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Generic revision and phylogenetic analysis of the Metriorrhynchinae (Coleoptera: Lycidae)

LADISLAV BOCAK

Faculty of Science, Palacký University, tř. Svobody 26, 771 46 Olomouc, Czech Republic; e-mail: ladislav.bocak@upol.cz

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Abstract. The subfamily Metriorrhynchinae is the most species-rich clade of Lycidae (Coleoptera). A recent proposal suggests that the Erotinae is a sister group of the Metriorrhynchinae. Within the Metriorrhynchinae, evidence is presented for the monophyly of the Conderini and Metriorrhynchini and their sister group position. The Trichalina, Hemiconderina and Metriorrhynchina form the tribe Metriorrhynchini. The relationships between the basal lineages of this group are poorly understood. Several clades are distinguished within the Metriorrhynchina, but there is only weak evidence supporting a relationships between them. The distribution of individual clades is discussed. *Carathrix* Kleine, 1926 (= *Pseudodontocerus* Pic, 1921), *Dilolycus* Kleine, 1926 (= *Metriorrhynchus* Gemminger et Harold, 1869), *Flabelloporrostoma* Pic, 1923 (= *Metriorrhynchus* Gemminger et Harold, 1869), *Rossioptera* Kasantsev, 1988 (= *Xylobanellus* Kleine, 1930), *Samanga* Pic, 1921 (= *Broxylus* C.O. Waterhouse, 1879), *Strophicus* C. O. Waterhouse, 1879 (= *Enylus* C.O. Waterhouse, 1879), and *Tapromenoeus* Bocak et Bocakova, 1989 (= *Prometanoeus* Kleine, 1925) are proposed as junior synonyms. *Pseudosynchonnus* Pic, 1922 is transferred to the Erotinae (Taphini) and *Pseudosynchonnus* Pic, 1922, *Protaphes* Kleine, 1926, and *Parapyropterus* Kleine, 1926 are proposed to be junior subjective synonyms of *Lycoprogenthes* Pic, 1915. Redescriptions of Metriorrhynchinae genera and a key to genera are provided.

INTRODUCTION

The Metriorrhynchinae is the largest subfamily of Lycidae, both in the number of genera and number of species. Kleine (1933) listed in the last World Catalogue about 1200 species in 41 genera now classified in this subfamily. That is, in terms species this subfamily make up over 40 percent of the Lycidae. Most Metriorrhynchinae are from Southeast Asia, the Indonesian Archipelago, New Guinea and Northern Australia. Further species occur in Africa, Madagascar, temperate Asia, Ceylon, and India. Only one species occurs in Eastern Europe and in Siberia. Within Lycidae, Metriorrhynchinae are defined by their circular phallobase (Figs 91–132), flat, conspicuous, unpaired vaginal gland in most representatives (Figs 143–160), and a pronotum with lanceolate median areola, usually with lateral and frontolateral pronotal carinae (Figs 57–86). Metriorrhynchinae appear to be close to the Erotinae as they have very similar pronotal carinae in some forms, structurally similar elytral costae, male and female genitalia similar in some features, and generally similar larvae (Bocak and Matsuda, in press).

Fabricius (1775) described the first species that is now placed in Metriorrhynchinae (*Pyrochroa serraticornis* now classified in *Trichalus*) and later proposed several additional species (Fabricius, 1801). Numerous entomologists working on the material collected by scientific expeditions in the first half of the XIXth century (Dalman, Fåhraeus, Macleay, Hope, Klug, and Boisduval) followed Fabricius. They described few species and classified them in then genera *Lycus* F., 1787, *Calopteron* Castelnau, 1838, or *Dictyoptera* Latreille, 1829. Guérin-Méneville (1830, 1838) and Castelnau (1838), were the first to introduce the genera of Metriorrhynchinae to lycid classification: *Cladophorus* Guérin-Méneville, 1830, *Metriorhynchus* Guérin-Méneville, 1838, and *Porrostoma* Castelnau, 1838. Various authors disagreed with the dating of their descriptions, and the validity of these taxa was clarified much later by Bocak (1998c). Numerous authors added further species to various genera (e. g. Erichson, Blanchard, Thomson, Walker, Motschulsky, Redtenbacher, Kiesenwetter, and Kirsch). C.O. Waterhouse (1877, 1879) alone proposed thirteen new genera which still form the backbone of Metriorrhynchinae classification. He described also numerous new species from different parts of the Metriorrhynchinae range of distribution. Further species were proposed in the last decades of the XIXth century (Blackburn, Bourgeois, Fairmaire, Gorham, Harold, Kirsch, Kiesenwetter, Lea, W. M. Leay, and Schaufuss). Only two authors, R. Kleine and M. Pic, contributed substantially to the knowledge of Lycidae before World War II. They described hundreds of new species and several new genera. Kleine and Pic defined genera mostly on the basis of the presence or absence of secondary costae, flabellate antennae or the number of pronotal carinae. Congruence of these criteria with other characters needs to be established. Unlike Pic, Kleine dissected genitalia, but preferred other characters for classification. Consequently, Kleine (1926a) classified *Metriorrhynchus parallelus* in *Cladophorus* on the basis of its flabellate antennae, although it is the type species of *Metriorrhynchus*, which he recognised.

Only a few species were described after World War II. Nakane (1968, 1969a, b, 1971, 1980) studied the fauna of Japan and Taiwan, Kasantsev (1988) described the genus *Rossioptera* (= *Xylobanellus* Kleine) from Russia, but he did not classify it in the Metriorrhynchinae. Bocak &

Bocakova (1987b, 1989, 1990b, 1991, 1999), Bocak (1998a, b, d, e, 1999a, b, 2000a, b, c, d, 2001a, b), and Bocak & Matsuda (1998) published several geographically limited revisions and descriptions of new species from the Oriental Region and New Guinea. Bocak (1998c) solved the long lasting uncertainty about the status of the genera described by Guérin-Méneville. Calder (1998) compiled a catalogue of Australian Lycidae and proposed 85 new combinations within the *Porrostoma*. These new combinations were not based on the study of type specimens, and therefore the generic classification of Australian Lycidae remains obscure.

At present, the entire classification of the Metriorrhynchinae at the species and generic levels is chaotic. A large part of this confusion results from the inadequate nature of Pic's descriptions and unclear reasons for his proposals. He thought that as his descriptions were long they would be useful (W. Wittmer, pers. comm.). As Kleine usually ignored Pic's descriptions, revisions of most genera are urgently needed.

The subfamily Metriorrhynchinae was proposed by Kleine (1926a), along with the subfamily Dilolycinae (=Haplothoracinae, nomen nudum). Later he described the subfamilies Trichalinae and Cladophorinae (Kleine, 1928). Kleine (1933) designated all these taxa as tribes of Lycinae. Bocak & Bocakova (1990a) proposed the tribe Conderini and subtribe Hemiconderina, synonymised Cladophorinae and Dilolycinae with Metriorrhynchinae and downgraded Trichalinae to the subtribal level. Metriorrhynchinae was made up of two tribes, Conderini and Metriorrhynchini, the later being divided to the subtribes Trichalina, Metriorrhynchina and Hemiconderina. Bocak (1998b) revised the generic classification of the Trichalina.

The species richness and high endemism in the transitional Austro-Oriental zone, as well as the restriction of Lycidae to moist forests and usually to mountainous habitats, suggest that Metriorrhynchinae could be a valuable model group for evolutionary and zoogeographical studies. This characteristic is combined with the fact that Lycidae are models in numerous mimicry complexes. Despite all this, the poor knowledge of Metriorrhynchinae has prevented them from being used for more general studies. Research on this group has suffered from the absence of comprehensive definitions of genera as well as the doubtful phylogenetic affinities between genera and tribes. This paper should establish the basis for further study of this extremely diverse group.

Natural history

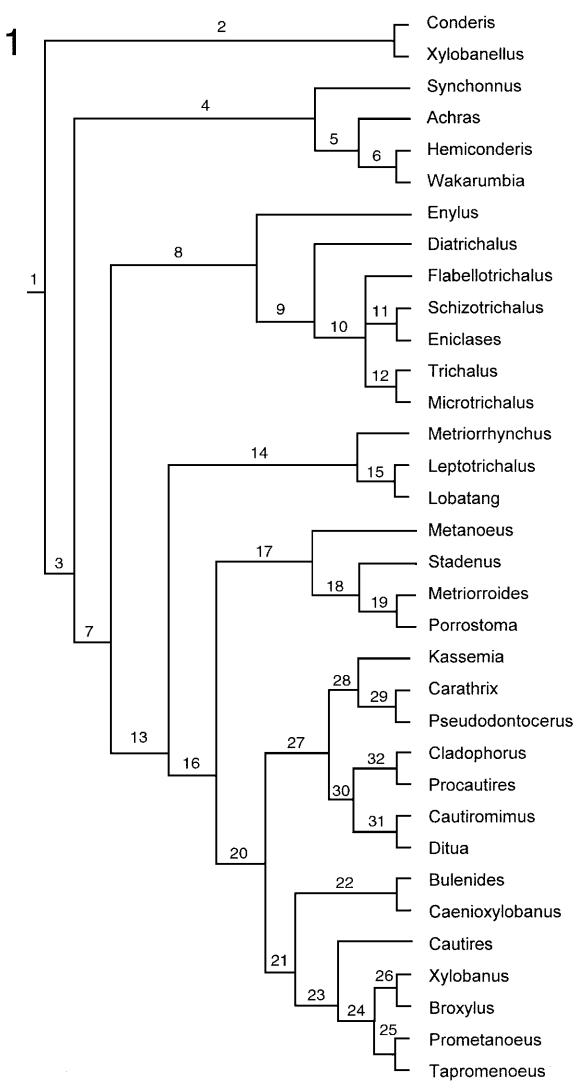
Metriorrhynchinae are one of the commonest groups of Lycidae in tropical Asia and Australia. The adults live mostly on the leaves of shrubs and herbs in dense forest canopy. Although most specimens in museum collections were collected individually or by sweeping of the lower strata of tropical forests, Metriorrhynchinae are active also in the upper strata as shown by the material obtained by insecticidal fumigation in Sulawesi (Bocak, 2000c). They are generally slow moving and fly only occasionally and reluctantly. The highest dispersal activity was observed in early morning and shortly before sunset. Some species are attracted to light but the proportion of Lycidae collected at lights is generally low. Unlike Lycinae, the Metriorrhynchinae are rarely attracted to flowers. *Leptotrichalus* are the only Metriorrhynchinae regularly collected on flowers in South East Asia. Flowers in Australia attract at least some species of *Porrostoma* and *Trichalus*. Larvae were collected in decaying wood. Lycidae generally seek moist conditions and inhabit rotten trunks or branches in shaded places, often laying on the ground and in close contact with moist soil. Several larvae of Metriorrhynchinae have been described. Burakowski (1988) described the larva and pupa of *Xylobanellus erythropterus*; Hayashi (1954), Fukuda & Hayashi (1981), and Hayashi (1986) described several Japanese species of *Cautires*. Potozkaja (1981) described the larva of *Xylobanus angusticollis* (Motschulsky). Other larvae of Metriorrhynchinae were reported recently by Bocak & Matsuda (in press). Metriorrhynchinae are often involved in Müllerian mimicry complexes, Lawrence & Britton (1991) mentioned those from Australia. Moore & Brown (1981) studied the antifeedants in the body of *Porrostoma rhippidium* (W. M. Leay, 1827).

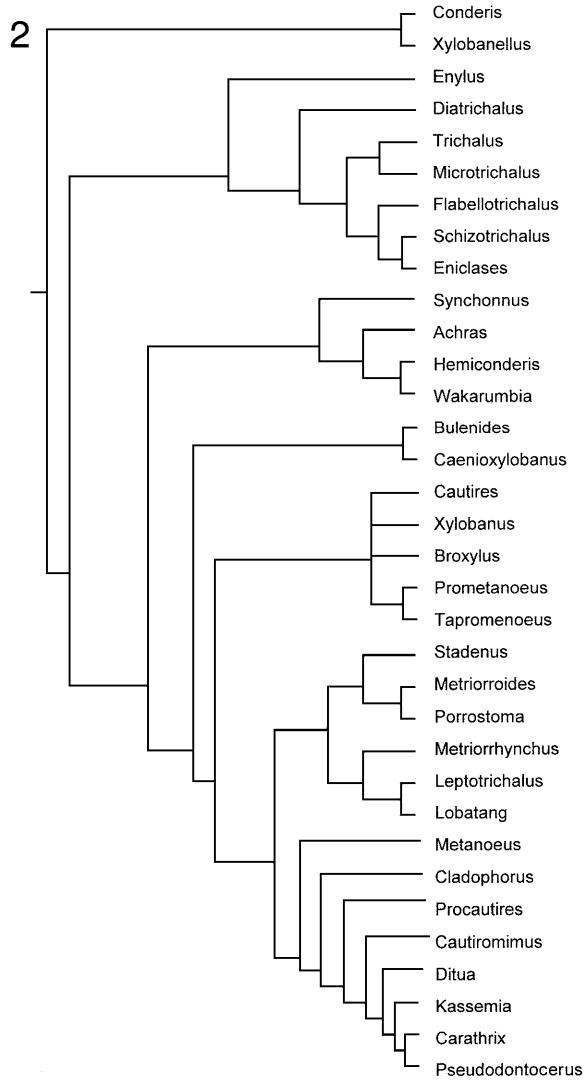
MATERIAL AND METHODS

Taxa

Altogether 45 genera were classified in the Metriorrhynchinae and Bocakova (in press) transferred *Broxylus* to the Metriorrhynchinae: for a list of genera see Appendix 1. The phylogenetic analysis deals with 34 genera of Metriorrhynchinae. One of Metriorrhynchinae genera was found to be a member of the Erotinae (*Pseudosynchonnus*). Four genera were synonymised prior the analysis, because they did not differ from genera included in the analysis: *Dilolycus* (= *Metriorrhynchus*), *Flabelloporrostoma* (= *Metriorrhynchus*), *Samanga* (= *Broxylus*), and *Strophicus* (= *Synchonnus*). One genus was not found in Pic's collection and its identity is unknown (*Falsolucidota*). The genera *Mimoxylobanus*, *Oriomum*, *Cladophorinus*, *Xylobanomorphus*, *Xylobanomimus*, and *Malacolycus* are available only as single specimens of one sex, and therefore they were excluded from the analysis. Their redescriptions and discussion of their possible systematic position are given in the taxonomic part. The proportion of unknown character states is very high for these genera and this uncertainty collapsed the basal part of the tree of Metriorrhynchini to the unresolved bush. Wiens (1998) discussed the consequence of a high proportion of missing data. All the genera excluded from the analysis as well as genus of unknown identity are monotypic, therefore their exclusion did not restrict substantially the scope of the analysis. All type species of Metriorrhynchinae genera were studied except *Falsolucidota* Pic, 1921b, which should be deposited in the National Museum of Natural History in Paris, but was not found in Pic's collection.

Bocak & Bocakova (1990a) reclassified the Metriorrhynchinae. Evidence for monophyly was sought in the morphology of the ingroup and trees were rooted using the outgroup method (Watrous & Wheeler, 1981). A sister-group for the Metriorrhynchinae was not suggested by previous authors and the possibility of a close relationship between Erotinae and Metriorrhynchinae based on larval characters was briefly discussed by Bocak & Matsuda (in press). In addition, Erotinae and Metriorrhynchinae have the same arrangement of elytral costae, carinae on the pronotum and slender parameres (present only in



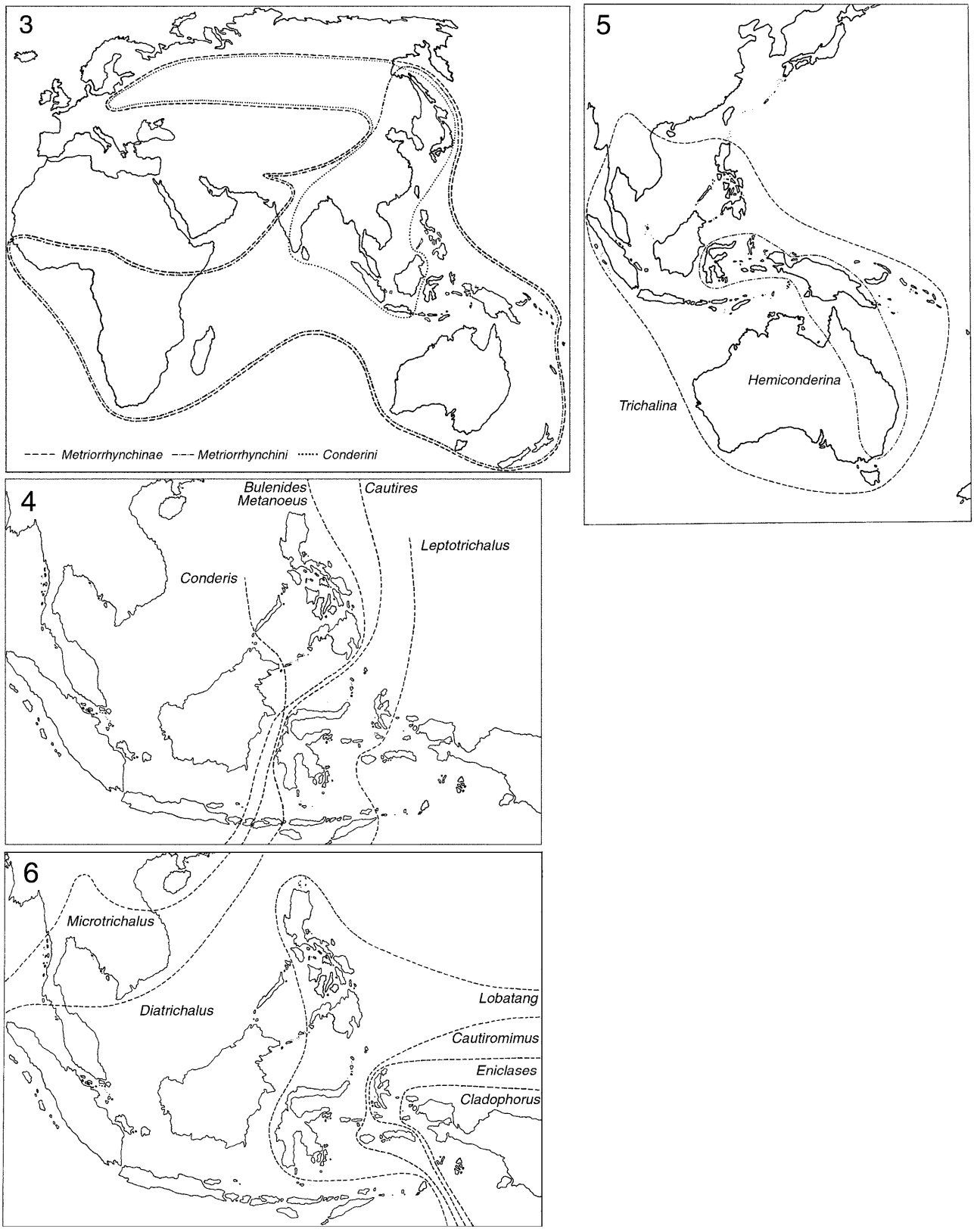


Figs 1–2: Cladograms. 1 – the strict consensus tree derived from three trees provided by an analysis of the matrix in Table 2 (mh*, bb*); 2 – the strict consensus tree based on two trees obtained after application of successive weighting. The numbers above branches correspond to node numbers in Tab. 3.

