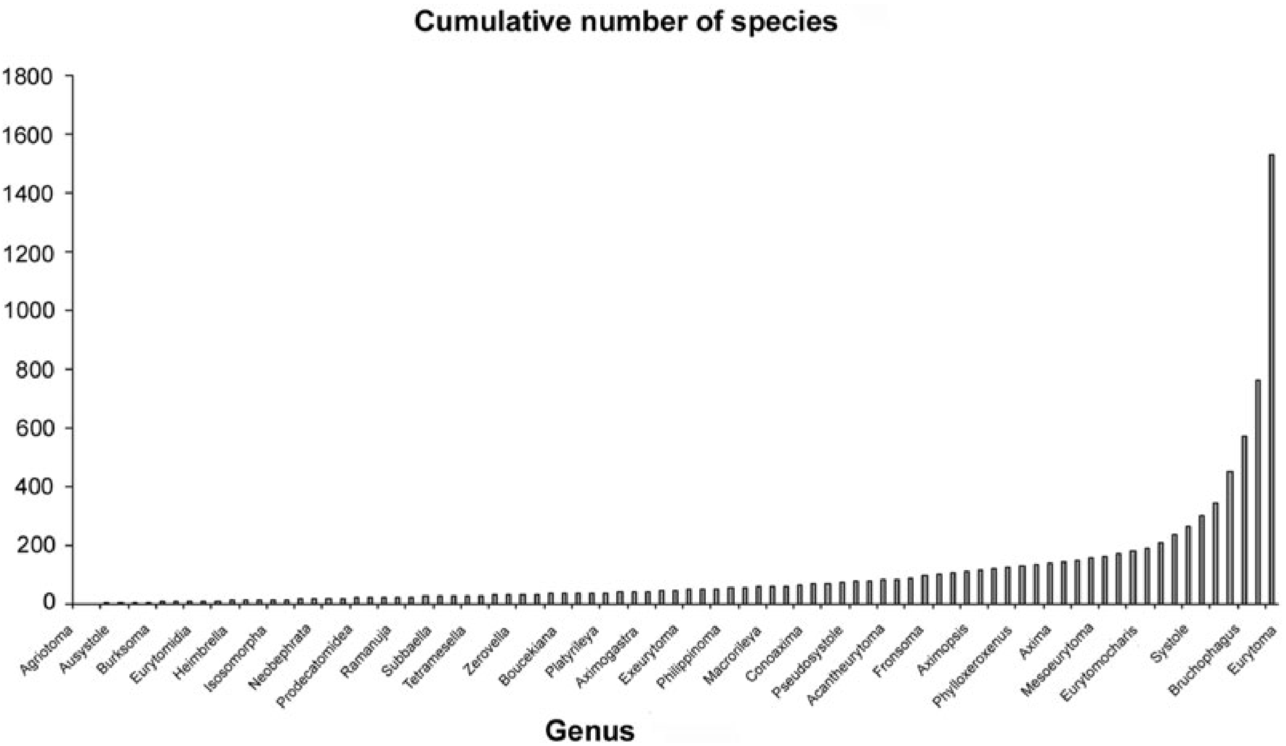

Figure 2. Cumulative number of described species of Eurytomidae distributed from less diverse genera to most diverse. Data from Noyes (2002).

placed in *Eurytoma* not because they are greatly like the type species, but because it has not yet been possible to place them elsewhere'. The problem is complicated by the apparently uniform habitus of the species and the intergradation of character states, which often form morphoclines.

The monophyly of Eurytomidae is still questioned because tangible synapomorphies are still lacking (Gates, 2007). Wijesekara (1997) proposed two features that might support the monophyly of Eurytomidae: (1) genal bridge completely covering the hypostomal bridge (found also in some Chalcididae); (2) anterior condyle of the petiole separated from the body only dorsally, so that the anterior ventral margin of the petiole abuts the propodeal foramen. His sampling of Eurytomidae was limited, however, being restricted to two species, respectively, belonging to *Eurytoma* and *Tetramesa*. Gates (2007) used 50 characters to investigate the relationships between Cleonyminae (one species), Leucospidae (two species), Chalcididae (ten species), Rileyinae *s.l.* (13 species), Heimbrinae (two species), and Eurytominae (nine species). The Eurytomidae were monophyletic but weakly supported by states being either plesiomorphic or highly homoplastic. In a another study presented at a recent workshop (Gates, 2005) the family was polyphyletic, i.e. the Rileyinae *s.s.* appeared as the sister group of a set of Chalcididae (*Acanthochalcis*, *Brachymeria*, and Haltichellinae), whereas the Heimbrinae + Eurytominae *s.l.* were the sister group of another set (*Dirhinus*, *Epitranus*, and Chalcidini).

Recently, Campbell *et al.* (2000) used the 28S-D2 rDNA to explore the phylogeny of the whole superfamily Chalcidoidea; they included five eurytomids. Despite this restricted sample the family was polyphyletic and split into two groups: Rileyinae and Eurytominae. Finally, Chen *et al.* (2004) carried out the first molecular phylogeny of the family. They used 24 species and four genes: 18S and 28S (nuDNA), and 16S and COI (mtDNA). Although most genes exhibit a very low level of variability, and the domains analysed strongly conflict, the authors concluded that the family was not monophyletic, with the Rileyinae being more closely related to Torymidae than to Eurytomidae.

The aim of our study is to propose the first phylogeny of the Eurytomidae based on morphology. As stated above, Heimbrinae (Stage & Snelling, 1986) and Rileyinae (Gates, 2007) were already revised, therefore we focused on the Eurytominae because it is by far the largest of the subfamilies and the least studied. The detailed objectives are therefore to infer: (1) monophyly of Eurytomidae; (2) relationships among the subfamilies; (3) monophyly of Eurytominae *sensu* Stage & Snelling (1986); (4) generic relationships within Eurytominae basing this on a large sample; (5) monophyly of large genera such as *Bruchophagus*, *Eurytoma*, *Sycophila*, *Systole*, and *Tetramesa* through shared synapomorphies.

MATERIAL AND METHODS

SPECIES SAMPLING

Our knowledge of the family includes over 800 species from the examination of 5000 specimens mainly housed in the INRA and CIRAD collections in Montpellier. The analysed species include types, specimens compared with types, and specimens accurately identified through type comparisons. The following acronyms are used to denote the depositories: AEI, American Entomological Institute, Gainesville, FL, USA; BMNH, The Natural History Museum (formely the British Museum of Natural History), London, UK; CIRAD, Centre de Coopération Internationale en Recherche Agronomique pour le Développement, Montpellier, France; FSAG, Faculté des Sciences Agronomiques, Gembloux, Belgium; HNHM, Hungarian Natural History Museum, Budapest, Hungary; INRA, Institut National de Recherches Agronomiques, Montpellier, France; MNHN, Muséum National d'Histoire Naturelle, Paris, France; USNM, United States National Museum, Washington DC, USA.

SPECIES NAMES

The species that could not be identified or are still undescribed were tentatively named according to the sampling localities (i.e. *Eurytoma* Gabon). When several unidentified species belonging to the same genus were collected in the same country we used either collection locality (e.g. *Bephratoides* Shushufindi, from Ecuador) or biological information (e.g. *Paradecatoma* Combretum for species reared from seeds of *Combretum*).

SPECIMENS EXAMINATION

Several characters never examined before within the Chalcidoidea were discovered in the course of this study. Many of them needed specimen dissections to be examined; we thererefore completely dissected the head, mesosoma, and gastral petiole of 141 species among the 178 included in the study. Structure of the antennal flagellum was examined using slide-mounted specimens and SEM (Zeiss DSM 950). The fine ornamentation on the back of the head, visible only at magnifications ranging from ×2000 to ×5000, was observed with the same equipment, which was also used to provide the illustrations. Thus, 576 SEM photographs from 67 species were made in order to scan their character states.

OUTGROUPS

The phylogeny of chalcidoid families is still unsolved. Noyes (1990) provided an intuitive phylogeny, and the first attempt to explore the molecular data was carried out by Campbell *et al*. (2000). Torymids, ormyrids, and chalcidids are often associated with Eurytomidae (Zerova, 1988; Noyes, 1990; Wijesekara, 1997; Gates, 2007). Therefore, we used one Torymidae (*Glyphomerus*) and one Chalcididae (*Hockeria*) as outgroups. One Pteromalidae Cleonyminae (*Lycisca*) was also added, as this group was stated to exhibit primitive features (Gibson, 2003); one Rileyinae *sensu* Gates (2007) (*Rileya*), two Rileyinae *s.l.* (*Buresium*, *Archirileya*), and two *Heimbra* (Heimbrinae) were selected as outgroups for the Eurytominae (Appendix 1).

TAXONOMIC SAMPLING

The species included in the analysis were chosen to illustrate, as far as possible, the morphological diversity of the subfamily throughout the world (Appendix 1). We included 178 species that represent 62 of the 73 described eurytomid genera. The remaining genera are monospecific or include very rare species that were not available to us (see the section Genera excluded from the study). *Eurytoma* and *Bruchophagus*, the two largest genera of the subfamily, are represented by 39 and 11 identified species, respectively, but the former also includes 25 species that could not be determined to species level. With the exception of monospecific genera, all genera were figured by several species, which have been chosen to represent the extreme variation encountered within them. Species are named according to the current nomenclature, with the exception of *Eurytoma squamea* Walker, 1834 and *Eurytoma phlei* Erdös, 1969, which belong to *Bruchophagus*, as demonstrated below.

CHARACTER SAMPLING

We mostly used females, as most males cannot be identified to species level and associated with females. We only examined external morphology. Male genitalia exhibit very little variation and consequently were not used. The terminology used follows that of Gibson (2003). Some structures had never been investigated and needed new names (see Appendix S1). Figures 10–17 illustrate the characters and terminology; Appendix S2 lists all the abbreviations used.

CHARACTER POLARIZATION

We used *Lycisca* and *Glyphomerus* to polarize the characters. Previous works (Wijesekara, 1997; Gibson, 2003; Gates, 2007) were also useful to help identify plesiomorphic states.

The existence of morphoclines concerning several characters (e.g. characters 4, 5, 82, 87, 89, 138, 148, 149) renders any partition into multistates as arbitrary. In Step 4 of Analysis 1 (see below) we screened the effect of grouping some states that were somewhat similar, but which were initially separated with the concern of including only truly homologous states. We sometimes split multistates characters into several characters in order to deal with binary states. This procedure was carried out when the pattern of distribution was quite different according to the states, e.g. one derived state of a character had a high rescaled consistency index (RC), whereas the others were highly homoplastic.

Appendix S3 lists the morphological characters and includes comments concerning their polarization. Most of the character states are illustrated (Figs 18–212). Appendix S4 includes the matrix of character-state distribution.

MISSING DATA

A number of characters used in this study can be examined only after the removal of some parts of the body, e.g. the head and the legs. Moreover, the characters concerning the postgenal bridge are visible only at high magnifications (> ×500) using an SEM. Some genera are monospecific and known only from the holotype or type series of their type species. Hence *Bruchophagus borealis* Ashmead, 1894, the type species of that genus, was replaced by another morphologically similar species – supposedly closely related to it – and called '*Bruchophagus* Alicante' to encode the characters of the back of the head. In others cases no similar species was found, thus generating missing data.

PHYLOGENETIC ANALYSIS

Analyses were run in PAUP 4.0b10 (Swofford, 2001), sometimes using the DOS version of this program compiled by Calendini & Martin (2005). All characters were treated as unordered, except for two characters for which reversals seemed impossible (because of loss and fusion of antennal segments). Analyses were run using a heuristic search, with tree bisection-reconnection (TBR) branch swapping, in conjunction with random addition sequences, holding one tree at each step. Maxtrees was set to 1000 in the initial runs and brought to 30 000 without improving the results, i.e. finding the shortest trees. Once an initial run was performed, we reweighted the characters according to their RC and carried out another run using the same options but storing only 100 trees, which proved to be sufficient as the reweighting reduces the number of possible equally weighted trees.

Despite the fact that the use of resampling methods to assess confidence limits on phylogenies has been questioned (Kluge & Wolf, 1993; Carpenter, 1996), support of the nodes was estimated with bootstrapping (Felsenstein, 1985) using the fully heuristic option of PAUP, with 100 replicates. Due to the size of the matrix we were unable to evaluate the Bremer support (Bremer, 1994) with AUTODECAY 4.0 (Eriksson, 1999).

We screened the effect of discarding characters with low RC. Removing the characters with RC < 0.025 had no effect on topology, but discarding characters with a higher RC (over 0.04) did affect the topology. Hence, 32 uninformative or homoplastic characters were discarded. We finally retained a total of 150 characters (Appendix S3).

Analysis 1

Analysis 1 used the complete data set; it is subdivided into five steps.

Step 1: All characters were given equal weight (#1). The trees obtained showed large multifurcations, pointing to a large level of homoplasy. Successive weighting (Farris, 1969) did not provide a stable solution. Checking the indices after the first iteration pointed to a bimodal distribution. Homoplastic characters generally exhibited low values (consistency index, CI less than 0.10), whereas the 15 nonhomoplastic characters have indices equal to 1. Moreover, we observed a decrease of the indices [CI, retention index (RI), and RC] for homoplastic characters at each step of the iteration process. Nevertheless, Källersjö, Albert & Farris (1999) showed that such characters are sometimes definitely informative; this was confirmed by our analysis (see above).

Step 2: These 15 nonhomoplastic characters were weighted as #2, and all other characters were weighted as #1. We carried out another parsimony analysis using the same procedure as above. By weighting the nonhomoplastic characters from Step 1 more heavily, the deeper nodes on the trees were better resolved. But, similarly, the successive weighting failed to find a stable solution. Checking CI, RI, and RC for each character, after the first iteration, showed that the new weightings reduced the gap between the values of homoplastic and nonhomoplastic characters. Using the same weighting we performed 30 runs, including ten random replicate searches for each run, which led to 30 sets of different equal-weight trees.

Step 3: Instead of implementing successive weighting we tried to find a 'consensus weighting'. The sets of equal-weight trees and associated indices (RC) provided the weighting values, using the most frequently encountered values. Ten separate runs including 100 random replicate searches were performed. The strict

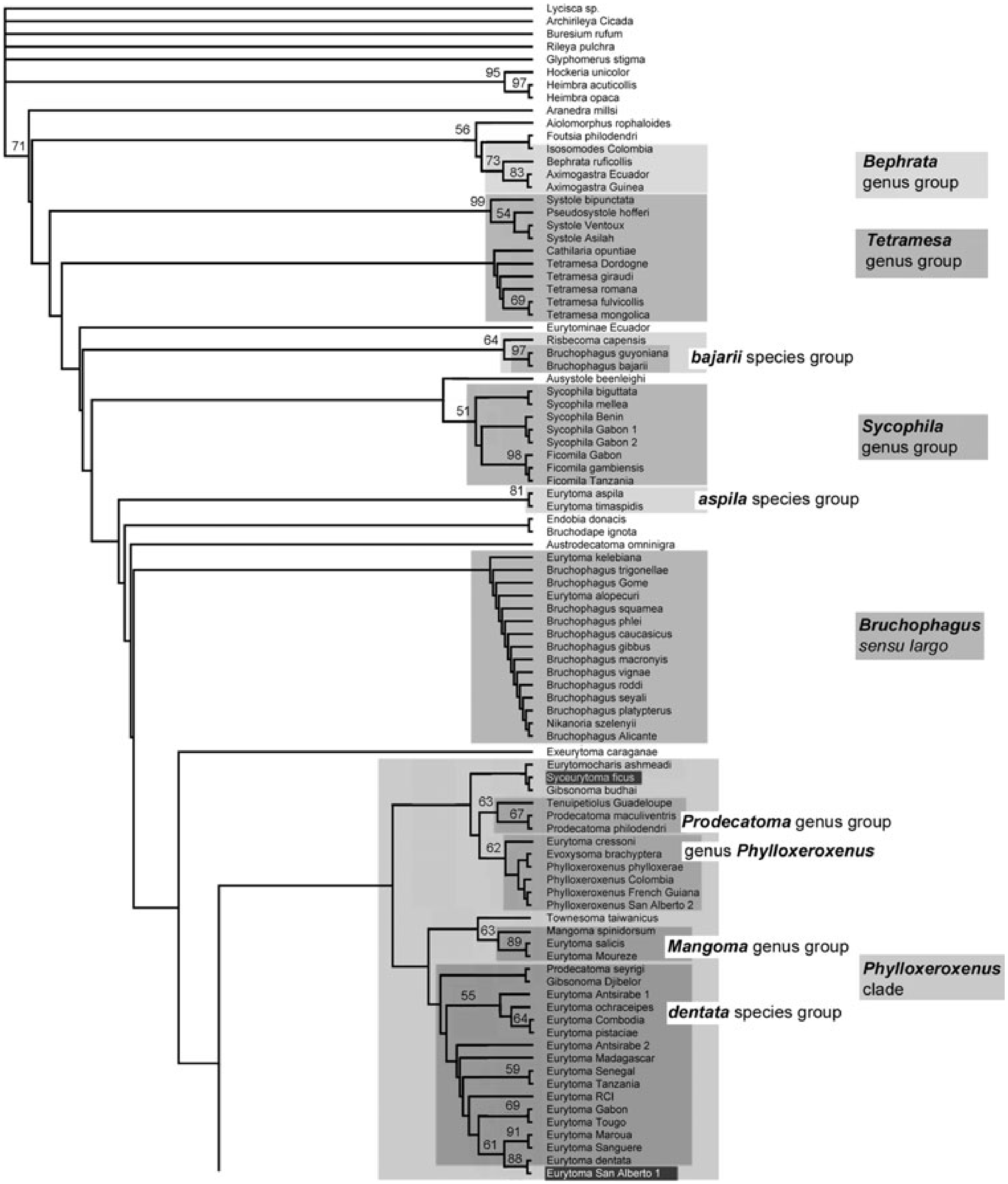

Figure 3. Cladogram 1. Phylogeny of the Eurytominae: strict consensus tree (= CS) of the equally weighted trees ($n = 35$). Study carried out with 150 morphological characters and 178 taxa using a 'consensus weighting approach' as defined in the text (Step 3 of Analysis 1). Boostrap values are given above the branches. Length of the tree: 165.96; consistency index, CI = 0.275; retention index, RI = 0.844; rescaled consistency index, RC = 0.232. The generic groups, large genera, and some species groups, as defined in the text, are shaded. The *Bephrata* group is not monophyletic on this cladogram. *Syceurytoma ficus* and the *Eurytoma* from San Alberto were finally excluded from the *Phylloxeroxenus* clade; they are shaded in dark grey to underline an ambiguous placement on this cladogram. *Plutarchia* always branches within the genus *Philolema sensu largo* in all cladograms. As this placement seems doubtful the genus is also superimposed. Putative placement of the type species for each of the largest genera is indicated.

Figure 3. *Continued*

Figure 4. Cladogram 2. Phylogeny of the Eurytominae: strict consensus tree (CS) of the equally weighted trees ($n = 35$). Study carried out with 150 morphological characters and 56 taxa using a 'successive approach' as defined in the text (Step 4 of Analysis 1). Bootstrap values are given above the branches. Length of the tree: 262.92; consistency index, CI = 0.353; retention index, RI = 0.856; rescaled consistency index, RC = 0.302.

consensus tree (CS) of the equal-weight trees is cladogram 1 (Fig. 3).

Step 4: Aimed to (1) find alternate hypotheses of relationships, and (2) stabilize the deep nodes that were found to be unstable at Step 3 and were not supported in cladogram 1. Instead, we used a successive approach. Farris (1969) reported that the final stable solution when a successive weighting is implemented depends greatly on the initial set of weights. It is also known that using indices (especially CI) may not be an accurate procedure for weighting characters. Källersjö *et al*. (1999) showed that homoplastic characters are even more informative than synapomophies. Character ranking was proposed to establish a hierarchy of characters (Wilkinson, 1994; DeGusta, 2004), but either the procedure to link ranking and weighting is lacking or it is inapplicable to large data sets because of computation limits.

Consequently, we came back to our data set and preliminary results. Steps 2 and 3 showed that whatever the trees achieved, stables nodes were always recovered. These nodes were mostly superficial and supported either less speciose genera of Eurytominae (*Systole*, *Ficomila*, *Bephratelloides*, *Paradecatoma*, *Aximopsis*, etc.) or species groups within large genera (i.e. *aspila* and *rosae* groups for *Eurytoma*, and the *bajarii* group for *Bruchophagus*).

We used the option 'Character reconstruction' to discriminate 'superficial homoplasy' from 'deep homoplasy' through the distribution of the character states: the former was recovered above the stable nodes; the latter below them. Fifty-six taxa were chosen to represent all of the stable nodes from Steps 1 and 2. The selected taxa were chosen based on the absence of missing data, and for their relative position within these stabel clades. This allowed us to discard most of the superficial homoplasy. The remaining homoplasy was discarded manually through the examination of the distribution of homoplastic derived states using cladogram 1. The characters were reweighted with the new CI. All the stable nodes recovered in cladogram 1 of Step 3 were also recovered in the following reconstructions. Few characters appeared composite and were subdivided. In the case of the metafurcal pits we finally considered both their relative placement towards the front margin of the metapleuron and their size. The last data set included 156 characters and 265 derived states. A run with 100 replicates led to a single tree (cladogram 2; Fig. 4).

Step 5: Cladogram 2 of the previous step was used to reweight the characters according to their RC. Implementing this weighting, 30 runs of PAUP, each with a single replicate, were performed. The CS of the equal-weight trees is cladogram 3 (Fig. 5); a suboptimal tree, interesting from a biogeographical point of view, is cladogram 4 (Fig. 6).

Moreover, we carried out further analyses with partial data sets.

Analysis 2

Analysis 2 dealt with the basal nodes of Eurytominae. We used 44 taxa, *Buresium* and *Archirileya* as outgroups, a few species branching on the terminal nodes, and all the taxa branching on the basal nodes of the Eurytominae in the preceding cladograms. We implemented different weightings for some characters to evaluate the effect on topology. One hundred replicates, each using four different sets of weightings, were performed. Two sets of equal-weight trees were found; their CS are illustrated in cladograms 5A and 5B (Fig. 7A, B).

Analysis 3

Analysis 3 is only devoted to the genus *Eurytoma* as currently understood. The genus has always been considered a diverse but homogenous assemblage of species. We wanted to test the monophyly and relationships of taxa within *Eurytoma*, discarding the potential homoplasy introduced from the other genera. To do so, we introduced all described species of the genus previously sampled ($n = 37$), used *Archirileya* as the outgroup, and selected various taxa which, in the former cladograms, branched on stable nodes together with some *Eurytoma* species. One hundred replicates were performed leading to two most parsimonious trees (MPT), the CS of which is the cladogram 6 (Fig. 8).

Analysis 4

Analysis 4 is devoted to the taxa branching on the terminal nodes. We used *Archirileya* as the outgroup, five taxa previously branching on basal or intermediate nodes, two species of *Eurytoma s.s.*, and all the taxa branching on the terminal zone. Again, 100 replicates were performed leading to the equally weighted tree that is cladogram 7 (Fig. 9).

RESULTS

As quoted above, results are illustrated in cladograms 1, 3, and 4 (Figs 3, 5, 6, respectively), which represent a CS of 35 and 45 trees (the number of equal-weight trees is the same in the cladograms 3 and 4). The last cladogram (Fig. 6) was achieved with the same data and parameter values as the preceding one and is longer (L = 464.43 steps vs. L = 463.46 steps). It is presented here because it comprises two large branches, including (mostly) New World taxa on one hand and Old World species on the other; it therefore maps out

Figure 5. (A) Cladogram 3A. Phylogeny of the Eurytominae: strict consensus tree (CS) of the equally weighted trees ($n = 45$). Study carried out with 156 morphological characters and 178 taxa using a 'successive approach' as defined in the text (Step 5 of Analysis 1). Bootstrap values are given above the branches. Length of the tree: 463.459; consistency index, CI = 0.201; retention index, RI = 0.813; rescaled consistency index, RC = 0.164. The generic groups, the large genera, and some species groups, as defined in the text, are shaded. The *bajarii* species group is included here in the *Tetramesa* genus group, whereas it branches within the *Risbecoma* genus group in other cladograms. It is therefore shaded in dark grey to denote an ambiguous placement. The same is true for *Aiolomorphus rhopaloides*, which generally branches on a basal node of Eurytominae, not within the *Phylloxeroxenus* clade. Putative placement of the type species for each of the largest genera is indicated.

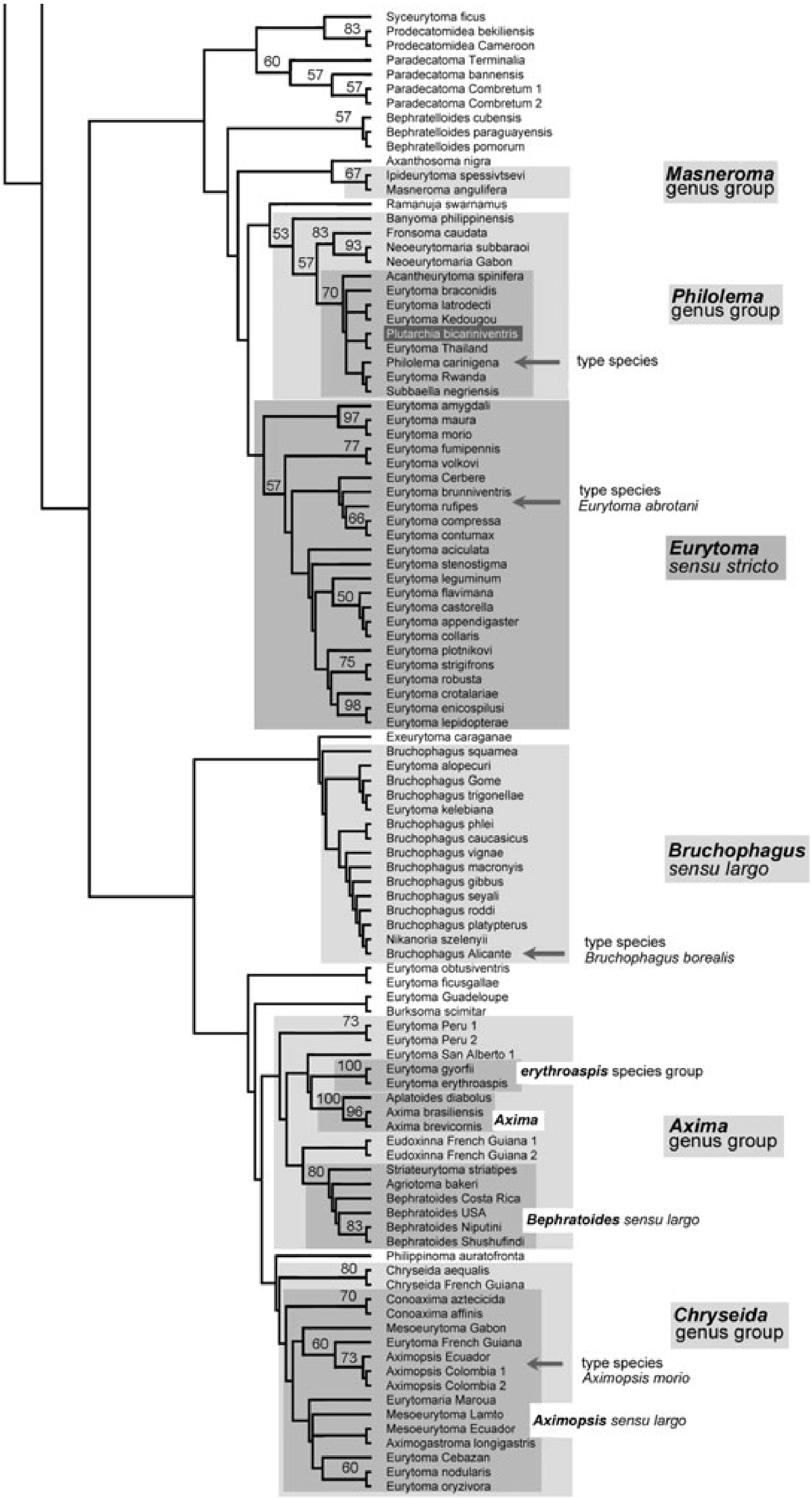

Figure 5. (B) Cladogram 3B. Cladogram 3 with feeding habits, when known, mapped on cladogram 3: phytophagous vs. entomophagus. Taxa not shaded or surrounded denote unknown or ambiguous feeding habit.

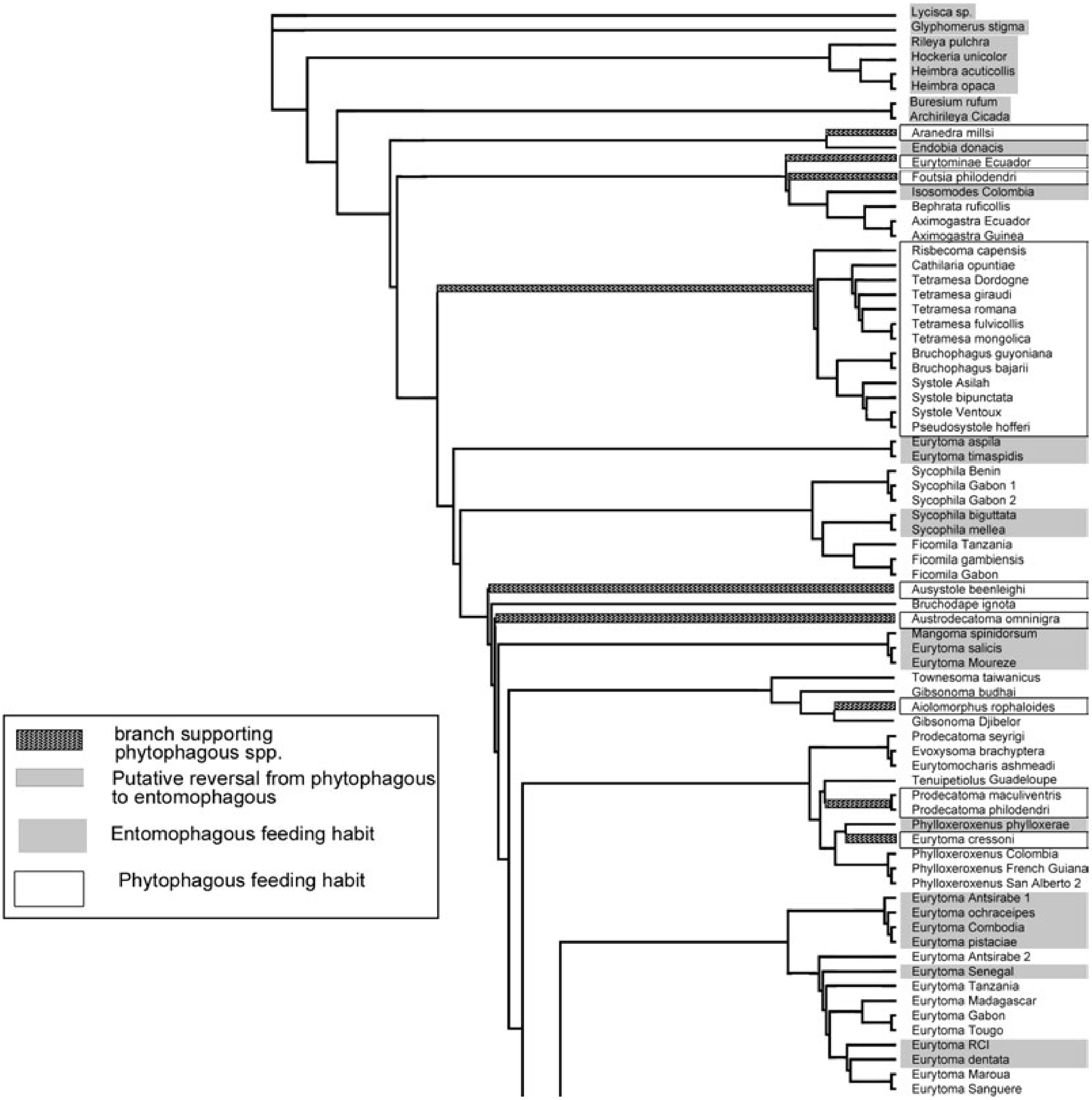

Figure 5. *Continued*

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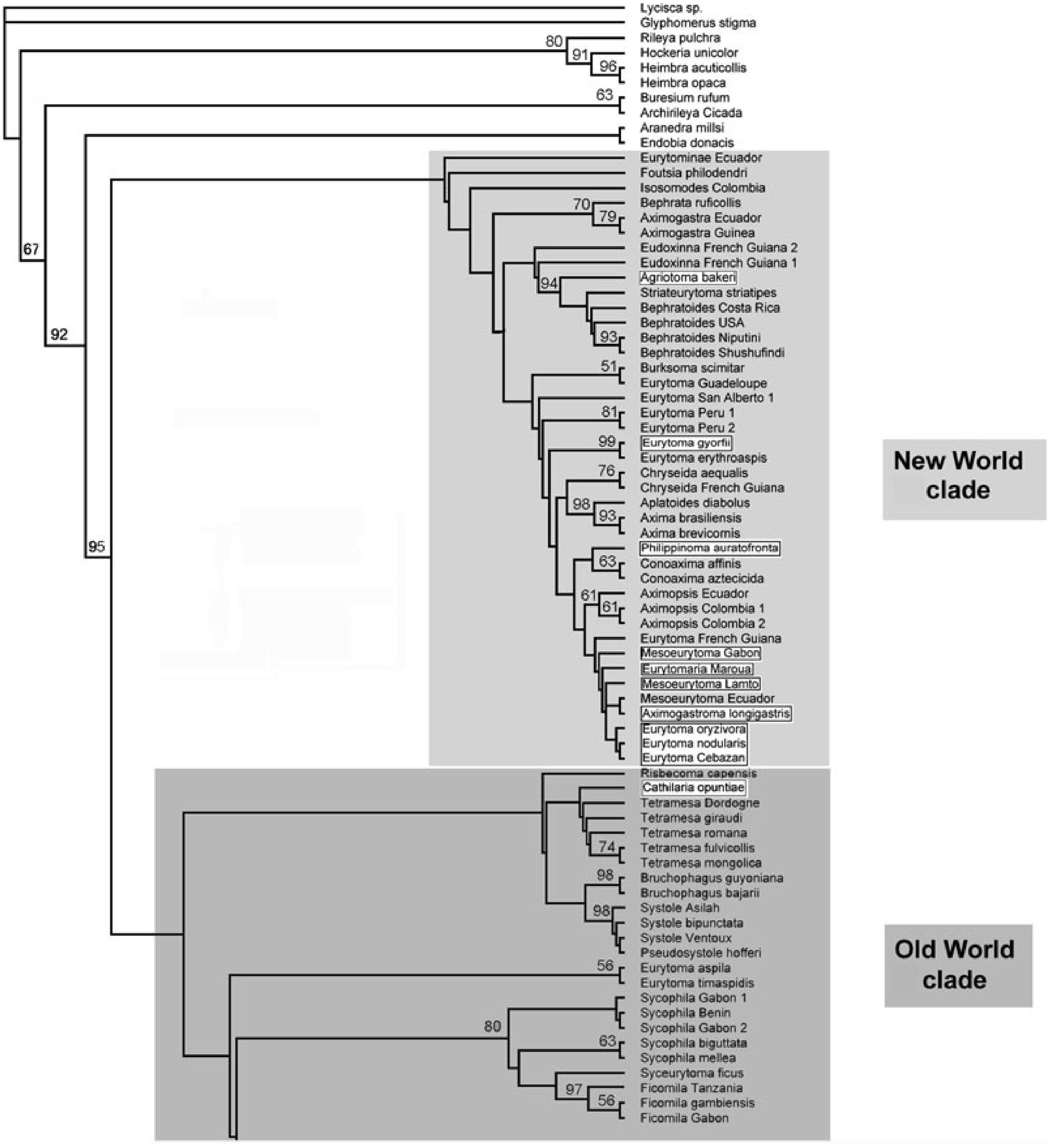


Figure 6. Cladogram 4. Phylogeny of the Eurytominae: strict consensus tree (CS) of the equally weighted trees ($n = 45$). Study carried out with 156 morphological characters and 178 taxa using a 'successive approach' as defined in the text (Step 5 of Analysis 1). Bootstrap values are given above the branches. Length of the tree: 464.433; consistency index, CI = 0.204; retention index, RI = 0.814; rescaled consistency index, RC = 0.166. Two large clades, including species distributed in the New World and in the Old World, respectively, are shaded. Species or genera conflicting with the general distribution are outlined.