Conderini within the Metriorrhynchinae). The phylogeny of Lycidae has not yet been analysed, and therefore multiple outgroups were chosen and the impact of switching to different outgroups tested. The following taxa were used as outgroups: *Dictyoptera* (represented by *D. aurora* (Herbst)) and *Pyropterus* (*P. nigroruber* (Degeer)) from Erotinae as presumably the closest sister-group, *Lyponia* (*L.* (*Ponyalis*) *laticornis* Fairmaire), which is considered to be the most basal member of Platerodinae (Bocakova, 2001), and *Calochromus* (*Calochromus* sp. from Yunnan) from the Calochrominae. *Dictyoptera* and *Pyropterus* represent genera that have and lack secondary elytral costae. This character was thought to be important for the generic classification of Lycidae. The selected outgroups represent all potential relatives of Metriorrhynchinae. The remaining subfamilies of Lycidae differ substantially in adult and larval characters (Lycinae: Lycini and Macrolycini) and in addition some of them have neotenous females (*Dulticola*, *Platerodrilus*, presumably Ateliinae, Leptolycinae: Dexorini).

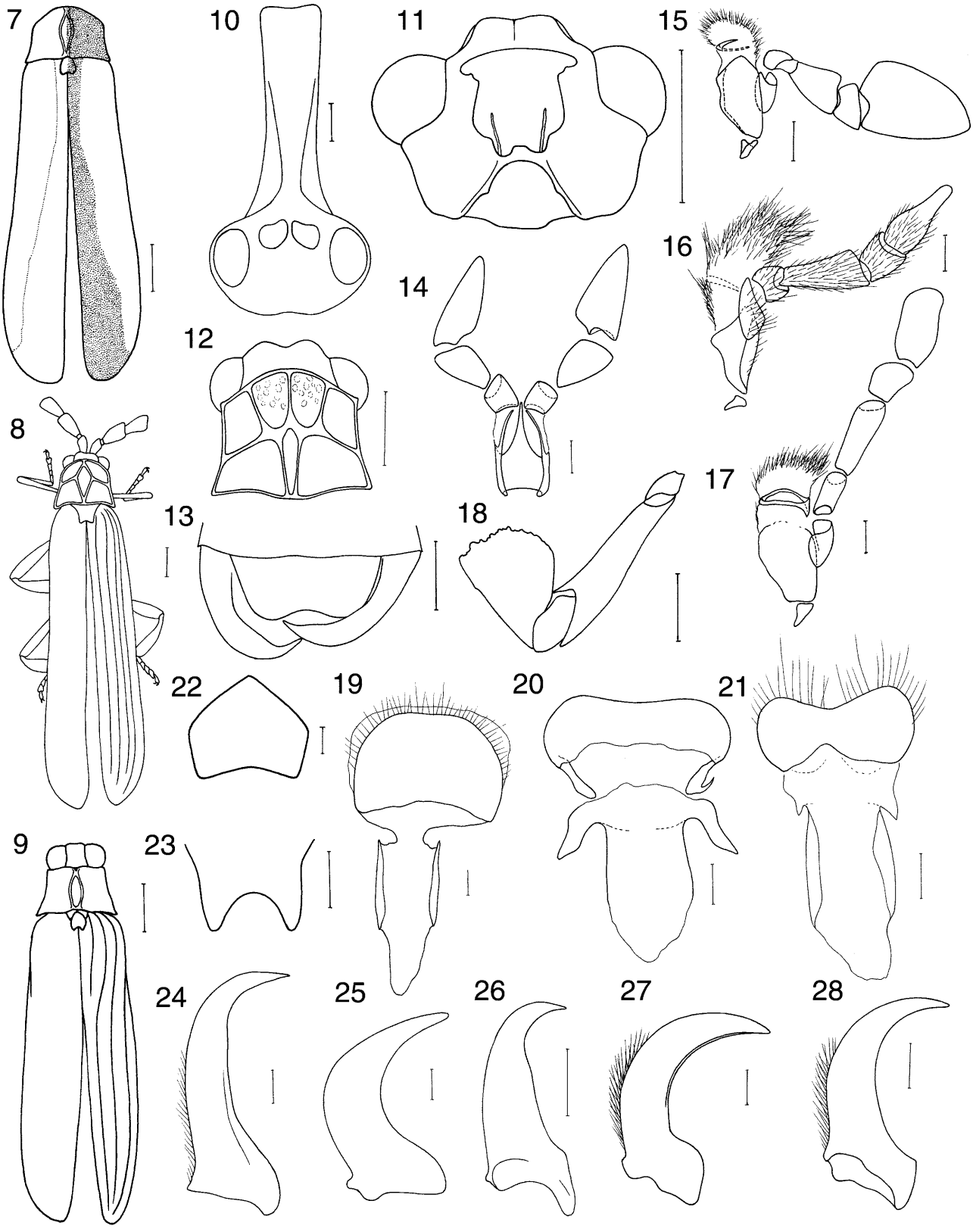
Characters

I identified 72 characters, 67 potentially informative for the relationships within an ingroup and five of them constant within an ingroup and used for its definition. Polymorphic characters in terminal taxa were coded as "-" in the matrix, and all characters are described in Table 1. Autapomorphic characters of individual genera were not included and they are discussed in the taxonomic part. When possible, several species of each genus were scored for each character. The genera included in the analysis were always available as type(s) or identified specimens of type species of both sexes. In several cases, data from disarticulated closely related species were compared with the type species. Because of the danger of inappropriate sampling, the examination of several representatives of each genus was preferred. This was easy in case for recently revised genera, but difficult in the case of the very large genera used by M. Pic (*Metriorrhynchus*, *Cladophorus*, *Cautires*), for genera typologically consisting of very diverse groups of unrelated species (*Procautires*) or genera formally monotypic but based on numerous undescribed species. I preferred to score the group of species closely related to the type-species. An alpha-taxonomic study of such genera was beyond the scope of this paper.



Figs 3–6: Distribution. 3 – distribution of subfamily and tribes; 4 – eastern limit of range of Asian continental elements; 5 – distribution of Hemiconderina and Trichalina; 6 – western limit of range of Australian elements.

The present study is based exclusively on adults. Both male and female genitalia of all available type specimens were dissected and the membranous parts stained lightly with chlorazol black. Important characters were drawn using an ocular grid-screen or illustrations were derived from photographs taken with an Olympus DP-10 or Camedia 3000 digital camera attached to an Olympus SZX-12 stereoscopic microscope.



Figs 7–28: 7–9. General appearance. 7 – *Enylus amplus*; 8 – *Wakarumbia grandis*; 9 – *Lobatang sordescens*; 10–11. Head. 10 – *Porrostoma rhippidium*; 11 – *Diatrichalus* sp.; 12 – pronotum, *Metriorrhynchus fessus*; 13 – labrum, *Pseudodontocerus pulcher*; 14 – labium, *Metriorrhynchus parallelus*; 15–17. Maxilla. 15 – *Broxylus fenestratus*; 16 – *Prometanoeus ochraceus*; 17 – *Metanoeus* sp.; 18 – maxillary palpus, *Pseudodontocerus pulcher*; 19–21. Labrum and hypopharynx. 19 – *Metriorrhynchus parallelus*; 20 – *Conderis signicollis*; 21 – *Metanoeus* sp.; 22–23. Scutellum. 22 – *Schizotrichalus nigrescens*; 23 – *Metriorrhynchus mirabilis*; 24–28. Mandible. 24 – *Metriorrhynchus parallelus*; 25 – *Conderis signicollis*; 26 – *Broxylus fenestratus*; 27 – *Pseudodontocerus* sp.; 28 – *Cladophorus* sp. Scale 0.5 mm (Figs 1–6, 17), 0.2 mm (Figs 7, 12), 0.1 mm (Figs 8–11, 13–16, 18–22).

TABLE 1. List of characters and character states used in the cladistic analysis of Metriorrhynchinae

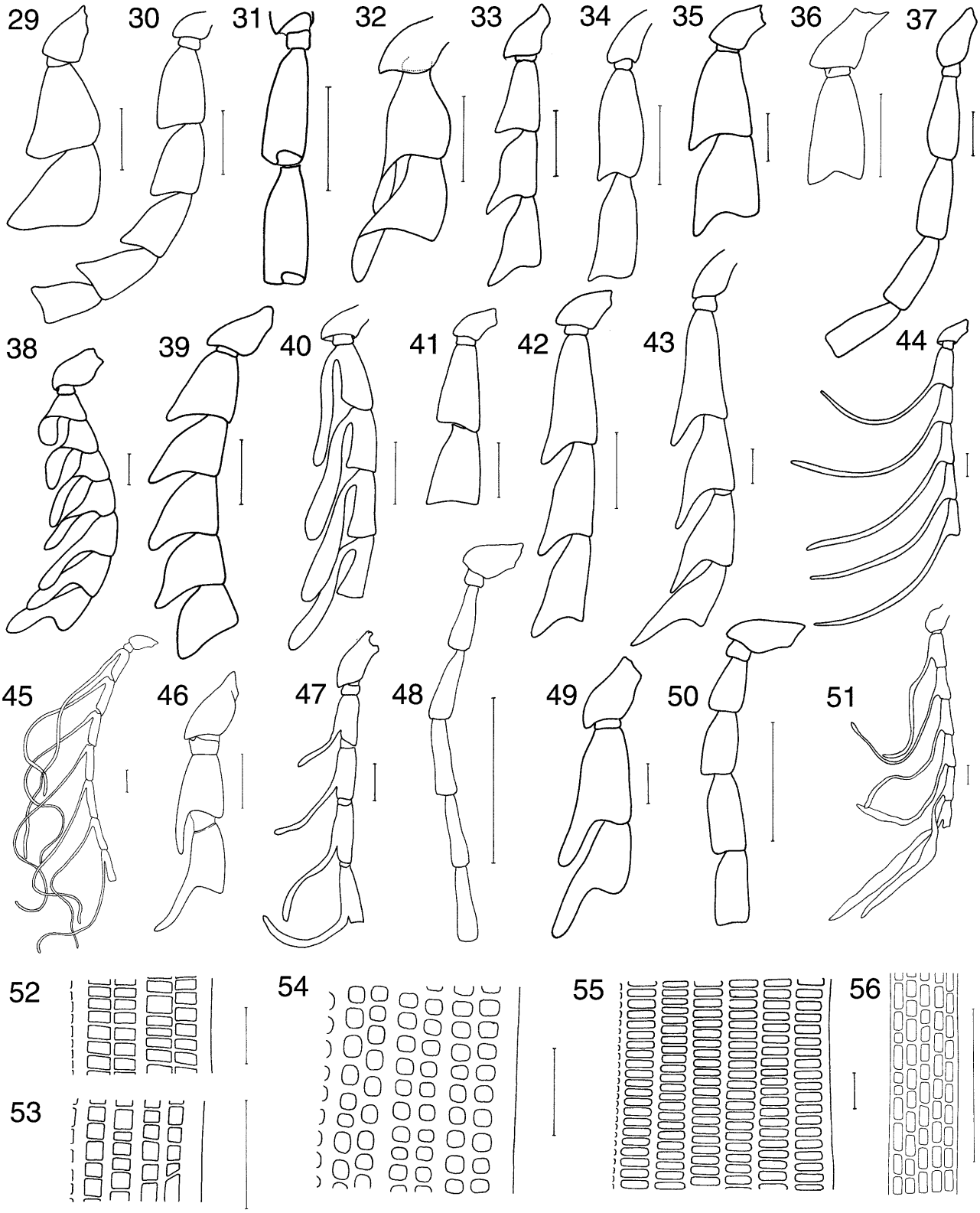
1	Rostrum	0, absent (Fig. 11); 1, present (Fig. 10)
2	Clypeo-genal suture	0, absent or unclear; 1, short; 2, long
3	Gula	0, longitudinal or rectangular; 1, transverse (Fig. 11)
4	Frontal margin of clypeus	0, convex; 1, concave; 2, straight; 3, bisinuate; 4, shallowly emarginate
5	Apex of labrum	0, simply rounded; 1, emarginate (Figs 19–21)
6	Labral arms	0, long, slender; 1, with stout base; 2, fused with lateral margin of labrum
7	Mandibles	0, long, stout, considerably curved (Fig. 25, 27, 28); 1, small, slender (Fig. 24); 2, small, slender with apex curved at a right angle
8	Molar	0, present, or at least mandibular base robust (Figs 25–28); 1, absent (Fig. 24)
9	Ventral mandibular condyle	0, ventrally directed; 1, caudally directed, robust; 2, caudally directed, weak
10	Apical segment of maxillary palpus	0, robust (Fig. 15); 1, slender (Fig. 16–17)
11	Tubercles on margin of terminal maxillary palpomere	0, absent (Fig. 15–17); 1, present (Fig. 18)
12	Tubercles on margin of terminal labial palpomere	0, absent (Fig. 14); 1, present
13	Antennae	0, rounded in cross-section; 1, considerably compressed
14	Male antennomeres 3–10 lamellae	0, with wide lamellae, serrate, filiform (Figs 29–39); 1, with slender lamellae
15	Male antennomeres 3–10	0, filiform or serrate; 1, flabellate (Fig. 38)
16	Length of antennomere 2	0, comparable with antennomere 3; 1, considerably shorter (Fig. 29–51)
17	Female antennae	0, serrate or filiform (as in Fig. 30); 1, flabellate (Figs 46–47)
18	Frontolateral pronotal carinae	0, absent (Figs 57–65); 1, present or at least vestigial (Figs 69–83)
19	Lateral pronotal carinae	0, present (Figs 57–59, 69–83); 1, absent or vestigial (Figs 61–68)
20	Frontal margin of pronotum	0, simple Figs 57–66, 69–86); 1, strengthened, formed by two carinae (Figs 67–68)
21	Median areola	0, constricted at base; 1, not constricted (Figs 87–86)
22	Median areola/frontal margin	0, directly attached (Fig. 61); 1, connected by costa (Figs 57–59, 62–86)
23	Shape of median areola	0, in middle, usually large (Figs 57–61); 1, small, short, attached to pronotal base (Figs 68–73, 77–86); 2, slender, *Trichalus* type (Figs 62–65)
24	Base of pronotum	0, with symmetrical bulges; 1, without symmetrical bulges
25	Number of pronotal areoles	0, less than seven (Figs 57–68); 1, seven (Figs 71–83)
26	Shape of pronotum	0, with apparent frontal angles and elevated lateral margins (Figs 57–73, 75–80); 1, rounded frontal angles, compact lateral margins (Figs 74, 81)
27	Pronotal carinae	0, robust, obtuse; 1, slender, straight (Figs 59–60)
28	Lateral margins of pronotum	0, without tubercles (Figs 57–59); 1, with tubercles (Figs 61–66); 2, slightly widened before base (Figs 76, 78)
29	Secondary elytral costae	0, fully developed (Figs 52–55); 1, present only close to humeri; 2; completely absent (Fig. 87); 3; absent only in middle part
30	Primary elytral costa 1	0, fully developed (Fig. 8); 1; considerably shortened (Fig. 9)
31	Primary elytral costa 3	0, full; 1, weaker at apex; 2; considerably shortened; 3, absent
32	Strength of costae	0, equal; 1, costae 2 and 4 much stronger, or at least costa 2 stronger
33	Elytral cells	0, transverse or rectangular (Fig. 55); 1, rounded, small (Fig. 54)
34	Process of mesothoracic spiracular plate	0, absent; 1, short; 2, long; 3, without process, spiraculum in form of large tube
35	Metascutellar hind margin	0, emarginate with keel; 1, straight without keel; 2, straight with keel
36	Mesoscutellar lateral process	0, absent or short; 1, long
37	Lenght of alacrista	0, as long as scutoscutellar suture or longer; 1, distinctly shorter

Table 1 (continued).