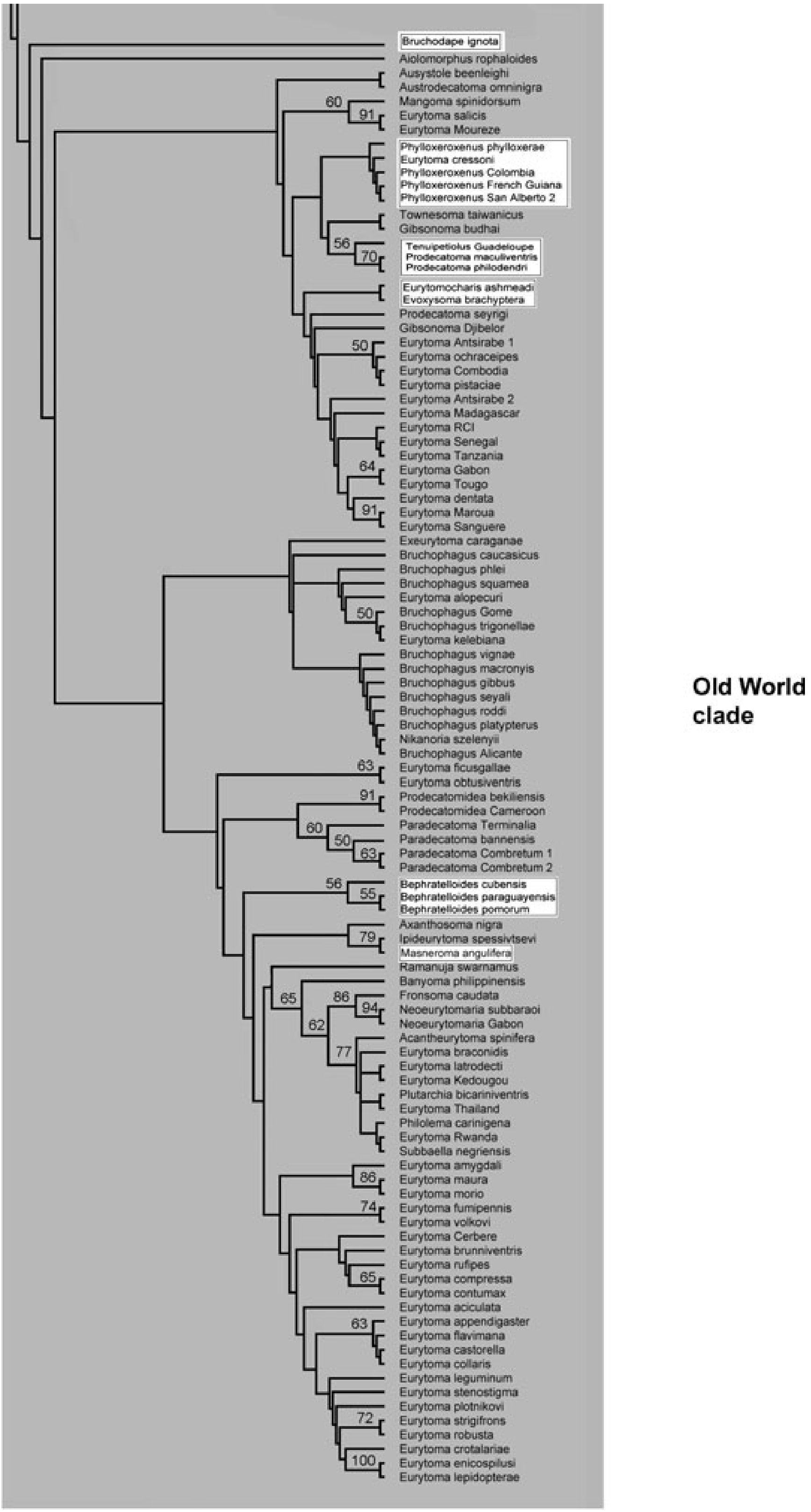


Figure 6. *Continued*

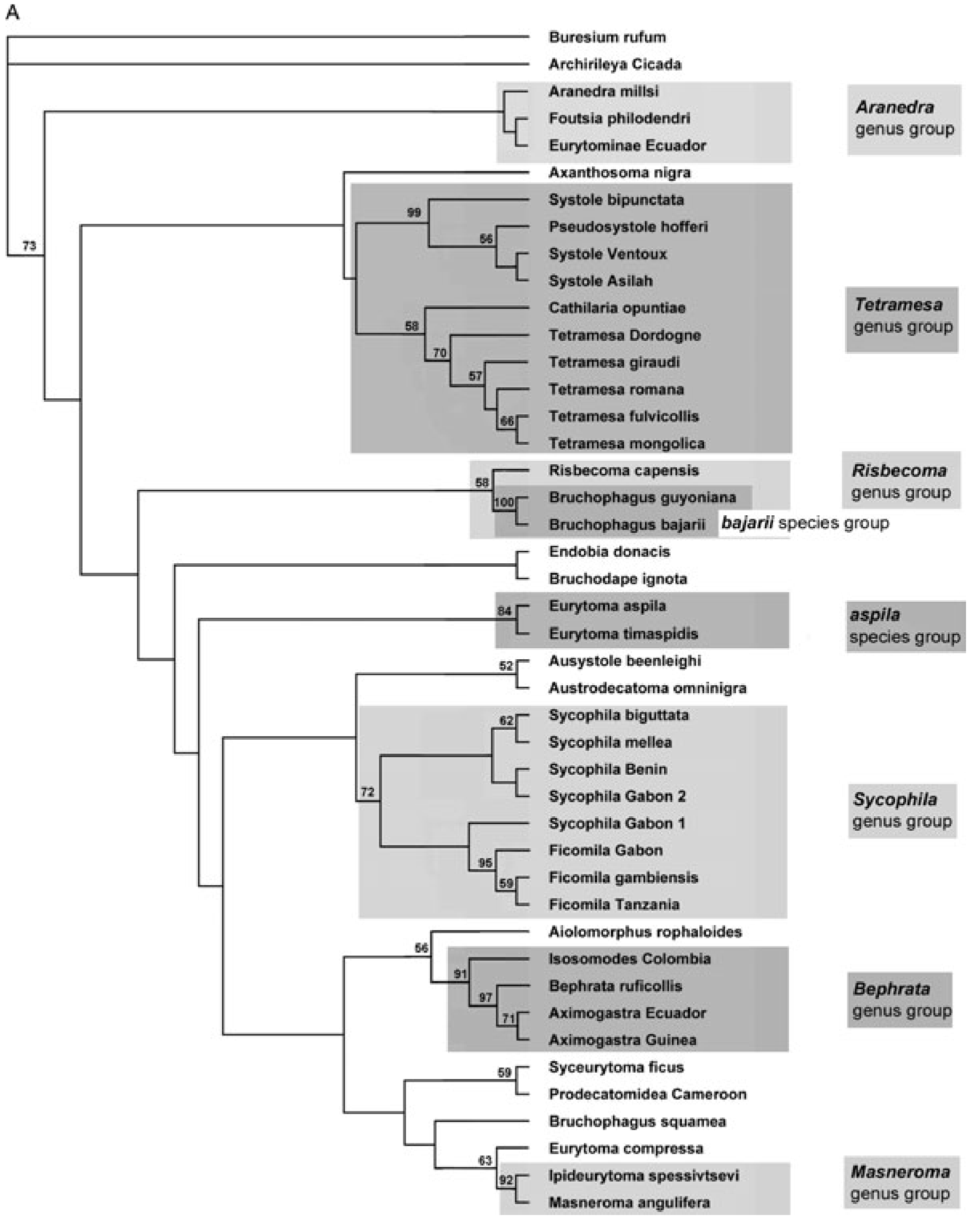


Figure 7. (A) Cladogram 5A. Phylogeny of the basal zone of the Eurytominae: strict consensus tree (CS) of the equally weighted trees ($n = 3$). Study carried out with 156 morphological characters and 44 taxa (Analysis 2). Bootstrap values are given above the branches. Length of the tree: 170.255; consistency index, CI = 0.425; retention index, RI = 0. 766; rescaled consistency index, RC = 0.325. The generic groups, the large genera, and some species groups, as defined in the text, are shaded. (B) Cladogram 5B. Phylogeny of the basal zone of the Eurytominae: CS of the equally weighted trees ($n = 9$). Study carried out with 156 morphological characters and 44 taxa (Analysis 2), implementing another weighting for some characters. Bootstrap values are given above the branches. Length of the tree: 217.700; CI = 0.491; RI = 0.775; RC = 0.380. The generic groups, large genera, and some species groups, as defined in the text, are shaded. The *Aranedra* genus group is paraphyletic here.

the distribution of large groupings of eurytomid taxa and sets up an interesting alternate hypothesis concerning the evolution of the subfamily. Local cladograms (Figs 7–9) are also presented to provide other alternate topologies that can be used in the discussion.

The trees are generally quite well resolved; with one basal island in cladogram 1 that concerns only the outgroups of Eurytominae. In the following cladograms this is better resolved, and concerns only the outgroup of the set (Eurytomidae + Chalcididae); however, one

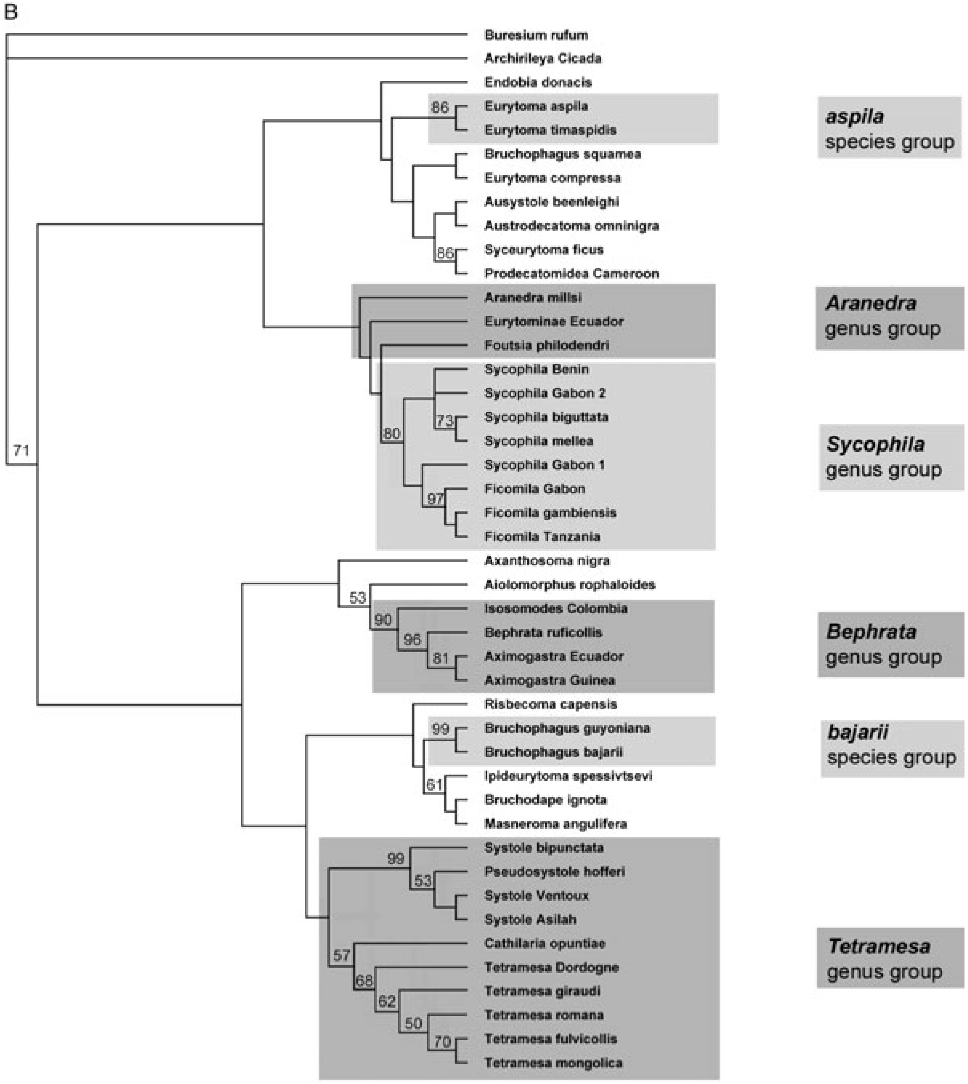


Figure 7. *Continued*

small island is found in both cladograms, which concerns the *Philolema* genus group (see the list of the taxa included below). Finally, another very small island is present in cladogram 4 within the genus *Bruchophagus*. Despite successive weighting, the CI are relatively low (ranging from 0.20 to 0.275), but this is to be expected in such large sets of data. Conversely, the RI values are relatively high (0.81–0.84). The nodes are not well supported. Nevertheless, many of the superficial nodes are conserved in the three cladograms obtained with the complete data set (cladograms 1, 3, 4; Figs 3, 5, 6).

EFFECT OF MISSING DATA

Wiens (1998) simulated the effect of adding taxa or characters with missing data on phylogenetic inference. He found that adding missing data generally increases the phylogenetic accuracy, but that this benefit quickly disappears when increasing the proportion of missing data. Overall, the proportion of these data in our matrix is 5.70% (1582 among 27 768 occurences); it is hence in the range of the benefit when adding incomplete characters. In our matrix these characters are mostly found on the back of the head (characters 41–57). By using the option 'Character reconstruction' in the program, we examined the states on the internal nodes and terminal taxa when character coding was incomplete. In most cases the coding generated by the program is unambiguous. One can postulate that the missing data have no influence on the resolution for stable nodes, e.g. nodes supported by a relatively high number of apomorphies. This is the case for the nodes supporting *Bephrata ruficollis*

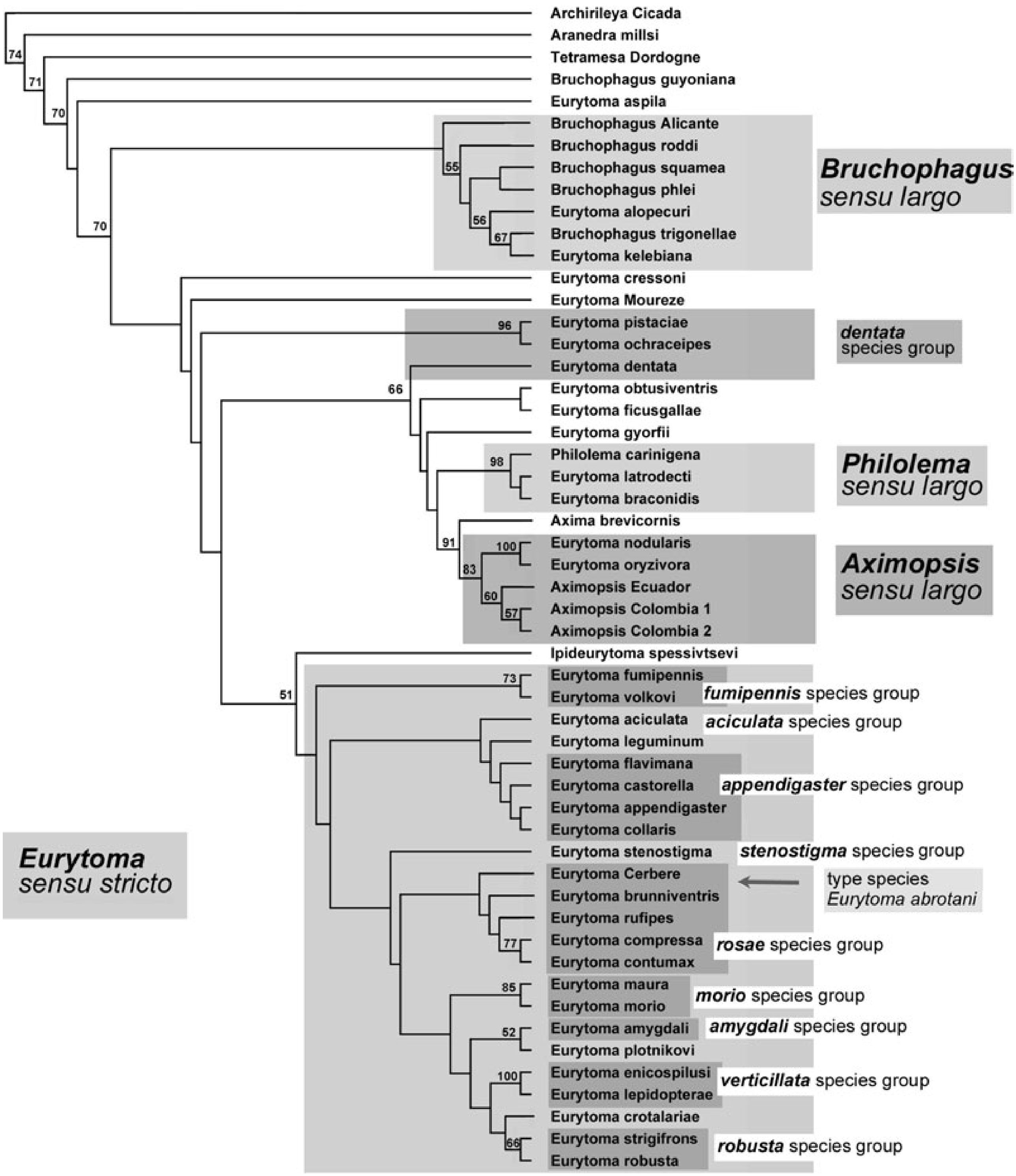


Figure 8. Cladogram 6. Phylogeny of the species classified in *Eurytoma*: strict consensus tree (CS) of the equally weighted trees ($n = 2$). Study carried out with 156 morphological characters and 37 taxa (Analysis 3). Bootstrap values are given above the branches. Length of the tree: 188.58; consistency index, CI = 0.388; retention index, RI = 0. 791; rescaled consistency index, RC = 0.307. The generic groups, the large genera, and some species groups, as defined in the text, are shaded. The *dentata* species group is not monophyletic on this cladogram.

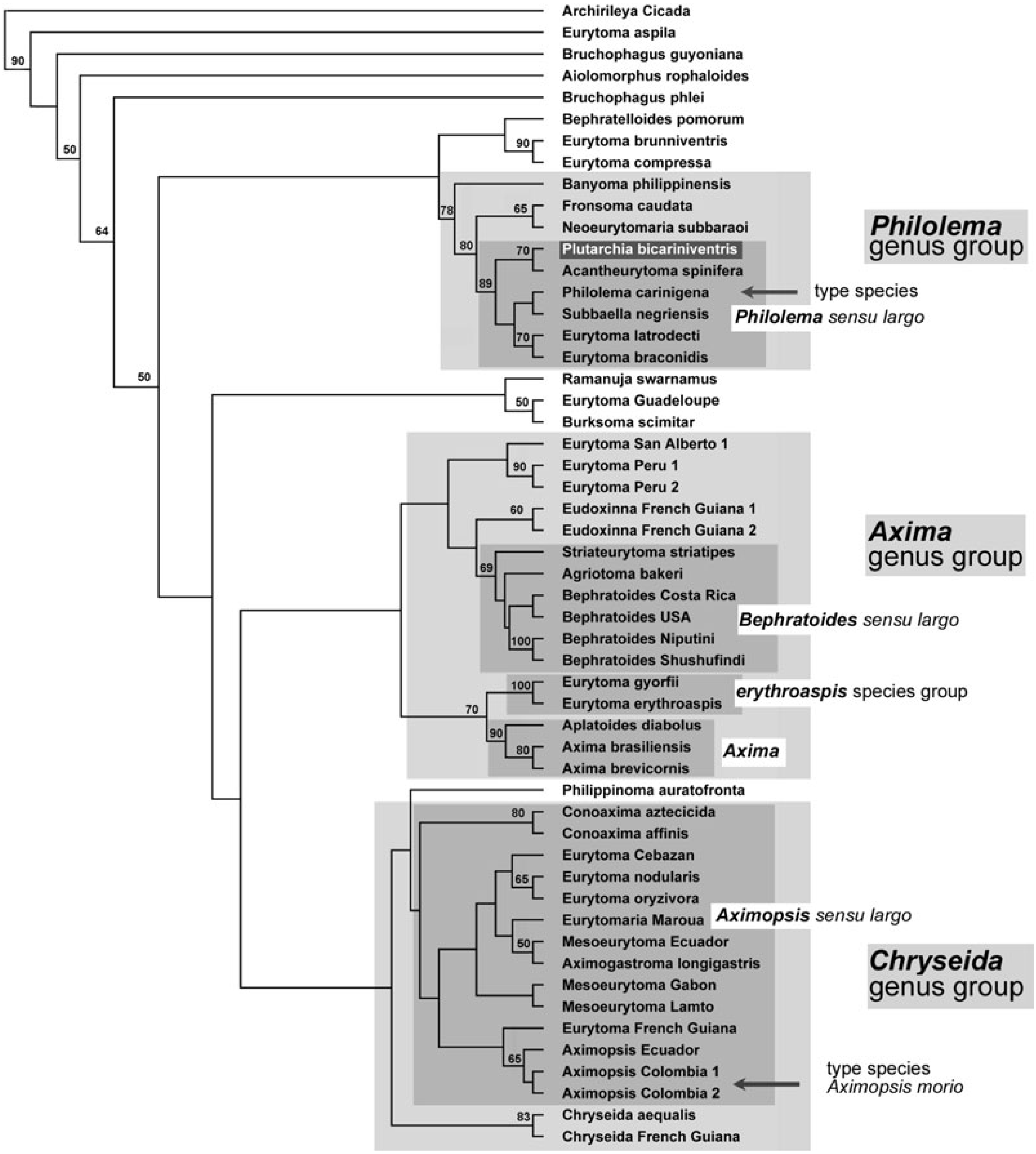


Figure 9. Cladogram 7. Phylogeny of the terminal zone of the Eurytominae: unique tree obtained. Study carried out with 156 morphological characters and 44 taxa (Analysis 4). Bootstrap values are given above the branches. Length of the tree: 168.672; consistency index, CI = 0.356; retention index, RI = 0.780; rescaled consistency index, RC = 0.280. The generic groups, large genera, and some species groups, as defined in the text, are shaded.

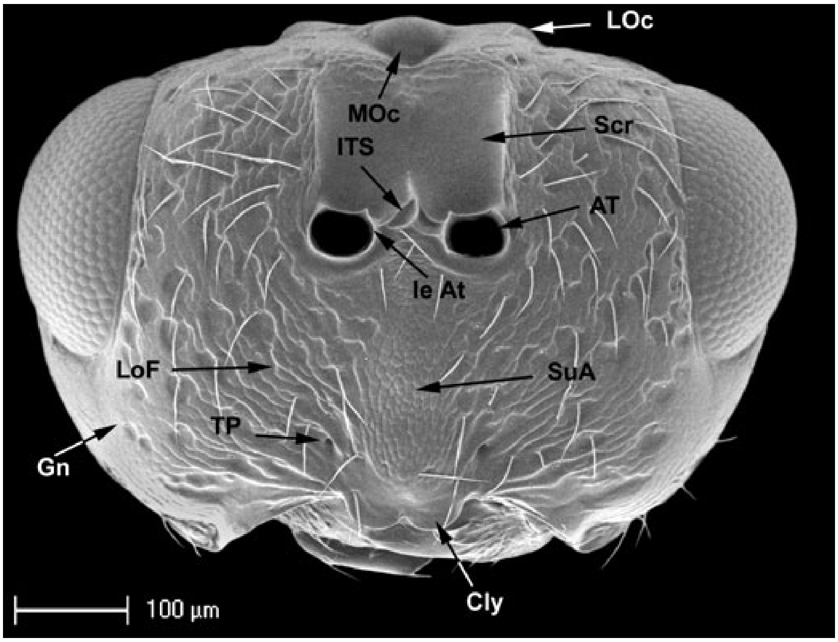


Figure 10. Eurytominae from Ecuador, head in frontal view: AT, antennal torulus; Cly, clypeus; Gn, gena (= malar space); Ie At, inner edge of antenna torulus; ITS, intertorular space (= interantenal projection, interantennal space); LOc, Lateral ocellus; LoF, lower face; MOc, median ocellus; Scr, scrobal depression (= antennal scrobes); SuA, supraclypeal area; TP, tentorial pit.

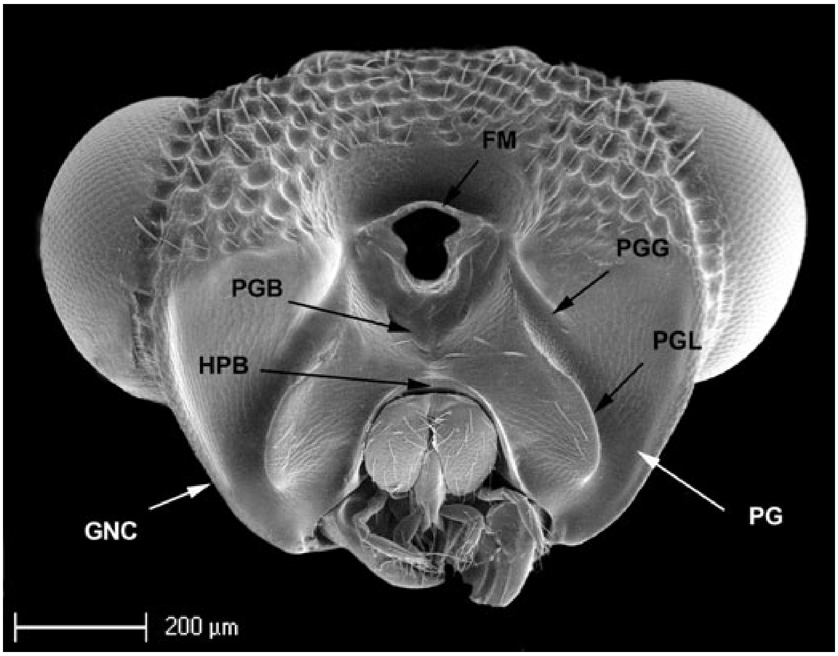


Figure 11. *Aximopsis* from Colombia, head in posterior view: FM, *Foramen magnum*; GNC, genal carina; HPB, hypostomal bridge; PG, postgena; PGB, postgenal bridge; PGG, postgenal groove; PGL, postgenal lamina.

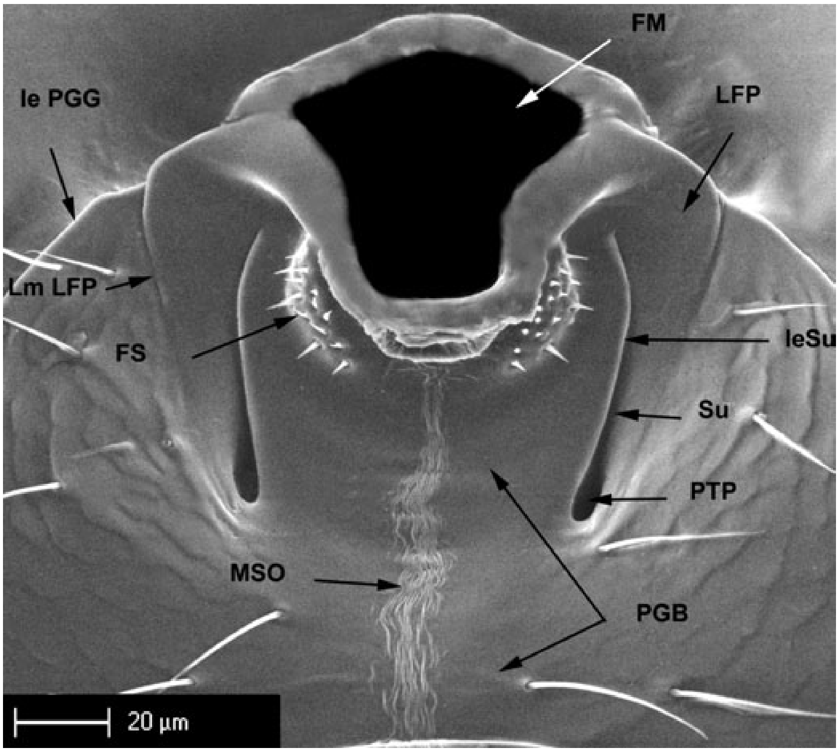


Figure 12. *Eurytoma aspila*, postgenal bridge (PGB): FM, *Foramen magnum*; FS, foraminal setae; Ie PGG, inner edge of the postgenal groove; IeSu, inner edge of the sulci; LFP, lateral foraminal plate; Lm LFP, Lateral margin of the lateral foraminal plate; MSO, median stripe of ornamentation on the postgenal bridge; PGB, postgenal bridge; PTP, posterior tentorial pits; Su, Sulci of the postgenal bridge.

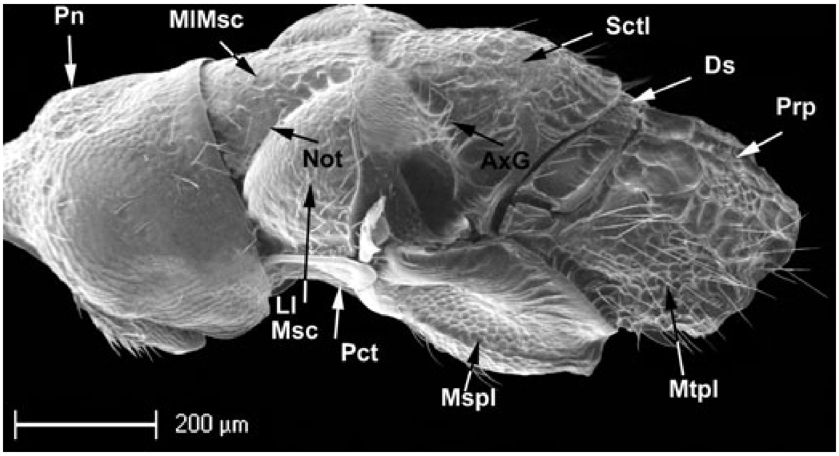


Figure 13. *Tetramesa fulvicollis*, mesosoma in lateral view: AxG, axillar groove; Ds, dorsellum; Ll Msc, lateral lobe of mesoscutum; MlMsc, midlobe of mesoscutum; Mspl, mesopleuron; Mtpl, metapleuron; Not, notaulus; Pct, prepectus, Pn, pronotum; Prp, propodeum; Sctl, scutellum.

or *Eurytoma salicis*, *Aximopsis* spp., etc. Conversely, the lack of data might have affected the local topology for unstable nodes, e.g. supporting *Foutsia philodendri, Evoxysoma brachyptera*, *Prodecatoma bekiliensis*, etc.