38	Width of mesosternal process	0, wide; 1, narrow
39	Tibial spurs on hind legs	0, present; 1, absent; 2, very short
40	Apical part of phallus	0, rounded in cross section or dorsoventrally compressed; 1, considerably laterally compressed
41	Phallus short, wide, robust	0, no; 1, yes (Figs 122, 125, 127)
42	Phallus lanceolate, widest at apex	0, no; 1, yes (Figs 92, 107, 108, 109)
43	Phallus slender, narrows at apex, membranous ventrally	0, no; 1, yes (Figs 103, 104)
44	Phallus slender, tubular	0, no; 1, yes (Figs 117–120)
45	Internal sac	0, membranous, without sclerotized structures (Fig. 91); 1, with two apical paired spines (Figs 107–110); 2, with two basal paired spines (Figs 125, 127); 3, linearly arranged spines; 4, spines fused (Fig. 94); 5, with stick-like structure (Fig. 121); 6, phallus with unique structure apically (Figs 100–101)
46	Internal sac with sclerotised plates or ducts	0, no; 1, yes (Figs 121–123, 125–126)
47	Phallus very slender, with weakly bulbous base, apex often rotated	0, no; 1, yes (Fig. 94)
48	Process at bases of paramerae	0, absent; 1, present
49	Phallus with dorsal keel	0, no; 1, yes (Figs 105, 106)
50	Base of phallus	0, straight; 1, hook-like (Fig, 91)
51	Basal tubercle of phallobase	0, absent; 1, present
52	Internal sac	0, completely membranous, colourless, retracted in phallus (Fig. 91); 1, exposed, at least partly sclerotized or coloured
53	Primary gonoporus	0, membranous; 1, sclerotized (Figs 122, 125, 126)
54	Parameres	0, present; 1,absent (Figs 92–132)
55	Shape of basal part of phallus	0, fused with basal part of parameres; 1, simply narrowed (Fig. 112); 2, obtuse or widened (Fig. 121, 127]
56	Symmetry of basal part of phallus	0, symmetrical (Fig. 112); 1, asymmetrical, type *Metriorrhynchus* (Fig. 114–116); 2, asymmetrical type *Trychalus* (Fig. 104)
57	Phallobase	0, elongate; 1, circular
58	Basal margins of coxites	0, strengthened; 1, simple; 2, plate-like
59	Phallobasal membrane	0, soft, colourless; 1, pigmented, sometimes sclerotised (Figs 114–116)
60	Valvifers fused with coxites	0, no; 1, yes (Fig. 156, 159)
61	Valvifers distinctly widened medaslly	0, yes; 1, no (Fig. 133)
62	Valvifers	0, much longer than coxites; 1, moderately long (Figs 151–153); 2, shortened, widened at apex (Fig. 136); 3, vestigial (Fig. 150)
63	Lateral glands with narrow ducts	0, no (Fig. 142); 1, yes (Figs 147–160)
64	Unpaired gland	0, absent or minute, filiform (Fig. 142); 1, flat, distinct (Fig. 147)
65	Lateral glands	0, inserted apically or laterally (Fig. 147); 1; inserted dorsally
66	Spermatheca	0, bulbous at least apically (Figs 142–144); 1, very slender
67	Paraproctus	0, with lateral sclerites fused to valvifers; 1, with free lateral sclerites; 2, simple, without lateral sclerites
68	Basal part of male sternum S8	0, very narrow basally; 1, quite wide, simply rounded; 2, wider, short; 3, widened, constricted before apex
69	Sternum S7	0, emarginate; 1, straight
70	Window in male sternum S8	0, present; 1, absent
71	Spiculum gastrale	0, present (Fig. 162); 1, absent
72	Apex of female sternum S7	0, simple; 1, shallowly emarginate; 2, deeply emarginate

Phylogenetic analysis

A total of 72 characters, as given in Table 2 were run unordered and unweighted. The minimum length trees were searched using computer program Hennig86 ver. 1.5 (Farris, 1988) using the Wagner parsimony analysis. The procedure of "mh*" (multiple hennig) and "bb*" (branch breaking) were used in all analyses. The results obtained by this procedure are uncertain to be of minimal length, but the implicit enumeration was not used because the matrix was too extensive and the computer equipment unable to deliver the results in a reasonable time. Subsequently using the "xstep" command each character was weighted according to its fit to the tree in the preceding run. The



Figs 29–56: 29–51. Basal antennomeres. 29 – *Conderis signicollis*, male; 30 – *Achras limbatus*, male; 31 – *Hemiconderis gracilis*, male, ventral view; 32 – *Diatrichalus salomonensis*, male; 33 – *Diatrichalus assimilis*, male; 34 – *Microtrichalus griseus*, male; 35 – *Trichalus flavopictus*, male; 36 – *Metriorrhynchus mirabilis*, female; 37 – *Prometanoeus ochraceus*, male; 38 – *Cautires ratus*, male; 39 – *Caenioxylobanus ater*, female; 40 – *Metanoeus pallidus*, male; 41 – *Metriorrhynchus inaequalis*, male; 42 – *Porrostoma lateralis*, male; 43 – *Metriorrhynchoides helleri*, male; 44 – *Cladophorus elegantulus*, male; 45 – *Pseudodontocerus* sp., male; 46 – *Pseudodontocerus pulcher*, female; 47 – *Pseudodontocerus* sp., female; 48 – *Malacolycus paululus*, male; 49 – *Porrostoma rhipidium*, male; 50 – *Mimoxylobanus reticulatus* , male; 51 – *Cladophorus* sp., male; 52–56. Elytral reticulation. 52 – *Porrostoma* sp.; 53 – *Pseudodontocerus pulcher*; 54 – *Pseudodontocerus* sp.; 55 – *Metriorrhynchoides* sp.; 56 – *Malacolycus paululus*. Scales 0.5 mm.

TABLE 2. Data matrix

	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	77
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	12
Dictyoptera	0000000010	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	01
Calochromus	0002000120	0000000010	---00000--	--00000000	0000000000	0000000000	1000000001	02
Lyponia	0001100010	00-0100010	---0000000	1000100000	0000000000	0-01100200	0100000100	02
Pyropterus	0001000010	0000000000	0000000010	0000000000	0000000000	0000000000	0000000001	00
Conderis	0110100010	00-0010000	1101000000	0001000001	0000000101	1000001000	0110000010	02
Xylobanellus	0111100010	00-0010000	1101000020	0001000001	0000000101	1000001000	0110000010	02
Diatrichalus	0211100100	1110-10010	11210001-1	0001011010	0000600000	0101111100	1111012101	01
Enylus	0011100111	0010010010	1-01000100	2101111110	000020-000	0101121100	1111012201	11
Flabellotrich.	0203102121	0010110010	1121000101	0001111010	0010000000	0101121100	1111102201	01
Schizotrichalus	0203102121	0010010110	1111000101	0002-11010	0010000010	0101121100	1111102201	01
Eniclases	0003102121	0010-10110	1--1000101	0001111010	0010000010	0101121100	1111102201	01
Trichalus	0203102121	0010010010	1121000101	0002011010	0010200000	0101121100	1111102301	00
Microtrichalus	0003102121	0010010010	1121000101	0002011010	0010200000	0101121100	1111102201	00
Synchonnus	0211100100	0110010000	1001000000	1101011010	0100100000	0101201100	1111001201	10
Achras	0111102000	0110010000	1101001000	1102011010	0100100000	0101201100	1111001201	11
Hemiconderis	0211102000	0110010000	1101001000	2102011010	0000301000	0101201100	1111002201	11
Wakarumbia	0211102000	0110010000	1101001010	1101011110	0000401000	0101201100	1111002301	11
Bulenides	0211100001	0010110111	1111000000	0002111020	0100100000	0101101100	1111001201	00
Caenioxylobanus	0211100000	0110110011	1111000020	0002111010	0100100000	0101101100	1111001101	00
Cautires	0111000001	001011010-	1111100000	0002011020	0100100000	0101101100	1111001201	0-
Xylobanus	0111000010	0010-101-0	1111100020	0002-11020	0100100000	0101201100	1111001101	0-
Broxylus	0111100000	00100101-0	1111100020	0002111010	0100100000	0101101100	1111002101	00
Prometanoeus	0111000101	0010010100	1111100000	3000011010	0100100000	0101101100	1111001201	00
Tapromenoeus	0111000101	0010010100	1111100020	3000111010	0100100000	0101101100	1111001201	00
Metanoeus	0211100101	0011110100	1111100-00	1002111000	-000200000	0101201110	1311002201	11
Stadenus	0214000111	01101101-0	1111-00200	1-04111000	0001000000	0101101101	1111002201	10
Metriorrhynchoid.	1004121121	0010110100	1111100200	0004200000	0001000000	0101101101	1111001201	11
Porrostoma	1004121121	0010110100	1111100200	1004201000	0001000000	0101-01101	1111002201	1-
Metriorrhynchus	0210101001	0010-10100	1111110000	0002100000	0001000000	0101111100	1111001301	10
Leptotrichalus	0202021021	0010010010	1121000001	0002111010	0001000000	0101111110	12110---01	11
Lobatang	0202021021	0010010010	1121000001	0002111110	0001000000	0101111110	1211001301	11
Cladophorus	0214100000	001-110100	1111100-00	0002111100	0000510000	0111211110	1111001301	10
Procautires	0211100000	0010110100	1111100-30	0002111110	1000010000	0111101110	1111001301	00
Cautiromimus	0110010000	0110110100	1111110000	0002111110	1000010000	0111-01100	1111001301	1-
Kassemia	0111110010	0110110100	1111100021	1001111010	1000210000	0111201100	1111002211	00
Ditua	0110010001	0010010100	1111100000	0012111100	1000210000	0111201100	1111001301	00
Carathrix	0210010001	0011111100	1111110000	001-011010	1000210000	0111201110	1111001201	11
Pseudodontocerus	0210110010	1111111100	1111110000	0011011010	1000210000	0111101110	1111001201	11

weights were reassigned until the topology of the resultant trees did not change. The program Tree Gardener ver. 2.2 (Ramos, 1997) was used for matrix edition and control of Hennig86 program. The Clados ver. 1.9 program (Nixon, 1998) was used for mapping of characters on a tree and a program default setting "hom0" was applied. This setting indicates as homoplasious only those changes that are designated as of independent origin.

Depositories

Material was examined from the following institutions and collections: BMNH, Natural History Museum, London; BPBM, State Museum of Natural and Cultural History, Honolulu, Hawaii; DEIE, Deutsches Entomologisches Institut, Eberswalde; HNHM, Hungarian Natural History Museum, Budapest; MHNG, Muséum national d'histoire naturelle, Geneva; MHNP, Muséum national d'Histoire naturelle, Paris; MNHU, Museum für Naturkunde, Humboldt Universität, Berlin; MHNB, Museum d'Histoire naturelle, Brussels; MSNG, Museo civico di storia naturale, "Giacomo Doria", Genova; NHMB, Naturhistorisches Museum, Basel; NHMW, Naturhistorisches Museum, Vienna; RMNH, Natural History Museum, Leiden; SMNS, Staatliches Museum für Naturkunde, Stuttgart; SMTD, Staatliches Museum für Tierkunde, Dresden; USNM, National Museum of Natural History, Washington, D.C.; ZMAN, Zoological Museum, Amsterdam; ZMPA, Instytut Zoologii PAN, Warsaw; LMBC, author's collection.

PHYLOGENETIC ANALYSIS

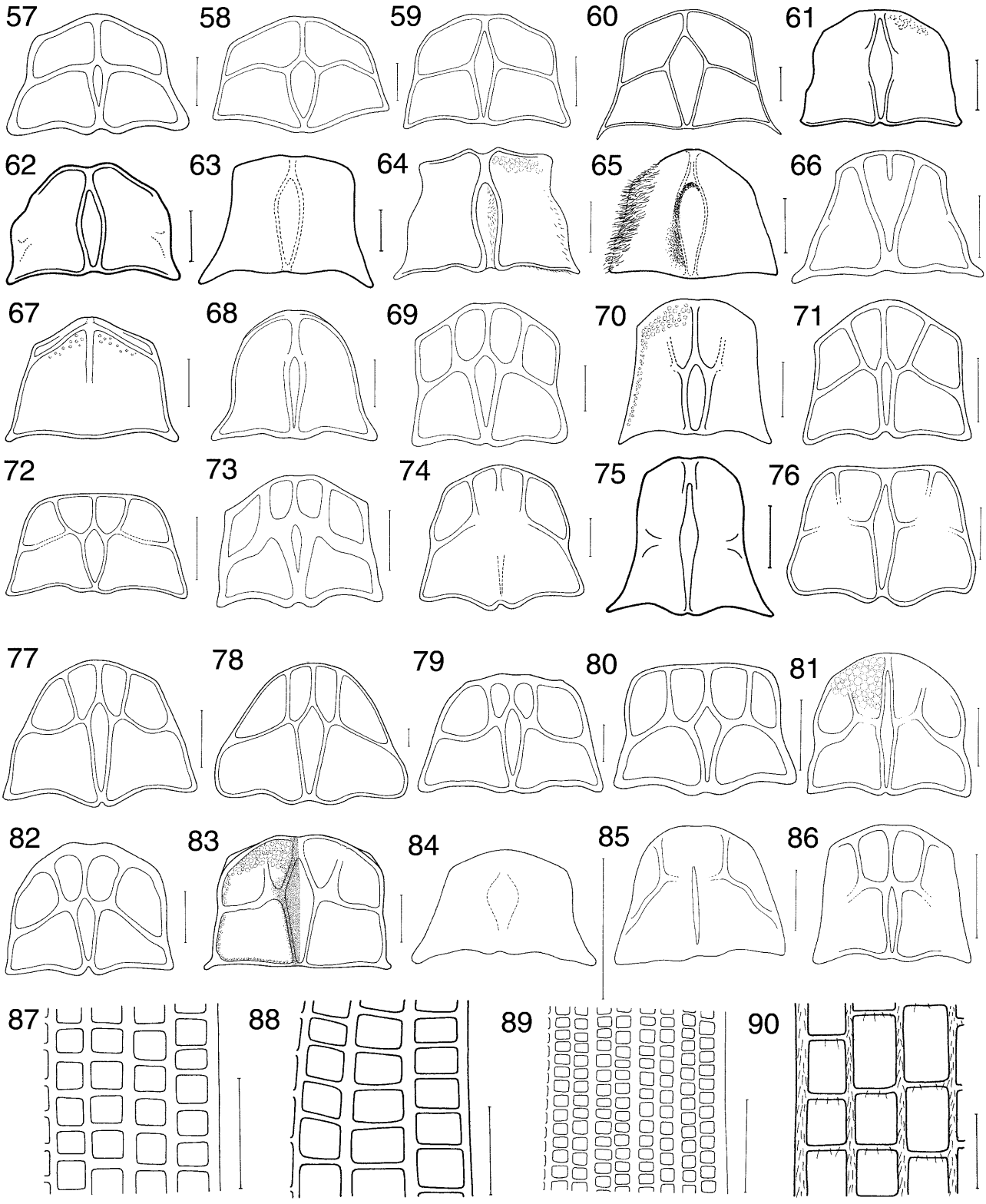
Results

When *Calochromus*, *Lyponia*, *Dictyoptera*, and *Pyropterus* were used to root cladograms, the analysis (mh*, bb*) yielded three parsimonious trees, each with 261 steps, a CI = 0.39 and a RI = 0.69. The strict consensus tree derived from them was identical with one of the original trees and included a polytomy in Trichalina (Fig. 1), and therefore the length, CI and RI of these trees did not differ. When only one of the original outgroup taxa was designated as an outgroup, the topology of the tree did not change. The mapping of characters is given in table 3, and the number of clades in Fig. 1.

Further, successive weighting was applied to the matrix after mh* and bb* (again with *Calochromus*, *Lyponia*, *Dictyoptera* and *Pyropterus* as outgroups). Two trees with length 651, a CI = 69 and a RI = 86 were obtained. These trees differed in the position of *Xylobanus*, either being a sister-group of *Cautires* or *Broxylus*. The consensus tree was slightly longer (length 653) and had identical indexes. The strict consensus tree differs in that it has a polytomy in the *Cautires* clade.

Discussion

The present analysis is the first attempt to investigate the phylogeny of the Metriorrhynchinae using a cladistic approach. The only classification of Lycidae (Bocak & Bocakova, 1990a) is not based on phylogenetic principles but on the need to diagnose supergeneric taxa for a comparative morphology of the major groups of Lycidae, and their identification. Nevertheless, the monophyly of the Metrirrhynchinae as understood by Bocak & Bocakova (1990a), as well as their constitutive tribes and subtribes is supported by the present phylogenetic analysis. The



Figs 57–90: 57–86. Pronotum. 57 – *Xylobanellus erythropterus*; 58 – *Conderis signicollis*; 59 – *Synchonnus clientulus*; 60 – *Hemiconderis explicatus*; 61 – *Enylus amplus*; 62 – *Diatrichalus salomonensis*; 63 – *Microtrichalus acutangulus*; 64 – *Microtrichalus patricius*; 65 – *Flabellotrichalus bilineatus*; 66 – *Eniclases nigriceps*; 67 – *Caenioxylobanus ater*; 68 – *Bulenides inapicalis*; 69 – *Xylobanus benignus*; 70 – *Broxylus fenestratus*; 71 – *Cautires ratus*; 72 – *Prometaneus ochraceus*; 73 – *Metanoeus dispar*; 74 – *Metriorrhynchus thoracicus*; 75 – *Leptotrichalus accuratus*; 76 – *Stadenus puncticollis*; 77 – *Porrostoma lateralis*; 78 – *Metriorrhynchoides helleri*; 79 – *Cladophorus praecipuus*; 80 – *Ditua deplanata*; 81 – *Cautiromimus reticulatus*; 82 – *Procautires toxopei*; 83 – *Pseododontocerus pulcher*; 84 – *Malacolycus paululus*; 85 – *Dilolycus lamellatus*; 86 – *Mimoxylobanus reticulatus*; 87–90. Elytral reticulation. 87 – *Xylobanellus erythropterus*; 88 – *Caenioxylobanus ater*; 89 – *Cautires sinensis*; 90 – *Broxylus fenestratus*. Scales 0.5 mm.

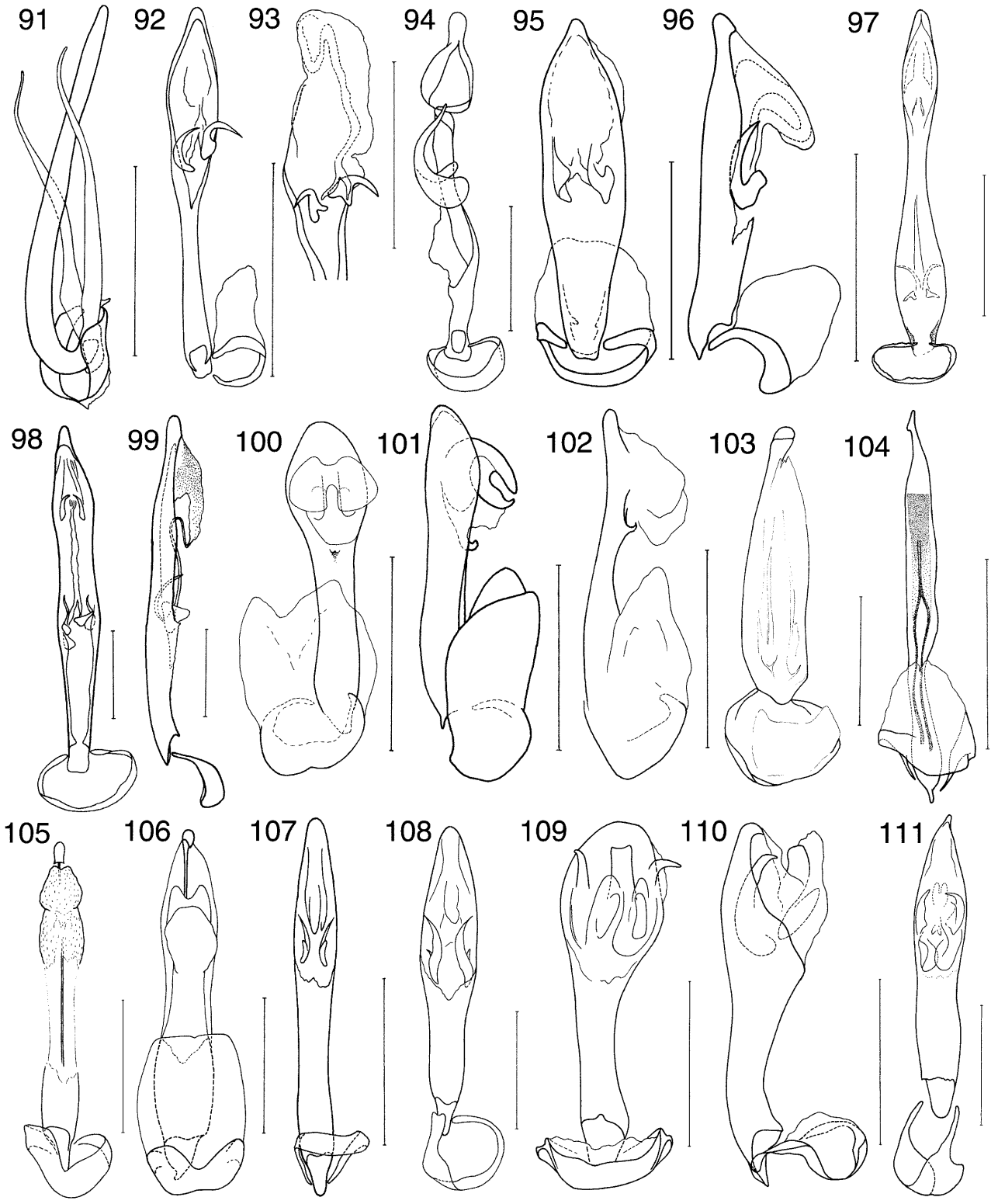
TABLE 3. Synapomorphies and homoplastic changes listed by nodes for the cladogram in Fig. 1.