MONOPHYLY OF EURYTOMIDAE

In all results the family is polyphyletic, as *Hockeria* (illustrating the Chalcididae) is the sister group of *Heimbra* (illustrating the Heimbrinae) with high

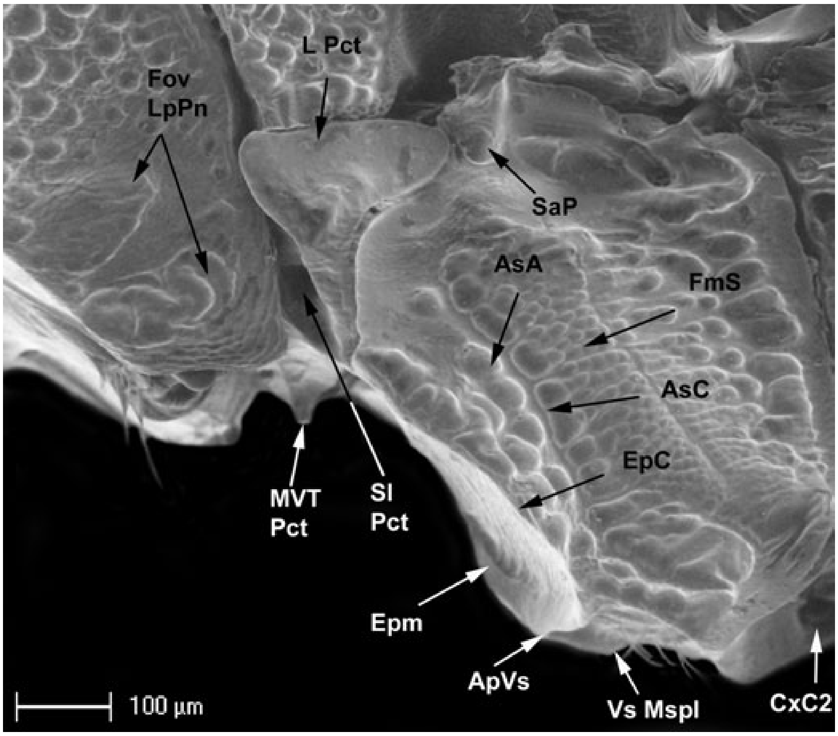


Figure 14. *Eurytoma* Cébazan, pronotum and mesonotum in lateral view: AsA, adscrobal area; AsC, adscrobal carina; ApVs, anterior projection of the ventral shelf; CxC2, midcoxal cavities; EpC, epicnemial carina; Epm, epicnemium; FmS, femoral scrobe (= femoral depression); Fov LpPn, foveae on lateral panel of pronotum; L Pct, lateral prepectus; MVT Pct, medioventral tooth of prepectus; SaP, subalar pit; Sl Pct, sublateral prepectus; Vs Mspl, ventral shelf of mesopleuron.

bootstrap support (= 91–95). Such a relationship was also obtained in a study dealing with the phylogeny of Chalcididae (Delvare, 2004). Altogether this relationship is corroborated by numerous derived states, seven of which are synapomorphies: (1) structure and articulation of the mandible (see Wijesekara, 1997 for details); (2) pronotum with posterolateral projection (Fig. 143); (3) parascutal and axillar carinae forming an arch; (4) mesopleuron with differentiated adscrobal area (homoplastic); (5) epicnemium completely delimited (homoplastic); (6) epicnemium with a median crest; (7) mesopleuron with a ventral shelf (homoplastic); (8) mesofurcal pits reduced or evanescent (Fig. 143; (9) metafurcal pits absent through secondary reduction (Fig. 143); (10) discrimen lamella quite high (a component of the internal skeleton within metapectus; see Krogmann, 2005, for details).

In cladograms 3 and 4, *Rileya* is placed as the sister group of (*Hockeria* + *Heimbra*). The support is moderate (76–80) and one putative synapomorphy is the short prepectus (more reduced in Chalcididae), both on its lateral panel and its ventral part (Fig. 151).

In the same cladograms (Eurytomidae + *Hockeria*) are monophyletic. This weakly supported relationship (bootstrap = 67) is, however, sustained by several synapomorphies: (1) mesothoracic spiracle hidden by a posterolateral flange of the pronotum (Figs 133–138); (2) mesocoxal cavities closed posteriorly (Figs 143, 144); (3) metapleuron at least partially fused with propodeum (Fig. 142); (4) metapleuron with a ventral shelf (Figs 157–159); (5) petiole completely closed and tube-like (Figs 187–193). The first character is also shared by Eulophidae Entedoninae (Gumovsky, 2002), and the last ones are probably found within a number of chalcidoid families, e.g. the Podagrionini have a ventral shelf (Grissell, 1995), and the species with petiolate gaster also share a tube-like petiole. Moreover, the mesothoracic spiracle is exposed in the Cratocentrini (Chalcididae): either a possible reversion in that tribe or an independent evolution in both groups? Further evidence for a close relationship between these families is the special structure of the syntergum, shared by the Rileyinae *s.l.* and several taxa in Chalcididae (Cratocentrini, *Brachymeria*, and Haltichellinae): the segment has a transverse carina in front of the cercal plates, which are situated within foveae; this carina might represent a trace of the fused sclerites that constitute the syntergum. The Eurytomidae as presently understood therefore appear paraphyletic

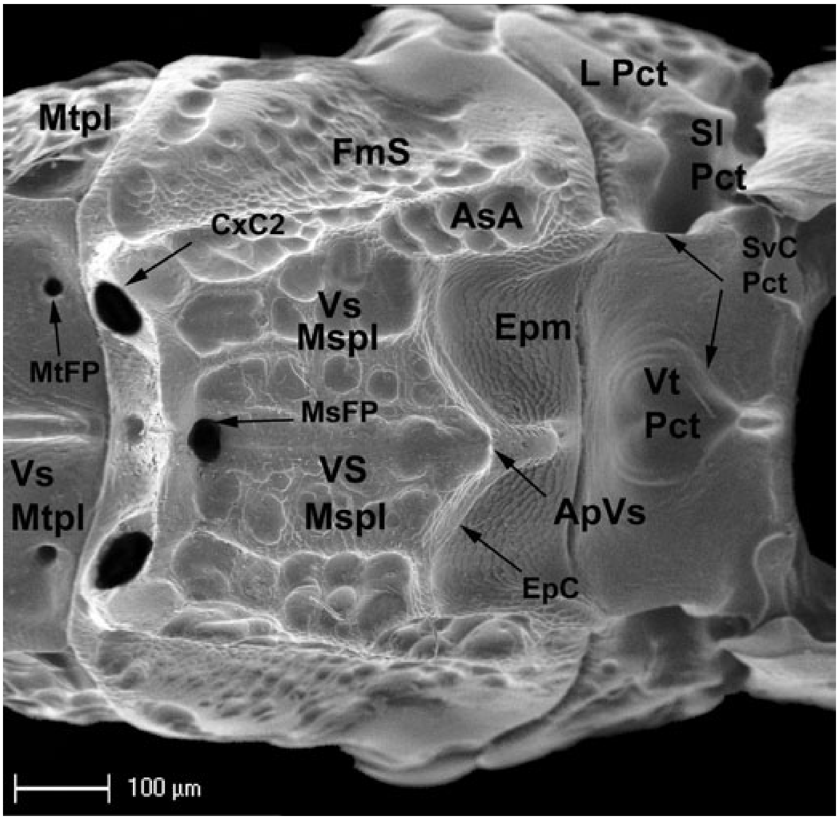


Figure 15. *Aximopsis* sp. from Colombia, mesopleuron in ventral view: AsA, adscrobal area; ApVs, anterior projection of ventral shelf; CxC2, midcoxal cavities; EpC, epicnemial carina; Epm, epicnemium; FmS, femoral scrobe (= femoral depression); L Pct, lateral prepectus; MsFP, mesofurcal pit; MtFP, metafurcal pit; Mtpl, metapleuron; Sl Pct, sublateral prepectus; Pct, subventral carinae of prepectus; VS Mspl, ventral shelf of mesopleuron; VS Mtpl, ventral shelf of metapleuron; Vt Pct, ventral prepectus.

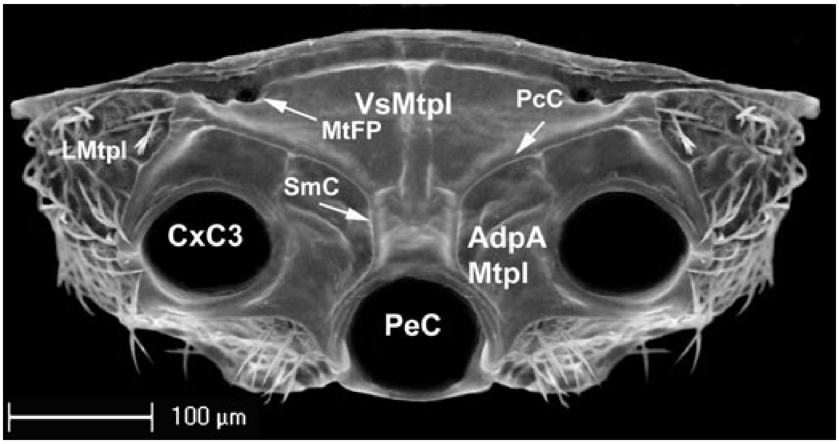


Figure 16. *Eurytoma cressoni*, metapleuron in ventral view: AdpA, adpetiolar area; CxC3, hind coxal cavities; PcC, precoxal carinae; PeC, petiolar cavity; LMtpl, lateral metapleuron; MtFP, metafurcal pit; SmC, submedian carinae; VS Mtpl, ventral shelf of metapleuron.

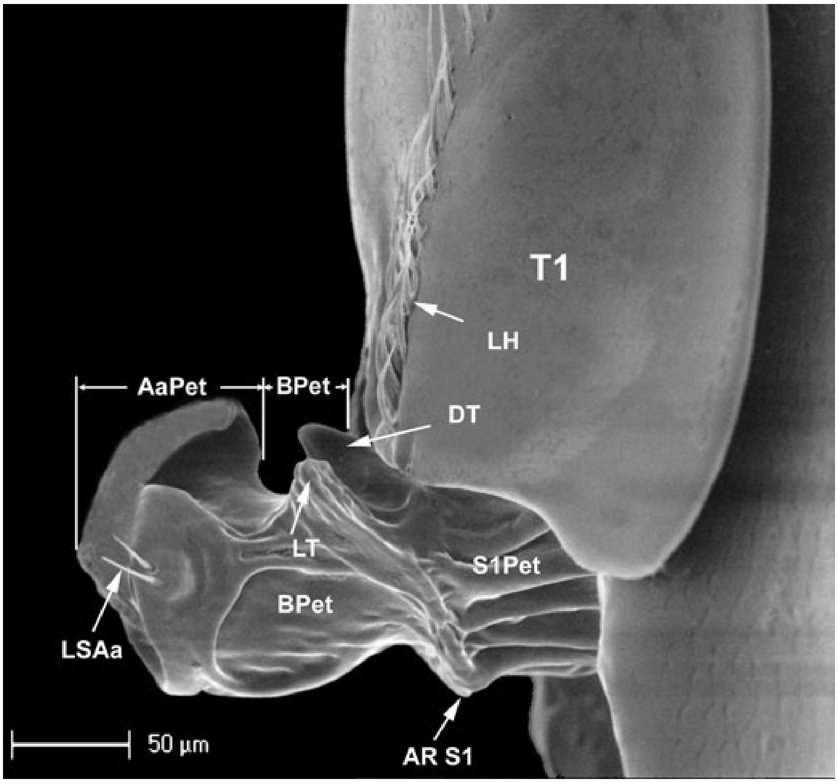


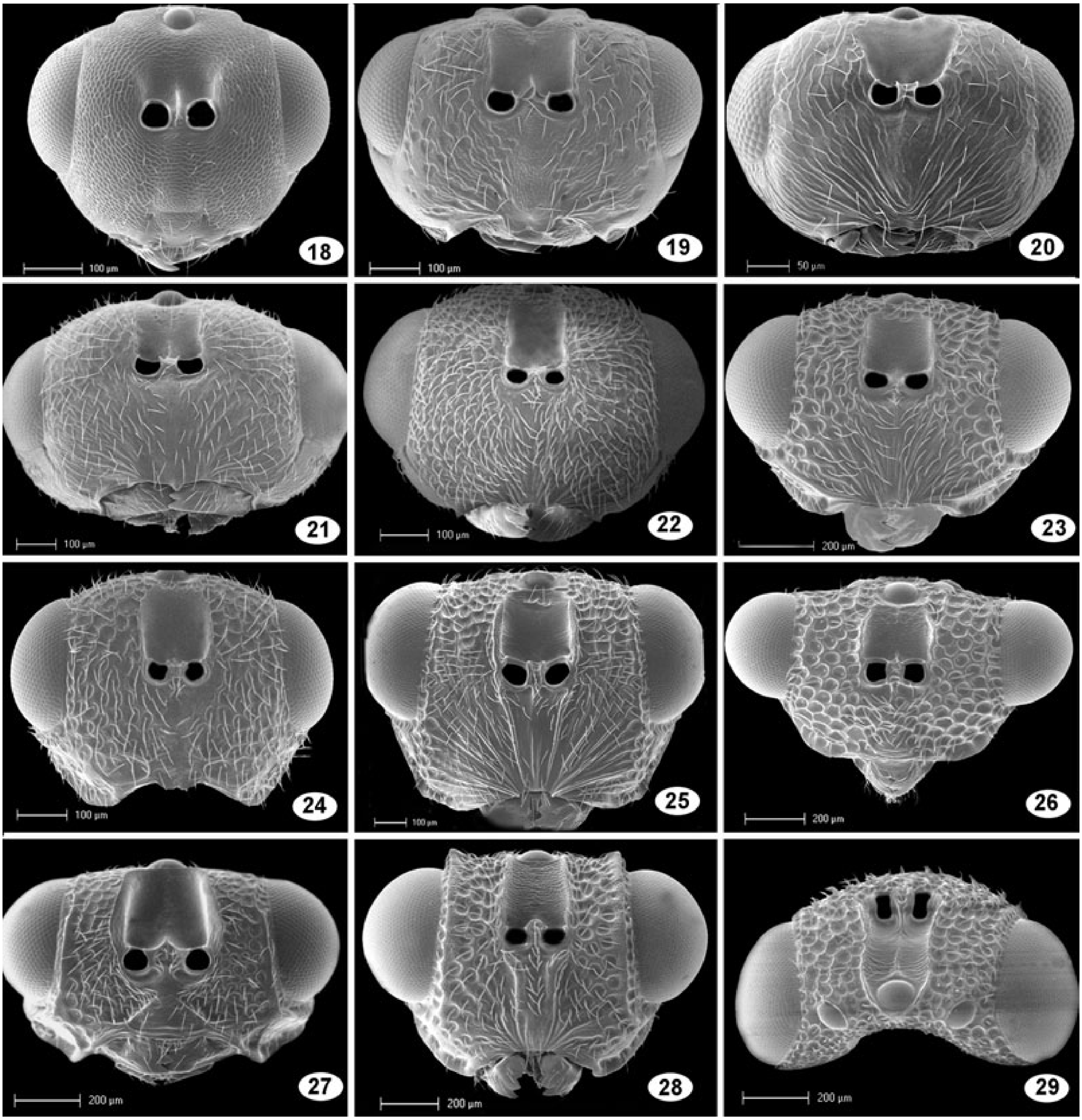
Figure 17. *Bruchophagus caucasicus*, gastral petiole in lateral view: AaPet, articular area of petiole; AR S1, anterior ridge delimiting petiolar part of first gastral sternum (S1) from petiole; BPet, body of petiole; DT, dorsal tooth; LH, line of hairs; LSAa, lateral setae on articular area; LT, lateral tooth; S1Pet, Petiolar part of the first gastral sternite; T1, first gastral tergite.

relative to the Chalcididae, and may even be polyphyletic. This corroborates recent results reported by Gates (2005, 2007) in which Rileyinae are polyphyletic and consist of two different lineages: (1) the Rileyinae *s.s.*, the limits of which were redefined by the same author; (2) the genera *Macrorileya*, *Archirileya*, and *Buresium* included in what we called the *Macrorileya* genus group.

The *Macrorileya* genus group is monophyletic in cladograms 2, 3, and 4 (bootstrap = 63–69). It is corroborated by the very small metafurcal pits that are only visible at strong magnification (> ×1000) (Fig. 167). The sister-group relationship for the *Macrorileya* genus group + Eurytominae is sustained by another feature of the metafurcal pits that are slightly to distinctly moved backwards (Figs 160–164), whereas they are placed along the anteroventral margin of the metapleuron in most chalcidoids (Krogmann, 2005). One of us (JYR) recently found that similar pits occurred in all Sycophaginae he examined (an unplaced family of figwasps, see Rasplus *et al.*, 1998), but they are closer to each other and their orientation is oblique (vertical in Eurytomidae).

MONOPHYLY OF THE EURYTOMINAE

In all cladograms the Eurytominae were retrieved as a monophyletic group, and they are supported by a moderate to high bootstrap (= 69–94, depending on the analytical permutation). The species belonging to the subfamily share the following synapomorphies: (1) reduced number of flagellar segments, with loss of two funicular segments (Figs 94–97); (2) prepectus with two subventral carinae (Fig. 15; subventral carinae of prepectus, SvC Pct); (3) enlarged metafurcal pits, slightly removed from the front ventral margin of the metapleuron, and consequently easily visible (Figs 16, 163, 164); (4) metapleuron with precoxal and submedian carinae on its ventral panel, the precoxal carinae separating the horizontal shelf from the sloping adpetiolar region (Fig. 16; precoxal carinae, PcC; submedian carinae, SmC); (5) metatibia with dorsal setae somewhat thickened and longitudinally impressed (Fig. 184); (6) articular part of the petiole bearing a pair of small hairs laterally (Fig. 17; lateral setae on articular area, LSAa) (this condition is only visible at high magnification with SEM and could not be checked in all taxa). In female Eurytomidae, the



Figures 18–29. Figures 18–28: head in frontal view – 18, *Buresium rufum*; 19, Eurytominae Ecuador; 20, *Eurytoma* Mourèze; 21, *Bruchophagus* Guyoniana; 22, *Eurytoma cressoni*; 23, *Phylloxeroxenus* San Alberto; 24, *Eurytoma dentata*; 25, *Eurytoma braconidis*; 26, *Axima brevicornis*; 27, *Eurytoma gyorfii*; 28, *Aximopsis* Colombia 2. Figure 29. Head in dorsal view; *Bephratoides* Shushufindi.

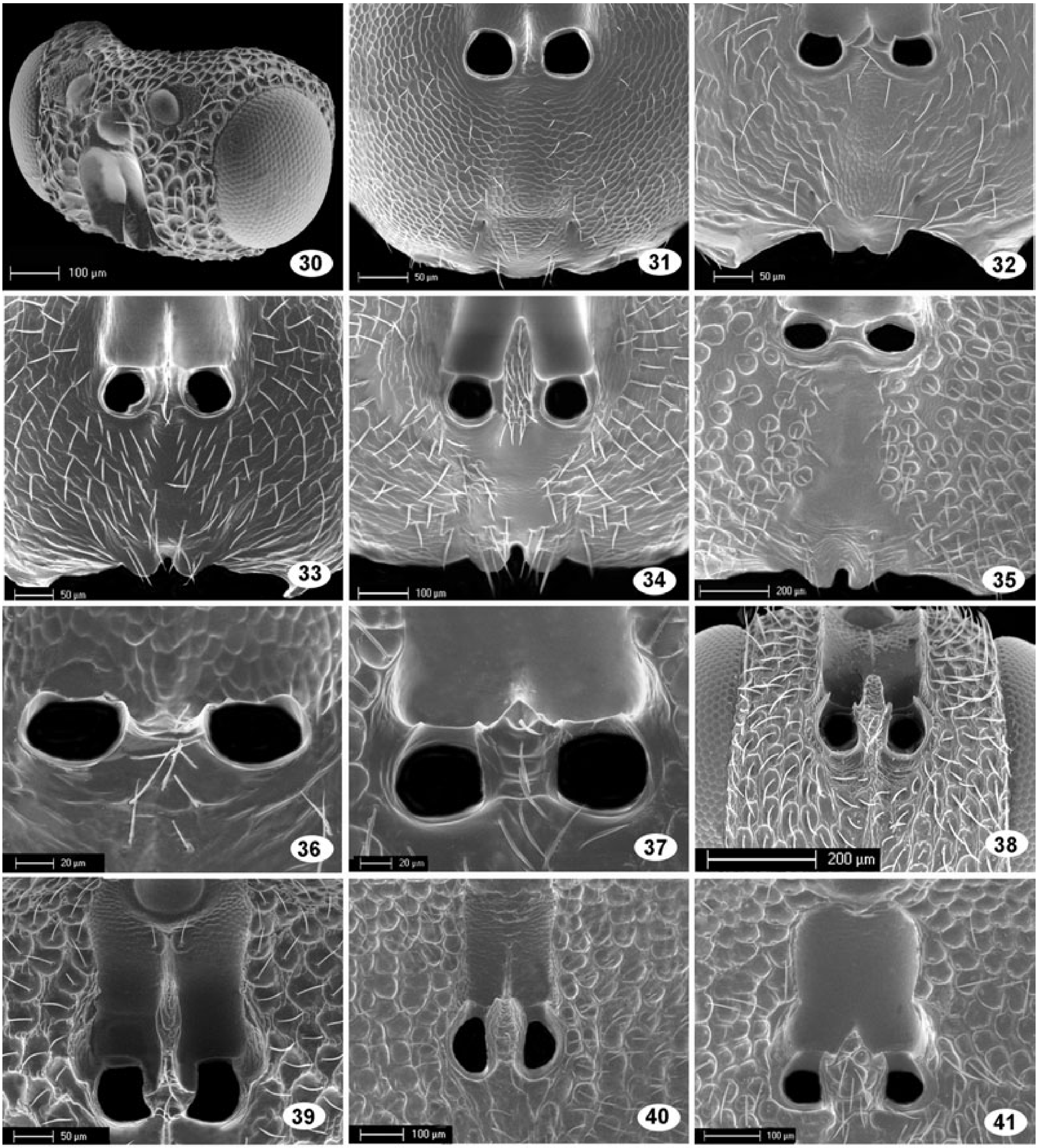
funicle is mostly five-segmented, less frequently six-segmented, and in that case the 7th flagellar segment is separated from the clava.

PHYLOGENY OF THE EURYTOMINAE

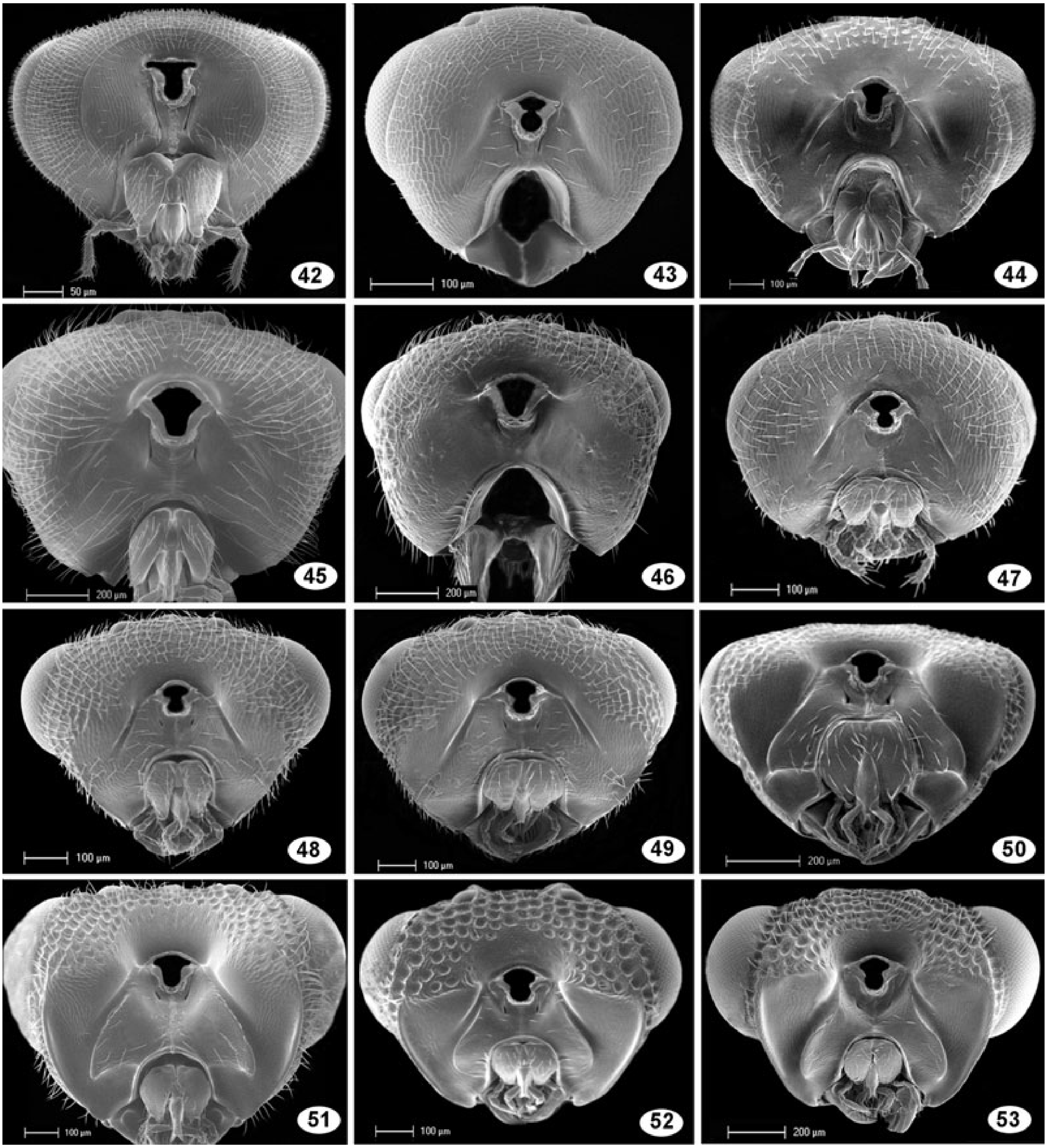
The subfamily exhibits a gradual evolution, with many clades branching from a main trunk and short distances between nodes. Moreover, although superficial nodes are stable in all cladograms, and often well supported, most of the deep nodes are not supported.

The basal nodes

We include here the species retaining the primitive state of genal carina (gena not carinate



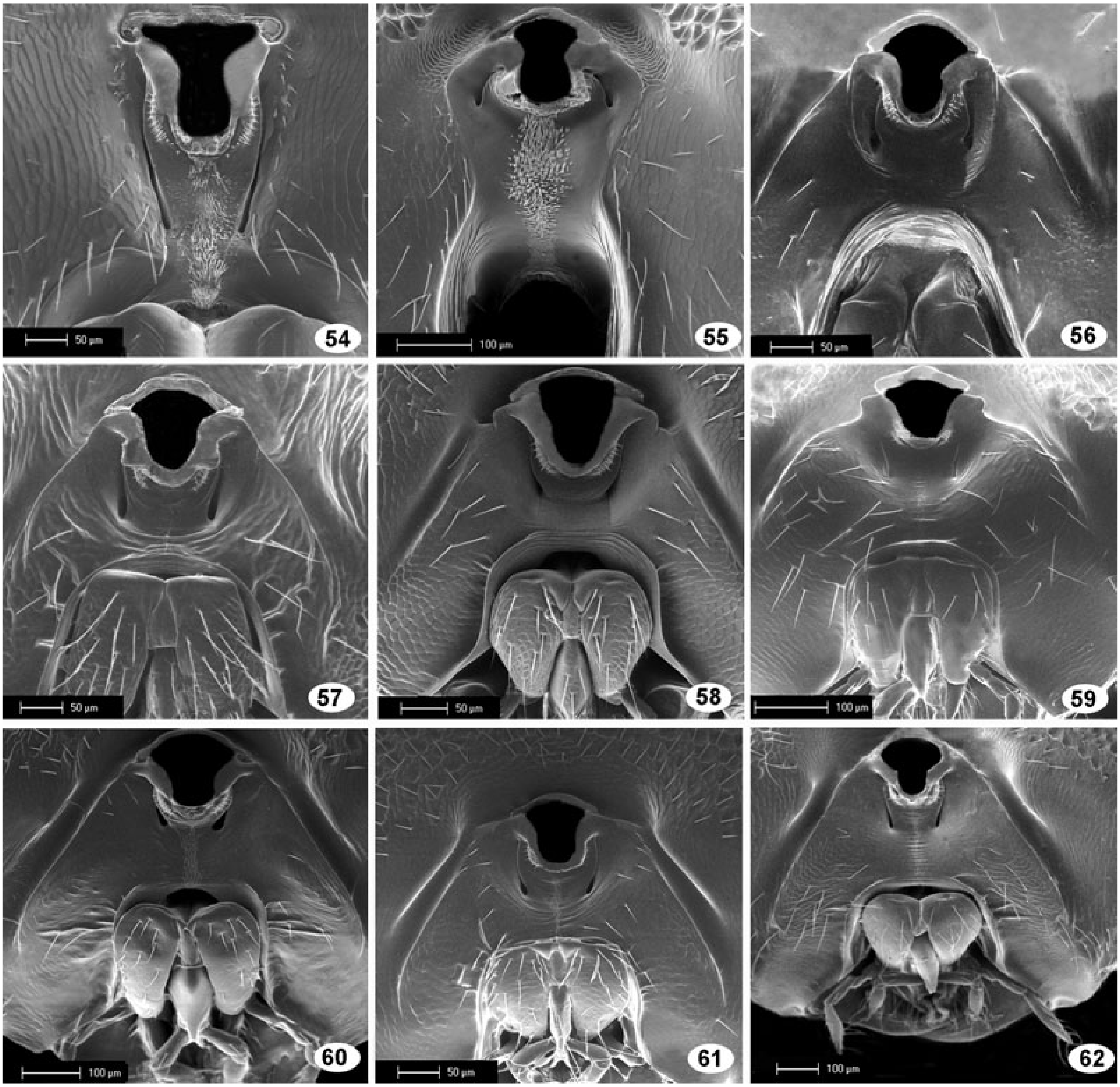
Figures 30–41. Figure 30: head in laterodorsal view – 30, *Prodecatoma maculiventris.* Figures 31–35: lower face and intertorular space (ITS); 31, *Buresium rufum*; 32, Eurytominae Ecuador; 33, *Sycophila* Benin; 34, *Ficomila* Gabon; 35, *Bephratelloides pomorum*. Figures 36, 37: ITS – 36, *Tetramesa fulvicollis*; 37, *Eurytoma collaris*. Figures 38–41: antennal scrobes – 38, *Aximogastra* Ecuador; 39, *Prodecatoma philodendri*; 40, *Paradecatoma* Combretum 2; 41, *Eurytoma nodularis*.



Figures 42–53. Head in posterior view: 42, *Glyphomerus stigma*; 43, *Buresium rufum*; 44, *Aranedra millsi*; 45, *Aiolomorphus rhopaloides*; 46, *Tetramesa romana*; 47, *Bruchophagus Alicante*; 48, *Bruchophagus phlei*; 49, *Bruchophagus caucasicus*; 50, *Eurytoma compressa*; 51, *Bephratoides* Shushufindi; 52, *Conoaxima affinis*; 53, *Aximopsis* Colombia 1.

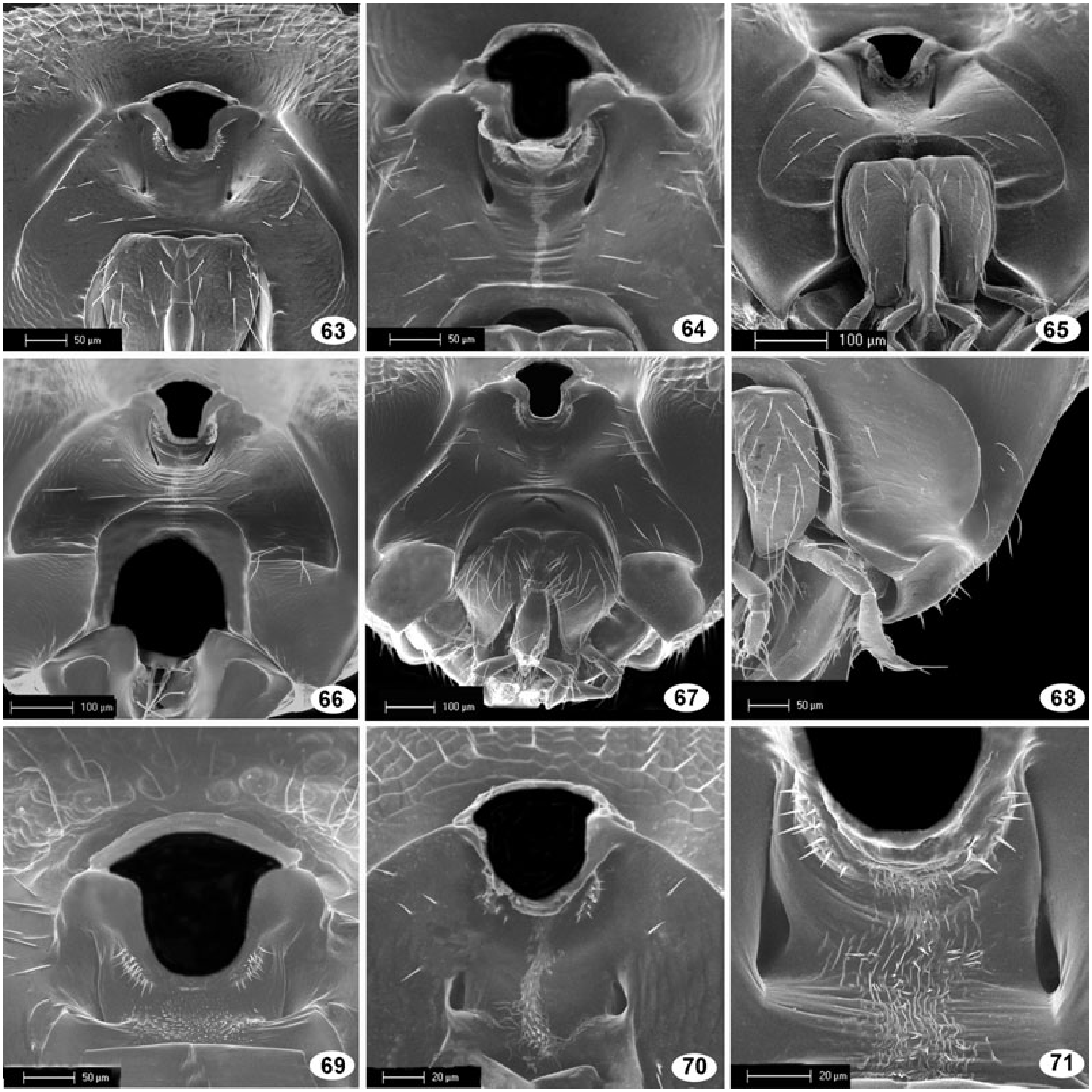
posteriorly) and axillar grooves (not step-like and without deep pit in the middle). This is the most unstable part of the cladograms and different topologies were found.

The genus Aiolomorphus: Aiolomorphus may occupy several different positions: it is usually placed in a clade with *Isosomodes*, *Bephrata*, *Aximogastra*, and sometimes *Foutsia* (cladograms 1, 5A, 5B; Figs 3, 7A,



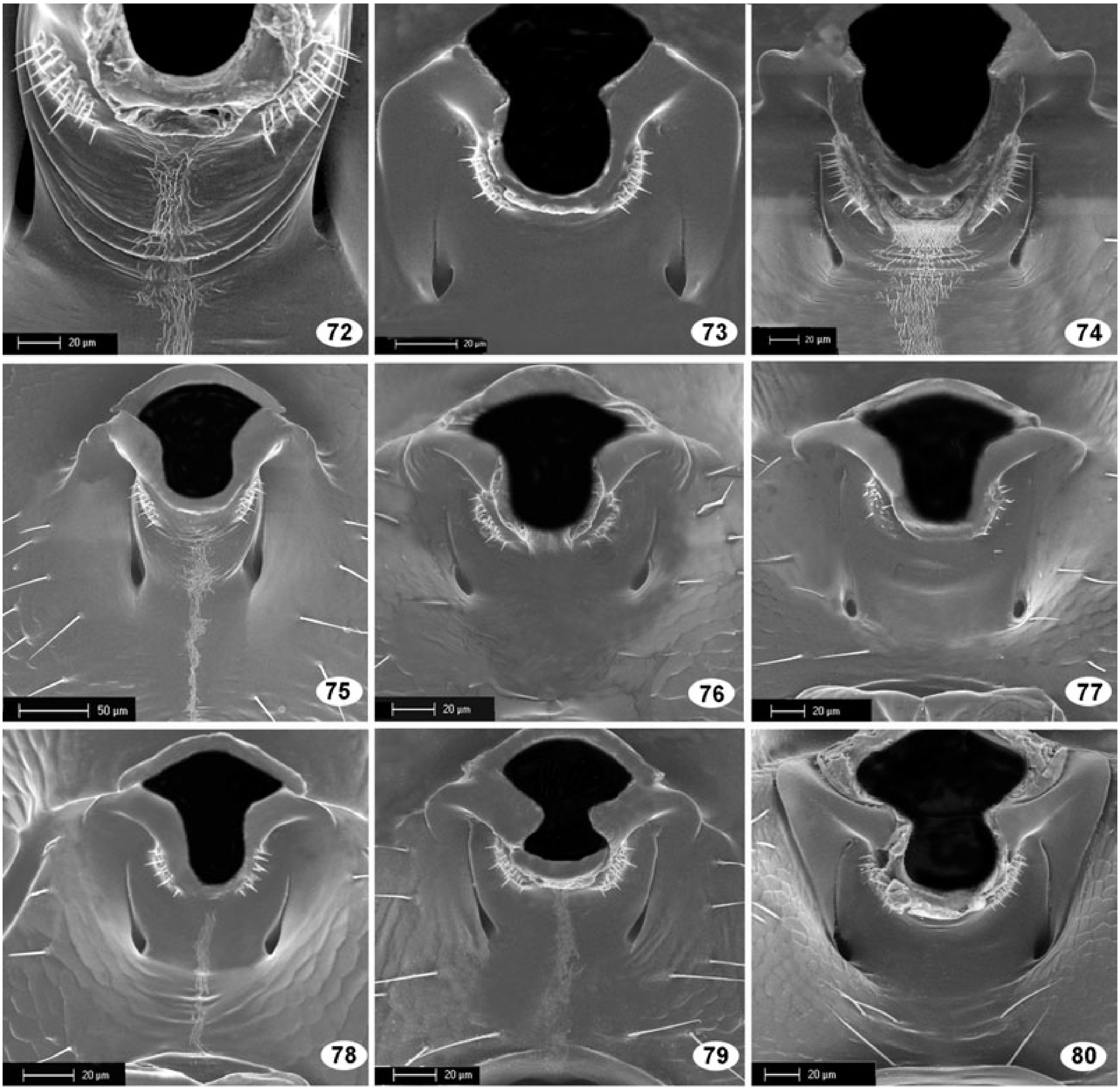
Figures 54–62. Postgena and postgenal bridge (PGB): 54, *Glyphomerus stigma*; 55, *Hockeria unicolor*; 56, *Aranedra millsi*; 57, *Tetramesa* Dordogne; 58, *Isosomodes* Costa Rica; 59, *Sycophila biguttata*; 60, Prodecatomidea Cameroon; 61, *Eurytoma ficusgallae*; 62, *Paradecatoma* Combretum 2.

B). This relationship is probably based on homoplastic characters: filiform flagellum, elongate mesosoma, acute angle between the stigmal and the postmarginal veins of the forewing (Fig. 205). Furthermore, *Aiolomorphus* is Oriental, whereas the other genera are mainly distributed in the New World. It sometimes branches independently (cladogram 4; Fig. 6) or as a sister group of *Gibsonoma* spp. (cladogram 3; Fig. 5A). In preliminary molecular results (Heraty, 2005) the genus merges from a basal node of the Eurytominae. The genus shares with *Archirileya* and *Macrorileya* a long PM, which is a putative plesiomorphic state. *Aiolomorphus* is well characterized by several synapomorphies: (1) squat pedicel that has a basal bottleneck (Fig. 101); (2) filiform flagellum, including a six-segmented funicle; (3) reversed carinae on the ventral metapleuron; (4) tuft of lateral hairs on the articular area of the petiole. Larvae of this monospecific genus develop within bamboos.



Figures 63–71. Figures 63–67: postgena and postgenal bridge – 63, *Eurytoma obtusiventris*; 64, *Eurytoma* sp., *braconidis* species group; 65, *Eurytoma* San Alberto 1; 66, *Syceurytoma ficus*; 67, *Eurytoma plotnikovi*. Figure 68: ventral part of postgena – *Eurytoma braconidis*. Figures 69–71: postgenal bridge; 69, *Heimbra opaca*; 70, *Rileya pulchra*; 71, Eurytominae Ecuador.

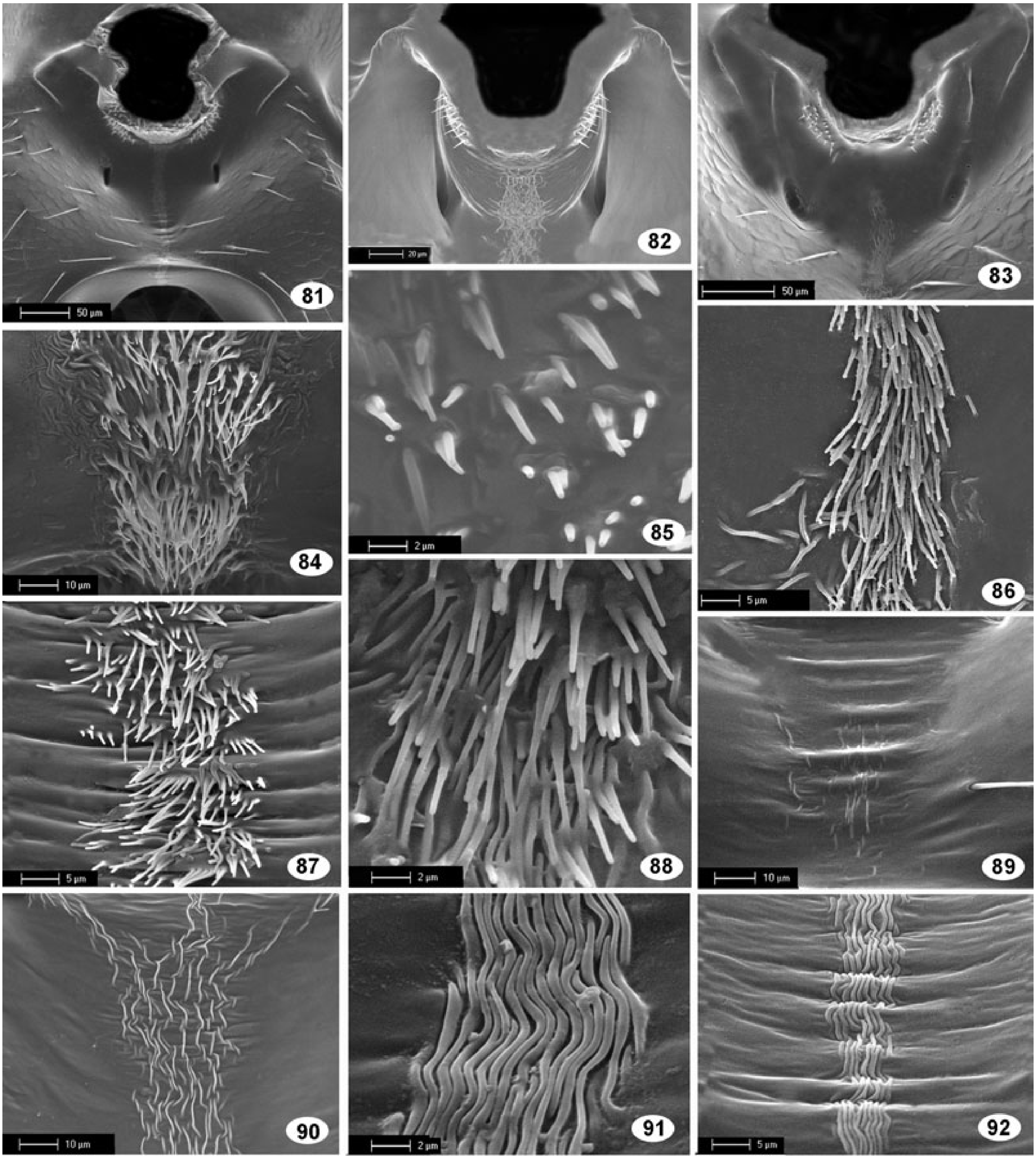
The Bephrata genus group: This group includes the genera *Isosomodes*, *Bephrata*, and *Aximogastra*. The group is retrieved in almost all cladograms (Figs 5A, 7A, B). Alternatively, *Isosomodes* is the sister group to (*Bephrata* + *Aximogastra*) (Fig. 5A). These genera share a number of derived states: (1) elongate body; (2) head subcircular in frontal view, with short malar space (at most half as long as the width of the oral fossa); (3) antennal toruli situated above the lower eye margin (Fig. 38); (4) relatively short antennal scrobes (hardly more than twice as long as toruli diameter); (5) presence of a median carina on the surface of the scrobes, above the intertorular space (ITS); (6) notauli at least partly obliterated, replaced by row of punctures in *Bephrata* and *Aximogastra* (Fig. 116), and obliterated posteriorly in *Isosomodes*; (7) scutellum



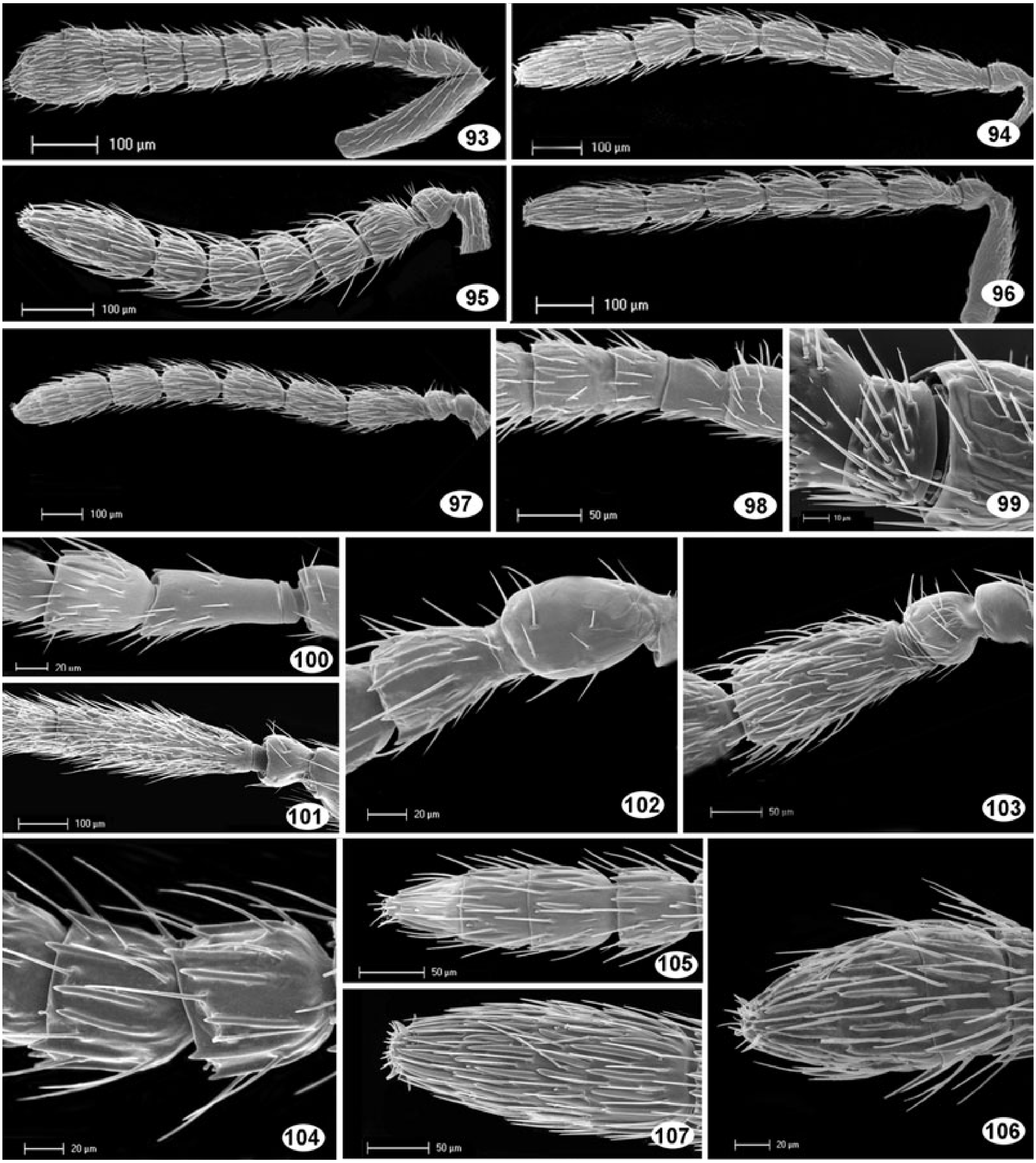
Figures 72–80. Postgenal bridge: 72, *Aiolomorphus rhopaloides*; 73, *Pseudosystole hofferi*; 74, *Ficomila Gabon*; 75, *Risbecoma capensis*; 76, *Eurytoma cressoni*; 77, *Eurytoma obtusiventris*; 78, *Eurytoma pistaciae*; 79, *Bruchophagus phlei*; 80, *Axima brevicornis*.

flattened, at most slightly convex; (8) axillar grooves partly or completely obliterated (Fig. 116); (9) subventral carinae of prepectus delimiting a raised area (Fig. 144); (10) long ST relative to the marginal vein of the forewing (M) (from slightly shorter to longer than this vein); (11) acute angle between ST and PM (of 40° or less). The sister-group relationship between *Bephrata* and *Aximogastra* is supported by a weak to high bootstrap value (= 57–91). Species are mostly found in the New World; however, one species of *Aximogastra* was found in Guinea and several *Bephrata* were described from India, but their identity is doubtful (Narendran, 1994). *Isosomodes brasiliensis* Ashmead, 1904 is an egg parasitoid of Orthoptera, and some *Bephrata* species are possibly egg parasitoids (S. Hanson, pers. comm.).

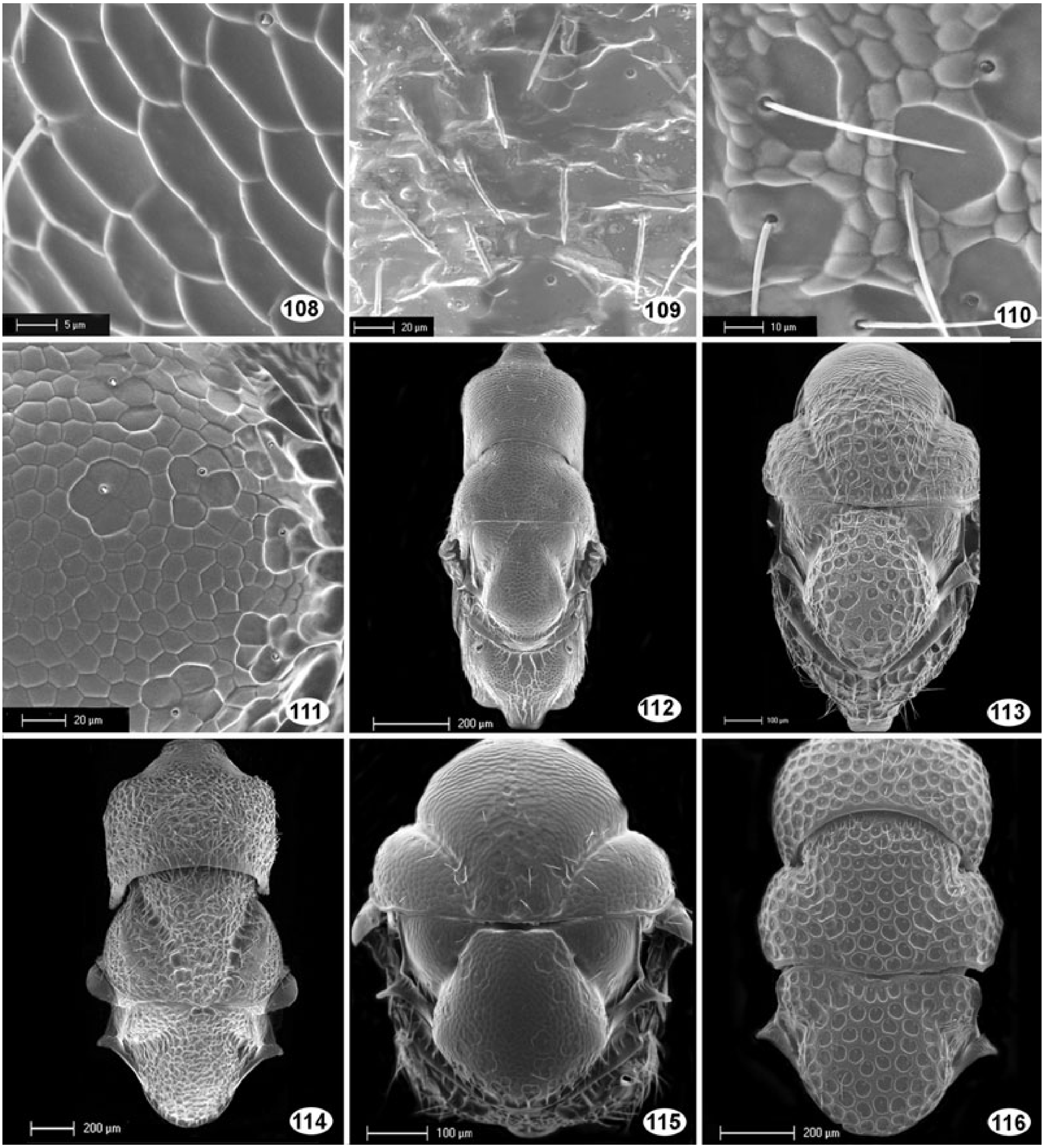
In our opinion *Aximogastra* must be synonymized with *Bephrata*, as they share several apomorphies: (1) gena with a carina (sometimes short) on posterior margin; (2) intertorular space narrow, compressed



Figures 81–92. Figures 81–83: postgenal bridge – 81, *Eurytoma* Cébazan; 82, *Risbecoma capensis*; 83, *Aximopsis* Colombia 1. Figures 84–92: postgenal bridge, ornamentation of median stripe – 84, *Glyphomerus stigma*; 85, *Heimbra opaca*; 86, *Rileya pulchra*; 87, *Aximogastra* Guinea; 88, *Bephratoides* Shushufindi; 89, *Eurytoma cressoni*; 90, *Prodecatomidea* Cameroon; 91, *Eurytoma morio*; 92, *Eurytoma braconidis*.

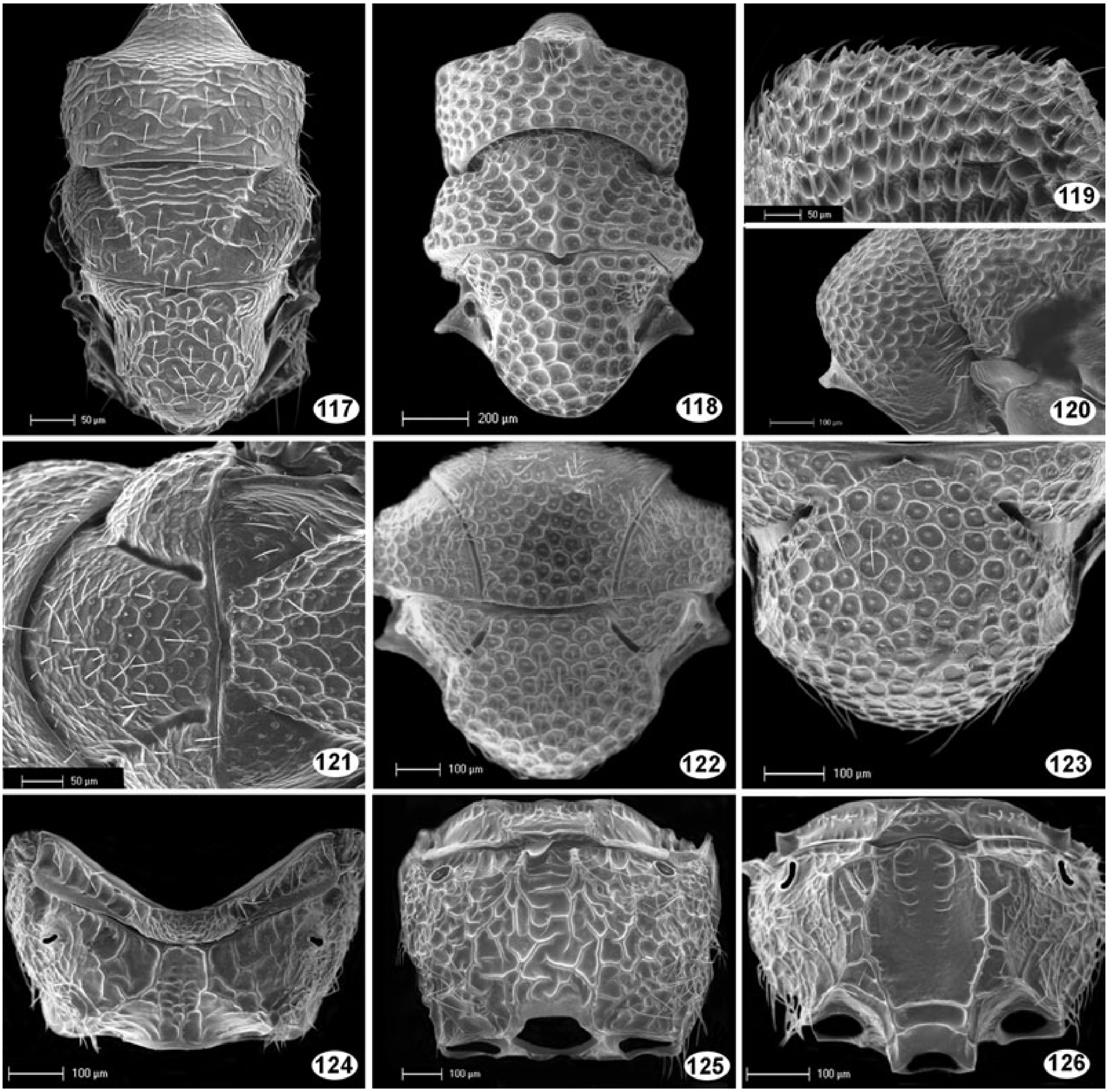


Figures 93–107. Figures 93–97: female antenna – 93, *Archirileya* Cicada; 94, *Eurytoma ochraceipes*; 95, *Eurytoma volkovi*; 96, *Eurytoma leguminum*; 97, *Eurytoma braconidis.* Figures 98, 100–103: pedicel and flagellomeres 1–3 – 98, *Archirileya* Cicada; 100, *Systole* Asilah; 101, *Aiolomorphus rhopaloides*; 102, *Bruchophagus* Alicante; 103, *Eurytoma braconidis*. Figure 99: first flagellomere; *Eurytoma* Cébazan. Figure 104: flagellomeres 5–6; *Tetramesa linearis.* Figures 105–107: female clava – 105, *Systole* Asilah; 106, *Bruchophagus* Alicante; 107, *Eurytoma* Cébazan.



Figures 108–116. Figures 108–111: patterns of sculpture – 108, *Buresium rufum* (lower face); 109, *Bruchophagus bajarii* (scutellum); 110, Eurytominae Ecuador (scutellum); 111, *Pseudosystole hofferi* (scutellum). Figures 112–116: Mesosoma in dorsal view; 112, *Buresium rufum*; 113, Eurytominae Ecuador; 114, *Tetramesa romana*; 115, *Pseudosystole hofferi*; 116, *Aximogastra* Guinea.

above into a laminate projection (Fig. 38); (3) postgenal bridge (PGB) with median stripe of ornamentation formed by rows of digitiform expansions (Fig. 87); (4) notauli and axillar grooves as rows of punctures; (5) procoxa with a basal S-like carina (and sometimes a tubercle) on anterior surface, together with an oblique groove or channel; (6) tip of hypopygium near apex of gaster. Moreover, the body is bi- or multicolored, and

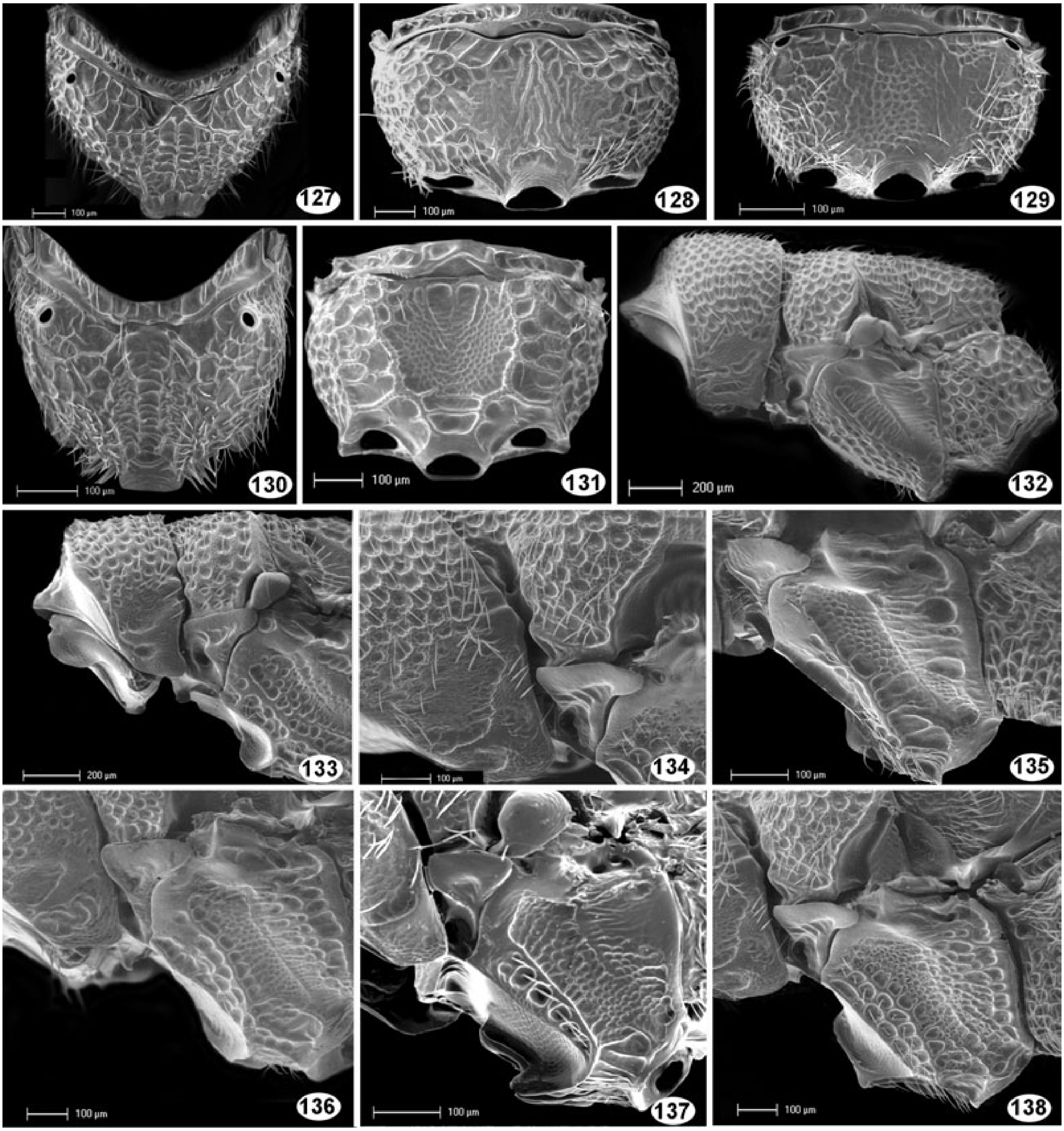


Figures 117–126. Figures 117, 118: mesosoma in dorsal view – 117, *Eurytoma* Mourèze; 118, *Aximopsis* Colombia 2. Figure 119: Dorsal part of pronotum in lateral view; *Bephratoides* Shushufindi. Figure 120: pronotum in lateral view; *Eurytoma dentata.* Figures 121, 122: mesonotum in dorsal view – 121, *Eurytoma aspila*; 122, *Eurytoma ochraceipes*. Figure 123: scutellum; *Eurytoma fumipennis*. Figures 124–126: Propodeum in dorsal view; 124, *Archirileya* Cicada; 125, *Tetramesa romana*; 126, *Sycophila* Benin.

the weakly sclerotized gaster often collapses and is strongly compressed laterally in dried specimens. The petiole is transverse to elongate (more than twice as long as it is broad).

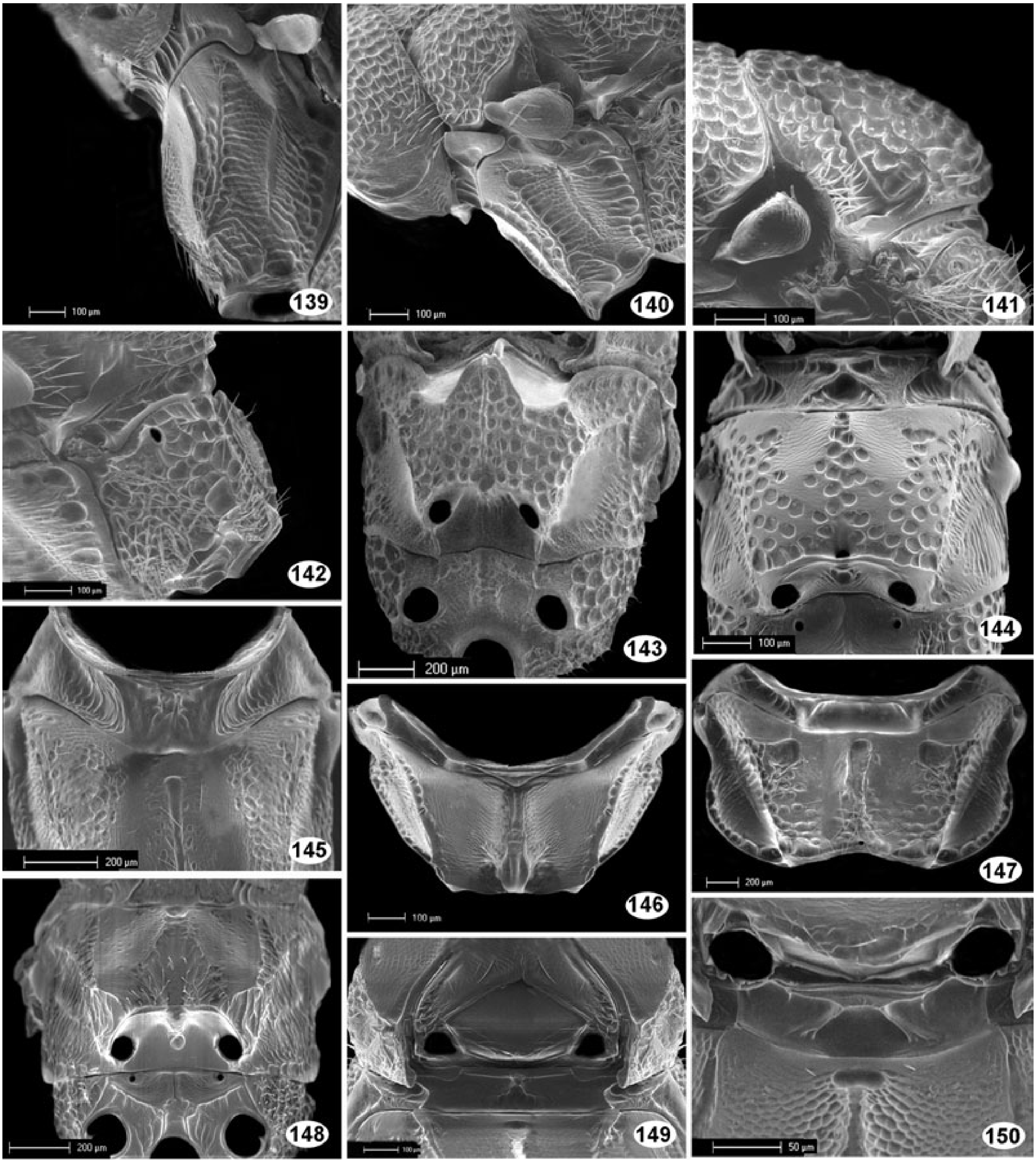
Isosomodes is supported by a few derived states: (1) subforaminal plate (SFP) present on PGB (but not well-delimited medially); (2) median stripe of ornamentation absent on PGB (Fig. 58); (3) marginal vein short (clearly shorter than stigmal vein). The combination of the two first apomorphies is unique within the subfamily.