Nodes	Synapomorphies	Homoplastic changes
1 Metriorrhynchinae	3.1, 13.1, 16.1, 21.1, 24.1, 57.1	34.1
2 Conderini	40.1, 48.1, 50.1, 51.1	2.1, 69.1
3 Metriorrhynchini	2.2, 9.0, 36.1, 37.1, 39.1, 52.1 58.1, 63.1, 64.1, 68.2	54.1, 55.1, 61.1, 67.1 70.1, 71.1, 72.1
4 Hemiconderina	-	12.1, 31.1, 32.1, 45.1, 55.2
5	27.1	7.2
6	47.1	67.2
7	-	10.1, 35.1
8 Trichalina	28.1, 56.2	8.1, 19.1, 67.2
9	-	23.2, 30.1, 71.0
10	4.3, 43.1, 65.1	3.0, 7.2, 9.2
11	-	34.2, 35.0, 45.2, 72.0
12	49.1	18.1, 23.1
13 Metriorrhynchina	-	23.1, 34.2
14	-	4.0, 7.1, 44.1, 56.1, 68.3
15	62.2	3.0, 4.2, 5.0, 6.2, 9.2, 19.1, 23.2, 30.1,59.1
16	-	15.1, 18.1, 25.1
17	-	8.1, 31.1, 39.0, 67.2
18 Porrostoma-group	28.2, 34.4, 60.1	4.4, 44.1
19	1.1, 35.2	2.0, 3.0, 6.2, 7.1, 9.2, 36.0
20	-	71.0, 72.0
21	-	42.1, 45.1
22 Bulenides-group	20.1	19.1, 25.0
23 Cautires-group	-	2.1, 5.0
24	-	15
25	31.3	8.1, 34.0
26	-	10.0, 29.2, 68.1
27 Ditua-group	41.1, 46.1, 53.1	10.0, 55.2
28	-	6.1, 34.1, 45.2
29	17.1	4.0, 14.1, 26.1, 33.1, 35.0, 59.1, 71.1, 72.1
30	-	38.1, 68.3
31	-	2.1, 4.0, 5.0, 6.1
32	-	59.1

monophyly of the Cladophorini as defined by Kleine (1933) and elsewhere was rejected by both hypotheses (Figs 1, 2).

The monophyly of the Metriorrhynchinae is supported by several synapomorphic characters: transverse gula (Fig. 11), considerably compressed antennae, antennomere 2 much shorter than antennomere 3 (Figs 29–51), unconstricted base of median areola (Figs 57–86), median areola connected to frontal margin of the pronotum by a keel (Figs 57–60, 62–86), symmetrical bulges at base of pronotum absent, circular phallobase (Figs 91–132). The shape of the phallobase is very characteristic and unlike that of other Lycidae. In addition, the shape of the pronotal carinae is very characteristic and only specimens of *Enylus* is these an indistinct frontal keel, but even in such cases the general appearance of the pronotum is different. The very short antennomere 2 is possibly a synapomorphic character state, although Ateliinae have a very short antennomere 2 as have several Leptolycinae. Both groups differ substantially in the shape of their cranium, male genitalia and Ateliinae have pobably neotenous females (Bocak & Matsuda, in press). These groups are unrelated to the Metriorrhynchinae, therefore an independent origin of these character states in the Metriorrhynchinae is suggested.

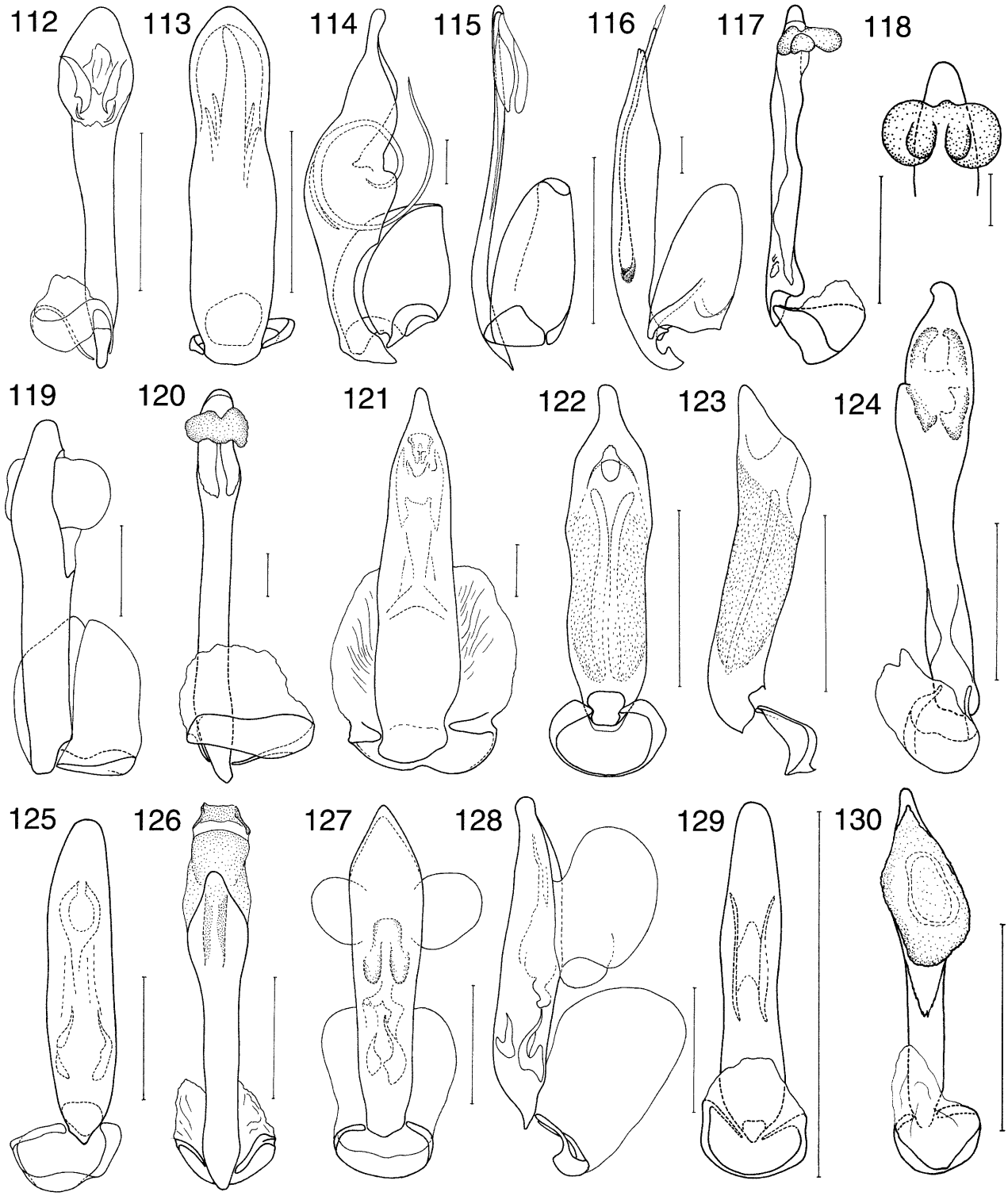
The Conderini, according to the present phylogenetic hypothesis (Figs 1, 2), have a basal placement within the Metriorrhynchinae. That the phallus has a laterally compressed apical part, and a hook-like base, and there are processes on the phallobase support their monophyly. All these characters are unique within the Lycidae. Additionally, the shape of the pronotal carinae is very characteristic in most species (Figs 57, 58), but the shape of the carinae is not the same in all specimens of some species and therefore was not coded in the matrix. Conderini share several symplesiomorphic character states with the



Figs 91–111: Male genitalia. 91 – *Conderis signicollis*; 92– 93 – *Synchonnus clientulus*; 94 – *Wakarumbia angustior*; 95– 96 – *Achras limbatus*; 97 – *Enylus segregatus*; 98 – 99 – *Enylus amplus*; 100 –101 – *Diatrichalus assimilis*; 102 – *Diatrichalus* sp.; 103 – *Microtrichalus bicoloripes*; 104 – *Flabellotrichalus notatithorax*; 105 – *Schizotrichalus nigrescens*; 106 – *Eniclases apertus*; 107 – *Bulenides* sp.; 108 – *Cautires sinensis*; 109 –110 – *Xylobanus costifer*; 111 – *Broxylus fenestratus*. Scales 0.5 mm.

Erotinae. The female genitalia have a very similar shape and the basal part of coxites is strenghthened, male genitalia have long parameres, and a completely membranous internal sac.

The monophyly of the clade forming the tribe Metriorrhynchini is supported by the regularly exposed, sclerotized or at least pigmented internal sac (Figs 92–132), the flat, apparent, unpaired vaginal gland (e.g. Figs



Figs 112–130: Male genitalia. 112 – *Prometanoeus ochraceus*; 113 – *Metanoeus* sp.; 114 – *Metriorrhynchus thoracicus*; 115 – *Leptotrichalus adolescens*; 116 – *Lobatang dubitabilis*; 117 –118 – *Stadenus triareolatus*; 119 – *Porrostoma rufipennis*; 120 – *Metriorrhynchoides helleri*; 121 – *Cladophorus* sp.; 122–123 – *Cautiromimus reticulatus*; 124 – *Cladophorinus cyanescens*; 125 – *Ditua deplanata*; 126 – *Procautires* sp.; 127–128 – *Pseudodontocerus* sp.; 129 – *Malacolycus paululus*; 130 – *Xylobanomorphus transformis*. Scales 0.5 mm.

143–146), lateral vaginal glands with a narrow, usually slightly sclerotized base (e. g. Figs 143–146), simple basal margin to coxites (Figs 134–140), mesoscutellum with long lateral processes, and short alacrista. The complete set of synapomorphic character states is given in Tab. 3, and the characters not mentioned here have undergone multiple reversions. The absence of parameres are hypothesised to be a homoplasy, because this character state has evolved independently in *Lyponia* (Platerodinae, char. 54) and is known also in the Platerodini, which were

not included as an outgroup in the analysis. Metriorrhynchini differ in this character from all similar Lycidae. However, the loss of parameres has occurred independently in other groups.

The tribe Metriorrhynchini is formed by three subtribes: Trichalina, Hemiconderina and Metrirrhynchina. Their relationship is unresolved. When no successive weighting was applied, the Trichalina had a basal position as a sister-group of the remaining Metriorrhynchini, and the Hemiconderina were the next basal clade. After successive weighting the relative position of these subtribes changed (Figs 1, 2). But in all analyses these clades remained stable. Unfortunately the larvae of these groups are unknown and I have not found a character to corroborate the hypotheses. Both hypotheses can be interpreted in the same way in the formal classification.

Kleine (1928, 1933) defined the Trichalina as a group of Metriorrhynchinae genera with a short elytral primary costa 1. Bocak (1998b) showed that the shortened costa 1 evolved several times in the Metriorrhynchinae and therefore restricted Trichalina to the terminal clade *Trichalus* + *Microtrichalus* + *Flabellotrichalus* + *Schizotrichalus* + *Eniclases* and provisionally classified *Enylus* and *Diatrichalus* as incertae sedis in the Metriorrhynchini. The present analysis placed *Enylus* and *Diatrichalus* basally in this clade because of two synapomorphic character states: tubercles on the lateral margin of the pronotum (Figs 61–66) and the shape of the basal part of phallus (Figs 104, 106). The tubercles may or may not be distinct in individual specimens but are regularly present, and together with the characteristically elevated lateral margins give the uniform pronotal appearance of the Trichalina. Considering the topology of the trees produced by the present analysis (Figs 1, 2), *Enylus* and *Diatrichalus* must be classified in the Trichalina.

The Hemiconderina as proposed by Bocak & Bocakova (1990a) was monotypic. Later, Bocak (1999b) described *Wakarumbia* from Sulawesi put it in the Hemiconderina. This was supported by the present analysis and additionally the Australian *Achras* was added to the terminal clade which is characterised by straight slender costae (char. 27). In both cladograms (Figs 1, 2) *Synchonnus* is a basal member of the Hemiconderina. Although genera classified in the Hemiconderina have many similar characters, it can not be defined as a monophyletic group, as the Hemiconderina clade has no autapomorphic character state.

That the Metriorrhynchina is monophylic is not well founded, as I have not found any synapomorphic character state to support the cladistic definition. In addition, the relationships between the individual clades within the Metriorrhynchina remain obscure.

Most members of this clade have a complex pattern of pronotal carinae forming four areoles on the frontal margin of the pronotum (i. e., frontolateral costae are present on the pronotum, character 18). This character is useful for identifying most Metriorrhynchina. On the cladogram in Fig. 1 the Metriorrhynchina without basal clade *Bulenides* and *Caenioxylobanus* share the state 18.1, after successive weighting (Fig. 2) the state 18.1 is not shared by the basal *Metriorrhynchus+Lobatang+Leptotrichalus* clade. Additionally, this character is a homoplasy as it is a similar arrangement of carinae in *Schizotrichalus* and *Eniclases* (Fig. 66). The arrangement of carinae in *Eniclases* is quite different from that of most Metriorrhynchina - only two diverging keels are present (Fig. 66). *Schizotrichalus* has similar longitudinal carinae but its median frontal carina is forked apically and connected with longitudinal carinae. Consequently, three carinae are attached to the frontal pronotal margin. Having no evidence to the contrary, both situations were scored as an identical character state. Further evidence will be needed to support or refute the Metriorrhynchina. As few larvae of the Metriorrhynchina have been described (Bocak & Matsuda, in press) they will not help to solve this ambiguity. The larvae of most known *Cautires* and *Xylobanus* are very similar and they share some characters with *Metriorrhynchus*. *Porrostoma* differs in having characteristic processes on the hind margins of its terga. Most of them share with *Xylobanellus* terga that are divided in two parts by a membranous line.

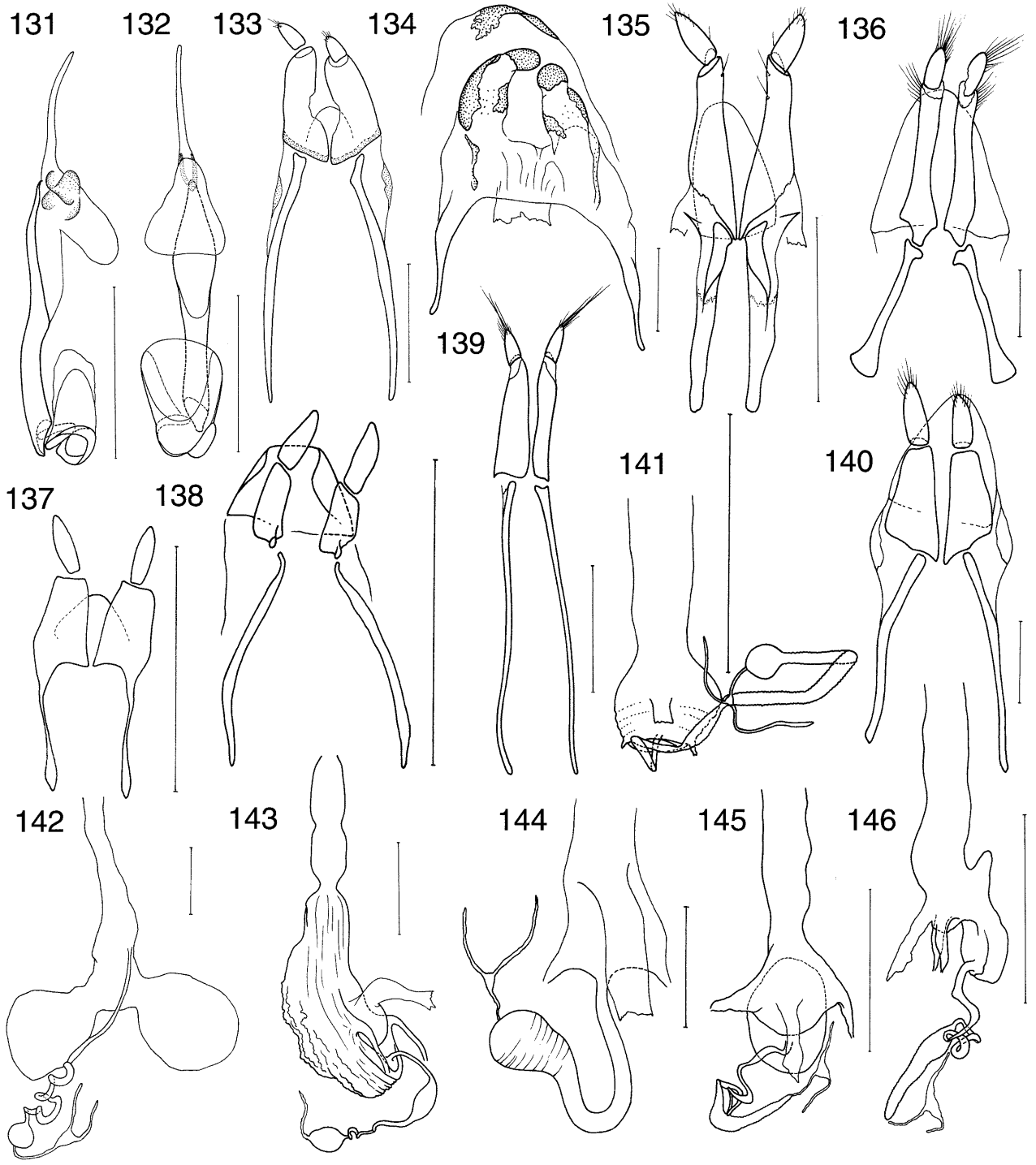
Only two constitutive clades give robust support to both cladograms (Figs 1, 2): the *Ditua* group formed by almost exclusively Papuan genera and the *Porrostoma* group with a restricted Austro-Papuan distribution. The clade *Bulenides* + *Caenioxylobanus* is either a basal group (Fig. 1) with the *Cautires* clade as the next clade, or they are a basal group within the *Cautires* clade (Fig. 2).

The position of *Metanoeus* is variable and it is attached as a basal member either to the *Porrostoma* or *Ditua* clade. In any case, *Metanoeus*, has an Oriental distribution, and is not related to the Afro-Oriental clade (*Cautires*, *Bulenides*, *Prometanoeus*, etc.). Some characters present only in some members of these genera could not be coded in the matrix: several *Metriorrhynchus* species share with *Metanoeus* very obtuse, indistinct pronotal carinae and both have shorter (*Metriorrhynchus*) to vestigial (*Metanoeus*) valvifers. Further evidence is needed to clarify the position of *Metanoeus*.

Zoogeography

Unfortunately, the very fragmentary knowledge of Lycidae at the alpha taxonomic level and consequently the doubtful information on generic distribution limit the following discussion. I have used unpublished information gathered by studying collections in the above institutions. The data in the lycid catalogue (Kleine, 1933) are inapplicable. The typological species concept applied to most genera by Kleine and the problems originating from Pic's confused work means that these data has to be confirmed by studying the original type material. Information on the distribution of genera is given in the systematic part.

On the other hand, Lycidae appear incapable of crossing natural barriers such as sea straits or deserts. Lycidae are often limited to humid mountain habitats and when these mountains are isolated, Lycidae easily speciate. Unlike many other groups, there are very few lycid species with a very wide range. The few widely distrib-



Figs 131–146: 131–132. Male genitalia, *Mimoxylobanus reticulatus*; 133–140. Ovipositor. 133 – *Xylobanellus erythropterus*; 134 – *Metriorrhynchus* sp.; 135 – *Caenioxylobanus ater*; 136 – *Metriorrhynchoides* sp.; 137 – *Strophicus nigellus*; 138 – *Synchonnus appositus*; 139 – *Pseudodontocerus pulcher*; 140 – *Cladophorus* sp.; 141–142. Female genitalia. 141 – *Caenioxylobanus ater*; 142 – *Xylobanellus erythropterus*; 143 – *Pseudodontocerus pulcher*; 144 – *Cladophorus* sp.; 145–146 – *Synchonnus appositus*. Scales 0.5 mm.

uted species are usually from lowlands and in this case the size of range is not impressive. I know only of one species that occurs in two zoogeographical regions.

The substantial part of the Metriorrhynchinae is an east Gondwanan element (distribution of Conderini is discussed further) with some representatives distributed in East Asia and a single species widely distributed from Russian Far East through Siberia to Belarussia and Poland (Fig. 3). The highest species and generic diversity occurs in the humid tropics of the Old World, but the generic species diversity is low in the Afrotropical Region. There are also substantial differences in the contribution of Metriorrhynchinae to the total representation of Lycidae in the zoogeographic regions.

The striking observation is that Conderini as a basal group within the Metriorrhynchinae have the distribution similar to Erotinae, although they are not recorded from the Nearctic Region. Most species are known from the south-eastern part of the Palaearctic Region and the northern part of the Oriental region, fewer species occur distributed in the north-eastern part of the Palaearctic. Unlike the Erotinae they are not known from the Afrotropical and Nearctic Regions (Fig. 3).

The range of Metriorrhynchini is limited to the Afrotropical, Oriental, Australian and eastern part of Palaearctic Regions. It seems reasonable to assume that the Metriorrhynchini dispersed to the Palaearctic Region after they evolved somewhere on the Gondwana continent. There are no endemic genera in the Palaearctic, and generally both the species and generic diversity of Palaearctic fauna are extremely low and decreases with the distance from the Oriental Region. Additionally, the Metriorrhynchinae form usually a small fragment of the Lycidae collected in the Palaearctic Region, unlike in the Oriental Region. The distribution of the Metriorrhynchini is given in Fig. 3.

Another important observation is that within the Metriorrhynchinae the two Australian lineages, Hemiconderina and Trichalina, have a basal position and that the diversity of Australian fauna is much higher than Afrotropical one. The Hemiconderina are endemic to the Australian Region (Fig. 5) and within the subtribe the basal lineage represented by *Synchonnus* is restricted to continental Australia as well as *Achras*, which also has several plesiomorphic characters. The remaining genera of Hemiconderina are recorded from New Guinea and the Indonesian Archipelago east of the Wallace line. Both, *Hemiconderis*, known from New Guinea and the Yapen Island, and *Wakarumbia*, from Sulawesi and the Buton Island, have undergone considerable speciation. At present, 23 *Wakarumbia* species are recorded from Sulawesi. Although, they show three different colour patterns, the substantial differences are in the male genitalia. Considering the tectonic history of Sulawesi and the limited range of *Wakarumbia*, we can presume that a part of Sulawesi of Australian origin or a part having contact with some part forming today New Guinea brought the ancestor of *Wakarumbia* to Sulawesi. I have not found any group of species restricted to one part of an island (Bocak, 1999b, 2000c, 2001b), therefore the simultaneous speciation on various mountain ranges of widespread lowland species is possible.

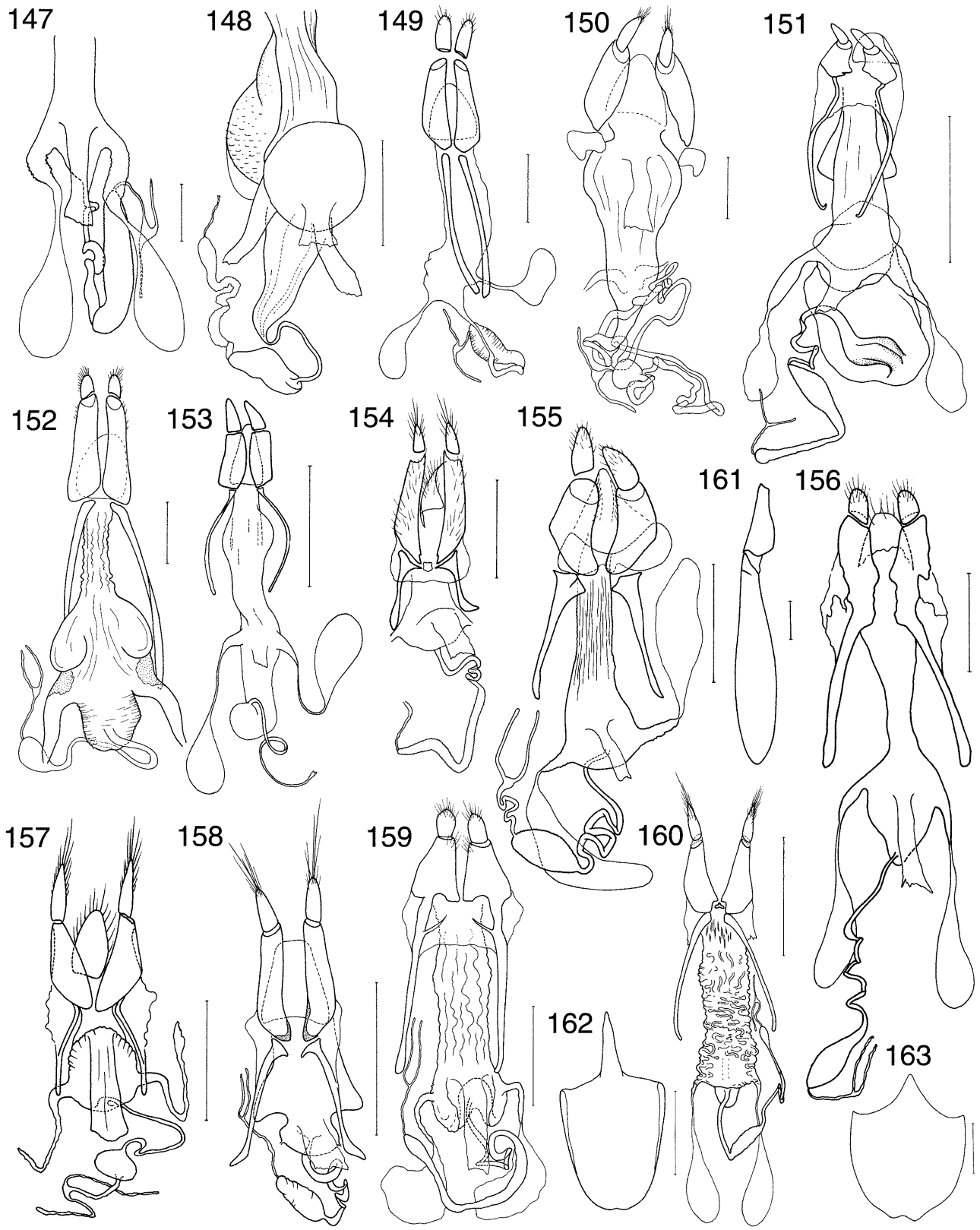
The Trichalina are the other basal group of presumably Australian origin. All genera constituting the Trichalina are known from the Australian Region, only some of them, *Diatrichalus* and *Microtrichalus* are present also in the Oriental Region (Fig. 5). The highest diversity is generally found in tropical parts of the Australian Region. After the revision of the Papuan fauna almost forty *Diatrichalus* species are recorded from the Australian Region (Bocak, 2001a), and further species can be expected from Australia. On the other hand, only five *Diatrichalus* species were recently reported from the Philippines (Bocak, 2000a) and only one species from the Asian continent and the Great Sundas. The distribution of *Microtrichalus* is similar. Although its range reaches further to the north and recently one species was found in southern Yunnan and northern Laos, the diversity of the Oriental fauna is very low and the number of species decreases gradually from the Wallace line to the northwest. Congruent with patterns found in other groups and the tectonic history, *Microtrichalus* is rich in species in the Philippines (Bocak, 1998d).

The range of Metriorrhynchina is almost coincident with that of the Metriorrhynchinae (Fig. 3). The Palaearctic fauna of Metriorrhynchina is poor, both in number of species and genera. Only *Cautires* and *Xylobanus* are reported from China, Japan and the Russian Far East. Metriorrhynchina are quite rare in the Palaearctic Region and form a small part of the Palaearctic lycid fauna considering the number of species. Dispersal from the south offers a possible explanation for the present distribution of Metriorrhynchina in the Palaearctic Region.

The Afrotropical fauna of Metriorrhynchina has not yet been revised and according to Kleine (1933) 192 species are reported from the Afrotropical Region. These species are classified in genera *Cladophorus*, *Cautires*, *Procautires*, *Caenioxylobanus*, and *Xylobanus*. I have studied available material in Pic's and Kleine's collections and I found that the Afrotropical species placed in *Cladophorus* and *Procautires* are not congeneric with Australian representatives of these genera and should be placed in *Cautires*. Afrotropical species of *Stadenus* were transferred to the Erotinae (Bocak & Bocakova, 1992). Therefore, only genera *Cautires* (about 150 species), *Xylobanus* (about 40 species), and *Caenioxylobanus* (2 species) are now confirmed for the Afrotropical Region. The Afrotropical fauna seems species rich, but multiple synonyms can be expected as Pic often described common species several times. *Caenioxylobanus* reported from Madagascar is the only genus endemic to the region.

The Afrotropical and Indian faunas of Metriorrhynchina are similar regarding the representation of genera. *Cautires*, *Xylobanus*, and *Prometaneus* are the only genera occuring west of the low Brahmaputra River, and *Prometanoeus* is the only genus endemic to the western part of the Oriental Region. *Cautires* is a widely distributed genus known from West Africa to the Philippines (Fig. 4) and Japan. *Xylobanus* has a similar distribution, but unlike *Cautires*, *Xylobanus* crosses the Wallace line to the east. This genus has not yet been revised and the real relationship of the Australian representatives is unknown.

Metriorrhynchina from the eastern part of the Oriental Region are more diverse. In addition to *Cautires* and *Xylobanus*, two endemic genera are common in South East Asia - *Metanoeus* and *Bulenides*. Both do not cross the Wallace line (Fig. 4). *Metriorrhynchus* is the only genus in the Metriorrhynchina which has its centre of distribution in the Australian Region and reaches continental Asia. Although this genus is reported from India (Kleine,



Figs 147–163: 147–160. Female genitalia. 147 – *Metriorrhynchoides* sp.; 148 – *Metriorrhynchus mirabilis*; 149 – *Cautires* sp.; 150 – *Metanoeus* sp.; 151 – *Achras limbatus*; 152 – *Pseudodontocerus* sp.; 153 – *Wakarumbia gracilis*; 154 – *Xylobanus costifer*; 155 – *Bulenides obsoletus*; 156 – *Stadenus puncticollis*; 157 – *Leptotrichalus accomodatus*; 158 – *Broxylus fenestratus*; 159 – *Stadenus triareolatus*; 160 – *Cautiromimus reticulatus*. 161 – trochanter and femur. *Pseudodontocerus pulcher*; 162–163. Female sternum A7. 162 – *Procautires* sp.; 163 – *Cautires* sp. Scales 0.5 mm.

1933), it was not found in collections from localities west of Burma.

There are several endemic lineages of Metriorrhynchina in the Australian Region: *Pseudodontocerus*, *Stadenus*, *Ditua*, *Cladophorus*, *Cautiromimus*, *Broxylus*, *Kassemia*, *Porrostoma*, and *Metriorrhynchoides*. The ranges of these genera extend to the west in various degrees (Fig. 6). *Metriorrhynchus* and *Lobatang* have most of their representatives in the Australian Region but a very small proportion of them cross the Wallace line onto the Asian continent (*Metriorrhynchus*) or to the Philippines (*Lobatang*). The distribution of *Leptotrichalus* is a bit different. Most species of *Leptotrichalus* are reported from the Philippines, several from Sulawesi, the Lesser Sundas, Java, Sumatra and Borneo, and several from the Asian continent, only one of which occurs beyond the Isthmus of Kra (Bocak, 2000b). Recently, several undescribed species were collected in Halmahera. This supports the conclusion about the relationship between *Lobatang* and *Leptotrichalus* inferred from morphological data in phylogenetic analysis. *Lobatang*, is a closely related genus known from the Papuan Subregion, Wallacea, and the Philippines. Most species are known from the eastern part of the region. Dispersal followed by speciation of an ancestor inhabiting islands north of Australia possibly lead to the present distribution and species richness of *Leptotrichalus*.

Two clades are restricted to the Australian Region. The clade *Porrostoma*, *Stadenus* and *Metriorrhynchoides* is the most common group in Australia with few species known from New Guinea. The *Ditua* clade (node 27, Fig. 1) is recorded mainly from New Guinea and adjacent islands. Few species occur in Australia. *Metanoeus* has an ambiguous position in the present analysis and is the only genus endemic to the Oriental Region, but related to clades whose centre of distribution is the Australian Region.

There are substantial differences in the relative representation of Metriorrhynchinae within the Lycidae. Metriorrhynchinae are relatively poorly represented in Afrotropical and Palaearctic Regions, where they usually form 10–20 per cent of collected specimens. They are more common in humid areas of South East Asia where they make up slightly over 50 per cent of the specimens. Their relative abundance increases to the east. East of the Wallace line the Lycidae are almost exclusively represented by the Metriorrhynchinae. The Metriorrhynchinae form 95 per cent of the specimens collected in New Guinea and a substantial part of the Australian lycid fauna. Metriorrhynchinae form 90 per cent of the lycid species recorded from Australia.

Conclusion

A. All ingroup terminal taxa form a monophyletic group characterised by the presence of a circular phallobase (Figs 91–132) and an antennomere 2 much shorter than antennomere 3 (Figs 29–51). Further apomorphic character states of Metriorrhynchinae are given in Table 3.

B. The present analysis supports the tribes Conderini and Metriorrhynchini. Three subtribes, Hemiconderina and Trichalina with a basal placement, form the Metriorrhynchini. The Hemiconderina concept is redefined. The genera *Diatrichalus* and *Enylus* are returned to the Trichalina. The resulting cladograms varied but some clusters within the Metriorrhynchina were relatively robust (*Ditua* clade, *Porrostoma* clade and *Cautires* clade).

C. The distribution of clades was discussed. Conderini are restricted to East and South East Asia, Metriorrhynchini are considered to be an East Gondwanan element with only a few species reaching northern East Asia. All these species are members of widespread genera known from the Afrotropical and Oriental regions. All major clades classified as subtribes of Metriorrhynchina are either exclusively Australian or at least have most of their endemic taxa in the Austro-Papuan Region.

D. The cladistic analysis showed that characters used for a long time to define genera (presence and/or absence of elytral secondary costae, shortened primary elytral costae, and serrate of flabellate antennae) evolved several times in the Metriorrhynchinae.

This study aimed to establish phylogenetic relationship between the genera of Metriorrhynchinae in order to study further individual clades within the subfamily. More extensive sampling and new sources of data, especially on immature stages and molecular data, will corroborate or refuse the proposed phylogeny. Additionally, further studies are need to establish new combinations and to enlarge the data base available for cladistic analyses.

TAXONOMY

Metriorrhynchinae Kleine, 1926

Metriorrhynchinae Kleine, 1926a: 97.
Type genus. *Metriorrhynchus* Gemminger et Harold, 1869.

Cladophorini Kleine 1928: 222; Bocak & Bocakova, 1990a: 641.
Type genus. *Cladophorus* Guérin-Méneville, 1830: Plate II, fig. 9.

Dilolycinae Kleine, 1926: 186; Bocak & Bocakova, 1990a: 641.
Dilolycini: Kleine, 1933: 84.
Type genus. *Dilolycus* Kleine, 1926a: 186.

Haplothoracinae Kleine, 1926a: 95 (nomen nudum); Bocak & Bocakova, 1990a: 641.
Type genus. *Haplothorax* Kleine, 1926a: 95 (nomen nudum).