The Tetramesa genus group: We include here the genera *Cathilaria*, *Tetramesa*, and *Systole.* The former

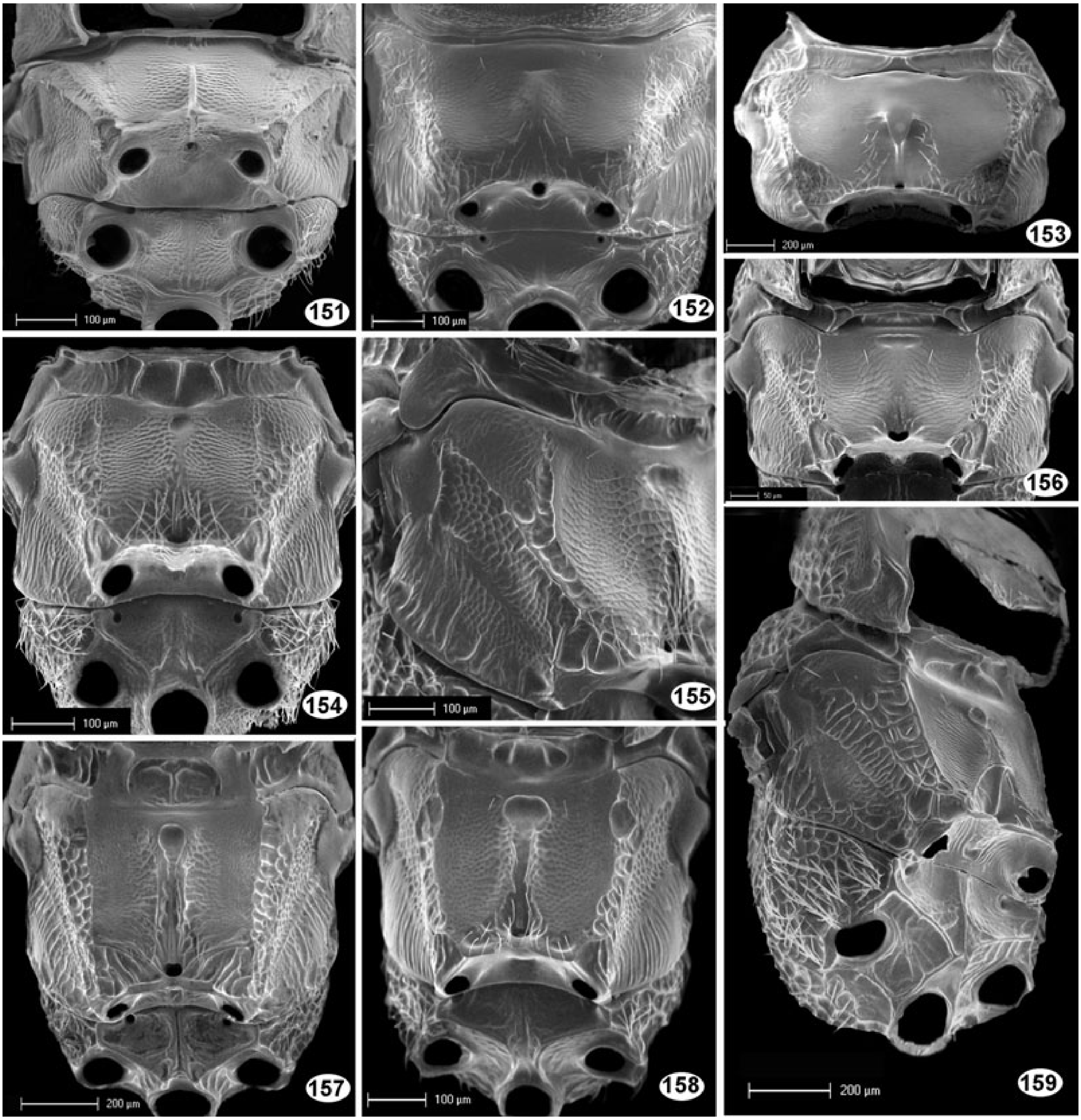


Figures 127–138. Figures 127–131: propodeum – 127, *Sycophila biguttata*; 128, *Eurytoma ochraceipes*; 129, *Bruchophagus roddi*; 130, *Eurytoma collaris*; 131, *Conoaxima affinis*. Figure 132: mesosoma in lateral view; *Bephratoides* Shushufindi. Figure 133: Mesosoma, anterior part in lateral view; *Aximopsis* Colombia 1. Figure 134: Pronotum and prepectus in lateral view; *Eurytoma braconidis.* Figures 135–138: mesopleuron in lateral view; 135, *Eurytoma dentata*; 136, *Eurytoma* Cébazan; 137, *Plutarchia bicariniventris*; 138, *Eurytoma braconidis*.

genera are always sister groups, but the clade (*Cathilaria* + *Tetramesa*) is sometimes the sister group of *Systole* (cladogram 1; Fig. 3), a result independently corroborated by Heraty (2005) using ribosomal data. The whole group is not supported by the bootstrap and is sustained by few derived states: (1) flagellar segments with suberect hairs (Fig. 104); (2) flagellar segments with few elongate sensilla

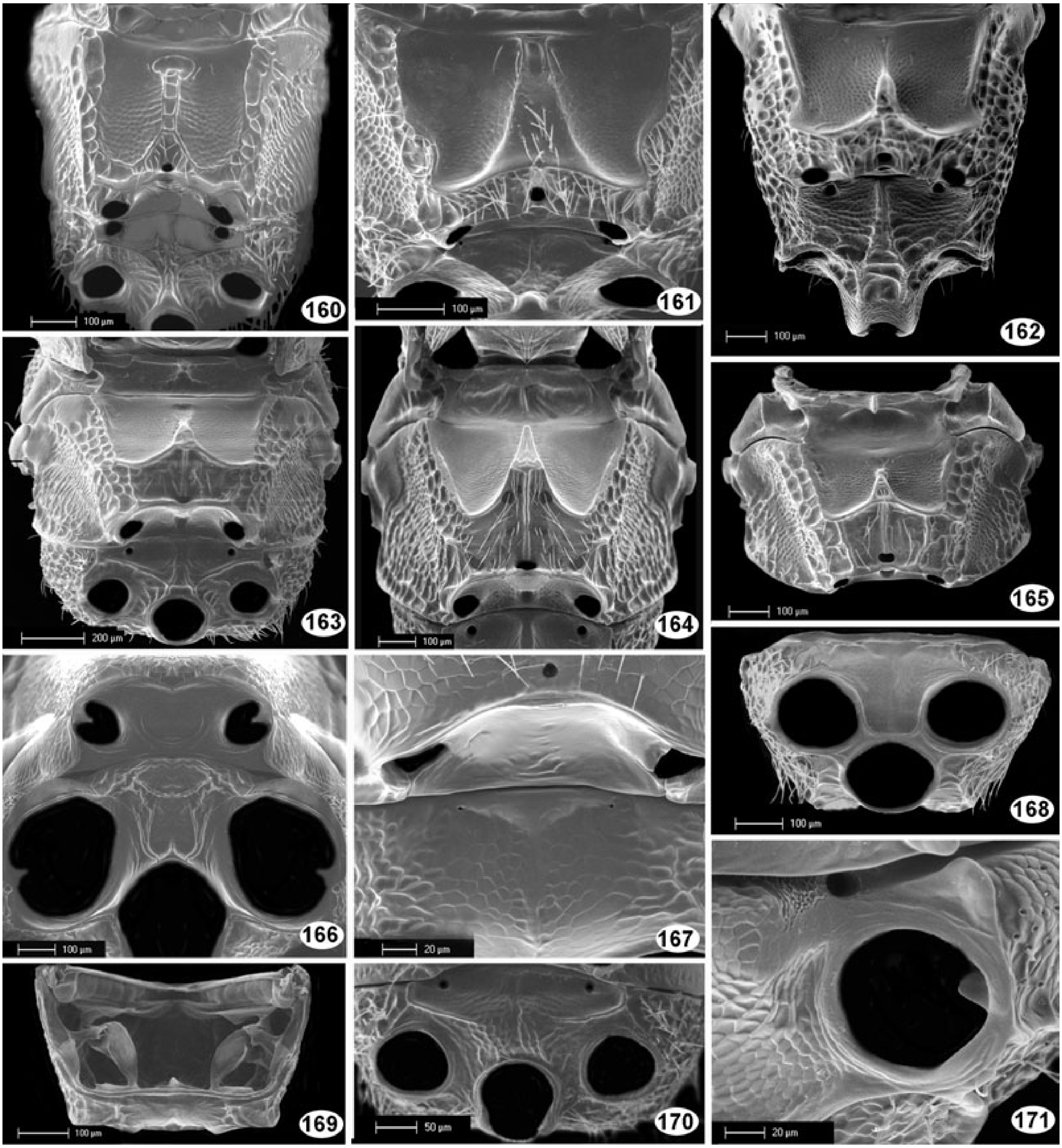


Figures 139–150. Figures 139, 140: Mesopleuron in lateral view – 139, *Bruchophagus squamea*; 140, *Eurytoma compressa*. Figure 141: scutellum in lateral view; *Eurytoma* Peru 1. Figure 142: propodeum in lateral view; 142, *Eurytoma dentata*. Figures 143, 144, 148: meso- and metapleuron in ventral view – 143, *Heimbra opaca*; 144, *Aximogastra* Guinea; 148, *Prodecatomidea* Cameroon. Figures 146, 147: mesopleuron in anterior view; 146, *Syceurytoma ficus*; 147, *Bephratelloides pomorum*. Figures 145, 149, 150: prepectus in ventral view; 145, *Tetramesa romana*; 149, *Bruchophagus* Alicante; 150, *Phylloxeroxenus* San Alberto 2.

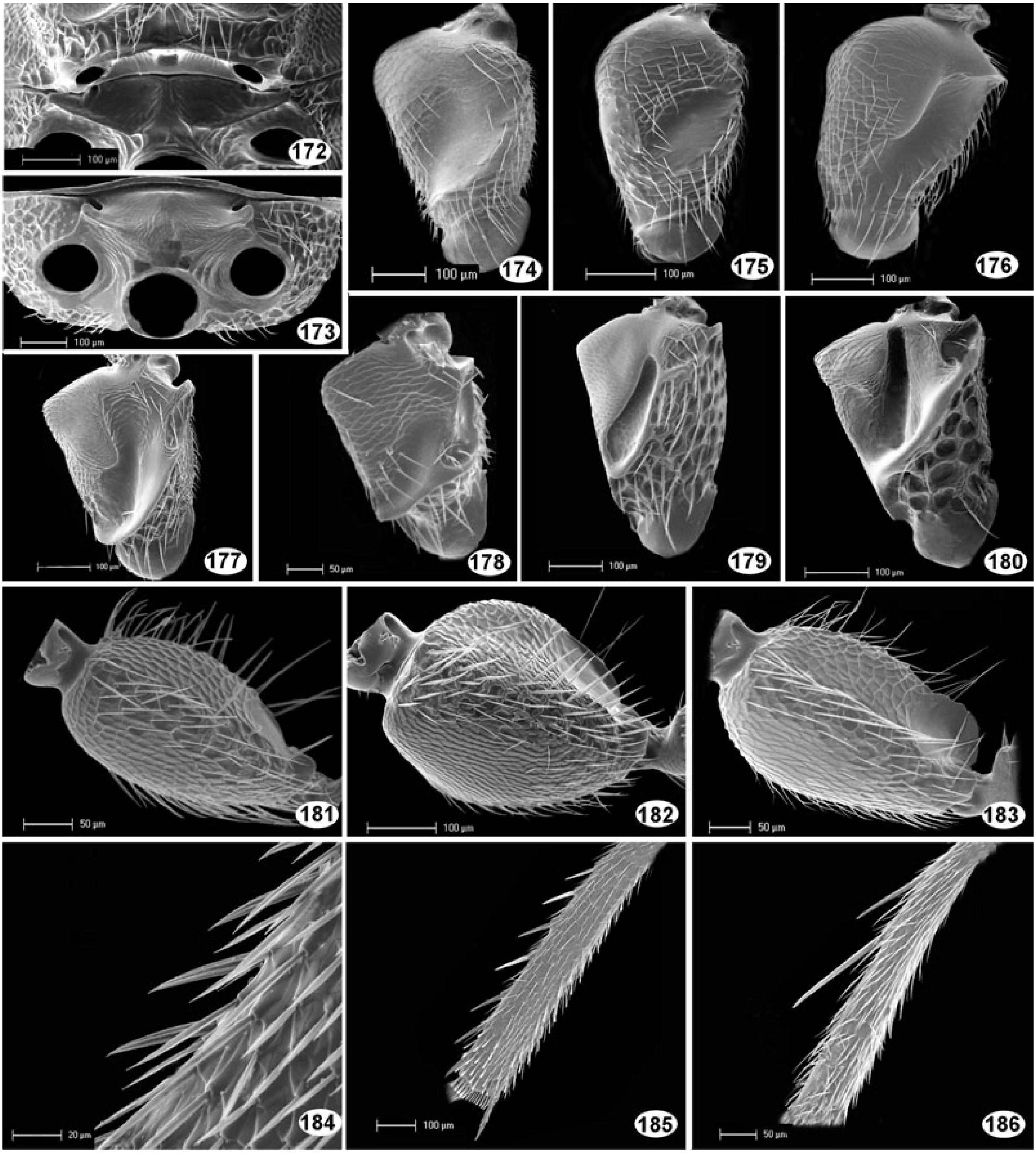


Figures 151–159. Figures 151, 152, 154, 157, 158: meso- and metapleuron in ventral view – 151, *Rileya pulchra*; 152, *Bruchophagus* Guyoniana; 154, *Bruchophagus phlei*; 157, *Eurytoma lepidopterae*; 158, *Tenuipetiolus* Guadeloupe. Figures 153 and 156: mesopleuron in ventral view – 153, *Ficomila* Gabon; 156, *Eurytoma* Senegal. Figure 155: mesopleuron in lateroventral view; *Bruchophagus caucasicus.* Figure 159: mesosoma in lateroventral view; *Eurytoma* San Alberto 1.

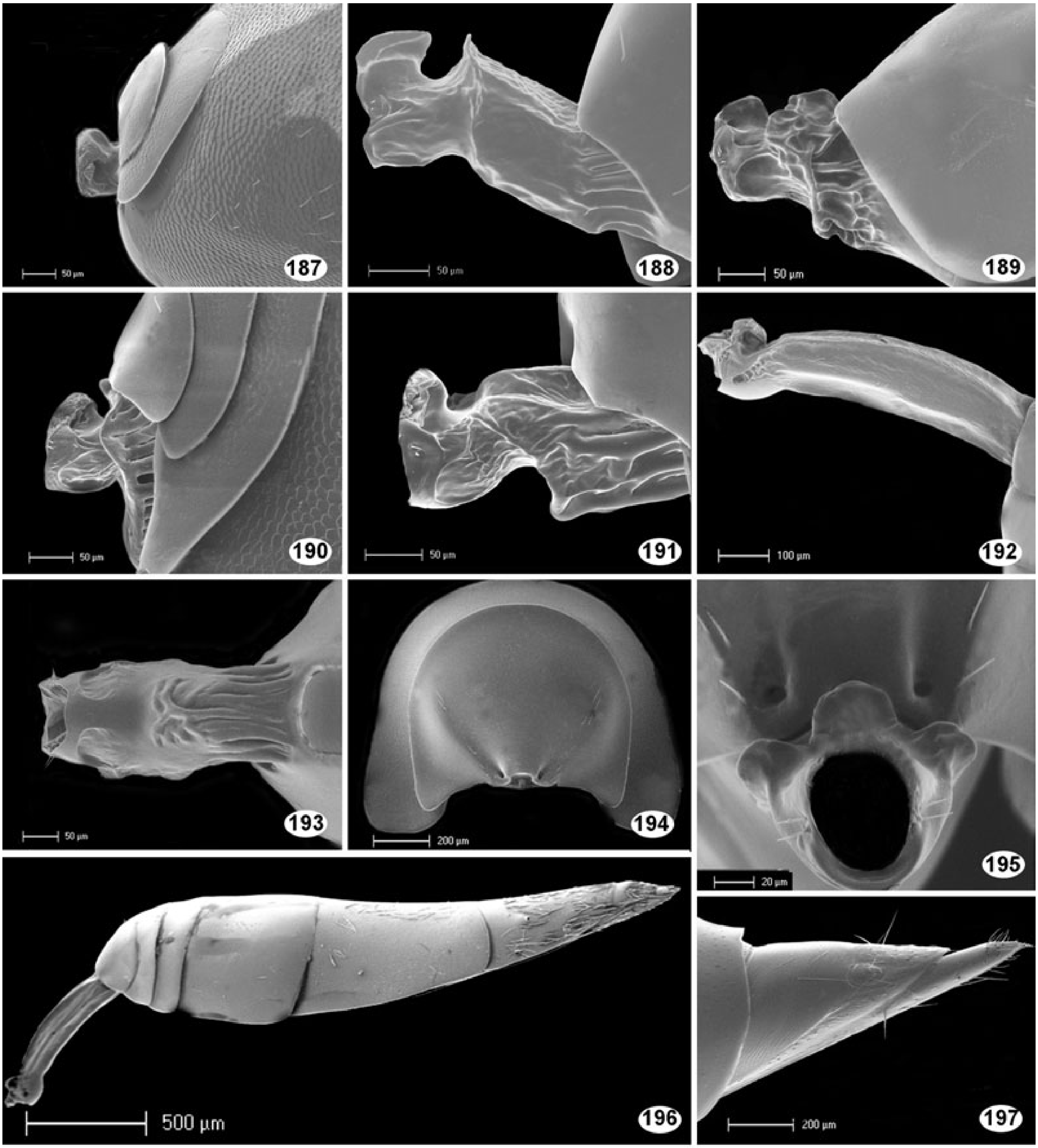
(Fig. 100); (3) notauli deep and broad (Fig. 114). *Tetramesa* and *Cathilaria* share the following derived states: (1) head and mesosoma with long, thin, and erect pilosity (Figs 13, 45); (2) ITS with a transverse carina (Fig. 36); (3) lateral foraminal plates (LFP) completely delimited dorsally and laterally (Fig. 57) (with a number of further reversals in *Tetramesa*). *Tetramesa* is a speciose, cosmopolitan genus, greatly diversified in the Holarctic region (Zerova, 1976; Noyes, 2002). The presence of three hairs on each side of the articular area of the petiole (Fig. 189) (instead of two in the other Eurytominae) is the only



Figures 160–171. Figures 160–164: meso- and metapleuron in ventral view – 160, *Prodecatoma maculiventris*; 161, *Eurytoma ficusgallae*; 162, *Axima brevicornis*; 163, *Eurytoma* Cébazan; 164, *Eurytoma braconidis*. Figure 165: mesopleuron in ventral view; *Conoaxima affinis*. Figures 166, 167, 168, 170: metapleuron in ventral view; 166, *Glyphomerus stigma*; 167, *Buresium rufum*; 168, *Archirileya* Cicada; 170, *Bruchophagus* Alicante. Figure 169: metapleuron (after dissection) in anterior view (internal skeleton visible) – *Archirileya* Cicada. Figure 171: hind coxal cavity and metafurcal pit (enlarged) – *Rileya pulchra*.



Figures 172–186. Figures 172, 173: metapleuron in ventral view – 172, *Eurytoma obtusiventris*; 173, *Eurytoma ochraceipes*. Figures 174–180: fore coxa in anterior view – 174, *Bruchophagus squamea*; 175, *Bruchophagus* Alicante; 176, *Eurytoma robusta*; 177, *Eurytoma* Cébazan; 178, *Eurytoma dentata*; 179, *Axima brevicornis*; 180, *Aximopsis* Colombia 1. Figures 181–183: hind coxa in lateral view – 181, *Bruchophagus phlei*; 182, *Eurytoma* Cébazan; 183, *Eurytoma morio*. Figure 184: hind tibia, part (enlarged) – *Eurytoma* Cébazan. Figures 185, 186: hind tibia in lateral view – 185, *Sycophila biguttata*; 186, *Eurytoma* Combodia.



Figures 187–197. Figures 187–192: petiole and base of gaster in lateral view; 187, *Rileya pulchra*; 188, Eurytominae Ecuador; 189, *Tetramesa fulvicollis*; 190, *Eurytoma cressoni*; 191, *Phylloxeroxenus* San Alberto; 192, *Axima brevicornis.* Figure 193: petiole in ventral view – *Eurytoma nodularis*. Figure 194: base of gaster in frontal view – *Bruchophagus squamea*. Figure 195: petiole and median part of first gastral tergite in frontal view – *Eurytoma volkovi.* Figure 196: petiole and gaster – *Axima brevicornis.* Figure 197: syntergum in lateral view – *Eurytoma amygdali*.

Figures 198–212. Figures 198, 199: head in frontal view – 198, *Philolema carinigena*; 199, *Aximogastroma longigastris*. Figures 200, 201: head and pronotum in lateral view; 200, *Masneroma angulifera*; 201, *Banyoma philippinensis*. Figure 202: female antenna – *Endobia donacis.* Figures 203, 204: mesosoma in dorsal view – 203, *Ramanuja swarmanus*; 204, *Banyoma philippinensis*. Figures 205–208: marginal, stigmal, and postmarginal veins of forewing – 205, *Aiolomorphus rhopaloides*; 206, *Eurytoma* sp., *rosae* species group; 207, *Eurytoma* sp., *morio* species group; 208, *Sycophila kestraneura*. Figure 209: gaster in dorsal view – *Prodecatomidea bekiliensis*. Figures 210, 211: gaster in lateral view – 210, *Gibsonoma budhai*; 211, *Aximogastroma longigastris*. Figure 212: hind tarsus; *Endobia donacis*.

synapomorphy characterizing the genus. In our opinion *Cathilaria* might just be a species group of *Tetramesa.* These genera differ mostly in body shape: elongate in *Tetramesa*, with the wings narrow, the axillar grooves narrowly separated on the transscutal line, and the propodeum moderately sloping; compact in *Cathilaria* (resembling some species of *Systole*), with the wings relatively broad, the axillar grooves widely separated on the transscutal line, and the propodeum strongly sloping. Larvae of both genera develop within stems of Poaceae (Claridge, 1961c; Zerova & Seregina, 1994); *Cathilaria* is specialized on *Hilaria* (Zerova, 1999).

Systole (including *Pseudosytole*) is always monophyletic. The genus is supported by several synapomorphies: (1) ITS without any ornamentation; (2) PGB with vestigial sulci (Fig. 73); (3) PGB without median stripe of ornamentation (Fig. 73); (4) first funicular segment (F1) tapering at base (Fig. 100). Moreover, the larvae develop in seeds of Apiaceae (Claridge, 1959b; Zerova & Seryogina, 1994). Some species of *Systole* are reported as seed-eaters of Lamiaceae (Zerova & Seregina, 1994). One of us (GD) examined the type of *Systole nikolskayae* Zerova, 1968, which has this feeding habit. This species proved to be quite similar to *B. borealis*, the type species of *Bruchophagus*. It is therefore possible that all *Systole* species associated with Lamiaceae seeds actually belong to that genus. *Pseudosystole* shares all the derived states defining *Systole*; its four-segmented funicle is autapomorphic. *Pseudosystole* is consequently synonymized with *Systole*.

The Risbecoma genus group: A sister-group relationship between *Risbecoma* and the *bajarii* species group was recovered in most cladograms (cladograms 1, 2, 5A, 5B; Figs 3, 4, 7A, B) with a weak bootstrap value (= 50–64). Such a relationship is supported by the following derived states: (1) lower face strigose (homoplastic) (Fig. 21); (2) ITS narrow (homoplastic) (Fig. 21); (3) LFP raised and shoulder-like (Fig. 75); (4) mesonotum with sculpture showing transverse crests or rugae (Fig. 109); (5) prepectus ventrally very short (Fig. 152); (6) forewing with short and sparse pilosity (homoplastic); (7) relatively thickened marginal vein (as in Fig. 207) (homoplastic); (8) petiole lacking dorsal tooth and basal teeth (reversals). Moreover, the median stripe of ornamentation on the PGB is narrow ventrally in *Risbecoma* (Fig. 75) and almost vestigial in the *bajarii* species group.

In some cladograms (3, 4; Fig. 5A, 6) the following topology was recovered: {*Risbecoma* + [(*Cathilaria* + *Tetramesa*) + (*Systole* + *bajarii* species group)]}. These taxa share a reversal concerning the subventral carinae of the prepectus, and are all phytophagous.

Risbecoma is unambiguously supported by the raised ITS, and the petiolate gaster with long first tergum. *Risbecoma* larvae are phytophagous and develop in seeds of Mimosoideae (Fabaceae).

The *bajarii* species group includes two species, *Eurytoma bajarii* Erdös, 1957 (not *bajariae*, unjustified emendation) and an undescribed species from Morocco, hereafter called *Bruchophagus* Guyoniana. Their sister-group relationship is supported by a high bootstrap value (= 94–100); both species share a clypeus with a distinct median tooth (Fig. 21), and their mesotibiae bear a long apical spur. Zerova (1996) included *E. bajarii* in *Eurytoma* as a specialized form of the *fumipennis* species group; indeed the clypeus also has a short medioventral tooth, and the larvae develop in seeds of *Euphorbia*. Graham (1996) transferred *E. bajarii* to *Bruchophagus* on the basis of the absence of the postgenal laminae. The *bajarii* species group consistently branches on the basal part of the cladogram, on a node distant from *Bruchophagus*. Our results demonstrate that the group belongs neither to *Eurytoma* nor to *Bruchophagus*.

The Aranedra genus group (Fig. 7A, B)*:* We include three monospecific genera (but a few species await description): *Aranedra*, *Foutsia*, and an undetermined genus from Ecuador. This group is not supported and is monophyletic only in one of the local analyses concerning the basal nodes (cladogram 5A; Fig. 7A). The protruding clypeus, and the deep and broad notauli, would support such a relationship. This putative monophyly is confirmed by their distribution and biology: all species are neotropical and phytophagous (gall-makers on *Philodendron* for the first two genera). *Aranedra* retains the same condition of the syntergum as found in Rileyinae (see above). A transverse syntergal carina is also found in *Conoaxima* and *Chryseida*, but is possibly not homologous (the carina is absent laterally and elbowed in the middle). Because a similar syntergum is exhibited by *Endobia*, this genus often appears as the sister group of *Aranedra* (Figs 5A, 6). Such a relationship however, conflicts with their distribution and biology patterns: *Endobia donacis* Erdös, 1964 is known from the Old World and parasitizes bostrichid beetles in the twigs of *A. donax* L. (Poaceae). *Aranedra* is characterized by a loss of ornamentation on the median stripe of the PGB (Fig. 56). *Foutsia* is a rare genus, known only from a few specimens. Many characters, usually hidden, could not be examined; its placement is therefore uncertain. The genus exhibits some distinctive derived states: (1) antennal scrobes with a long median crest; (2) M thickened; (3) forewing enfumated below the marginal vein (both states shared by *Sycophila* and *Ficomila*). The undetermined Eurytominae from Ecuador shows a very broad median stripe of ornamentation on the PGB, including both folds and digitiform expansions of the cuticle (Fig. 71), a state mostly found outside Eurytominae but apparently unique within the subfamily. The submedian carinae of the prepectus are distinctive: the inner carinae strongly diverge from the outer carinae, and are almost parallel to the anterior margin of the prepectus. This species is a seed-eater developing on *Luma apiculata* (DC.) Burret (Myrtaceae).

The Sycophila genus group: We include here the genera *Sycophila* and *Ficomila*. The species included in the analysis always branch on the same node (Figs 3, 5A, 6), which is supported by a weak to moderate boostrap value (51–80). The group is corroborated by several apomorphies: (1) clypeus bilobed (Figs 33, 34) (homoplastic); (2) LFP with dorsal margin forming, together with the inner edge of postgenal grooves (PGG), a strongly wavy line (Figs 59, 74) (possibly a synapomorphy); (3) PGG somewhat curved in their upper parts (Fig. 59); (4) metatibia with dorsal enlarged setae (Fig. 185) (homoplastic); (6) thickened marginal vein (Fig. 208) (homoplastic); (7) forewing with a more-or-less broadly infumated spot behind the marginal vein (homoplastic).

Ficomila is monophyletic in all cladograms and well supported (bootstrap = 93–97). This monophyly is based on the presence of a ring-like process on the epicnemium (homoplastic with *Syceurytoma*) together with a broad areola on the prepectus, delimited by the widely spaced subventral carinae (Fig. 153).

Sycophila is monophyletic relative to *Ficomila* only in the local study of the basal nodes (Fig. 7B). As a result of the morphological diversity of *Sycophila*, and of our limited sampling, it is difficult to assess its relationships. However, no evident synapomorphy supports the genus. Tropical species were mostly reared from figs (Moraceae), but their biology is poorly known: some are possibly true parasitoids, whereas others might be inquilines in Epichrysomallinae galls. The Holarctic species are mostly associated with cynipid galls (Claridge, 1959a; Nieves-Aldrey, 1983; Pujade i Villar, 1994), but their exact biology must be elucidated. For a long time they were included in *Eudecatoma*, until the genus was synonymized with *Sycophila* by Bouček (1974). This synonymy was challenged by Zerova (1996) as the type species of *Sycophila* has enlarged pro- and metafemur. However, this character was removed from our matrix because it is highly homoplastic, and we confirm the synonymy. Assessing clearly the monophyly of *Sycophila* requires a larger sample and is above the purpose of this study. For the time being and with the available data it seems reasonable to keep the genera separated.

The *Aranedra* genus group is paraphyletic, once relative to the *Sycophila* genus group in cladogram 5B (Fig. 7B), but the relationship is not supported by the bootstrap. As a whole this pair is sustained by the following derived states: (1) clypeus protruding; (2) PGG with sharp inner edge on their upper part; (3) PGG expanded (down to the hypostomal bridge); (4) propodeum with a distinct nucha; (5) gaster petiolate. Moreover, a morphocline was found between *Aranedra* and the *Sycophila* genus group concerning the dorsal margin of LFP: straight in *Aranedra* (Fig. 56), slightly sinuate in the undetermined Eurytominae from Ecuador, and forming a wavy line in the *Sycophila* genus group (Figs 59, 74). The last group is sometimes the sister-group of *Ausystole* (cladogram 1; Fig. 3); see the discussion below concerning the latter genus. In one case (cladogram 4; Fig. 6) *Syceurytoma* is the sister group of *Ficomila*. See comments below.

The aspila species group: The two species selected branch together with a weak to high bootstrap value (= 50–91). The peculiar structure of the notauli (deep and groove-like) is the only synapomorphy defining the group (Fig. 121). It exhibits many plesiomorphic characters: it branches on a relatively basal node, most often on an independent clade (cladograms 1, 3, 4, 5A; Figs 3, 5A, 6, 7A). In the Palearctic Region, the species were reared from cynipid galls on herbaceous plants. They were included in *Eurytoma* (Zerova, 1995; Noyes, 2002) or in *Bruchophagus* (Ferrière, 1950; Szelényi, 1976). Our study demonstrates that they cannot belong to these genera.

The genus Endobia: This rare genus includes two described species (Bouček, 1983) from France and India, respectively, and an undescribed species from West Africa (G. Georgen, pers. comm.). They are parasitoids of Anobiidae in bamboos. *Endobia* is supported by several autapomorphies: (1) propodeum with deep furrow, similar to human buttocks (!); (2) basitarsi long and thickened (Fig. 212); (3) petiole with basal teeth large and flattened. *Endobia* branches on a basal or subbasal node, as a sister group of *Aranedra* (cladograms 3, 4; Figs 5A, 6), or of *Bruchodape* (cladograms 1, 5; Figs 3, 7). The long F1 (Fig. 202) supports the former relationship. *Endobia* also shares with *Aranedra* a similar structure of the syntergum (see comments above). A deep median furrow of the propodeum is also found in *Bruchodape*.

The genus Bruchodape: This enigmatic genus exhibits highly specialized structures, especially on the gaster. Only one species is described from the Neotropical Region (Burks, 1971). According to M. Gates (pers. comm.), *Bruchodape* might be associated with xylophagous beetles as at least one specimen was reared in Guatemala from dead wood. The genus sometimes branches on an independent node (cladogram 3; Fig. 5A), at other times is the sister group of *Endobia* (cladograms 1, 5; Figs 3, 7), or of

Masneroma (cladogram 2; Fig. 4) within the following topology: *Axanthosoma* + [*Ipideurytoma* + (*Bruchodape* + *Masneroma*)]. This sister-group relationship is corroborated by the following derived states: (1) pro- and metafemorae enlarged but short; (2) metatibial spurs enlarged; (3) claws somewhat enlarged and curved. These characters might, however, be adaptative and associated with phoretic habits. Moreover, enlargment of the femora is clearly homoplastic in Eurytominae. The main autapomorphies of *Bruchodape* are: (1) upper tooth of mandible truncate and separated from mid-tooth by a broad emargination; (2) gena with a sharp tooth on posterior margin, associated with an evident depression of the postgena; (3) ITS and ocellar triangle broad, in comparison with the transverse head; (4) adscrobal area convex; (5) propodeum long, bearing large spiracles and a fairly deep median furrow; (6) mesopleuron with ventral shelf and differentiated epicnemium, with the remainder of the mesopleuron otherwise densely and finely strigose on femoral scrobe and mesepimeron; (7) forewing veins short; (8) T4 large, bearing a spheric projection in the centre of a depressed area; (9) apical angulation of the gaster, the apex of T4, and following segments vertical. These derived states are amazingly associated with primitive ones for the subfamily.

The genus Ausystole: The genus was described (Bouček, 1988) for an Australian species developing in seeds of *Eutaxia microphylla* (R.Br.) C. H. Wright & Dewar (Leguminosae). It branches either on an independant node (cladogram 3; Fig. 5A), as the sister group of (*Sycophila*, *Ficomila*) (cladogram 1 as Fig. 3), or as the sister group of *Austrodecatoma* (cladograms 4, 5A, B; Figs 6, 7a, B) (bootstrap = 52). The sister-group relationship with the *Sycophila* genus group is supported by the bilobed clypeus, the sparsely punctured scutellum, and the presence of enlarged dorsal setae on the hind tibia. Phytophagous habits and Australasian distribution support a relationship between *Ausystole* and *Austrodecatoma*.

The genus Austrodecatoma: The genus includes three species of Indopacific distribution that gall seeds of *Atalantia* spp. (Rutaceae) (Bouček, 1988). *Austrodecatoma* appears on an independent branch, just basal to the *Bruchophagus* node (cladogram 1; Fig. 3), or the *Mangoma* genus group (cladogram 3; Fig. 5A); it is otherwise the sister group of *Ausystole* (Figs 6, 7A, B) in the final cladograms. A close relationship with *Bruchophagus* was suggested by Bouček (1988), and the somewhat sinuate posterior margin of the gena together with the concave postgena support this. However, *Austrodecatoma* exhibits a bilobed clypeus never recovered in *Bruchophagus*; the ITS is also different and shows a transverse ridge in *Austrodecatoma,* whereas it is raised above the surface of the scrobes in *Bruchophagus*.

The intermediate nodes

The species included here have the gena at least slightly carinate posteriorly, the last two segments of the clava are fused, and the axillar grooves are deep; however, the species lack the raised and long postgenal laminae displayed by species branching on the terminal nodes.

The following group of taxa is most often recovered on the same branch, which is, however, never supported by the boostrap. It includes the *Mangoma* genus group, the genus *Phylloxeroxenus*, *Eurytoma obtusiventris*, the *Prodecatoma* genus group, the genera *Townesoma* + *Gibsonoma*, and the *dentata* species group. The species belonging to this clade share several apomorphies, most of them being homoplastic: (1) clypeus emarginate ventrally, often bilobed (Figs 20, 22–24); (2) genal carina raised (Fig. 23); (3) PGB with sulci superficial and tending to be vestigial (Figs 76, 78); (4) PGB with inner edge of sulci not raised and not overlapping them; (5) funicular segments fusiform (Fig. 94); (6) flagellomeres bearing long appressed hairs; (7) mesopleuron flattened anteriorly, the epicnemium being almost completely delimited (Fig. 135); (8) T4 greatly enlarged, often more than twice as long as T3, and almost completely overlapping T5 (Fig. 210).

All these species have a raised carina on the gena, and consequently they were often and still are included in the genus *Eurytoma*. However, they do not display the synapomorphies of *Eurytoma*-type species [PGG constantly diverging downwards, raised postgenal laminae (PGL), and ventral depression on the postgena]. Faint PGL can be found, but are never raised above the surface of the postgena. Moreover, the orientation of the laminae is different: when present they converge downwards (Fig. 63). The absence of PGL in many species prompted some authors to include them in *Bruchophagus*, i.e. *E. pistaciae* Rondani, 1877 (Szelényi, 1976). Again members of the group do not exhibit the derived states characterizing *Bruchophagus* [first gastral tergum (T1) with sublateral lines of hairs]. Finally some species were wrongly included in *Prodecatoma*; see comments below concerning this genus.

The clade includes both parasitoids of gall-forming insects (especially Cecidomyiidae) and phytophagous wasps, which gall the seeds on a variety of plants. The clade is extremely diversified in the tropics and most of the *Eurytoma* described from tropical countries belong to it. One of us (GD) examined the types of *Eurytoma* described by Risbec (1952) from Madagascar and found that most of the described species actually belong to the *dentata* species group.

The Mangoma genus group: This group includes *Mangoma* and species presently classified within the *salicis* species group of *Eurytoma*. This monophyletic lineage is supported by weak bootstrap values (= 60–63) and is based on three apomorphies: (1) mesoscutum with differenciate sculpture on its anterior part (Fig. 117); (2) narrow but deep notauli; (3) scutellum with the punctures having narrow walls (raised into crests in *Mangoma*).

All species of the *salicis* species group are distributed in the Palearctic region, where they are quoted as parasitoids (but might be inquilines) of sawflies of the genus *Pontania* Tenthredinidae), which are leaf gall-formers on *Salix* spp. (Salicaceae) (Graham, 1970). Their head is globose in dorsal view, their clypeus bilobed, and their lower face is strigose (Fig. 20). The pair of included species is always retrieved as monophyletic (bootstrap = 98–93).

Mangoma includes only *Mangoma spinidorsum* Subba Rao, 1986 reared from *Procontarinia matteiana* Kieffer & Cecconi, 1906 (Cecidomyiidae), a leaf-gall midge of mango trees in the Oriental Region (Subba Rao, 1986). *Mangoma* shows evident autapomorphies (carinate anterior margin on the collar, and transverse crests on the mesonotum).

The sister-group relationship between *Mangoma* and the *salicis* species group is surprising because the former exhibits very outstanding states, which might have evolved from features also present in the *salicis* species group: i.e. faint carina on the pronotal collar leading to a raised carina; narrow walls of the scutellar cells leading to transverse crests. Moreover, both genera include parasitoids of leaf gall-makers.

The genus Phylloxeroxenus: This genus includes species distributed in the New World, where they are probably highly diversified. The group is recovered once (cladogram 1; Fig. 3) (bootstrap = 62) and supported by five apomorphies: (1) lower face strigose (Fig. 23); (2) PGB with median stripe of ornamentation either vestigial or even absent (Fig. 89); (3) prepectus with subventral carinae diverging strongly, the inner ones joining the medioventral tooth when present (Fig. 150); (4) metapleuron with precoxal carinae close to its anterior margin (as in Fig. 172); (5) petiolar part of the first gastral sternum (S1) enlarged, often greatly so (Fig. 190).

The type species of *Eurytomocharis* (*Eurytomocharis minuta* Ashmead, 1894) and *Evoxysoma* (*Systole brachyptera* Ashmead, 1886) were described from Florida (USA); they are known only from their type specimens, which are glued on their ventral side. It was therefore not possible to examine important characters on the mesopleuron, the back of the head, the clypeus, and the lower face. Nevertheless, the enlarged first gastral sternite of *S. brachyptera* undoubtedly confirms its placement within *Phylloxeroxenus*. *Evoxysoma* is therefore synonymized here with *Phylloxeroxenus*.

Eurytoma obtusiventris: The relationship of *E. obtusiventris* with other eurytomines is puzzling. This species and a few related ones are parasitoids of Tephritidae in Asteraceae, and are distributed in the New World (Peck, 1963; J. Etienne, pers. comm). *E. obtusiventris* is sometimes recovered as the sister group of *Eurytoma ficusgallae* (cladograms 3, 4; Figs 5A, 6), or branches on a node adjacent to the *Chryseida* genus group (cladogram 1; Fig. 3). Such relationships are supported by the presence of a complete epicnemial carina on the mesopleuron, a ventral shelf, and an oblique groove and raised carina on the procoxae. But these characters are certainly interdependent (they are always correlated). *E. obtusiventris* shares with *Phylloxeroxenus* superficial sulci and a vestigial stripe of ornamentation (Fig. 89) on PGB (Fig. 77), and identical LFP; in both taxa the precoxal carinae of the ventral metapleuron are moved forwards (Fig. 172). We therefore strongly suspect *E. obtusiventris* to be closely related to *Phylloxeroxenus*. Cladogram 4 (Fig. 6) shows a different relationship, with *E. obtusiventris* as the sister group of a species belonging to the *salicis* species group. Nevertheless, the taxa involved branch on a common node.

The Prodecatoma genus group: The genera *Tenuipetiolus* and *Prodecatoma* are included here. This group is retrieved in all cladograms but is supported by a weak bootstrap value (= 56–70). It is based on the following derived states: (1) adscrobal area with a dorsal depression or areola (Fig. 158); (2) epicnemium with a large and circular median areola dorsally (Fig. 160); (4) precoxal carinae close to anterior margin of metapleuron, and consequently the metafurcal pits are close to its front margin (Fig. 158) (an apparent reversal); (5) submedian carinae close to each other (Fig. 160). Moreover, in many species the petiole is elongate (particularly in *Tenuipetiolus*).

The first two gastral tergites are supposed to be fused dorsally in *Tenuipetiolus* (Burks, 1971); however, several Neotropical species have T1 and T2 completely separated. Consequently the tergite fusion might be a synapomorphy for a group of the species only. *Eurytomocharis* might be a senior synonym for *Tenuipetiolus*, as both genera share the petiolar apomorphies (with a petiole clearly longer than wide and, related to this, basal and dorsal teeth of the petiole either reduced or absent, and no ventral ridge between petiole and petiolar part of S1). Nevertheless, these taxa never group together and *Eurytomocharis* is the sister group of either *Evoxysoma* (cladograms 3, 4; Fig. 5A, 6) or *Prodecatoma seyrigi*.

Prodecatoma is considered here in a restricted sense. We include only Neotropical and phytophagous species, and exclude several oriental and afrotropical species that in our opinion are wrongly classified in this genus. *Prodecatoma s.s.* is supported by: (1) lower face strigose with a median carina continued on ITS; (2) ITS raised into a broadly laminate and discoid projection continuing dorsally on the scrobal depression (Fig. 39); (3) prepectus with subventral carinae distinctly diverging anteriorly. *Prodecatoma* species display a different set of characters. In *Prodecatoma maculiventris* the epicnemium is flattened, similar to *Tenuipetiolus*, the procoxa is not impressed, and the petiole is elongate. In *Prodecatoma philodendri* the mesopleuron has a ventral shelf that protrudes forward medially, the procoxae show a deep oblique groove and an oblique carina, the petiole is transverse, and the gaster is strongly compressed laterally. The examination by one of us (GD) of the Neotropical species housed in USNM and BMNH neverless showed that these species exhibit the extreme states of morphoclines. Hence in *Prodecatoma diospyri* the mesopleuron bears an H-like ventral carina delimiting a short and sloping ventral shelf, the procoxa is not impressed, the petiole is subquadrate, and the gaster is also strongly laterally compressed.

The genera Gibsonoma and Townesoma: The Oriental genera *Townesoma* and *Gibsonoma* are known only from the type specimens *Townesoma taiwanicus* Narendran, 1994 and *Gibsonoma budhai* Narendran, 1994, respectively. The examination of their body parts was therefore incomplete as it was impossible to dissect these types. *Townesoma* is the sister group of *Gibsonoma* in the final cladograms, obtained after successive weighting (cladograms 2, 4; Figs 4, 6). In the initial cladogram (Fig. 3), *Townesoma* is the sister group of the *Mangoma* genus group, whereas *Gibsonoma* is clustered with *Syceurytoma*. Evidently, more material is needed to better examine the characters and clarify the relationships. The sister-group relationship of (*Gibsonoma* + *Townesoma*) is based on homoplastic characters: (1) propodeum with distinct nucha; (2) petiolar body at least twice longer than broad (Fig. 210); (3) petiole without basal teeth, sometimes with a carina; (4) petiole without a ventral ridge delimiting it from S1. These characters are interdependent (found together in several independent groups), possibly biasing the results in parsimony. We suspect the palaeotropical *Gibsonoma* and *Townesoma* to be distantly related to the New World *Tenuipetiolus* and *Prodecatoma*. We examined several species from the island of Réunion that probably belong to *Gibsonoma*. In these species the males exhibit strong sexual dimorphism: their marginal vein is enlarged. This might be another apomorphic character supporting the genus, but again further material is needed.

The dentata species group: We included in our analysis a relatively large number of species ($n = 15$) belonging to this group, which exhibit a mosaic of character states. Being morphologically diverse the group is only supported once by the bootstrap (= 61) on cladogram 2 (Fig. 4). *P. seyrigi* always branches on a basal node of the stem supporting the group, and it exhibits putative plesiomorphic states: clypeus bilobed, lower face punctured, supraclypeal area smooth, antennal toruli with raised inner margins, ITS sulcate, notauli superficial, prepectus with subventral carinae enclosing a trapezoidal areola, transverse petiole bearing basolateral teeth and delimited from S1 by a ridge. Further transformations within the group include: lower face with horizontal carinae merging from the clypeus (in *Eurytoma dentata*) (Fig. 24); PGG expanded, with inner edges forming laminae, and converging to each other downwards (as in Fig. 53); subventral carinae of prepectus joined and Y-like (in *E. dentata* and related species); mesopleuron with short projecting tooth (in *E. dentata*) (Fig. 135); procoxa with oblique groove and raised carina (in *E. dentata* and related species) (Fig. 178); reversals concerning the carinae on the ventral metapleuron (in *E. pistaciae* and related species) (Fig. 173); metatibiae bearing large spiniform setae at their base (in *E. pistaciae* and related species) (Fig. 186). Because these characters often evolved independently, relationships between these taxa are still unresolved.

Nevertheless, *P. seyrigi* and another species – initially identified as a *Gibsonoma* and collected at Djibelor – branch on basal nodes (cladograms 1, 4; Figs 3, 6). They share together a long marginal vein. *Gibsonoma* Djibelor shows derived states found independently in several taxa: the Y-like submedian carinae of the prepectus are shared with *E. dentata*, whereas reversals concerning the ventral carinae of the metapleuron are shared with *E. pistaciae*.

The group is mostly palaeotropical with few species reaching the warmer regions of the Palearctic region. They are possibly parasitoids of gall-forming insects including Cecidomyiidae, but some species are phytophagous, galling seeds of various plants (A. Kirk and J. Etienne, pers. comm.).

The genus Bruchophagus s.l.: In our new definition of the genus several species groups are presumed to belong here:

1. The *borealis* species group includes *B. borealis* Ashmead, 1894, which is the type species of the genus. As quoted earlier, *Bruchophagus* Alicante was used to encode characters. *Bruchophagus nikol-*

skayae, described in *Systole* (see above), also belongs to this group, as shown by the head shape (relatively transverse in frontal view as in Fig. 21), the parallel sides of the pronotum, the superficial axillar grooves (as in Fig. 115), and the short marginal vein (at most, as long as the stigmal vein). These last states are possibly correlated to the small size of the specimens observed (see below concerning this point).

2. The *metallica* species group is currently classified in *Nikanoria*. Species have metallic reflections on the integument, which are often very faint. The *metallica* and *borealis* species groups share the same derived characters and are always sister groups. The *metallica* group includes parasitoids (possibly inquilines) associated with gallmakers (Cynipidae or Cecidomyiidae) developing on plants growing on salty soils (Zerova, 1979).

3. The *gibbus* species group is by far the largest group including several dozens species in all zoogeographical regions. It is recovered at best paraphyletic with respect to (*Bruchophagus* Alicante + *Nikanoria*) (cladogram 1; Fig. 3). The mesosoma is squat; the strongly sloping propodeum has a flat transverse outline and a broad basal carina. The group is mostly supported by a biological character, all species being seed eaters of Leguminosae. *Exeurytoma*, which also develops on legumes and displays these characters, might also belong to the *gibbus* species group (Zerova & Seryogina, 1994). The genus was erected on the basis of its elongate syntergum (Burks, 1971).

4. The *squamea* species group includes *E. squamea* Walker, 1834 (transfered here to *Bruchophagus*), and at least three undescribed species from Europe. Monophyly of the group is supported by the raised genal carina, the raised adscrobal carina of the mesopleuron partly delimiting a ventral shelf (Fig. 139), the presence of a depressed, step-like (but not carinate) surface on the procoxae (Fig. 174), and the punctulate sculpture of the gaster. Szelényi (1975) reported *Bruchophagus squamea* as a parasitoid of *Cephus pygmaeus* (L.) (Cephidae) developing in wheat stems. Otherwise *B. squamea* shares all the apomorphies of *Bruchophagus s.l.*

5. The *atra* species group includes three described species presently classified in different genera. One of us (GD) examined the types of *Isosoma atrum* Walker, 1832 and *Eurytoma alopecuri* Erdös, 1969: both belong to the same species, and we used the better preserved type of the latter species to encode the characters. *I. atrum* was designated by Claridge (1961a) as the type species of *Ahtola*, which was later considered to be a subgenus of *Eurytoma* (Bouček & Graham, 1978); *E. alopecuri* was transfered to *Tetramesa* by Szelényi (1974). This group is supported by two apomorphies: the short antennal scrobes that are hardly longer than broad, and the very deep median furrow on the propodeum. Both species are parasitoids of *Tetramesa* spp. living in stems of *Alopecurus* sp. (Poaceae); they occur only in the Palearctic region.

6. The *kelebiana* species group includes at least three species (one undescribed) from Europe and West Africa. *Bruchophagus trigonellae* was reared from seeds of *Medicago medicaginoides* (Retz.) E. Small (= *Trigonella tenuis*) (Fabaceae) (Szelényi, 1976); the biology of the other species is unknown. This species exhibits some outstanding characters: the ITS is not raised above the surface of the antennal scrobes, the procoxae have an oblique groove, and T1 bears no lines of hairs. Consequently *B. kelebiana* was sometimes not placed within *Bruchophagus* (cladogram 1; Fig. 3). However, the group is supported by several apomorphies: (1) clypeus with a medioventral tooth; (2) pronotum very large, about 1.5 times as long as the mesoscutum (a synapomorphy); (3) notauli step-like. The group is retrieved as monophyletic in the final trees (cladograms 3, 4; Figs 5A, 6).

7. The *phlei* species group includes a dozen of Palearctic species; as far as we know they are parasitoids of *Tetramesa* larvae developing within stems of Poaceae (Szelényi, 1968, 1974). They are superficially similar to *Eurytoma* of the *appendigaster* species group, which share the same biology. Their genal carina is raised, the mesosoma is moderately elongate, and the propodeum is sloping and shows an areolate median groove; hence, the basal carina is short and wedge-like. All these states are shared with the *kelebiana* and *atra* species groups.

Bruchophagus s.l. is supported by: (1) ITS raised above the surface of the antennal scrobes, ending dorsally in a sharp or blunt tooth (as in Fig. 37) (with further reversals in the *metallica* and *borealis* species groups); (2) PGG with inner edge step-like on upper part, separated from the dorsal margin of FLP by a very slight emargination (Fig. 79); (3) propodeum with a brush of hairs on each side of the petiolar cavity (Fig. 129) (hairs sometimes reduced); (4) metacoxa dorsally hairy at base (Fig. 181); (5) first gastral tergite with sublateral lines of hairs on each side of the submedian pits (Fig. 17). Some of these states are sometimes reversed. This is possibly a result of the small size of the species, which renders most characters evanescent (sculpture, carinae, sulci, hairs) and led to homoplasy between small-sized species, e.g. *Bruchophagus platypterus* (Walker, 1834) (from the *gibbus* species group) and the clade (*Bruchophagus* Alicante + *Nikanoria*). The genus as considered above is monophyletic in all trees achieved after successive weighting; it is, however, not supported by the boostrap (< 50).

The allocation of the species included in the data set to the above species groups appears in Appendix 3.

The genus Syceurytoma: Syceurytoma includes only one Afrotropical species (South Africa), reared from a *Sycophila* within *Ficus* stem galls (Bouček, 1988). The position of *Syceurytoma* is unstable: it is a sister group of either *Gibsonoma* (cladogram 1; Fig. 3) or *Prodecatomidea* (cladograms 3, 5A, B; Figs 5A, 7A, B; bootstrap = 58). The somewhat curved PGG in the upper part, the wavy dorsal margin of LFP, the ring-like process on the mesopleuron (Fig. 146), the wedge-shaped basal carina of the propodeum, which otherwise shows a nucha, the thickened marginal vein, and the host plant association suggest a close relationship with *Ficomila*. However, such a relationship was rarely recovered (cladogram 4; Fig. 6). A close relationship with *Prodecatomidea* is supported by the strigose lower face, the laminate posterior margin of the gena, the raised and regular adscrobal carina delimiting a short ventral shelf, and the Afrotropical distribution. The series of derived states of the petiole, which *Syceurytoma* shares with members of the *Prodecatoma* genus group, partly explains its inclusion there in parsimony. We explained earlier why such a series is misleading. The postgenal laminae of *Syceurytoma* are very distinctive (Fig. 66).

The genus Prodecatomidea: The genus only includes two Afrotropical species: *Prodecatomidea bekiliensis* Risbec, 1952 from Madagascar, and an undescribed species from Cameroon known only from males. The biology of *Prodecatomidea* is unknown but the globose gaster of *P. bekiliensis* suggests a phytophagous biology. The monophyly of the genus is supported by a high bootstrap value (= 83–91). An original combination of apomorphies supports it: (1) lower face strigose and without tentorial pits; (2) posterior margin of gena with a raised and slightly sinuate carina; (3) antennal scrobes carinate laterally and dorsally; (4) postgena depressed; (5) LFP with dorsal margin continuing as sharp inner edge of PGG without emargination, but remains of lateral margins visible; (6) PGB with folds on the median strip distant from each other (Fig. 90); (7) mesopleuron with adscrobal carina raised and complete, partially delimiting a short ventral shelf (Fig. 148); (8) forewing with a sparse pilosity; (9) marginal (and sometimes parastigma) thickened; (10) petiole very broad; (11) gaster broad and short (Fig. 209). *Prodecatomidea* occupies several positions: it branches on an independent node (cladogram 1; Fig. 3), is the sister group of *Syceurytoma* (cladograms 3, 5A, 5B), or is the sister group of *Paradecatoma* (cladogram 4; Fig. 6).

Eurytoma ficusgallae: Eurytoma ficusgallae was reared from galled figs of *Ficus burkei* (Miq.) Miq. in the Afrotropical region (Bouèek, Watsham & Wiebes, 1981). It branches on a common stem together with *Paradecatoma* and *Eudoxinna* (cladogram 1; Fig. 3) or is the sister group of *E. obtusiventris* (cladograms 3, 4; Fig. 5A, 6). It shares with these species the states linked with the presence of a ventral shelf on the mesopleuron (Fig. 161). Amazingly, the postgena of *E. ficusgallae* is similar to the postgena of *Bruchophagus*, but not to that of *E. obtusiventris* and *Paradecatoma*. *E. ficusgallae* does not share the synapomorphies of *Eurytoma s.s.*, and does not belong to this genus.

The genus Paradecatoma: Only *Paradecatoma bannensis* Masi, 1943, the type species of *Paradecatoma*, is formally described, but we know of at least three undescribed Afrotropical species. They were reared from seeds of *Combretum* and *Terminalia* (Combretaceae); *Eurytoma werauhia* Gates & Cascante-Marin (2004), a phytophagous species associated with floral buds of *Werauhia gladioliflora* (Wendl.) (Bromeliaceae), probably belongs to *Paradecatoma*. Therefore the genus is also distributed in the Neotropical region and could be exclusively phytophagous. Bouček *et al.* (1981) briefly redescribed the type species and underlined some characters. *Paradecatoma* is retrieved as monophyletic in all cladograms, but is supported by a weak bootstrap value (= 60–62). It is corroborated by several characters: (1) ITS narrow (Fig. 40); (2) antennal toruli with strongly raised margin; (3) LFP not delimited because its dorsal margin continues without emargination as the inner edge of the PGG (Fig. 62); (4) PGB with median strip vestigial, with folds distant from each other (Fig. 90). The genus is either the sister group of (*Eudoxinna* + *Bephratoides*) (cladogram 1; Fig. 3) or of *Prodecatomidea* (cladograms 3, 4; Figs 5A, 6). The transverse carina delimiting anteriorly the ventral shelf of the mesopleuron is the continuation of the adscrobal carina, not of the epicnemial carina. These structures of the PGB and mesopleuron better support the close relationship with *Prodecatomidea*. *Paradecatoma* is morphologically diversified: *P. bannensis* is the only species with a medioventral tooth on the clypeus, the ventral shelf of the mesopleuron may be partly or completely delimited, and the procoxa may or may not have an oblique carina. The postgenal grooves are mostly like those of *Bephratelloides*.

The terminal nodes

The species merging from these nodes share several derived states: gena with strong posterior carina, PGG expanded downwards below the dorsal margin of the hypostomal fossa (Figs 50–53), and procoxae with an oblique groove delimited basally by an S-shaped ridge or carina (Figs 176, 177, 180).

Four clades are recognized in most cladograms (cladograms 3, 4, 7; Figs 5A, 6, 9). These clades are mostly characterized by the structure of the postgena. In *Eurytoma* and the *Philolema* genus group: (1) the LFP is hardy raised over the surface of the postgena and has a flat surface (Figs 64, 67); (2) its dorsal margin is narrowly separated from the inner edge of the PGG, which is therefore obliterated in its upper part (Fig. 64); (3) the PGB is moderately concave dorsally; (4) its median strip is formed by folds (Fig. 91). In the *Axima* and *Chryseida* genus groups: (1) the body is strongly sclerotized; (2) the LFP has a convex surface (Fig. 80); (3) is as least partly delimited laterally; (4) is broadly separated from the inner edge of the PGG (Fig. 53); (5) the PGB is strongly concave; (6) the prepectus has a strong medioventral tooth (Fig. 156); (7) its subventral carinae are strongly diverging anteriorly and delimit a raised surface (Fig. 165) (but the inner ones are hardly visible because they are obliterated); (8) the mesopleuron most often has a horizontal ventral shelf and a completely delimited epicnemium (Figs 162, 163); (9) the petiole is frequently longer than broad, and the ridge delimiting the petiolar part of S1 is absent (Fig. 193). In the *Axima* genus group the median stripe of ornamentation includes both folds and digitiforms expansions (Fig. 84). In the *Chryseida* genus branch the subventral prepectus is a deep pit, the bottom of which is not visible (Fig. 136).

The genus Bephratelloides: The genus includes Neotropical species reared from seeds of Annonaceae (Grissell & Schauff, 1990; Grissell & Foster, 1996). The genus is weakly supported by the bootstrap (= 52–56). *Bephratelloides* is only supported by homoplastic characters: (1) clypeus bilobed (Fig. 35); (2) PGB relatively long.

The genus Axanthosoma: This Indopacific genus is frequently the sister group of (*Masneroma* + *Ipideurytoma*) (cladograms 1, 3, 4, 5; Figs 3, 5A, 6, 7), but this relationship is not supported by the bootstrap (< 50). The three genera branch on a node on the terminal part of the cladograms, just basal to *Eurytoma*. This relationship is confirmed by preliminary molecular results (Heraty, 2005). *Axanthosoma* includes very small-sized species in which the structures (carinae, grooves, sculpture) tend to collapse, and apparently reverse to plesiomorphic states for the subfamily. These seemingly primitive features are associated with the presence of a postgenal lamina, as found in *Eurytoma*. This state, if considered a synapomorphy, implies that the apparent plesiomorphic states of *Axanthosoma* result from reversals resulting from the small size of their hosts (eggs of the cicadid genus *Melampsalta*). The genus sometimes branches alone on a basal clade (cladogram 5B; Fig. 7B).

The Masneroma genus group: Included here is the pair (*Masneroma* + *Ipideurytoma*) that always forms a clade, supported by a weak to high bootstrap value (= 67–92). This sister-group relationship is based on: (1) head shape distinctly transverse in frontal view; (2) vertex flat, more or less angulate with the frons (carinate in *Masneroma*), and in the same plane as the dorsal part of the pronotum (Fig. 200); (3) funicular segments slightly transverse; (4) scutellum with sparse puncturation (interspaces much larger than the diameter of the points). As stated above, together with *Axanthosoma*, this group branches on a node most often adjacent to the genus *Eurytoma*. Both genera are Holarctic in distribution (Bouček & Novicky, 1954; Bouček, 1983). *Ipideurytoma* was synonymized with *Eurytoma* by Zerova (1995), but was recognized as a valid genus by Yang (1996); this hypothesis is validated here.

The genus Eurytoma s.s.: All species with a carinate gena and that show no other outstanding characters were included in this genus. Claridge (1961a) was the first author relying on the habitus of the postgena to characterize *Eurytoma*; he was followed by Bouček (1988). The genus is redefined here in a narrower sense (cladograms 3, 4, 6; Figs 5A, 6, 8). *Eurytoma s.s.* exhibits the following derived states: (1) PGL present and raised ventrally over the surface of the postgena (Figs 50, 67), with the postgenal lamina therefore visible as a tooth in lateral view; (2) postgena with a ventral depression between the posterior margin of the gena and the hypostomal fossa, with the depression delimited dorsally by a ridge or a step (a true synapomorphy) (Fig. 67); (3) gena with posterior margin slightly angulate above oral fossa. These characters are shared by all members of the *rosae* species group, to which *Eurytoma abrotani* (Panzer, 1801), the type species of the genus, belongs (Bouček *in* Noyes, 2002). The first apomomorphy is shared with some Neotropical species belonging to *Bephratoides*, *Chryseida*, or those named here as *Eurytoma* Peru. These taxa branch on relatively distant nodes as they otherwise have quite distinct apomorphies.

Eurytoma as understood here includes the following species groups.

1. The *aciculata* species group presents no autapomorphies. In Europe, it includes a pair of species presumed to be parasitoids of *Pontania* spp. (Tenthredinidae) galling *Salix* leaves (Noyes, 2002). These *Eurytoma* might be inquilines as well.
2. The *stenostigma* species group includes at least four Palearctic species, the clava of which are truncate at the apex (Zerova, 1995); nothing is known about their biology.
3. The *appendigaster* species group is highly diversified in the Holarctic region; its members are

parasitoids of *Tetramesa* spp. developing in grass stems (Claridge, 1959b). The group is otherwise characterized by the fusiform shape of the flagellomeres (Fig. 96), the relatively long M (at least 1.4 times as long as ST), and the horizontal ovipositor (ascending backwards in most eurytomids). The group is sometimes retrieved as monophyletic (cladograms 4, 6; Figs 6, 8).

4. The *morio* species group includes parasitoids of xylophagous beetles, especially Curculionidae Scolytinae (Noyes, 2002). It is supported by the hairy metacoxa (Fig. 183), the relatively inflated M (Fig. 207), and the distinctive costal cell bearing numerous white hairs on its ventral surface. The monophyly of the group is supported by a high bootstrap value (> 80) in all cladograms. Most species lack the characteristic postgenal depression of *Eurytoma*. The group is diversified in temperate regions, but is also distributed in the Afrotropical and the Neotropical regions where a few species have been collected.

5. The *amygdali* species group only occurs in the Palearctic region. It includes seed feeders associated with Rosaceae (Zerova & Fursov, 1991). The female antenna has a six-segmented funicle and a one-segmented clava (the 1st segment of the clava being removed from the 2nd); they also lack the postgenal depression.

6. *Eurytoma plotnikovi* Nikols'kaya, 1934, a species associated with *Pistacia vera* (Anacardiaceae), shares the long pilosity on the head and mesosoma and broad notauli with the members of the *amygdali* species group. It displays the typical postgenal depression of *Eurytoma* (Fig. 67). *E. plotnikovi* is the sister group of *Eurytoma amygdali* (Enderkin, 1907) in the final tree (cladogram 6; Fig. 8).

7. The *rosae* species group is mostly diversified in the Holarctic region (at least 40 European spp.), and includes parasitoids of gall-making cynipids and of tephritids or weevils developing in stems and flowers of Asteraceae (Claridge, 1961b). Members of the *rosae* species group are recognized by the precoxal tooth visible in lateral view and formed by the raised adscrobal carina (Fig. 140). The group is monophyletic in all cladograms.

8. The *verticillata* species group is mostly Afrotropical, but also includes the Palearctic *Eurytoma verticillata* (Fabricius, 1798). The species are parasitoids or hyperparasitoids of Lepidoptera (Delvare, 1988). It is a monophyletic group with a high bootstrap value (= 100). Species look similar to the *rosae* species group but lack the ventral depression of the postgena. The mesopleuron is distinctive, with the epicnemium completely delimited, and the elbowed adcrobal carina incompletely delimits a ventral shelf (Fig. 157).