Diagnosis. Body small to large (3–30 mm), mostly slender, flat (Figs 7–9), weakly sclerotized. Head small, partly concealed by pronotum. Cranium mostly compact (Fig. 11), seldom rostrate (Fig. 10). Antennae compressed, filiform, serrate or flabellate (Figs 29–51). Mouthparts well developed, mandibles small, moderately curved (Figs 24–28), maxillary palpi 4-segmented (Figs 15–17), labial palpi 3-segmented. Labium simple (Fig. 14). Pronotum with carinae (Figs 57–86). Elytra with four primary and five secondary longitudinal costae (e. g. Figs 52–56), sometimes secondary costae absent (Figs 56, 87, 88, 90) or primary costae reduced. Longitudinal costae connected by transverse costae. Male genitalia with para-

meres and retracted, membranous internal sac (Fig. 91) or parameres absent and internal sac sclerotized or exposed (Figs 92–132). Ovipositor with plate-like coxites, small movable styli and sclerotized, rod-shaped valvifers (Figs 133–140). Vagina mostly membranous, seldom sclerotized (Figs 141–160). Spiculum gastrale moderately long to absent (Figs 162–163).

Distribution. Afrotropical, Oriental, and Australian Regions, eastern part of Palaearctic Region, Siberia, Eastern Europe (Fig. 3).

Remarks. Metriorrhynchinae are easily recognisable within the Lycidae as they have pronotal carinae (Figs 57–86) and a very short antennomere 2 (Figs 30–51). In addition all representatives have a circular phallobase (Figs 91–132), and parameres that are characteristically slender or absent (Figs 91–132).

Conderini Bocak et Bocakova, 1990

Conderini Bocak et Bocakova 1990a: 643.
Type genus. *Conderis* C. O. Waterhouse, 1879: 59.

Diagnosis. Body small to medium-sized, most species cinnabar red. Rostrum absent, antennae filiform to weakly serrate (Fig. 29), almost circular in cross-section to weakly compressed. Pronotum with five areoles, median areola often reduced in size, connected with pronotal and basal margins by long carinae (Figs 57, 58). Elytra with four strong primary costae, secondary costae present (*Conderis*) or absent (*Xylobanellus*, Fig. 87). Male genitalia with long parameres, base of phallus curved, phallobase with process at base, bases of parameres fused with phallus to form a unique process (Fig. 91). Ovipositor robust, with stout valvifers, small sclerites attached to valvifers (Fig. 133). Vagina membranous, unpaired gland very small, inconspicuous, lateral glands very delicate and very wide at base (Fig. 142).

Distribution. Palaearctic and Oriental Regions. Over 30 species described at present; mainly from China and continental South East Asia.

Remarks. Two genera, *Conderis* and *Xylobanellus* are classified as Conderini. Their close relationship is well supported by the unique shape of male (Fig. 91) and female genitalia (Figs 133, 142). They are easily distinguished by the presence or absence of secondary elytral costae. The absence of secondary costae is the only advanced feature found in *Xylobanellus*, but this occurs independently in many lineages within the Lycidae (several occurences in the Metriorrhynchinae). Unfortunately, *Conderis* does not have any synapomorphic character state and therefore *Conderis* can be paraphyletic with respect to *Xylobanellus*.

Conderis C. O. Waterhouse, 1879

Conderis C. O. Waterhouse, 1879: 59.
Type species. *Calopteron signicolle* Kirsch, 1875: 36; C. O. Waterhouse, 1879: 59 (by original designation).

Pseudoconderis Pic, 1921a: 8, hors texte; Bocak, 1998a: 18.
Type species. *Pseudoconderis gorhami* Pic, 1921a: 8; Bocak, 1998a: 18 (by subsequent designation).

Diagnosis. Body small to medium sized, most species cinnabar red. Antennae filiform to slightly serrate (Fig. 29). Pronotum with five areoles (Fig. 58), sometimes median areola reduced in size (as in Fig. 57), narrow, connected with frontal and lateral margins by stout carinae. Elytra parallel-sided to slightly widened posteriorly, each elytron with four stout, longitudinal primary costae and five much weaker, sometimes interrupted, secondary costae. Transverse costae dense, sometimes irregular, bottom of elytral areoles bald. Terminal male abdominal sternite with hole in basal part. Phallus almost straight in middle, parameres long (Fig. 91). Valvifers with attached sclerites, widened in middle part, basal margin of coxites strengthened (Fig. 133). Vagina membranous.

Distribution. Eastern part of the Palaearctic Region (China, Japan), Oriental Region (mainly continental South East Asia, less common in Himalayas and India, as well as in Sundas; easternmost record from Lombok). Over 20 species known from the range of the genus.

Remarks. Many *Conderis* species share the same characteristic elytral structure. The transverse costae are usually very dense and the bottoms of elytral areoles are bald, mat and the surface has a fungus-like structure. This is the only apomorphic character of *Conderis* but not all species.

Xylobanellus Kleine, 1930

Xylobanellus Kleine, 1930a: 171.
Type species. *Xylobanellus atricolor* Kleine, 1930a: 171 (by original designation).

Rossioptera Kasantsev, 1988: 169, **syn. n.**
Type species. *Eros erythropterus* Baudi, 1871 (by monotypy).

Chuzenjianus Kôno, 1932: 61; Nakane, 1969a: 176.
Type species. *Chuzenjianus tenuis* Kôno, 1932: 61 (by original designation).

Diagnosis. Body small to medium-sized, slender, parallel-sided. Antennae slender, long, slightly serrate. Apical maxillary palpomere triangular. Pronotum almost parallel-sided, posterior angles rectangular. Median areola small, very slender (Fig. 57). Elytra flat, with four stout longitudinal costae, transverse costae well marked, only 20–25 costae per interspace, elytral areoles squared to longitudinal (Fig. 87), their bottom flat, matt, finely chagrined. Male genitalia with slender curved phallus, its apex widened in lateral view. Parameres well developed. Ovipositor robust, vagina membranous.

Distribution. Five species are placed in *Xylobanellus*, one occurring in Eastern Europe and Siberia, the rest in China, Thailand, Malaysia, Borneo and Java.

Remarks. All *Xylobanellus* species share several characters, which potentially could be present in a common ancestor: secondary costae absent, rectangular reticulate cells and male segment A7 with straight margin. The similarly structured elytral costae is also encountered in unrelated lineages within the Metriorrhynchinae (e. g. *Broxylus, Caenioxylobanus, Xylobamus*) and in other subfamilies of Lycidae (Lycinae: Calopterini, part; Erotinae, part). *Rossioptera* is based on *Eros erythropterus*, previously classified in *Dictyoptera*. Bocak & Bocakova

(1987a) transferred *E. erythropterus* to *Xylobanellus*. *Rossioptera* is considered to be a junior subjective synonym of *Xylobanellus*.

Metriorrhynchini Kleine, 1926

Metriorrhynchini Kleine, 1926a: 97.
Type genus. *Metriorrhynchus* Gemminger et Harold, 1869: 1629.

Diagnosis. Body small to large. Head mostly lack a rostrum, seldom has a more or less long rostrum. Antennae serrate to flabellate in males, serrate in females, seldom flabellate in females. Pronotum with only median areola and lateral costae present (Figs 61–65, 84), with slender costae forming five areoles (Figs 59–60) or with seven areoles (e. g. Figs 76–83). Elytra with longitudinal and transverse costae. Secondary costae weak to absent (Figs 52–56, 87–90). Male genitalia without parameres (Figs 92–132), with partly sclerotized internal sac, or large, usually finely setose sac exposed on apical part of phallus (Fig. 118). Vagina with paired, lateral, narrowly attached glands (Figs 143–160), and with apparent, flat, unpaired gland (e. g. Figs 143, 145).

Distribution. Afrotropical, Oriental, and Australian Regions and eastern part of Palaearctic Region (Fig. 3).

Remarks. Metriorrhynchini are easily recognisable by the absence of parameres, presence of characteristic pronotal carinae forming up to seven areoles, flat unpaired vaginal gland and narrowly attached lateral glands. *Metriorrhynchus* Guérin-Méneville, 1838 was considered to be the type genus by Kleine (1926a). Bocak (1998c) discussed the validity of the name.

Hemiconderina Bocak et Bocakova, 1990

Hemiconderina Bocak et Bocakova 1990a: 645.
Type genus. *Hemiconderis* Kleine, 1926a: 162.

Diagnosis. Body small to medium-sized, mostly slender, parallel-sided (*Wakarumbia*, *Hemiconderis*, Fig. 8, and *Achras*), seldom shorter, more robust (*Synchonnus*). Head small, without rostrum. Antennae serrate (Figs 30, 31), antennomeres triangular to parallel-sided, always apparently compressed, similar in both sexes. Pronotum with five areoles, carinae straight, slender, median areola small, narrow (Figs 59, 60). Elytra parallel-sided to slightly widened posteriorly (Fig. 8). Elytral costae 2 and 4 stronger, always reaching apex of elytra, costae 1 and 3 always apparently weaker in apical half of elytra, seldom shortened. Secondary costae present in most genera, absent in *Wakarumbia*. Legs slender, strongly compressed. Male genitalia with simple, slender phallus (Figs 92–96). Internal sac with pair of basal spines, seldom fused in one complex structure (*Wakarumbia*, Fig. 94). Ovipositor wide, valvifers apparently divergent, vagina membranous, simple (Figs 151, 153).

Distribution. Australian Region: Australia, New Guinea, Yapen Island, Sulawesi, Buton Island (Fig. 5); there was no overlap in the distribution of *Wakarumbia*, *Achras*, and *Hemiconderis*.

Remarks. Hemiconderina are easily distinguished by the shape of their pronotum, with characteristic, slender, straight carinae forming only five areoles on the pronotal disc (Figs 59–60), head without rostrum, and primary costae 1 and 3 weaker apically; rarely also a costa 1 partly shortened (*Hemiconderis bipustulatus* Bocak & Bocakova, 1990b). Additionally, all genera placed here share a slender, delicate appearance, with parallel-sided elytra, very slender legs, slender and relatively long maxillary palpi, slightly securifom apical maxillary palpomere, minute labial palpi, and absence of tibial spurs.

Synchonnus C. O. Waterhouse, 1879

Synchonnus C. O. Waterhouse, 1879: 59.
Type species. *Synchonnus clientulus* C. O. Waterhouse, 1879: 59 (by monotypy).

Diagnosis. Body small, quite robust, slightly widened posteriorly. Head small, without rostrum. Antennae robust, strongly compressed, serrate. Maxillary palpi slender, apical palpomere slightly widened. Pronotum with strongly projected hind angles, with five areoles, median areola slender, long. Four primary and five secondary costae extant whole length of the elytra, primary costa 2 and 4 much stronger, costa 3 very weak apically. Secondary costae weak, transverse costae irregular. Male genitalia very slender, phallus widened in apical third, internal sac with two large spines in basal part. Ovipositor with small coxites and long valvifers (Fig. 138), vagina with dorsal sac (Figs 145–146).

Distribution. Australian Region. Five species reported from Australia, New Guinea, and Jobi Island.

Remarks. *Synchonnus* has a basal position in Hemiconderina. As in *Achras* the male genitalia has a pair of spines (Figs 92–93, 95–96), but unlike this genus it has more robust body and obtuse pronotal carinae.

Achras C. O. Waterhouse, 1879

Achras C. O. Waterhouse, 1879: 61.
Type species. *Achras limbatus* C. O. Waterhouse, 1879: 62 (by monotypy).

Diagnosis. Body medium-sized. Head without rostrum. Antennae strongly compressed, slender, only antennomeres 3 and 4 broad, subsequent antennomeres narrow, acutely pointed. Maxillary palpi quite robust. Pronotum with almost straight basal margin and posterior angles acutely projected. Disc with five areoles. Elytra with strong primary costae on humeral third of elytra, much weaker further back, primary costae 1 and 3 much weaker apically, secondary costae on apical third of costa 3 absent, on costa 1 irregular. Transverse costae on elytra weak, irregular, elytral cells mostly slightly transverse. Male genitalia robust, short, with two large spines on basal part of internal sac. Ovipositor with short coxites and long, slender valvifers, vagina large, membranous (Fig. 151).

Distribution. Australian Region: Australia (New South Wales). Monotypic.

Remarks. *Achras* was classified with *Metriorrhynchus* and *Metriorrhynchoides* in the Metriorrhynchini (Kleine, 1933) and later was not studied but kept in the Metriorrhynchina (Bocak & Bocakova, 1990a). Based on the pre-

sent analysis it is transferred to the subtribe Hemiconderina. *Achras* is characterised by sclerotized, widened basal part of spermaduct and lateral sacks at base of vagina. The second character can very between species analogous to the situation in other genera. *Achras* seems to be very closely related to *Wakarumbia* but retains several plesiomorphic character states, i. e. vestiges of secondary costae, unrotated phallus, pair of basal spines on internal sac.

Wakarumbia and *Achras* both have characteristically shaped valvifers (Fig. 151), vagina with unpaired gland located on independent frontal sac, both genera have much weaker costae 1 and 3, but which extent the whole length of elytra. They have similar, characteristic labrum and slender lateral processes on mesoscutum.

Hemiconderis Kleine, 1926

Hemiconderis Kleine, 1926a: 162.
Type species. *H. explicatus* Kleine, 1926a: 162 (by monotypy).

Diagnosis. Body small to medium-sized, slender, coloration usually bright, seldom dull. Head small, without rostrum. Antennae considerably compressed, weakly serrate, reaching beyond elytral apex. Maxillary palpi relatively long, slender, terminal palpomere slightly widened. Pronotum with slender, conspicuous carinae forming 5 areoles. Median areola slender (Fig. 60). Elytra long, slender, with 4 primary costae at base, primary costa 3 shortened, reaching middle of elytra. Primary costa 1 seldom short. Secondary costae well developed, reticulate cells small, regular. Phallus lanceolate, internal sac with two large spines linearly arranged. Female genitalia broad, well sclerotized, coxites free. Valvifers thin, their bases with various projections, widened.

Distribution. Australian Region: New Guinea, Yapen Island. Altogether 9 species known (Bocak & Bocakova, 1990b).

Remarks. *Hemiconderis* is the only member of the Hemiconderina having entire secondary costae, shortened primary costa 3 and two spines on internal sac linearly arranged; the first located at base of phallus, the second on apical half. Basal part of valvifers of all females widened to some degree (Bocak & Bocakova, 1990b). *H. bipustulatus* Bocak & Bocakova, 1988 has additionally a shortened costa 1, but to a considerably smaller degree than encountered in Trichalina.

Wakarumbia Bocak, 1999

Wakarumbia Bocak, 1999b: 166.
Type species. *Wakarumbia gracilis* Bocak, 1999b: 167 (by original designation).

Diagnosis. Body small, very slender, delicate, with slender legs and antennae. Head without rostrum. Antennae slightly serrate to parallel-sided. Pronotum with five areoles, pronotal carinae straight and slender. Elytra almost parallel-sided, with four primary costae, primary costae 1 and 3 weak, secondary costae absent, only vestiges present at base of elytra. Transverse costae well developed, regular, elytral cells mostly square-shaped. Phallus with one, complex basal spine on internal sac, in most species apical part of phallus rotated to various degrees.

Distribution. Australian Region: Sulawesi, Buton Island. Altogether 23 species classified in *Wakarumbia*.

Remarks. *Wakarumbia* is the only genus of Hemiconderina that lacks secondary costae. Apical part of phallus in most species is characteristically rotated and there is one complex spine at base of the phallus.

Trichalina Kleine, 1928

Trichalinae Kleine, 1928: 222.
Trichalini Kleine 1933: 69.
Trichalina Bocak et Bocakova, 1990a: 646

Type genus. *Trichalus* C. O. Waterhouse, 1877: 82.

Diagnosis. Body small to medium-sized. Head without rostrum. Antennae serrate, seldom with short lamellae (several *Diatrichalus*, Fig. 32), or flabellate (*Flabellotrichalus*). Pronotum with slender median areola (Figs 62–65), with two divergent carinae (*Eniclases*, Fig. 66) or with five areoles (*Schizotrichalus*). Elytra regularly with considerably shortened primary costa 1 (Fig. 9), secondary costae usually well developed, absent in some *Diatrichalus*. Male genitalia slender with basal spines (Figs 97–99), widened apically with complex sclerotized internal sac (Figs 101–102) or slender, with partly sclerotized apical part, internal sac without basal spines (Figs 104–106) or basal spines apparent (Fig. 103). Ovipositor with simple coxites, valvifers usually long and slender, vagina always membranous, lateral glands usually dorsally attached (*Microtrichalus* etc.), sometimes laterally attached (*Diatrichalus*, *Enylus* only).

Distribution. Australian Region and eastern part of the Oriental Region: Indochina, Thailand, southernmost Yunnan, Peninsular Malaysia, the Philippines, and the Great Sundas (Fig. 5). Highest diversity in New Guinea and Australia, the number of species decreases to the west of the range and only a few species are known from continental Asia.

Remarks. The genera with shortened elytral costa 1 previously classified in the tribe Trichalina were revised recently by Bocak (1998b). Only genera with the characteristic slender phallus and dorsally attached lateral vaginal glands belonged in the Trichalina in the restricted sense, and the sister-group position of *Diatrichalus* and *Enylus* was confirmed. The present analysis of the whole subfamily Metriorrhynchinae confirmed the monophyly of the restricted Trichalina and also supports the close relationship of genera *Enylus* and *Diatrichalus* to the Trichalina clade. Although the relationship of these genera needs confirming using larval characters and molecular data, the genera *Enylus* and *Diatrichalus* are here classified in the Trichalina.

Enylus C. O. Waterhouse, 1879

Enylus C. O. Waterhouse, 1879: 72.
Type species. *E. segregatus* C. O. Waterhouse, 1879 (by monotypy).

Strophicus C. O. Waterhouse, 1879: 73, **syn. n.**
Type species. *Strophicus nigellus* C. O. Waterhouse, 1879: 73 (by monotypy).

Diagnosis. Body small to medium-sized. Head small, without rostrum. Antennae strongly compressed, similar in both sexes, serrate or antennomeres almost parallel-sided, never flabellate. Maxillary palpi robust, apical palpomere with an oblique apex, broad. Pronotum only with median areola, lateral carinae absent, weak lateral tubercles on lateral margins of pronotum. Elytra with four primary costae, primary costa 1 strong over whole length, costae 2 and 4 much stouter than costae 1 and 3, costa 3 much weaker apically. Legs slender, strongly compressed. Male genitalia always with slender, long phallus, with pair of basal spines, partly sclerotized apically, phallobasal membrane inconspicuous. Ovipositor with short, rather stout valvifers, fused with coxites (Fig. 137), vagina relatively short, bases of glandular ducts robust, accessory glands inserted laterally. Spermatheca slender, very long.

Distribution. Australian Region: New South Wales, New Guinea, and Mysool Island. Only four species are at present classified in *Enylus*, two of them were originally classified in *Strophicus*.

Remarks. *Enylus* is the only genus classified in Trichalina not having a shortened elytral primary costa 1. Only the holotype of *Strophicus nigellus* was available, and therefore *Strophicus* was not included in the phylogenetic analysis. *Strophicus* is externally very similar to *Enylus* and the only differs in the size of its eyes: very small in males of *Strophicus* and very large in *Enylus*. The presence and/or absence of sexual dimorphism in eye size ise regularly observed in genera of Lycidae. This character is correlated with when in the day they fly. Males of species active at night have large eyes. Therefore, I propose that *Strophicus* is a junior subjective synonym of *Enylus*.

Diatrichalus Kleine, 1926

Diatrichalus Kleine, 1926a: 167.
Type species. *D. xylobanoides* Kleine, 1926 (by original designation).

Mimotrichalus Pic, 1930: 92, hors texte; Bocak, 1998b.
Type species. *M. tenimberensis* Pic, 1930 (by monotypy).

Diagnosis. Body medium-sized, coloration variable but mostly black or black with metallic blue shine, only a few species have a brightly coloured pronotum and basal part of elytra. Never light concolour. Head small, without rostrum. Antennae strongly compressed, antennomeres parallel-sided to acutely serrate in both sexes, seldom very shortly flabellate in male. Maxillary palpi with broad apical palpomere bearing papillae at apex. Pronotum with one more or less broad longitudinal areola in the middle, lateral margins elevated. Elytral primary costa 1 considerably shortened, reaching at most one third of elytral length, secondary costae irregular to completely absent in some species. Legs relatively strong and short, strongly compressed. Male genitalia with relatively short and robust phallus, internal sac lacks basal spines, regularly strongly sclerotized apically (Figs 100–101). Ovipositor with slender, long valvifers, sometimes incompletely fused at base, vagina relatively short, vaginal glands inserted laterally. Spermaduct robust at base, spermatheca slender, very long.

Distribution. Australian and eastern part of the Oriental Region. Only one species found in continental Malaysia, Java, Borneo and Sumatra. All other Oriental representatives occur in the Philippines. The highest diversity is found in New Guinea. Kleine (1933) placed six species in *Diatrichalus*. Later, it was found that many Oriental and Papuan species previously classified as *Trichalus* belonged to *Diatrichalus* (Bocak, 2000a, 2001a). At present over 40 species are classified in this genus.

Remarks. In all *Diatrichalus* the basal part of spermaduct is widened and this unique character is considered to be apomorphic state. This genus originally included only species that lacked secondary costae. A study of most species showed that in *Diatrichalus* there are transitional states between strong secondary costae, weak irregular secondary costae and complete absence of costae. The internal sac and basal part of female spermaduct in *Diatrichalus* has a very characteristic and unique shape of and both species that have and lack secondary costae are included in this genus.

Trichalus C. O. Waterhouse, 1877

Trichalus C. O. Waterhouse, 1877: 82.
Type species. *T. flavopictus* C. O. Waterhouse, 1877: 82; C. O. Waterhouse 1878: 103 (by subsequent designation)

Xantheros Fairmaire, 1877: 167
Type species. *X. ochreatus* Fairmaire, 1877: 167; Bourgeois 1891: 347 (by subsequent designation).

Diagnosis. Body medium-sized, slightly widened posteriorly, antennae serrate in both sexes. Pronotum with one longitudinal median areola, first elytral primary costa shortened, secondary costae always well developed, regular. Male genitalia with slender phallus, internal sac membranous, with pair of spines at base, internal sac exposed, free. Ovipositor with extremely robust valvifers, fused in basal third, flat, closely attached to coxital processes. Vagina robust, lateral glands attached dorsally, their bases widened, unpaired vaginal gland short, spermathecal duct short, spermatheca large, bulbous.

Distribution. Australian Region: only continental Australia.

Remarks. Kleine (1933) cited 112 *Trichalus* species from the Oriental and Australian Regions. Recent studies indicate that most Oriental and Papuan species previously classified as *Trichalus* belong to *Microtrichalus* (Bocak, 1998b, d, 2000d). The Australian *Trichalus* is badly in need of revision. Widened bases of lateral glands and fused valvifers are the unique apomorphic character states of *Trichalus*.

Microtrichalus Pic, 1921

Microtrichalus Pic, 1921b: 9, hors texte.
Type species. *M. singularis* Pic, 1921b: 9 (by monotypy).

Falsoenylus Pic, 1926: 29, hors texte; Bocak, 1998b.
Type species. *F. basipennis* Pic, 1926: 30; (by monotypy).

Diagnosis. Body small to medium-sized, very often with dorsal part of body at least partly yellow to lightly brown. Antennae serrate in both sexes, labial palpi slender, apical palpomere slightly narrowed at apex, com-

pressed. Pronotum with one longitudinal median areola. First elytral primary costa shortened, secondary costae regularly present. Male genitalia very uniform within genus. Phallus slender, only basally completely sclerotized, ventrally open apically, internal sac exposed, with pair of sickle-like thorns at base, sometimes with V-shaped rod in membrane. Whole of male genitalia often very slightly pigmented and sclerotized, rendering structure of internal sac inconspicuous. Ovipositor with slender valvifers. Vagina slender to moderately robust, with dorsally attached lateral accessory glands whose bases are more sclerotized, proper glands very fine. Two lateral pockets of unknown function are present in lateral part of vagina. Very slender unpaired gland attached to base of vagina.

Distribution. Australian and Oriental Regions: Sunda Islands, the Philippines, Peninsular Malaysia, Thailand, Indochina, and the southernmost part of Yunnan.

Remarks. Many species formerly placed in *Trichalus* were transferred to *Microtrichalus* (Bocak, 1998d, 2000 d). At present, 40 species are classified in *Microtrichalus*, but the faunas of New Guinea and Australia, where the highest diversity is found, have not yet been revised. Lateral pockets and unpaired basal vaginal gland are the unique apomorphic character states of *Microtrichalus*.

Flabellotrichalus Pic, 1921

Flabellotrichalus Pic, 1921b: 9, hors texte.
Type species. *F. notatithorax* Pic, 1921b: 9; Kleine, 1936: 4 (by subsequent designation).

Stereotrichalus Kleine, 1926a: 183; Kleine, 1930a: 330.
Type species. *S. evidens* Kleine, 1926a: 184 (by subsequent designation)

Villosotrichalus Pic, 1921b: 9, hors texte; Bocak, 1998.
Type species. *V. reductus* Pic, 1921b: 9 (by monotypy).

Diagnosis. Body medium sized to large, slightly widened posteriorly. Usually dark brown to black with humeral part of elytra lighter. Head without rostrum, antennae flabellate in male (Fig. 27). Pronotum with one longitudinal median areola, frontal and lateral margins of pronotum very often with dense short to very long pubescence. Elytral primary costa 1 shortened, secondary costae always present. Male genitalia very slender, phallobase usually covered with extensive membrane. Phallus very long, narrow, sclerotized completely only basally, apically sclerotized dorsally, internal sac exposed, pigmented at apex, sometimes with strengthened rod in membrane, never with pair of spines at base. Vagina with two dorsally attached accessory glands, glands very fine, spermaduct long, curved, spermatheca lemon-shaped.

Distribution. Australian Region. *Flabellotrichalus* is recorded only from New Guinea and Moluccas. At present 13 species are classified in this genus.

Remarks. Long antennal lamellae in male, pubescence on pronotum, and shape of male genitalia are unique characters of *Flabellotrichalus* within the Trichalina.

Schizotrichalus Kleine, 1926

Schizotrichalus Kleine. 1926a: 183.
Type species. *T. nigrescens* C. O. Waterhouse, 1879: 70 (by original designation).

Diagnosis. Body small to medium sized, dark brown to black. Antennae slightly serrate in both sexes. Maxillary palpi slender. Pronotum with five areoles. Elytral primary costa 1 shortened, usually secondary costae developed, in one (presently undescribed) species irregular transverse costae and mostly absent secondary costae. Male genitalia with long, slender, only basally well sclerotized phallus, dorsally one strengthened pigmented keel, bearing reversed cup-like apex (Fig. 105). Middle part membranous, with internal sac pigmented apically, no basal spines present. Phallobase without extensive membrane. Ovipositor with long slender valvifers, sometimes connected at bases. Vagina long, slender, lateral accessory glands inserted dorsally, apical gland short. Spermaduct short, straight, spermatheca robust.

Distribution. Australian Region: New Guinea. Monotypic, but several undescribed species have been collected.

Remarks. *Schizotrichalus* differs in five pronotal areoles from other genera classified in the in Trichalina.

Eniclases C. O. Waterhouse, 1879

Eniclases C. O. Waterhouse, 1879: 66.
Type species. *Lycus* (genus 35) *luteolus* C. O. Waterhouse, 1878 (by original designation).

Trichalolus Pic, 1923: 36, hors texte; Bocak & Bocakova, 1991.
Type species. *T. apertus* Pic, 1923: 36 (by monotypy).

Diagnosis. Body medium-sized. Head without rostrum, antennae with parallel-sided to serrate antennomeres 3–10, only a few species antennomeres flabellate in male. Labial palpi slender, apical palpomere parallel-sided. Pronotum divided by two divergent carinae into three fields (Fig. 66). Elytra with first elytral primary costa shortened, with complete secondary costae. Male genitalia with apparent keel on dorsal surface of phallus, with free, membranous internal sac, without sclerotised structures or spines (Fig. 106). Ovipositor with basal processes of coxites attached to valvifers, lateral glands of vagina attached into the middle part of vagina, glands very fine.

Distribution. Australian Region. At present, 26 species are known from New Guinea and one from the Moluccas. Although I have seen very extensive lycid material from the Solomon Islands it contained no species of this genus.

Remarks. *Eniclases* is characterised by a unique arrangement of pronotal costae. Bocak & Bocakova (1991) revised this genus.

Metriorrhynchina Kleine, 1926

Metriorrhynchina Kleine, 1926a: 97; Bocak & Bocakova, 1990a: 644.

Type genus. *Metriorrhynchus* Gemminger et Harold, 1869: 1629.

Diagnosis. Body small to large. Head usually without rostrum, several genera with a very small (*Leptotrichalus*) or long rostrum (*Porrostoma*, Fig. 10, *Metriorrhynchoides*, *Oriomum*). Male antennae often flabellate, the position of lamellae or antennomeres variable within genera,

lamellae usually robust (Fig. 38), seldom extremely slender and long (*Pseudodontocerus*, Fig. 45, *Cladophorus*, Figs 44, 51). Pronotum usually with distinct frontolateral and lateral carinae and small, slender median areola attached to basal margin of pronotum (e. g. Figs 69–74, 76–83), several genera with either only median areola present and lateral costae vestigial (*Leptotrichalus*, *Lobatang*, Fig. 75), only frontal keel and median areola strongly marked and lateral and frontolateral carinae vestigial (*Bulenides*, Fig. 68), or only frontal keel distinct (*Caenioxylobanus*, Fig. 67). Elytra with primary and secondary longitudinal costae connected by transverse costae (Figs 52–55, 89), secondary costae sometimes absent (Figs 56, 88, 89). Male genitalia without parameres, often lanceolate with pair of spines apically (Figs 107–12), robust, with basal spiens (Figs 125–28) or tubular with exposed membranous internal sac (Figs 115–20). Female genitalia with simple coxites, membranous or more or less sclerotized vagina, large unpaired gland and pair of lateral glands.

Distribution. Afrotropical, Oriental, Australian Regions and eastern part of the Palaearctic Region. Coincident with distribution of Metriorrhynchini (Fig. 3).

Bulenides C. O. Waterhouse, 1879

Bulenides C. O. Waterhouse, 1879: 34.
Type species. *Lycus* (genus 21) *obsoletus* C. O. Waterhouse, 1878: 109; Bourgeois, 1891: 345 (by subsequent designation).

Diagnosis. Body small to medium sized. Head without rostrum. Antennae robust, flabellate in male, lamellae short and robust (as in Fig. 38), serrate in female. Maxillary palpi slender, apical palpomere pointed. Pronotum often narrowed anteriorly, with robust frontal margin (Fig. 68), disc with one small median areola, regularly with vestiges of frontolateral costae. Elytra with four strong, entire primary costae and weak but regular secondary costae. Elytral cells minute. Phallus slender, lanceolate, internal sac with two spines on apical third of phallus. Vagina membranous, spermaduct short, spermatheca lemon-shaped (Fig. 155).

Distribution. Eastern part of Oriental Region: Burma, Thailand, Indochina, Taiwan, Peninsular Malaysia, Sumatra, Java, Borneo, and the Philippines.

Remarks. *Bulenides* is characteristic in having only a small, narrow areola in middle of pronotum, the carinae forming the areola can be obtuse to absent and consequently only a strong frontal keel is present on pronotum. The shape of pronotum is variable, but often distinctly narrowed frontally. The shape of pronotum is similar to that of *Caenioxylobanus*, which differs in the complete absence of secondary elytral costae and tibial spurs. Additionally, the form of the frontal margin of the pronotum in *Bulenides* and *Caenioxylobanus* is unique (Figs 67–68). This character state was confirmed in *B. obsoletus* (type species) and some other species but is absent from some species included in *Bulenides*. Only a complete revision of *Bulenides* will clarify the limit of the genus.

Caenioxylobanus Pic, 1922

Caenioxylobanus Pic, 1922: 13, hors texte.
Type species. *Caenioxylobanus ater* Pic, 1922 (hereby designated).

Diagnosis. Body medium-sized, completely dark brown to black. Head without rostrum. Antennae robust, strongly compressed, flabellate in male, serrate in female (Fig. 39). Maxillary palpi robust. Pronotum trapezoidal, with a distinct protruding frontal margin, which is formed by a robust vertical surface (Fig. 67). One longitudinal keel present on disc, anterior half of keel sharp and narrow, higher than wide at base, in basal part almost absent, transformed into a very wide, flat mound. Elytra flat, with four longitudinal costae and slender transverse costae. All costae very regular, slender and sharp. Reticulate cells quadrate to slightly transverse (Fig. 88), all costae shiny, black, bottom of cells velvet, dark brown. Male genitalia slender, lanceolate, internal sac with two spines on apical third. Ovipositor robust (Fig. 135), vagina membranous, spermatheca long, bulbous apically (Fig. 140).

Distribution. Afrotropical Region: Madagascar. Two species are endemic to Madagascar.

Remarks. Pronotal carinae of *Caenioxylobanus* have a unique shape and this genus differs from the closely related *Bulenides* in the absence of secondary costae and in the mat, velvet bottoms to the elytral cells.

Xylobanus C. O. Waterhouse, 1879

Xylobanus C. O. Waterhouse, 1879: 38.
Type species. *Lycus costifer* Walker, 1858: 282 (by original designation).

Invalid designation. *Xylobanus fastidiosus* C. O. Waterhouse, 1879: 39; Bourgeois, 1891: 345.

Diagnosis. Body small to medium-sized, often slender, parallel-sided. Head without rostrum. Antennae serrate to flabellate in male, lamellae if present short, robust (as in Fig. 38), more or less serrate in female. Maxillary palpi robust, apical palpomere almost parallel-sided to considerably widened. Pronotum trapezoidal, usually with seven strongly marked areoles (Fig. 69), in some species lateral and frontolateral carinae obtuse to reduced. Elytra with four well developed, strong longitudinal primary costae, secondary costae absent, elytral reticulate cells transverse, regular. Male genitalia slender, phallus lanceolate as in *Cautires* (Fig. 108) or widened in apical part (Figs 109, 110). Ovipositor short, with robust valvifers (Fig. 154), vagina short, membranous, spermatheca long, slender to lemon-shaped.

Distribution. Afrotropical, Australian, and Oriental Regions, Palaearctic Region: China, Japan, Korea, and Russian Far East. Almost 300 species are described for this genus.

Remarks. *Xylobanus* is an extremely species rich and widespread genus. It is characterised by a pronotum with seven areoles (although the carinae can be obtuse to vestigial on some parts of the pronotum, frontolateral and lateral pronotal carinae are never completely absent) and elytra lack secondary costae (they are present at most vestigially on narrow humeral part). *Xylobanus* and *Cautires* have a similar shaped pronotum and male and female genitalia. Their close relationship is supported by their

very similar larvae (Potozkaja, 1981, Bocak & Matsuda, in press). The affinities with *Broxylus* are discussed further. Several characters of *Xylobanus* are variable. The phallus is widely rounded apically and primary gonoporus is sclerotized in many species, including the type species *Xylobanus costifer*, but the apex is pointed and the gonoporus membranous in *X. corporaali* Pic, 1922 from Sumatra. On the other hand these species both have phallus with a wide base. *Xylobanus costifer* has valvifers connected at base, as does one species from Bali and some other species, but this sclerite is vestigial or absent in other species. Also presence of spiculum gastrale is variable and some species have flabellate antennae (e. g. *X. nigrimembris* Pic, 1926d), or serrate antennae (*X. humifer* Walker, 1858). Only an extensive, detailed alpha-taxonomical study can clarify the concept of *Xylobanus*. The absence of secondary costae is an advanced feature, which has evolved several times in Lycidae.

Broxylus C. O. Waterhouse, 1879

Broxylus C. O. Waterhouse, 1879: 20.
Type species. ?*Calopteron pfeifferi* C. O. Waterhouse, 1878: 106 (by monotypy). The name was cited by Waterhouse (1878) with a question mark before the generic name indicating provisional generic classification.

Samanga Pic, 1921b: 9, hors texte, **syn. n.**
Type species. *Samanga fenestrata* Pic, 1921b: 9 (by monotypy).

Diagnosis. Body medium-sized. Head small, antennae reach beyond the middle of the elytra, compressed. Palpi strongly compressed, maxillary palpi with long, spoon-like apical palpomere, palpomere 4 as long as combined length of palpomeres 1–3, labial palpi short, apical palpomere large (Fig. 15). Pronotum with partly reduced carinae, frontolateral carinae present on areola only, lateral carinae weak (Fig. 70). Elytra flat, widest in apical tenth or strongly hemispherically widened, with four longitudinal, sharp primary costae and thin, sharp transverse costae of similar strength. Elytral cells quadrate to apparently longitudinal (Fig. 90). Legs slender, strongly compressed. Trochanters very slender, long. Male genitalia as figured (Fig. 111).

Distribution. Australian Region: Sulawesi. Altogether 11 species known from Sulawesi (Bocak & Jašš, in press).