9. The *robusta* species group is distributed in the Palearctic and Afrotropical regions. In the former the species parasitize Tephritidae associated with the same habitat as for the *rosae* species group; in Africa the species are mostly parasitoids of Bruchidae developing in seeds of Fabaceae (Delvare, 1988; Rasplus, 1988). The group is always monophyletic in all cladograms. It is supported by the following derived states: the emarginate clypeus, the strigose lower face, the narrow ITS, a medioventral tooth on the prepectus, a ventral shelf on the mesopleuron (Fig. 135), and its completely delimited epicnemium.

10. *Eurytoma crotalariae* Risbec, 1951 exhibits distinctive states and its postgena has no ventral depression; it branches outside the *Eurytoma* stem in cladogram 1 (Fig. 3). However, it shares many derived states with the *robusta* species group. The species develops as seed eaters of *Crotalaria* spp. (Fabaceae) in West Africa (Delvare, 1988), and is found simultaneously with *Eurytoma* spp. of the *robusta* species group parasitizing bruchids. The shared morphological characters and habitat let us hypothesize a shift from entomophagy to phytophagy.

11. The *fumipennis* species group includes seed eaters of *Euphorbia* species (Zerova, 1994). They are distributed only in the Palearctic region. The group is supported by the following derived states: the protruding ventral margin of the clypeus (sometimes bearing a short median tooth), the squat mesosoma, and the propodeum strongly sloping and flat. It is always recovered as monophyletic with a high bootstrap value.

The allocation to species groups of the species included in our analysis is presented in Appendix 3.

The Philolema genus group: This group is supported by the presence of a small depression of the postgena at the corner of the oral fossa, in relationship with the habitus of the PGL, which smoothly joins the posterior margin of the gena downwards (Fig. 68); the lower face has two submedian carinae delimiting the supraclypeal area (Fig. 25). The group (excluding *Ramanuja*) is retrived in all cladograms with a weak to moderate bootstrap value (= 53–78). The whole group is mostly palaeotropical, with a few species present in the southern parts of the Palearctic region.

The genus Ramanuja: This genus is only known from the female holotype of *Ramanuja swarnamus* Narendran, 1989, described from the Oriental region. The type has dense patches of golden pilosity on the head and mesosoma; therefore some parts of the body are not visible and many characters could not be encoded, and the postgena especially could not be observed. In cladogram 1 (Fig. 3) it is found on a node immediately basal to *Eurytoma*; in the other complete trees (cladograms 3, 4; Fig. 5A, 6) it branches on the basal node of the *Philolema* genus group.

The pair Fronsoma + Neoeurytomaria: These genera from the Oriental Region were only known from a few species. We included one species from Africa, which is close to *Neoeurytomaria subbaraoi* Narendran, in the matrix. In all reconstructions this pair is on a subbasal node of the branch, and is supported by a moderate bootstrap value (= 79–86). *Fronsoma* was erected because its antenna supposedly has two anelli. We explain in Appendix S3 that this is incorrect. No synapomorphy distinguishes *Neoeurytomaria* from *Fronsoma*; these genera are therefore synomymized here.

The genus Banyoma: This monospecific genus is always the sister group of (*Plutarchia* + *Philolema*). It exhibits outstanding characters: i.e. the protuding disc-like ITS (Fig. 201), deeply concave propodeum in middle (Fig. 204), and a very long gaster (Burks, 1971: fig. 51).

The genus Philolema sensu largo: In the current generic classification, this genus includes few species that have raised preorbital carinae joining together above the median ocellus (Fig. 198). We consider this character unreliable because it is just the extreme state of a morphocline (all other states are found in closely related species). *Philolema* is the first valid generic name for species displaying the following apomorphies (in addition to those mentioned above for the whole genus group): (1) sublateral prepectus as a deep pit (Fig. 138); (2) mesopleuron with long but sloping ventral shelf (Fig. 164); (3) median part of ventral shelf strongly projecting anteriorly into a shoulder-like process when seen in lateral view (Fig. 138); (4) subalar pit present and deep, but mostly hidden by tegula; (5) procoxae with raised oblique carina delimiting ventrally an oblique groove; (6) procoxae with small areola on side of the carina.

All these apomorphies are shared by species belonging to the genera *Philolema*, *Acantheurytoma*, *Subbaella*, and to the *braconidis* and *lactrodecti* species groups of *Eurytoma* (the last group was previously assigned to the genus *Desantisca* before it was synomymized with *Eurytoma* by Bouček, 1988). *Acantheurytoma* exhibits an outstanding autapomorphy, i.e. the presence of a spine on the scutellum, which we consider only of specific value. *Subbaella* has a long gastral petiole, a character with no generic value as it is quite variable within various eurytomine genera (*Sycophila*, *Prodecatoma*, *Eurytoma*, and *Aximopsis*). We propose to synonymize all the above genera under *Philolema*. *Hexeurytoma* (not included in the matrix) also shares the derived states of *Philolema*, but has a distinctive petiolar region: petiole enlarged, propodeum with posterior margin concave, and T1 with a transverse basal ridge. These transformations are probably related to oviposition behaviour; they might therefore only be of specific value.

The genus Plutarchia: The included species always branches within *Philolema s.l.* However, *Plutarchia* has distinctive features: projection of the mesopleuron, giving it a characteristic appearance (Fig. 137); procoxa with depression quite large; T1 and T2 fused and with large basal pits. These specialized states point to another possible branching. An accurate placement of the genus evidently requires a more detailed phylogenetic analysis of related groups. As we cannot solve the problem, we propose to keep the generic name.

The Axima genus group: Here we include species exhibiting a unique ornamentation on the PGB: in these taxa the median stripe includes both folds and digitiform expansions (Fig. 88). The relevant species mostly have a Neotropical distribution, and are parasitoids of insects living in stems or branches (xylophagous beetles or aculeate Hymenoptera). The monophyly of the group needs confirmation as it is retrieved only in the final trees (cladograms 3, 4 and 7; Figs 5A, 6, 9).

The genus Eudoxinna: Only *Eudoxinna transversa* (Walker, 1862) is described, but we know of at least three other underscribed species that are all distributed in the Amazon basin; their biology is unknown. *Eudoxinna* is either the sister group of *Bephratoides s.l.* or a paraphyletic relative to it. *E. transversa* and the first species collected in French Guiana show some outstanding characters: head subtriangular with malar space long (longer than height of eyes); eyes and antennal scrobes short (they are only 2.5 times as long as the toruli diameter); clypeus with medioventral tooth; mesoscutum strigose, with deep notauli; PM long (nearly three times as long as ST); petiole elongate. Moreover, *E. transversa* has a laminate pronotal carina and a compressed hind tibia. The other species included do not show the above features. The genus is supported by the following derived states: (1) lower face strigose; (2) genal carina laminate; (3) mesopleuron with narrow adscrobal area delimited by parallel epicnemial and adcrobal carinae; (4) mesopleuron with short ventral shelf; (5) procoxa depressed, the depression delimited by a raised apical carina; (6) gaster very strongly compressed (collapsing when dry). The PGG are relatively short, with their inner edge not being raised into laminae. A sister-group relationship with *Bephratoides* can be hypothesized in that both share the following apomorphies: (1) narrow and raised ITS; (2) elongate basitarsi (nearly half as long as tibiae); (3) laterally compressed gaster. Nevertheless the *Bephratoides* + *Eudoxinna* relationship is generally not supported; it is weakly supported in cladograms 1 and 7 only (Figs 3, 9) (bootstrap = 53–60).

The genus Bephratoides (including Striateurytoma and Agriotoma): Bephratoides currently includes five described species from the New World, with one of them reared from Buprestidae (Peck, 1963). *Striateurytoma* includes only its type species, *Striateurytoma striatipes* Ashmead, 1904, described from Brazil. *Agriotoma* is also monospecific, including only *Agriotoma bakeri* Burks, 1971, but is distributed in the Oriental region (Malaysia) (Burks, 1971). According to their morphology it is possible that all these species are parasitoids of wood-boring beetles; the distinctive, cristate sculpture of the pronotum suggests such biological habits (Fig. 119). In all trees the group is monophyletic and supported by moderate to high bootstrap values (= 80–95), and several apomorphies corroborate its monophyly: (1) ITS narrow, sulcate, rounded off and dorsally broadened; (2) median ocellus located within the scrobal depression (Fig. 29); (3) antennal scrobes relatively long and narrow (Fig. 29); (4) occiput deeply excavated; (5) LFP reversed (Fig. 51); (6) PGB strongly concave and long (Fig. 51); (7) pronotal surface with transverse crests or rugae (Fig. 132); (8) pronotal collar ecarinate dorsally but angulate (or nearly so) with the collum; (9) mesopleuron with a long ventral shelf (sometimes reversed); (10) petiole elongate, much longer than wide. The gena has a laminate carina on posterior margin and the PGL are present and raised ventrally (Fig. 51). *Bephratoides* is morphologically diverse: the ventral shelf of the mesopleuron may be present or not, the sublateral prepectus is a deep pit or not, a medioventral tooth is present or not on the prepectus, together with a raised carina an oblique channel is present or not on the procoxae, and the marginal vein of the forewing may be thickened. *Striateurytoma* and *Agriotoma* share all synapomorphies listed above for *Bephratoides*. The former genus is based on enlarged and compressed protibiae: in our opinion this character is only of specific value, as is the exserted ovipositor used to define *Agriotoma* (Burks, 1971); this character is homoplastic and was discarded for this reason. *Striateurytoma* and *Agriotoma* are synonymized with *Bephratoides*.

The Eurytoma spp. from Peru: A pair of undescribed species was included in the sample to assess their phylogenetic placement. They were both reared from *Laemosaccus ebenus* Pascoe, 1786 (Curculionidae), a borer on *Myrciaria dubia* (HBK) McVaugh (Myrtaceae) on the Amazon slope of Peru. The monophyly of this group is always retrieved and is supported by moderate to high bootstrap values (= 73–91), although they share no evident synapomorphy. Their body is bicolored (yellow with black spots) and one species from Costa Rica has translucid integument on the gaster, which allows us to see the internal structures. Our results show that these species cannot be included in *Eurytoma* as they do not branch on the node supporting that genus.

The Eurytoma from San Alberto: Two rare Neotropical species of this group are presently known to us from Colombia and French Guiana, respectively; their biology is unknown. They share the following synapomorphy: the postgenal carinae are present but turn abruptly towards the hypostomal carina ventrally (Fig. 65). Otherwise, the mesopleuron has a completely delimited epicnemium that bears a short median tooth (Fig. 159) (identical with that of *E. dentata*), the prepectus has a sharp median tooth, and the petiole is elongate. The placement of this group is unstable. It is the sister group of *E. dentata* in cladogram 1 (Fig. 3), whereas it branches within the *Axima* genus group in the final trees (cladograms 3, 4, 7; Figs 5A, 6, 9). We tentatively used *Eurytoma* to name the species, but our data clearly show that it does not belong to this genus.

The erythroaspis species group: The group includes three species: *Eurytoma erythroaspis* Cameron, 1904, a closely related species from the Neotropical region, and the Palearctic *Eurytoma gyorfii* Erdös,1957. The latter species is a parasitoid of Anobiidae living in dead wood (Bouček, 1977). In cladogram 1 (Fig. 3) this group is the sister group of the *Philolema* genus group (excluding *Ramanuja*). This position is supported by the similar shape of the postgena (Fig. 68) and of the ventral prepectus. In the final trees (cladograms 3, 4, 7; Figs 5A, 6, 9) the group is the sister group of *Axima*. This position is supported by the structure of the head (Fig. 27) and the PGB. The pair of species included in our sampling was always retrieved as monophyletic with a high bootstrap value (= 99–100). Their sister-group relationship with *Axima* in cladogram 7 is supported by a moderate bootstrap (= 70).

The genus Axima (including Aplatoides): The genus was recognized early because of the transverse, distinctive head (Fig. 26) and the presence, in the type species *Axima spinifrons* Walker, 1862 (examined by GD) of sharp teeth on the vertex. This last character proved to be only of specific value. The genus is distributed in the New World and *Axima zabriskiei* Howard, 1890 was reared from *Ceratina* spp. (Apoidea) nesting in twigs (Peck, 1963). It is supported by the following apomorphies: (1) head quite transverse in frontal view, with protruding eyes (Fig. 26); (2) LFP completely delimited laterally (Fig. 80); (3) PGB without median stripe of ornamentation, and only a few digitiform expansions visible (Fig. 80); (3) propodeum with elongate nucha (Fig. 162); (4) metapleuron with ventral shelf very long; (5) petiole elongate and bent downwards posteriorly (Fig. 192); (6) T5 long (Fig. 196). The type species of *Aplatoides* shares all the synapomorphies of *Axima*. The shape of its head is the extreme state of a morphocline. The genus is therefore synomymized with *Axima*. The genus shares with the *Chryseida* genus group the same structure of the sublateral prepectus, which appears as a deep pit; hence, *Axima* branches within this group in cladogram 1 (Fig. 3). This placement nevertheless conflicts with the condition of the PGB found in the *Axima* genus group.

The Chryseida genus group:

1. The genus Chryseida. The genus was recognized early as it includes the largest and most beautiful eurytomids: their bodies have bright metallic reflections. *Chryseida* mostly has a Neotropical distribution with a few species reaching the southern part of the USA (Burks, 1956). Apart from body colour the only synapomorphy recognized (not included in the matrix because of the reduced sampling) concerns the ventral rim of the foramen magnum, which is expanded to form a sphere in the only species examined (this character needs the removal of the head to be examined and we were reluctant to do so on the only specimen available for the other species). The rim of the foramen magnum hence forms a condyle allowing the head to rotate; this is required as the occiput and postgena are strongly concave with the pronotal collum deeply inserted within them. The sulci of the PGB, although difficult to examine, are deep. The few known species are parasitoids of Bruchidae. The genus was recovered as monophyletic in all the reconstructions and was moderately supported (bootstrap = 64–80).
2. The genus *Aximopsis sensu largo* (including *Conoaxima*, *Eurytomaria*, *Mesoeurytoma, Aximogastroma*, and the *nodularis* species group of *Eurytoma*). Within the *Chryseida* genus group the species included here in *Aximopsis* exhibit a reversal in the sulci of the PGB, which are either superficial (in *Conoaxima*) (Fig. 52) or vestigial/absent (in other taxa) (Figs 81, 83). Although generally retrieved as monophyletic (cladograms 1, 3, 7; Figs 3, 5A, 9) *Aximopsis s.l.* is not supported by a robust node. It is sustained once by a moderate bootstrap (= 68) on cladogram 2 (Fig. 4). Moreover, the relationships between the included species could not be resolved because of the high level of homoplasy within the clade. Nevertheless, *Conoaxima* always branches on a basal node within *Aximopsis s.l.* Cladogram 7 (Fig. 9) shows two large clades within the genus, including Old World and Neotropical species, respectively.
3. The genera *Mesoeurytoma* Cameron, 1911 and *Eurytomaria* Masi, 1943 were erected for species with raised preorbital carinae (Burks, 1971); they were each monospecific at the time of their description. The type species of *Conoaxima* and *Aximopsis*, respectively, *Conoaxima aztecicida* Brues, 1922 and *Aximopsis morio* Ashmead, 1904, bear teeth or tubercles correspondingly on the scutellum and pronotum. In these four species the pronotal carina is raised laterally, either complete or nearly so, or is replaced medially by submedian teeth. The examination of a large sampling (over 150 species distributed in all zoogeographical regions) showed that these expansions or ornamentations are only of specific value: they are homoplastic and distributed according to various combinations in different taxa. Moreover, the states on which the above genera were erected only illustrate the extreme condition of morphoclines. The species presently classified in the *nodularis* group of *Eurytoma* exhibit various intermediate states of these morphoclines. They also share with *Aximopsis s.l.* the same derived states that are quoted above: ten apomorphies for the pair *Axima* genus group + *Chryseida* genus group, one derived state for the *Chryseida* genus group, and one apomorphy for *Aximopsis s.l.* itself. The existence of these morphoclines renders the generic identification difficult and risky using the available key to World genera (Burks, 1971), or even using regional keys (Narendran, 1994). Conversely, the *Eurytoma* spp. included in the *nodularis* group do not share the synapomorphies of that genus.

For the above reasons *Mesoeurytoma*, *Conoaxima*, and *Eurytomaria* are synonymized with *Aximopsis* and members of the *nodularis* species group are transfered to the same genus. *Aximogastroma* is known only from the holotype of its type species, *Aximogastroma longigastris* Narendran, 1994. As they were not visible on the holotype it was not possible to encode several characters, which explains the different positions of the genus in the trees. However, *A. longigastris* mostly branches within *Aximopsis s.l.* and it shares all its derived characters; we do not hesitate to synonymize it. One of us (GD) examined the type of *Stireurytoma carinata* Cameron, 1911; it is either the male of *Mesoeurytoma cariniceps* Cameron, 1911 or a closely related species, as their head and mesosoma are identical. Bouček (1988) mentions that the two species are congeneric but are not synonyms according to their different wing venation; however, a sexual dimorphism sometimes affects this character. In any case, *Stireurytoma* is a junior synonym of *Aximopsi*s.

After this manuscript was already written and submitted a paper was published (Gates *et al*., 2006) proposing a redefinition of the genus *Aximopsis*. Basing their statement on a phylogenetic study that included 31 eurytomid species and 48 morphological characters, the authors redefine the genus in a much narrower sense, comprising only eight Neotropical species, all of them being parasitoids of buprestid beetles mining the leaves of Arecaceae. Clearly *Aximopsis* as defined by Gates *et al*. (2006) is a monophyletic group, at least through this narrow specialization for a very narrow spectrum of hosts. The authors quote only a pair of morphological states that support the genus: upper frons and vertex showing umbilicate punctures, and male petiole with an anteroventral projection. The first state is shared with at least some *Chryseida* spp.; therefore, only the second state is a true synapomorphy.

Evidently the concept of *Aximopsis* proposed by Gates *et al*. (2006) is the reverse of our results and perception of the genus. We, however, maintain it because: (1) it is based on a much more representative sampling when considering the species and characters examined; (2) the narrow concept is based on one putative synapomorphy only; (3) the broad concept is based on a number of derived states; (4) the clade appears as a monophyletic group in the majority of the analyses; (5) the gradual and mosaic evolution encountered within the clade prevent us splitting it into smaller units that would be difficult to identify. *Aximopsis s.s.* is considered here as only a specialized group that evolved in narrow association with its hosts.

Aximopsis, as here understood, is extremely speciose in the tropics, and many species described in *Eurytoma* belong to it. *Aximopsis* species are parasitoids of endophytic insects, living in branches, stems or leafmines: xylophagous Coleoptera (mainly Cerambycidae and Buprestidae), aculeate Hymenoptera nesting in twigs or leaf-mining Buprestidae. We strongly suspect a first shift from a shared habitat from Coleoptera to Hymenoptera associated with the recurrent use of beetle galleries by nesting wasps. A second shift might be considered through a possible coevolution with some Buprestidae (genera *Taphrocerus* and *Pachyschelus*), which, in the Neotropical region, became leaf-miners on Arecaceae (Gates *et al*., 2006).

Incertae sedis nodes

The genus Philippinoma: This Oriental genus includes two species known only from their type series. It may be the sister group of the *Chryseida* genus group (cladogram 7; Fig. 9) and it shares many of its derived states: postgenal laminae raised, prepectus with a strong medioventral tooth, subventral carinae of prepectus delimiting a raised surface, mesopleuron with a horizontal ventral shelf, and a completely delimited epicnemium. The main morphological difference concerns the subventral prepectus, which is concave but has no deep pit; we could not examine the PGB. The definitive placement of the genus was not accurately determined, but the genus clearly belongs to the terminal zone of the cladogram.

The genus Burksoma: This monospecific genus is only known from the type series of the included species. It generally appears as the sister group of the *Eurytoma* sp. collected from Guadeloupe, both species branching on a node within the *Axima* genus group. The pair shares a series of characters related to the presence of a ventral shelf on the mesopleuron (adscrobal carina joining epicnemial carina, epicnemium completely delimited); this might explain this placement. We did not have enough specimens to examine the median stripe of ornamentation of the PGB using SEM. The position of the genus must be confirmed.

The Eurytoma from Guadeloupe: The species is either the sister group of *Burksoma scimitar* (cladograms 2 and 3 as Figs 4 and 5) or branches on a node adjacent to it (cladograms 1 and 4 as Figs 3 and 6). We suspect this species is not closely related to *Burksoma*. Both taxa differ in a number of derived states, i.e. the species from Guadeloupe has a strongly bilobed clypeus. The same reasons as stated above for *E. obtusiventris* led us to hypothesize that the species from Guadeloupe might be closely related to *Phylloxeroxerus*. The species is known to us from only one female, and more specimens are needed to assess its phylogenetic relationships.

CLASSIFICATION OF EURYTOMIDAE

Our analysis strongly suggests that the family as currently understood is not monoplyletic, a result consistent with previous morphological (Gates, 2005) or molecular studies (Campbell *et al*., 2000; Chen *et al*., 2004; Heraty, 2005). The Heimbrinae and Eurytominae *sensu* Stage & Snelling (1986) each appear to be monophyletic. The Heimbrinae are the sister group of the Chalcididae (or of some of the recognized taxa included within them).

The Rileyinae as traditionally understood are polyphyletic. Again, this result is in agreement with Gates (2007). The subfamily includes two unrelated taxa: the Rileyinae *s.s*. (redefined by the same author) and the *Macrorileya* genus group (as defined above), which was included in the Eurytominae by Gates (2007). The relationships between the Rileyinae *s.s.* and other chalcidoids are obviously not solved and need further analysis.

Gates (2007) synonymized the Buresiinae *sensu* Zerova (1988), which included only *Buresium*, with the Eurytominae. We propose to keep the subfamily valid for this well-supported monophyletic group. Consequently, the subfamily now includes three genera: *Buresium*, *Macrorileya*, and *Archirileya*. *Macrorileya* is subdivided in two groups of species that may not be closely related: the type species, *Macrorileya oecanthi* (Ashmead, 1894) (type examined) forms the first group, and *Macrorileya antanimorae* (type examined) and other undescribed Malagasy species forms the second group. *M. oecanthi* shares with *Archirileya* spp. the same sexual dimorphism: the pro- and hind femorae are enlarged in males. They also parasitize the same hosts (eggs of Orthoptera or Hemiptera) in twigs of herbaceous plants. The only morphological character that separates both genera is found in the structure of the antenna. In *Macrorileya* the flagellum includes one anellus and seven funicular segments, whereas the basal funicular segments are anelliform in *Archirileya*. A careful examination of the antenna with SEM showed that this character shows a morphocline from *Archirileya inopinata* Silvestri, 1920 to *M. oecanthi*. The undetermined *Archirileya* included in the analysis exhibits an intermediate state (Fig. 98). In all species the first flagellar segment bears no elongate (i.e. multiporous plate) sensilla, and the following segments vary only in length. We therefore consider *Archirileya* a junior synonym of *Macrorileya*. The Malagasy species included in *Macrorileya* are morphologically dissimilar. They show an extreme elongation of most parts of their body.

The Buresiinae has the following, unique combination of characteristics: flagellum with 11 flagellomeres; flagellomere 1 elongate or discoid, but without elongate sensilla (MPS); flagellomeres 2–4 elongate or anelliform, but with elongate sensilla; pronotum at least as long as mesoscutum; mesothoracic spiracle not visible; prepectus, including its ventral part, long; metapleuron partly separated from propodeum; meso- and metafurcal pits quite small (the latter visible at high magnifications only); gastral tergum 2 short; syntergum with a transverse carina in front of cercal plates.

The Buresiinae, as presently defined, are the sister group of the Eurytominae *sensu* Stage & Snelling (1986), a result consistent with that obtained by Gates (2007) who used a different data set.

None of the topologies obtained in this study support the classification proposed by Ashmead (1904), Burks (1971), or Zerova (1988). The gradual pattern of evolution, with many branchs merging from a common trunk and nodes separated by short distances, better confirms the concept proposed by Stage & Snelling (1986), and followed by Bouček (1988) and Noyes (2002).

To conclude, we propose that the classification of monophyletic Eurytomidae includes the following subfamilies.

1. Buresiinae, including *Macrorileya s.l.* and *Buresium.*
2. Eurytominae *sensu* Stage & Snelling (1986).

The taxonomic changes we proposed are listed in Appendix 2. The species removed from *Eurytoma* and *Bruchophagus*, but still awaiting a generic placement are listed in Appendix 4.

HOSTS, HOST HABITAT AND RELATIONS OF EURYTOMIDAE (FIG. 5B)

Phylogeny provides a framework to assess the evolutionary pattern of a group. Within Chalcidoidea this kind of information is relatively scarce, mostly because their relationships are still hypothetical. Grissell (1995) and G.A.W. Wijesekara (pers. comm.) superimposed biological information on the phylogeny of Torymidae and Chalcididae, respectively. Zerova (1992) hypothesized several evolutionary trends for the Eurytomidae. In our phylogenetic hypothesis of the family, Buresiinae are basal and are parasitoids of insects (most often of embryos) living in stems of herbaceous plants (Smith, 1930). Consequently, the common ancestor of Buresiinae + Eurytominae was probably entomophagous. Buresiinae are associated with grasslands, and this observation is compatible with Zerova (1992) who suggested that the earlier eurytomids lived in arid regions.

Within Eurytominae *Isosomodes*, *Axanthosoma*, and *Endobia* retain the biology of Buresiinae and are entomophagous in stems of herbaceous plants. Some genera, i.e. *Aiolomorphus* and *Tetramesa*, are phytophagous in stems of Poaceae, a biology that may easily occur through a shift. Otherwise an evident gap separates such biological features to those found in so many Eurytomidae living in tropical forests, which are associated with gall-forming insects or even form galls themselves on plants. A shift from entomophagy to phytophagy evidently occurred many times, and is found in different branches of the cladograms presented here.

The main difficulty we faced with Eurytomidae was to accurately assess the diet and behaviour of endophytic species. Only accurate observations and careful dissections allow us to assess the exact trophic relationships. We know of several examples concerning related species that display different feeding behaviour. Etienne & Delvare (1987) accurately studied the rich trophic web related with the flowering parts of a legume plant in Casamance (Senegal) and found two species of Eurytomidae (i.e. *Eurytoma* Senegal) belonging to the *dentata* species group, which were clearly entomophagous specialists. In contrast, in the same group, A. Kirk (pers. comm.) and J. Etienne (pers. comm.) also discovered species galling the ovaries of *Olea europapaea* L. (Oleaceae) in Namibia and *Haematoxylon campechianum* L. (Caesalpiniaceae) in Guadeloupe, respectively.

It is not possible at present to assess the number of shifts from entomophagy to phytophagy that occurred within Eurytominae, but according to the available data this number is certainly high. By considering cladogram 4 (Fig. 6) and superposing the known biologies we identified at least 15 switches from entomophagy to phytophagy. Phytophagy concerns species mostly branching on the basal or intermediate nodes of the cladogram (39 and 42%, respectively, when considering the available data), whereas entomophagy is more frequent in the terminal nodes (62%).

CONCLUSION

A number of characters studied in this paper had never been examined within Chalcidoidea and other Hymenoptera. In our opinion, they are probably of interest for future phylogenetic investigations in Hymenoptera. Some of them, such as the meso- and metafurcal pits, are related to the internal skeleton, the structure of which was examined in more detail and for the first time by Krogmann (2005), who emphasized their usefulness for phylogenetic studies.

The Eurytomidae, as they were classified until now, are at least paraphyletic relative to the Chalcididae, and may even be polyphyletic. Our results provide strong evidence for a sister-group relationship between the Heimbrinae and the Chalcididae. We agree with Gates (2007) that the Rileyinae *auct.* consist of two unrelated groups. The Rileyinae *s.s.* as redefined by Gates (2007) are excluded from the Eurytomidae. Thus, the family forms a monophyletic group consisting of two subfamilies (Buresiinae and Eurytominae). Both subfamilies were recovered as monophyletic groups. Within the Eurytominae we noticed a gradual and mosaic evolution connected with a large level of homoplasy; such a pattern does not allow further subdivision of the subfamily. Our results support the subfamily concept proposed by Stage & Snelling (1986). The gradual evolution of Eurytominae is also reflected in the numerous morphoclines, which makes somewhat arbitrary the coding of continuous characters into discrete variables. The short distances encountered between the nodes on the main branch of the cladograms are another expression of the gradual evolution. The biological plasticity of Eurytominae occurs simultaneously with the morphological diversity: very few derived states (less than 10%) are true synapomorphies.

Despite this large level of homoplasy, our data provide support for a formalized generic classification of the Eurytominae: the deep nodes of the cladograms were unstable, but many superficial nodes were stable and robust. The large genus *Eurytoma* as considered until now is clearly polyphyletic. It is redefined in a much narrower sense and supported by a few putative synapomorphies. The limits of the genera *Prodecatoma*, *Bruchophagus*, *Philolema*, and *Aximopsis* are also reconsidered.

Obviously the level of homoplasy encountered in the morphological data did not allow us to completely solve the phylogeny of the Eurytominae. The published molecular phylogenies of Eurytomidae are still unsatisfactory for at least two reasons: (1) the species sampling is clearly not representative and (2) the genes used have low discriminating power. We are presently investigating new genes, and we expect to propose a new hypothesis based on both morphological and molecular data soon.

GENERA EXCLUDED FROM THE STUDY (NOT ENCODED IN THE MATRIX)

Eurytomidia Masi, 1917: *Eurytomidia* is only known from the type specimen of *Eurytomidia dubia* Masi, 1917; one of us (GD) examined this male type, housed in BMNH. It belongs to the *robusta* species group of *Eurytoma*. *Eurytomidia* is synonymized here with *Eurytoma*.

Giraultoma Bouček, 1988: *Giraultoma* is a monospecific genus known only from a few specimens of the Australian *Giraultoma pulchricorpus* (Girault, 1915). According to Bouček (1988) the genus is very close to *Tetramesa*.

Houstonia Bouček, 1988: *Houstonia* is known from the female holotype of *Houstonia zani* Bouček, 1988. One of us (GD) examined it. The most distinctive character is the raised and regular adscrobal carina, which is similar to that displayed by *Prodecatomidea*. Too many parts of the body are not visible (hidden by appendices) to suggest any hypothesis about its relationships with other Eurytominae.

Isosomorpha Ashmead, 1888: *Isosomorpha* is also represented by a unique specimen, the holotype of *Isosomorpha europae* (Ashmead, 1894), housed in USNM and examined by GD. It is just a very teneral specimen of *Tetramesa*, and is unrecognizable at the specific level because the head, antennae and propodeum are strongly distorded. *Isosomorpha* is therefore synonymized with *Tetramesa*.

Stigmeurytoma Bouček, 1988: *Stigmeurytoma* is represented by *Stigmeurytoma eucalypti* (Ashmead, 1900), and is apparently known from seven specimens only (Bouček, 1988). It shares the same adscrobal carina as that found in *Prodecatomidea* and *Houstonia*, but again too much information is lacking to suggest any relationship with other eurytomine genera.

Tetramesella Zerova, 1974: *Tetramesella* includes only its type species *Tetramesella luppovae* Zerova, 1974, from Kazakhstan (Zerova, 1974). From the figures provided by the author this species seems very close to the *Tetramesa* from the Dordogne of the present study.

The Oriental and mostly monospecific genera: *Homodecatoma* Liao, 1979; *Neobephrata* Narendran & Padmasenan, 1989; *Phleudecatoma* Yang, 1996; *Ramdasoma* Narendran, 1994 and *Systolema*

Narendran, 1994; were not available to us. According to the illustration provided by the authors, this second genus is based on a teneral specimen with partially fused flagellomeres, which explains the four-segmented funicle.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1. Special terms used to describe some morphological structures of Eurytomidae or outgroups. (Word document)

Appendix S2. Abbreviations used. (Word document)

Appendix S3. Morphological characters used to infer the phylogeny of the Eurytomidae. CI, RI and RC calculated from cladogram 3. (Word document)

Appendix S4. Data matrix of 150 characters used to infer phylogeny of the Eurytominae. (Word document)

This material is available as part of the online article from: http://www/blackwell-synergy.com/doi/abs/10.1111/j.1096-3642.2007.00308.x

(This link will take you to the article abstract).

APPENDIX 1

List of outgroups and eurytomid species used in the phylogenetic study (nomenclature according to Noyes, 2006).

Species	Status of specimen examined (T, t)*	Depositary	Origin: Country	Origin: Locality	Host plant and host
Chalcididae					
Hockeria unicolor Walker, 1832	t	CIRAD	France	Hérault: Grabels	–
Pteromalidae					
Lycisca sp.	–	INRA	French Guiana	La Chaumière	collected on dead tree
Torymidae					
Glyphomerus stigma (Fabricius, 1793)	–	CIRAD	Iran	Azarbaijan-e-Sharghi: Marand	ex *Diplolepis fructuum* gall (Cynipidae)
Heimbrinae					
Heimbra acuticollis Cameron, 1909	–	INRA	Argentina	San Antonio	–
Heimbra opaca (Ashmead, 1894)	–	USNM	USA	Arizona: Ashfork	–
Rileyinae					
Archirileya Cicada	–	CIRAD	France	Vaucluse Cairanne	ex *Cicada orni* eggs (Cicadidae)
Buresium rufum Boucek, 1969	–	CIRAD	France	Hérault: Pégairolles-de-Buèges	–
Rileya pulchra (Ashmead, 1894)	t	CIRAD	Guadeloupe	Deshaies Clugny	ex *Ophiomyia* sp. (Agromyzidae)
Eurytominae					
Acantheurytoma spinifera Cameron, 1911	–	BMNH	India	Bengalore: Hebbat	ex wasp larva
Agriotoma bakeri Burks, 1971	–	USNM	Indonesia	Borneo	–
Aiolomorphus rophaloides Walker, 1871	t	USNM	China	Foochow	–
Aplatoides diabolus Yoshimoto & Gibson, 1979	–	USNM	Brazil	Para	–
Aranedra millsi Burks, 1971	T	USNM	Ecuador	Miami	ex root gall on *Philodendron*
Austrodecatoma omninigra Girault, 1928	–	BMNH	New South Wales	Pallamallawa	ex fruit galls of *Erimocitrus*
Ausystole beenleighi (Girault, 1926)	–	BMNH	Australia	S. Queensland: Stanthorpe	–
Axanthosoma nigrum Girault, 1913	–	BMNH	Australia	N. Queensland: Gordonvale	ex *Melampsalta puer* egg (Cicadidae)
Axima brevicornis Ashmead, 1904	t	CIRAD	Colombia	Santander: San Alberto	–
Axima brasiliensis Ashmead, 1904	t	CIRAD	Colombia	Santander: San Alberto	–
Aximogastra Ecuador	–	CIRAD	Ecuador	Napo: Shushufindi	–
Aximogastra Guinea	–	INRA	Guinea	Gaah	–
Aximogastroma longigastris Narendran, 1994	T	AEI	Malaysia	Negri S: Pasoh Forest Res.	–
Aximopsis Colombia 1	–	CIRAD	Colombia	Santander: San Alberto	–
Aximopsis Colombia 2	–	CIRAD	Colombia	Santander: San Alberto	–
Aximopsis Ecuador	–	CIRAD	Ecuador	Napo: Shushufindi	–

APPENDIX 1 *Continued*

Species	Status of specimen examined (T, t)*	Depositary	Origin: Country	Origin: Locality	Host plant and host
Banyoma philippinensis Burks, 1971	T	USNM	Philippines	Cuernos, Mts Negros	–
Bephratelloides cubensis (Ashmead, 1894)	–	CIRAD	Dominican Republic	La Romana	ex *Annona muricata*
Bephratelloides paraguayensis (Crawford, 1911)	–	INRA	French Guiana	Montagne de Kaw, Patawa	–
Bephratelloides pomorum (Fabricius, 1804)	–	CIRAD	French Guiana	ex *Annona* fruit	–
Bephratoides Niputini	–	USNM	Ecuador	Orellana: Niputini	canopy fogging
Bephratoides Venezuela	–	USNM	Venezuela	Aragua Cumboto	–
Bephratoides Costa Rica	–	USNM	Costa Rica	Puntaneras: Golfito National Park	Malaise trap
Bephratoides USA	–	USNM	USA	MD, Montgom. Co.	Malaise trap
Bephratoides Shuhufindi	–	CIRAD	Ecuador	Napo: Shushufindi	–
Bephrata ruficollis Cameron, 1884	–	BMNH	Costa Rica	Heredia: Chilamate	–
Bruchodape ignota Burks, 1971	–	CIRAD	French Guiana	Piste Bélizon PK 30	–
Bruchophagus bajarii (Erdös, 1957)	t	CIRAD	Iran	Azarbaijan-e-Sharghi: Marand	ex *Euphorbia* seeds
Bruchophagus caucasicus Zerova, 1992	–	CIRAD	France	Hérault: Saint-Pierre-de-la Fage	–
Bruchophagus gibbus (Boheman, 1836)	–	CIRAD	Turkey	Adana	–
Bruchophagus macronyis Fedoseeva, 1956	–	CIRAD	France	Hautes-Alpes: Arvieux	–
Bruchophagus phlei Erdös, 1969	t	CIRAD	France	Hautes-Alpes: Saint-Véran	–
Bruchophagus platypterus (Walker, 1834)	–	CIRAD	France	Hérault: Montagne Séranne	–
Bruchophagus roddi Gussakovskiy, 1933	–	CIRAD	France	Hérault: Montpellier	ex *Medicago* seeds
Bruchophagus seyali (Risbec, 1951)	t	CIRAD	Senegal	Thiès	ex *Indigofera suffructicosa* seeds
Bruchophagus squamea (Walker, 1834)	t	CIRAD	France	Aude: Peyriac-de-Mer	–
Bruchophagus trigonellae Zerova, 1970	–	CIRAD	France	Aveyron: Viala-du-Pas-de-Jaux	–
Bruchophagus vignae (Risbec, 1951)	t	CIRAD	Senegal	Thiès	–
Bruchophagus Alicante	–	CIRAD	Spain	South of Zaragoza	–
Bruchophagus Gomé	–	CIRAD	Benin	Gomé	–
Bruchophagus Guyoniana	–	CIRAD	Morocco	Road of Er Rachidia-Erfoud	females ovipositing on *Euphorbia guyoniana*
Burksoma scimitar Subba Rao, 1978	T	USNM	Brazil	Matto-Grosso: Proy	–
Cathilaria opuntiae (Muesebeck, 1932)	t	USNM	USA	New Mexico: N Rodeo	on *Hilaria mutica*
Chryseida aequalis (Walker, 1862)	–	INRA	French Guiana	–	–

APPENDIX 1 *Continued*

Species	Status of specimen examined (T, t)*	Depositary	Origin: Country	Origin: Locality	Host plant and host
Chryseida French Guiana	–	INRA	French Guiana	Montagne de Kaw, Patawa	–
Conoaxima affinis Brues, 1922	–	CIRAD	Colombia	Santander: San Alberto	–
Conoaxima aztecicida Brues, 1922	t	USNM	Colombia	Santander: San Alberto	–
Endobia donacis Erdös, 1964	T	MNHN	France	Var: La Garde	ex dry stem of *Arundo donax*
Eudoxinna French Guiana 1	–	FSAG	French Guiana	Montagne de Kaw, Patawa	Malaise trap
Eudoxinna French Guiana 2	–	FSAG	French Guiana	Montagne de Kaw, Patawa	Malaise trap
Eurytoma aciculata Ratzeburg, 1848	–	CIRAD	France	Notre-Dame-des-Songes	ex galls of *Salix* sp.
Eurytoma alopecuri Erdös	T	HNHM	Hungary	Lajasforras	ex *Tetramesa*
(= *Isosoma atrum* Walker, 1832)	T	BMNH	–	–	–
Eurytoma amygdali Enderlein, 1907	–	CIRAD	France	Vaucluse: Ville-sur-Auzon	ex *Amygdalus communis* seeds
Eurytoma appendigaster (Swederus, 1795)	–	CIRAD	France	Hautes-Alpes: Arvieux	–
Eurytoma aspila (Walker, 1836)	–	CIRAD	France	Hérault: Grabels	–
Eurytoma braconidis Ferrière, 1929	t	CIRAD	Chad	Bebededjia	ex *Apanteles syleptae* ex *Haritalodes derogata* (Crambidae)
Eurytoma brunniventris Ratzeburg, 1852	–	CIRAD	France	Hérault: Cazevielle	ex gall of *Plagiotrochus australis* (Cynipidae) *on Quercus ilex*
Eurytoma castorella Erdös, 1969	t	CIRAD	France	Hérault: Ferrière-les-Verreries	–
Eurytoma collaris Walker, 1832	t	CIRAD	France	Lot: Cahors	–
Eurytoma compressa (Fabricius, 1794)	t	CIRAD	France	Vaucluse: Bédoin	–
Eurytoma contumax Szelényi, 1974	t	CIRAD	France	Hautes-Alpes: Arvieux	–
Eurytoma cressoni Girault, 1915	t	CIRAD	Guadeloupe	Beausoleil, Sainte-Rose	ex fruit of *Palicourea crocea* and *Cordia* sp.
Eurytoma crotalariae Risbec, 1951	t	CIRAD	Senegal	Séfa	ex seeds of *Crotalaria retusa*
Eurytoma dentata Mayr, 1878	–	CIRAD	France	Hérault: Montferrier-sur-Lez	–
Eurytoma enicospilusi Risbec, 1952	T	MNHN	Madagascar	Békily	–
Eurytoma erythroaspis Cameron, 1904	T	CIRAD	Colombia	Santander: San Alberto	–
Eurytoma ficusgallae Bouček, 1981	T	BMNH	Zimbabwe	Salisbury	on *Ficus*
Eurytoma flavimana Boheman, 1836	–	CIRAD	France	Alpes-de-Haute-Provence: Digne	–
Eurytoma fumipennis Walker, 1836	t	CIRAD	France	Gard: Corconne	on *Euphorbia* sp.
Eurytoma gyorfii Erdös, 1957	T	CIRAD	France	Savoie: Méry	on dead wood

APPENDIX 1 *Continued*

Species	Status of specimen examined (T, t)*	Depositary	Origin: Country	Origin: Locality	Host plant and host
Eurytoma kelebiana Erdös, 1957	T	HNHM	Hungary	Darvas erdo füvein	–
Eurytoma latrodecti Fullaway, 1953	–	USNM	Australia	Townsville	ex egg sac of *Latrodectus hasserti* (Araneae)
Eurytoma leguminum Erdélyi & Szelényi, 1975	T	CIRAD	France	Hérault: Montpellier	–
Eurytoma lepidopterae Risbec, 1951	T	CIRAD	Burkina Faso	Farako-Bâ	ex *Anomis flava* on Cotton
Eurytoma morio Boheman, 1836	–	CIRAD	France	Ariège: Roquefixade	on dead wood
Eurytoma maura Boheman, 1836	–	CIRAD	France	Hérault: Montferrier-sur-Lez	on *Fraxinus excelsior* infested by *Phloeotribus scarabeoides*
Eurytoma nodularis Boheman, 1836	–	CIRAD	France	Lot: Cahors	on *Rubus* sp.
Eurytoma obtusiventris Gahan, 1934	T	CIRAD	Guadeloupe	Saint-François	ex Tephritidae on *Wedelia*
Eurytoma ochraceipes Kalina, 1970	–	CIRAD	France	Hérault: Grabels	–
Eurytoma oryzivora Delvare, 1988	T	CIRAD	Senegal	Ziguinchor, Djibélor	ex *Maliarpha separatella* (Pyralidae) on *Oryza sativa*
Eurytoma pistaciae Rondani, 1877	–	CIRAD	France	Hérault: Lespignan	–
Eurytoma plotnikovi Nikol'skaya, 1934	–	INRA	Iran	Qazvin	ex seeds of *Pistacia vera*
Eurytoma robusta Mayr, 1878	–	CIRAD	France	Lot: Lentillac, Lauzes	–
Eurytoma rufipes Walker, 1832	–	CIRAD	France	Lot: Cahors	–
Eurytoma salicis Thomson, 1876	–	CIRAD	UK	–	–
Eurytoma stenostigma Thomson, 1876	–	CIRAD	France	–	–
Eurytoma strigifrons Thomson, 1876	–	CIRAD	France	Hérault: Mauguio, Carnon	–
Eurytoma timaspidis (Mayr, 1904)	–	CIRAD	France	–	–
Eurytoma volkovi Zerova, 1994	–	–	France	Corsica: Galéria	females ovipositing within seeds of *Euphorbia characias*
Eurytoma Antsirabé 1	–	INRA	Madagascar	Route Antisirabé 35 km	–
Eurytoma Antsirabé 2	–	INRA	Madagascar	Route Antisirabé 35 km	–
Eurytoma Cambodia	–	CIRAD	Combodia	Pochentong RN 4	ex *Ophiomyia* sp. (Agromyzidae) on *Tephrosia purpurea*
Eurytoma Cébazan	–	CIRAD	France	Hérault: Cébazan	–
Eurytoma Cerbère	–	CIRAD	France	Pyrénées-Orientales: Cerbère	ex gall of *Phanacis phoenixopodes* (Cynipidae) on *Lactuca viminalis*

APPENDIX 1 *Continued*

Species	Status of specimen examined (T, t)*	Depositary	Origin: Country	Origin: Locality	Host plant and host
Eurytoma Colombia	–	CIRAD	Colombia	Santander: San Alberto	–
Eurytoma French Guiana	–	FSAG	French Guiana	Patawa	–
Eurytoma Gabon	–	CIRAD	Gabon	La Makandé	–
Eurytoma Guadeloupe	–	CIRAD	Guadeloupe	Petit-Bourg, Duclos	–
Eurytoma Kédougou	–	CIRAD	Senegal	Kédougou	–
Eurytoma Madagascar	–	INRA	Madagascar	Ambohimanga	–
Eurytoma Maroua	–	CIRAD	Cameron	Maroua, Zokok	–
Eurytoma Mourèze	–	CIRAD	France	Hérault: Mourèze	ex gall of *Salix*
Eurytoma Peru 1	–	MNHN	Peru	Loreto: Iquitos	ex *Laemosaccus ebenus* (Curculionidae) on *Myrciaria dubia*
Eurytoma Peru 2	–	MNHN	Peru	Loreto: Iquitos	ex Laemosaccus ebenus (Curculionidae) on *Myrciaria dubia*
Eurytoma RCI	–	CIRAD	Ivory Coast	Bimbresso	ex fruit of *Phragmenthera capitata*
Eurytoma Rwanda	–	CIRAD	Rwanda	Gi Kongoro	ex Braconidae ex *Gonomera carpi* (Lasiocampidae)
Eurytoma San Alberto 1	–	CIRAD	Colombia	Santander: San Alberto	–
Eurytoma Sanguéré	–	CIRAD	Cameroon	Sanguéré	–
Eurytoma Senegal	–	CIRAD	Senegal	Ziguinchor, Djibelor	ex *Ceratoneura* (Eulophidae) on *Solanum aethiopicum*
Eurytoma Tanzania	–	CIRAD	Tanzania	Magwashi	–
Eurytoma Thailand	–	CIRAD	Thailand	Farm Suwan	on Cotton
Eurytoma Tougo	–	CIRAD	Congo	Kivu: Tougo	–
Eurytomaria Maroua	–	CIRAD	Cameroon	Maroua	–
Eurytomocharis minuta Ashmead, 1894 (= *ashmeadi* Peck, 1951)	T	USNM	USA	Florida: Jacksonville	–
Evoxysoma brachypterum Ashmead, 1886	T	USNM	USA	Florida: Jacksonville	–
Exeurytoma caraganae Burks, 1971	T	USNM	Iran	Tehran	ex *Caragana* seeds
Ficomila gambiensis Bouček, 1981	T	BMNH	Zimbabwe	Salisbury	–
Ficomila Gabon	–	CIRAD	Gabon	Makokou	ex syconium of *Ficus artocarpoides*
Ficomila Tanzania	–	INRA	Tanzania	Magwashi	–
Fronsoma caudata Narendran (1994)	T	AEI	Malaysia	Negri S: Pasoh Forest Res.	–

APPENDIX 1 *Continued*

Species	Status of specimen examined (T, t)*	Depositary	Origin: Country	Origin: Locality	Host plant and host
Foutsia philodendri Burks (1971)	T	USNM	Mexico	Vera Cruz: Huatusco	ex root galls of *Philodendron*
Gibsonoma budhai Narendran (1994)	T	AEI	Taiwan	Meifeng	–
Gibsonoma Djibelor	–	CIRAD	Senegal	Ziguinchor, Djibelor	–
Ipideurytoma spessivtsevi Bouček & Novikyi, 1954	–	CIRAD	Hungary	Köszeg; Mts Irottko, 300 m	–
Isosomodes Colombia	–	CIRAD	Colombia	Santander: San Alberto	on *Solanum torvum*
Mangoma spinidorsum Subba Rao (1986)	T	BMNH	Thailand	Bangkok	ex leaf galls of *Mangifera indica*
Masneroma angulifera Bouček, 1983	–	USNM	USA	WV: Hardy Co	–
Mesoeurytoma Ecuador	–	CIRAD	Ecuador	Napo: Shushufindi	–
Mesoeurytoma Gabon	–	CIRAD	Gabon	Makokou	–
Mesoeurytoma Lamto	–	INRA	Ivory Coast	Lamto	–
Neoeurytomaria subbaraoi Narendran, 1994	T	AEI	Malaysia	Negri S: Pasoh Forest Res.	–
Neoeurytomaria Gabon	–	CIRAD	Gabon	Peni Nyoundou	–
Nikanoria szelenyii Zerova, 1974	–	CIRAD	France	Hautes Alpes: Arvieux	–
Paradecatoma bannensis Masi, 1943	t	INRA	Congo	Rutshuru	–
Paradecatoma Combretum 1	–	MNHN	Senegal	Fatick: PN Delta Satoum	ex *Combretum glutinosum* fruit
Paradecatoma Combretum 2	–	MNHN	Senegal	Fatick: PN Delta Satoum	ex *Combretum glutinosum* fruit
Paradecatoma Terminalia	–	MNHN	Senegal	Fatick: PN Delta Satoum	ex *Terminalia macroptera* fruit
Philippinoma auratofronta Narendran, 1994	T	AEI	Malaysia	Negri S: Pasoh Forest Res.	–
Philolema carinigena Cameron, 1908	T	BMNH	Borneo	Kuching	–
Phylloxeroxenus phylloxerae Ashmead, 1881	T	USNM	USA	Texas: Baton Rouge	ex *Phylloxera* galls
Phylloxeroxenus Colombia	–	CIRAD	Colombia	Santander: San Alberto	–
Phylloxeroxenus French Guiana	–	FSAG	French Guiana	Patawa	–
Phylloxeroxenus San Alberto	–	CIRAD	Colombia	Santander: San Alberto	–
Plutarchia bicariniventris Girault, 1925	–	CIRAD	Cambodia	Pochentong RN 4	ex *Ophiomyia* sp. (Agromyzidae) on *Tephrosia purpurea*
Prodecatoma philodendri Ferrière, 1924	T	CIRAD	Panama	Barro ColoI	ex *Philodendron oxycardium*
Prodecatoma maculiventris (Ashmead 1894)	T	CIRAD	Colombia	Santander: San Alberto	–
Prodecatoma seyrigi Risbec, 1952	T	MNHN	Madagascar	Békily	–

APPENDIX 1 *Continued*

Species	Status of specimen examined (T, t)*	Depositary	Origin: Country	Origin: Locality	Host plant and host
Prodecatomidea bekiliensis Risbec, 1952	T	MNHN	Madagascar	Békily	–
Prodecatomidea Cameroon	–	CIRAD	Cameroon	Piste Kounden-Koutaba	–
Pseudosystole hofferi Kalina, 1969	–	CIRAD	France	Lot: Cabrerets	–
Ramanuja swarnamus Narendran, 1994	T	AEI	Malaysia	Negri S: Pasoh Forest Res.	–
Risbecoma capensis (Walker, 1862)	t	CIRAD	Benin	Pobé	on *Ricinus communis*
Striateurytoma striatipes (Ashmead, 1904)	T	BMNH	Brazil	Para	–
Subbaella negriensis Narendran, 1994	T	AEI	Malaysia	Negri S: Pasoh Forest Res.	–
Syceurytoma ficus Bouèek, 1981	T	BMNH	Zimbabwe	Salisbury	ex twig galls on *Ficus natalensis*
Sycophila biguttata (Swederus, 1795)	–	CIRAD	France	Lot: Arcambal	–
Sycophila mellea (Curtis, 1831)	–	CIRAD	France	Lot: Saint-Géry	–
Sycophila Benin	–	CIRAD	Benin	route N'dali-Ina	ex *syconium* of *Ficus*
Sycophila Gabon 1	–	CIRAD	Gabon	Makokou	ex *syconium* of *Ficus artocarpoides*
Sycophila Gabon 2	–	CIRAD	Gabon	Makokou	ex syconium of *Ficus artocarpoides*
Systole bipunctata Erdös, 1952	T	CIRAD	France	Vaucluse: Monnieux	–
Systole Asilah	–	CIRAD	Morocco	Asilah	on Apiaceae
Systole Ventoux	–	CIRAD	France	Vaucluse: Beaumont-du-Ventoux	–
Tenuipetiolus Guadeloupe	–	CIRAD	Guadeloupe	Bouillante, Pigeon	ex seeds of *Palicourea crocea*
Tetramesa fulvicollis (Walker, 1832)	t	CIRAD	France	Lot: Labastide-Marnhac	–
Tetramesa giraudi (Schlechtendal, 1891)	–	CIRAD	France	Tarn-et-Garonne: Montauban	–
Tetramesa mongolica Szelényi, 1971	T	CIRAD	France	Hérault: Fabrègues	–
Tetramesa romana (Walker, 1873)	T	CIRAD	Spain	Grandia	on *Arundo donax*
Tetramesa Dordogne	–	CIRAD	France	Dordogne: Couze-et-Saint-Front	Malaise trap
Townesoma taiwanicus Narendran, 1994	T	AEI	Taiwan	Wushe	–
Eurytominae Ecuador	CIRAD	Ecuador	Laracunda	–	ex fruit of *Luma apiculata* (Myrtaceae)

*T, type specimen used in the present study; t, specimen compared with type.

APPENDIX 2

PROPOSED TAXONOMIC CHANGES

New generic synonymies

Axima Walker, 1862: Type species *Axima spinifrons* Walker, 1862 by monotypy (type examined).

= *Aplatoides* Yoshimoto & Gibson, 1979. Type species *Aplatoides diabolus* Yoshimoto & Gibson, 1979), by original designation (type examined). **Syn. nov**.

Aximopsis Ashmead, 1904: Type species *Aximopsis morio* Ashmead, 1904), by original designation (type examined).

= *Mesoeurytoma* Cameron, 1911. Type species *Mesoeurytoma cariniceps* Cameron, 1911, by original designation (type examined). **Syn. nov.**

= *Stireurytoma* Cameron, 1911. Type species *Stireurytoma carinata* Cameron, 1911, by original designation (type examined). **Syn. nov.**

= *Conoaxima* Brues, 1922. Type species *Conoaxima aztecicida* Brues, 1922, by original designation (type examined). **Syn. nov.**

= *Eurytomaria* Masi, 1943. *Eurytomaria aximoides* Masi, 1943, by original designation (type examined). **Syn. nov.**

= *Aximogastroma* Narendran, 1994. Type species *Aximogastroma longigastri*s Narendran, 1994, by original designation (type examined). **Syn. nov.**

Bephrata Cameron, 1884: Type species Bephrata ruficollis Cameron, 1884 by monotypy.

= *Aximogastra* Ashmead, 1904. Type species *Aximogastra bahiae* Ashmead, 1904, by monotypy (type examined). **Syn. nov.**

Bephratoides Brues, 1909: Type species *Bephratoides maculatus* Brues, 1909, by monotypy.

= *Agriotoma* Burks, 1971. Type species *Agriotoma bakeri* Burks, 1971 (type examined). **Syn. nov.**

= *Striateurytoma* Burks, 1971. Type species *Bephrata striatipes* Ashmead, 1904, by original designation (type examined). **Syn. nov.**

Bruchophagus Ashmead, 1888: Type species *Bruchophagus borealis* Ashmead, 1894, by subsequent designation (type examined).

= *Nikanoria* Nikol'kaya, 1955. Type species *Nikanoria pavlovskii* Nikols'kaya, 1955, by monotypy. **Syn. nov.**

= *Ahtola* Claridge, 1961. Type species *Isosoma atrum* Walker, 1832, by original designation (type examined). **Syn. nov.**

Eurytoma Illiger, 1807: Type species *Chalcis abrotani* Panzer, 1801, by subsequent designation.

= *Eurytomidia* Masi, 1917. Type species *Eurytomidia dubia* Masi, 1917, by monotypy (type examined). **Syn. nov.**

Fronsoma Narendran, 1994: Type species *Fronsoma caudata* Narendran, 1994, by original designation (type examined).

= *Neoeurytomaria* Narendran, 1994. Type species *Neoeurytomaria subbaraoi* Narendran, 1994, by original designation (type examined). **Syn. nov.**

Macrorileya Ashmead, 1900: Type species *Rileya oecanthi* Ashmead, 1894, by monotypy (type examined).

= *Archirileya* Silvestri, 1920. Type species *Archirileya inopinata* Silvestri, 1920, by monotypy (type examined). **Syn. nov.**

= *Anarchirileya* Bouček, 1952. Type species *Anarchirileya femorata* Bouček, 1952, by monotypy. **Syn. nov.** (synonymized with *Archirileya* by Bouček, 1958).

= *Sidonia* Erdös, 1957. Type species *Sidonia podagrica* Erdös, 1957, by monotypy (type examined). **Syn. nov.** (synonymized with *Archirileya* by Bouček, 1958).

Philolema Cameron, 1908: Type series *Philolema carinigena* Cameron, 1908, by monotypy (type examined).

= *Acantheurytoma* Cameron, 1911. Type species *Acantheurytoma spinifera* Cameron, 1911, by monotypy (type examined). **Syn. nov.**

= *Desantisca* Burks, 1971. Type species *Desantisca latrodecti* Burks, 1971, by original designation (type examined). **Syn. nov.**

= *Subbaella* Narendran, 1994. Type species *Subbaella negriensis* Narendran, 1994, by original designation (type examined). **Syn. nov.**

Phylloxeroxenus Ashmead, 1888: Type species *Eurytoma phylloxerae* Ashmead, 1881, by monotypy (type examined).

= *Evoxysoma* Ashmead, 1888. Type species *Systole brachyptera* Ashmead, 1886, by monotypy (type examined). **Syn. nov.**

Systole Walker, 1832: Type species *Systole albipennis* Walker, 1832. By monotypy.

= *Pseudosystole* Kalina, 1969. Type species *Pseudosystole hofferi* Kalina, 1969, by monotypy. **Syn. nov.**

Tetramesa Walker, 1848: Type species *Tetramesa iarbas* Walker, 1848, by monotypy (type examined).

= *Isosomorpha* Ashmead, 1888. Type species *Isosomorpha europae* Ashmead, 1894, by subsequent designation (type examined). **Syn. nov.**

New specific synonymy

Bruchophagus atra (Walker, 1832) (Isosoma) (type examined).

= *Eurytoma alopecuri* Erdös, 1969 (type examined). **Syn. nov.**

New combinations

Axima diabolus (Yoshimoto & Gibson, 1979), **comb. nov.** (from *Aplatoides*)

Aximopsis affinis (Brues, 1922), **comb. nov.** (from *Conoaxima*)

Aximopsis aximoides (Masi, 1943), **comb. nov.** (from *Eurytomaria*)

Aximopsis aztecicida (Brues, 1922), **comb. nov.** (from *Conoaxima*)

Aximopsis carinata (Cameron, 1911), **comb. nov.** (from *Mesoeurytoma*)

Aximopsis cariniceps (Cameron, 1911), **comb. nov.** (from *Mesoeurytoma*)

Aximopsis longigastris (Narendran, 1994), **comb. nov.** (from *Aximogastroma*)

Aximopsis nodularis (Boheman, 1836), **comb. nov.** (from *Eurytoma*)

Aximopsis oryzivora (Delvare, 1988), **comb. nov.** (from *Eurytoma*)

Bephrata bahiae (Ashmead, 1904), **comb. nov.** (from *Aximogastra*)

Bephratoides bakeri (Burks, 1971), **comb. nov.** (from *Agriotoma*)

Bephratoides striatipes (Ashmead, 1904), **comb. nov.** (from *Striateurytoma*)

Bruchophagus atra (Walker, 1832), **comb. nov.** (from *Isosoma*)

Bruchophagus kelebiana (Erdös, 1957), **comb. nov.** (from *Eurytoma*)

Bruchophagus nikolskayae (Zerova, 1968), **comb. nov.** (from *Systole*)

Bruchophagus pavlovskii (Nikols'kaya, 1955), **comb. nov.** (from *Nikanoria*)

Bruchophagus phlei (Erdös, 1969), **comb. nov.** (from *Eurytoma*)

Bruchophagus squamea (Walker, 1834), **comb. nov.** (from *Eurytoma*)

Bruchophagus szelenyii (Zerova, 1974), **comb. nov.** (from *Nikanoria*)

Eurytoma dubia (Masi, 1917), **comb. nov.** (from *Eurytomidia*)

Fronsoma subbaraoi (Narendran, 1994), **comb. nov.** (from *Neoeurytomaria*)

Macrorileya femorata (Bouček, 1952), **comb. nov.** (from *Anarchirileya*)

Macrorileya inopinata (Silvestri, 1920), **comb. nov.** (from *Archirileya*)

Macrorileya podagrica (Erdös, 1957), **comb. nov.** and **stat. rev.** (from *Sidonia*)

Mangoma salicis (Walker, 1934), **comb. nov.** (from *Eurytoma*)

Philolema braconidis (Ferrière, 1929), **comb. nov.** (from *Eurytoma*)

Philolema latrodecti (Burks, 1971), **comb. nov.** (from *Eurytoma*)

Philolema negriensis (Narendran, 1994), **comb. nov.** (from *Subbaella*)

Philolema spinifera (Cameron, 1911), **comb. nov.** (from *Acantheurytoma*)

Phylloxeroxenus brachypterus (Ashmead, 1886), **comb. nov.** (from *Systole*)

Phylloxeroxenus cressoni (Howard, 1897), **comb. nov.** (from *Eurytoma*)

Prodecatoma maculiventris (Ashmead, 1894), **comb. nov.** (from *Eurytoma*)

Systole hofferi (Kalina, 1969), **comb. nov.** (from *Pseudosystole*)

Sidonia podagrica Erdös, 1957 was synonymized with *Archirileya inopinata* Silvestri by Bouček (1958). A careful examination of their types by one of us (GD) showed that *inopinata* is a distinct species. Examination of the holotype of *Eurytoma maculiventris* Ashmead, 1894 proved that it is a *Prodecatoma,* as defined in the present study.

APPENDIX 3

Allocation of species included in the present study to species groups in the genera *Bruchophagus* and *Eurytoma*.

Species	Species group	Genus
Bruchophagus Alicante	*borealis*	*Bruchophagus*
Bruchophagus caucasicus Zerova, 1992	*gibbus*	*Bruchophagus*
Bruchophagus gibbus (Boheman, 1836)	*gibbus*	*Bruchophagus*
Bruchophagus macronyis Fedoseeva, 1956	*gibbus*	*Bruchophagus*
Bruchophagus platypterus (Walker, 1834)	*gibbus*	*Bruchophagus*
Bruchophagus roddi Gussakovskiy, 1933	*gibbus*	*Bruchophagus*
Bruchophagus seyali (Risbec, 1951)	*gibbus*	*Bruchophagus*
Bruchophagus vignae (Risbec, 1951)	*gibbus*	*Bruchophagus*
Bruchophagus squamea (Walker, 1834)	*squamea*	*Bruchophagus*
Bruchophagus kelebiana (Erdös, 1957)	*kelebiana*	*Bruchophagus*

APPENDIX 3 *Continued*

Species	Species group	Genus
Bruchophagus trigonellae Zerova, 1970	*kelebiana*	*Bruchophagus*
Bruchophagus phlei (Erdös, 1969)	*phlei*	*Bruchophagus*
Bruchophagus atra (Walker, 1832) (= *Eurytoma alopecuri* Erdös, 1969)	*atra*	*Bruchophagus*
Eurytoma aciculata Ratzeburg, 1848	*aciculata*	*Eurytoma*
Eurytoma amygdali Enderlein, 1907	*amygdali*	*Eurytoma*
Eurytoma plotnikovi Nikol'skaya, 1934	*amygdali*	*Eurytoma*
Eurytoma stenostigma Thomson, 1876	*stenostigma*	*Eurytoma*
Eurytoma appendigaster (Swederus, 1795)	*appendigaster*	*Eurytoma*
Eurytoma castorella Erdös, 1969	*appendigaster*	*Eurytoma*
Eurytoma collaris Walker, 1832	*appendigaster*	*Eurytoma*
Eurytoma flavimana Boheman, 1836	*appendigaster*	*Eurytoma*
Eurytoma leguminum Erdélyi & Szelényi, 1975	*appendigaster*	*Eurytoma*
Eurytoma maura Boheman, 1836	*morio*	*Eurytoma*
Eurytoma morio Boheman, 1836	*morio*	*Eurytoma*
Eurytoma fumipennis Walker, 1836	*fumipennis*	*Eurytoma*
Eurytoma volkovi Zerova, 1994	*fumipennis*	*Eurytoma*
Eurytoma brunniventris Ratzeburg, 1852	*rosae*	*Eurytoma*
Eurytoma contumax Szelényi, 1974	*rosae*	*Eurytoma*
Eurytoma rufipes Walker, 1832	*rosae*	*Eurytoma*
Eurytoma robusta Mayr, 1878	*robusta*	*Eurytoma*
Eurytoma strigifrons Thomson, 1876	*robusta*	*Eurytoma*
Eurytoma crotalariae Risbec, 1951	*crotalariae*	*Eurytoma*

APPENDIX 4

Species removed from genera *Prodecatoma*, *Bruchophagus*, or *Eurytoma* and awaiting generic placement.

Aspila Walker, 1836: Described in *Decatoma*; transferred to *Bruchophagus* by Szelényi (1976); included in *Eurytoma* by Bouček & Graham (1978); belongs to the *aspila* species group *bajarii* Erdös, 1957. Described in *Eurytoma*; transferred to *Bruchophagus* by Graham (1996); belongs to the *bajarii* species group.

Dentata Mayr, 1878: Described in *Eurytoma*; belongs to the *dentata* species group *ficusgallae* Bouček, 1981. Described in *Eurytoma*; species *sola*.

Obtusiventris Gahan, 1934: Described in *Eurytoma*; belongs to the *obtusiventris* species group.

Ochraceipes Kalina, 1970: Described in *Eurytoma*; belongs to the *dentata* species group.

Pistaciae Rondani, 1877: Described in *Eurytoma*; belongs to the *dentata* species group.

Seyrigi Risbec, 1952: Described in *Prodecatoma*; belongs to the *dentata* species group.

Timaspidis Mayr, 1904: Described in *Eurytoma*; transferred to *Bruchophagus* by Ferrière (1950); belongs to the *aspila* species group.