Remarks. *Broxylus* was classified in the Calopterini (Lycinae) and transferred to the Metriorrhynchinae recently by Bocakova (in press). *Samanga* and *Broxylus* are very closely related. They have similar shaped genitalia and large, flat apical palpomeres. These taxa also have quadrate elytral cells with distinct concave bottoms (these are unique in Metriorrhynchinae) and reduced lateral carinae on the pronotum. Thanks to the considerably dilated elytra *Broxylus* has a very characteristic general appearance. The last mentioned character is the only difference between *Broxylus* and *Samanga* and therefore I propose *Samanga* to be a junior synonym of *Broxylus*. Elytra of *Broxylus fenestratus* are less dilated and similar to those of *Xylobanus*.

Broxylus is very close to *Xylobanus* from which it differs in the shape of its terminal palpomeres. We do not have reliable synapomorphic character state for *Xylobanus*, and therefore *Broxylus* may be a modified member of *Xylobanus*.

Cautires C. O. Waterhouse, 1879

Cautires C. O. Waterhouse, 1879: 36.
Type species. *Lycus* (gen. 22) *excellens* C.O. Waterhouse, 1878: 110; Bourgeois, 1891: 345 (by subsequent designation)

Diagnosis. Body small to medium sized. Head without rostrum. Antennae flabellate in male (Fig. 38) and serrate in female. Maxillary palpi robust, apical palpomere widened, securiform. Pronotum trapezoidal, disc with seven areoles (Fig. 71), seldom lateral carinae partly reduced. Elytra with four entire longitudinal primary costae. Secondary costae considerably weaker, but well developed. Transverse costae regular, as strong as secondary longitudinal costae. Phallus slender, lanceolate, internal sac with two spines on apical third of phallus (Fig. 108). Ovipositor slender, valvifers subtle, vagina membranous, spermatheca lemon-shaped (Fig. 149).

Distribution. Afrotropical and Oriental Regions; Palaearctic Region: Russian Far East, China, Japan, Taiwan. Although *Cautires* was reported by Kleine (1926a, 1933) from New Guinea, I have not found any *Cautires* from this region and Kleine's illustrations of male genitalia are similar to those of *Cladophorus* or *Cautiromimus*. In the south-east, the furthermost records of *Cautires* are from the Philippines, Borneo and Lesser Sundas (Sumbawa). I have not found any representative in Sulawesi or Moluccas and it is not present in New Guinean material. The highest diversity occurs in continental South East Asia, Sumatra, Java and Borneo. *Cautires* is the commonest lycid in Madagascar, but it is rare in continental Africa, although many species are reported from there.

Remarks. All characters used for the definition of *Cautires* (seven pronotal areoles, entire elytral costae and shape of genitalia) are symplesiomorphic character states and at present no apomorphic character state is known. An alpha taxonomic study of the *Cautires* clade will lead to a better understanding of the relationships.

Prometanoeus Kleine, 1925

Prometanoeus Kleine, 1925c: 133.
Type species. *Prometanoeus ochraceus* Kleine, 1925c: 133 (by monotypy).

Tapromenoeus Bocak and Bocakova, 1989: 327, **syn. n.**
Type species. *Xylobanus hirtus* Kleine, 1928: 234 (by original designation).

Diagnosis. Body small. Head without rostrum. Antennae slender, weakly serrate, flattened (Fig. 37). Maxillary apical palpomere pointed (Fig. 16). Pronotum with short median areola attached to frontal margin by relatively long keel. Frontolateral carinae less apparent (Fig. 72). Elytra with three primary longitudinal costae. According to structure of basal part of costae, primary costae 1, 2 and 4 present, costa 3 absent, vestiges of it make base of costa 4 stouter. Secondary costae weak, irregular or absent. Transverse costae obtuse, weak, irregular to well developed. Elytra densely pubescent or with erect bristles. Phallus lanceolate, apical fourth wider,

internal sac with two spines. Ovipositor moderately slender, vagina membranous.

Distribution. Oriental Region: Ceylon. Two species classified in this genus.

Remarks. The shape of genitalia and pronotal carinae indicate a close relationship between *Prometanoeus* and *Cautires*. They differ in absence and/or presence of flabellate antennae in male. The flabellate antennae evolved several times in Lycidae. The monotypic genera *Prometanoeus* and *Tapromenoeus* are very closely related and although they are different in general appearance they have a similar shaped pronotum, pubescence on elytra, and a similar shaped aedeagus. Bocak & Bocakova (1989) based *Tapromenoeus* on the absence of secondary costae but the analysis showed that the reduction of secondary costae happened several times in the Metriorrhynchinae and is also often encountered in other subfamilies of Lycidae. *Prometanoeus* does not have any reliable apomorphic character state that separates it from *Tapromenoeus*. Therefore I consider *Tapromenoeus* to be a junior subjective synonym of *Prometanoeus*.

Metanoeus C. O. Waterhouse, 1879

Metanoeus C. O. Waterhouse, 1879: 73.
Type species. *Lycus* (gen. 37) *conformis* C. O. Waterhouse, 1878: 115; Bourgeois, 1891: 347 (by subsequent designation).

Diagnosis. Body small to medium-sized, elytra at most slightly widened posteriorly. Head small, without rostrum, with large eyes even in females. Male antennal lamellae long, narrowly attached to basal parts of antennomeres (Fig. 40). Maxillary palpi relatively slender, apical antennomere parallel-sided. Pronotum with seven areoles, carinae obtuse (Fig. 73). Phallus wide basally (Fig. 113). Phallobasal membrane extensive, at least partly sclerotized. Internal sac with three pairs of spines. Vagina often considerably sclerotized, form of sclerotisation highly species specific, narrowed to apex (if vagina rounded, then basal part of spermaduct is robust), unpaired gland attached basally to apically, basal position correlated with sclerotisation of vagina, lateral glands large to medium sized, attached ventrally, when vagina sclerotized, laterally if membranous, basal part of glandular ducts more or less sclerotized. Spermaduct usually extremely long, sometimes of medium length (in species with membranous vagina). Female valvifers considerably shortened, modified in plates (Fig. 150).

Distribution. Oriental Region. The highest diversity found in Borneo, Sumatra, and Peninsular Malaysia. *Metanoeus* is very rare in western part of Oriental Region. One species is common in Mindanao. Altogether over 20 species are classified in *Metanoeus*.

Remarks. The very obtuse pronotal carinae and vestigial valvifers are characteristic of *Metanoeus*. Similar obtuse carinae are found in some *Metriorrhynchus*, which differ in the much shorter lamellae of male antennae, long slender phallus and only shortened valvifers. The sclerotisation of vagina, long processes on scutellum and long, basally attached male antennal lamellae reminiscent of some Papuan representatives of the Metriorrhynchinae. No genera bearing similar characters were found within the range of *Metanoeus*. Further characters supporting the relationship of *Metanoeus* within Metriorrhynchina are need.

Metriorrhynchus Gemminger et Harold, 1869

Metriorrhynchus Gemminger et Harold, 1869: 1629.
Type species. *Lycus parallelus* Guérin-Méneville in Boisduval, 1835: 114; C. O. Waterhouse, 1878: 101 (by subsequent designation).

Metriorhynchus Guérin-Méneville, 1838: 72 (a junior homonym of *Metriorhynchus* Meyer, 1830).
Type species. *Lycus parallelus* Guérin-Méneville in Boisduval, 1835: 114; C. O. Waterhouse, 1878: 101 (by subsequent designation).

Invalid designation. *Metriorrhynchus cribripennis* C. O. Waterhouse, 1879: 52; Bourgeois, 1891: 347 (by subsequent designation).

Dilolycus Kleine, 1926a: 186, **syn. n.**
Type species. *Dilolycus lamellatus* Kleine, 1926a: 186 (by original designation).

Flabelloporrostoma Pic, 1923: 35, hors-texte (as subgenus of *Porrostoma*), **syn. n.**
Type species. *Porrostoma mirabilis* Pic, 1923: 35 (by monotypy).

Diagnosis. Body large, parallel-sided. Head small, with short, stout rostrum or without rostrum, galeae long, much longer than mandibles. Antennae serrate in both sexes or flabellate in male and serrate in female (Fig. 36). Maxillary palpi slender, long, apical palpomere slender, compressed, pointed at apex (as in Fig. 14). Pronotum with seven, in middle sometimes reduced, areoles on disc. Four strong elytral primary costae developed, costa 3 sometimes slightly shortened (by one eighth at most), slightly weaker in apical half of elytra. Secondary costae much weaker. Transverse costae dense, regular, a bit stronger than secondary costae, elytral cells transverse, regular. Phallus stout, internal sac without spines but with a sclerotised structure (Fig. 114) or similar structure accompanied by several pairs of short minute rods (Bocak, 1998c, Figs 1, 2). Ovipositor small, only partly sclerotized, with short valvifers (Fig. 134), vagina large, often at least partly sclerotized (Fig. 148; Bocak 1998c, Figs 6, 7).

Distribution. Australian Region and eastern part of Oriental Region: Peninsular Malaysia, Thailand, Laos, Sundas, and the Philippines. *Metriorrhynchus sericeus* C. O. Waterhouse, 1879 is reported from India (Kleine, 1933), but *Metriorrhynchus* was not found in the recently collected material from India. Highest diversity is found in the Papuan Subregion and Australia, but fauna of these regions is badly in need of revision at the species level. Calder (1998) combined all Australian species of *Metriorrhynchus* with *Porrostoma*, because of the doubtful status of the name *Metriorhynchus* Guérin-Méneville, 1838.

Remarks. There are two types of vagina in *Metriorrhynchus*: *M. parallelus* (type-species) has a completely sclerotized vagina but species in the *M. thoracicus* Fabricius, 1801 group have a completely membranous vagina. These groups have a similar shaped paraproctus, very

slender, reduced valvifers and a very strong membrane in which the ovipositor is enclosed.

Dilolycus was proposed for a species with considerably reduced carinae in the middle of the pronotum (Fig. 85). It has similar shaped male genitalia to the Papuan group of species (as in Bocak, 1998c, Figs 1, 2). Therefore I consider *Dilolycus* to be a junior subjective synonym of *Metriorrhynchus*.

The holotype of *Metriorrhynchus mirabilis* has damaged antennae, only the three basal antennomeres of each antenna remain preserved, antennomere 3 is serrate. Two fragments of antennae were glued on the separate label: the first fragment was serrate, corresponding to the remaining antennomeres on the holotype, the second fragment flabellate. It must be part of a different specimen, because it is made up by antennomeres 3–11. The name *Flabelloporrostoma* and its generic status are based on this incorrectly identified body part. Therefore, I propose *Flabelloporrostoma* to be a junior subjective synonym of *Metriorrhynchus*.

Lobatang Bocak, 1998

Lobatang Bocak, 1998b: 190.
Type species. *Lobatang papuensis* Bocak, 1998b: 190 (by original designation).

Diagnosis. Body slender, externally similar to *Trichalus* (general body form, shortened first elytral primary costa, only one longitudinal areola in middle of pronotum, Fig. 9), medium-sized to moderately large. Head without rostrum. Antennae long, strongly compressed, antennomeres 3–10 almost parallel-sided to serrate in both sexes. Maxillary palpi with slender apical palpomere. Pronotum with one longitudinal, median areola, lateral margins parallel-sided or pronotum much wider at base. Elytra flat, with shortened primary costa 1, usually with apparent secondary costae, in one species secondary costae distinctly weaker than transverse ones, irregular, interrupted. Legs long, slender, hind trochanters much wider apically. Phallus robust only at base, slender and apical two thirds very gradually narrowed, internal sac completely sclerotized. Phallobase robust, membrane partly sclerotized (Fig. 116). Ovipositor short and wide, valvifers robust, vagina wide, accessory glands inserted laterally, glandular ducts very short, unpaired apical gland as long as vagina.

Distribution. Australian Region: New Guinea, Moluccas, Sulawesi; Oriental Region: the Philippines.

Remarks. *Leptotrichalus* and *Lobatang* has same shaped female genitalia, especially the shortened, widened valvifers. *Lobatang* is characterised by the unique modification of the internal sac, which has not been found in other Lycidae.

Leptotrichalus Kleine, 1925

Leptotrichalus Kleine, 1925a: 296.
Type species. *Metriorrhynchus cyaniventris* Kirsch, 1875 (by original designation).

Diagnosis. Body medium-sized to large, slender, slightly widened posteriorly. Head small, without or with very short rostrum. Antennae compressed, antennomeres 3–10 parallel-sided to slightly serrate, never flabellate. Pronotum slender, long, apparently narrowed frontally (Fig. 75), only very slender longitudinal areola in middle of pronotum, sometimes less apparent lateral carinae present on middle of lateral pronotal margin. Elytra slender, with considerably shortened primary costa 1 and with entire secondary costae. Legs very long, slender, strongly compressed. Male genitalia very diverse in shape, often slender, tube-like, internal sac without any basal spines, rarely with strengthened sclerotized parts. Phallobase often with large, well sclerotized membrane. Ovipositor with short valvifers, vagina short, accessory glands attached laterally, unpaired vaginal gland large, spermatheca bulb-like.

Distribution. Australian Region: Lesser Sundas, Moluccas, and Sulawesi; Oriental Region: Sunda Islands, the Philippines, Malaysia, Thailand and Indochina. Altogether almost 60 species are classified in *Leptotrichalus* with highest diversity in the Philippines.

Remarks. The relationship between *Leptotrichalus* and *Lobatang* is supported by prolonged galees, very wide base of male sternum A8, strong, shortened valvifers and generally short and wide ovipositor and the slender and asymmetrical shape of basal part of phallus. They differ in the prolonged pronotum in *Leptotrichalus* and the sclerotized internal sac in *Lobatang*. Additionally, the apical maxillary palpomere is more slender in *Leptotrichalus*.

Stadenus C. O. Waterhouse, 1879

Stadenus C. O. Waterhouse, 1879: 61.
Type species. *Porrostoma dichroum* C. O. Waterhouse, 1877: 86 (by original designation).

Diagnosis. Body medium-sized. Head small, without rostrum. Antennae stout, serrate. Maxillary palpi with almost parallel-sided apical palpomere, without papillae, apex obliquely cut. Pronotum wide, almost straight at basal margin, widest before base, mostly only median areola present (see remarks), but at least small vestiges of frontolateral carinae are regularly present (Fig. 76). Primary costae strong, almost completely developed, costa 2 and 4 apparently stronger in apical part, other primary costae very slightly shortened, weaker. Phallus simple, slender, internal sac without spines or sclerotisation (Figs 117, 118). Female genitalia with very robust and wide valvifers, which are firmly fused with coxites, vagina membranous, large (Figs 156, 159).

Distribution. Australian Region. Five species are placed in *Stadenus*. The Afrotropical species previously classified in *Stadenus* are now placed in the tribe Slipinskiini (Erotinae) (Bocak & Bocakova, 1992).

Remarks. The very similar shape of male and female genitalia supports the affinity of *Stadenus* and *Porrostoma*. *Porrostoma* differs in presence of rostrum, *Stadenus* has completely fused coxites and valvifers. *Stadenus* was originally defined by three areoles on the pronotal disc, but this character is unreliable. I have studied male and female *Stadenus triareolatus* in copula

(BMNH). They are externally very similar and without any doubt they are conspecific. The female specimen has three areoles, the male seven areoles. But even the female specimen has some vestiges of frontolateral carinae.

Porrostoma Castelnau, 1838

Porrostoma Castelnau, 1838: 26.
Type species. *Lycus rufipennis* Fabricius, 1801 (by monotypy).
Invalid designation. *Porrostoma erythropterum* Erichson, 1842; C. O. Waterhouse, 1879: 44.

Diagnosis. Body medium sized to large. Head with long rostrum (Fig. 10). Antennae serrate to flabellate in male (Figs 42, 49), serrate in female. Maxillary palpi slender, apical palpomere slender, almost parallel-sided, hypopharynx very long, mandibles minute. Pronotum with seven strongly marked areoles, carinae usually very strong (Fig. 77). Elytra with entire primary and secondary longitudinal costae. Transverse costae regular, dense, cells usually strongly transverse (Fig. 52). Male genitalia short, robust to slender and long, but regularly simple, parallel-sided, internal sac membranous, without spines (Fig. 119). Female genitalia with robust valvifers, very closely attached to coxites, vagina membranous, relatively short (Bocak, 1998c, Fig. 14).

Distribution. Australian Region. *Porrostoma* is the commonest lycid in Australia, where the highest diversity is found. Several species are known from New Guinea.

Remarks. *Porrostoma* was for long time considered a junior synonym of *Metriorrhynchus*. The name was used by C. O. Waterhouse (1877) and later sometimes inconsistently by Pic. Kleine (1933) listed *Porrostoma* as a junior synonym of *Metriorrhynchus*. Calder (1998) used *Porrostoma* as a junior replacement name for *Metriorhynchus* Guérin-Méneville and proposed 85 new combinations with *Porrostoma* (only Australian fauna). Bocak (1998c) replaced *Metriorhynchus* Guérin-Méneville by *Metriorrhynchus* Gemminger et Harold, used *Porrostoma* as a valid taxon and differentiated between *Metriorrhynchus* and *Porrostoma*. The identity of most species classified in *Porrostoma* is unknown and this genus is badly in a need of revision.

Metriorrhynchoides Kleine, 1926

Metriorrhynchoides Kleine, 1926a: 118.
Type species. *Metriorrhynchoides helleri* Kleine, 1926a: 119 (by original designation).

Diagnosis. Body large, conspicuously widened posteriorly. Head small with long, laterally compressed rostrum (as in Fig. 10). Antennae slender, flattened, serrate in both sexes (Fig. 43). Apical maxillary palpomere flat, narrowed to apex. Maxillae long. Pronotum with seven strongly marked pronotal areoles, median areola large, widest in frontal part (Fig. 78). Frontolateral carinae short. Pronotum constricted in basal third. Elytra wide, much wider than abdomen, with elevated humeri. Four primary longitudinal costae strong over whole length, costae 2 and 3 sometimes fused before apex. Secondary costae weak but continuous (Fig. 55). Transverse costae very dense, regular. Elytral cells transverse (Fig. 55). Male genitalia slender, internal sac membranous (Fig. 120). Ovipositor with slender coxites and stout valvifers (Fig. 136), vagina membranous, short.

Distribution. Australian Region: New Guinea, only four species classified in *Metriorrhynchoides*.

Remarks. *Metriorrhynchoides* is closely related to *Porrostoma*. Its pronotal carinae are very similar to those of *Porrostoma* and additionally they both have a long rostrum. *Metriorrhynchoides* is characterised by a widened apical part of elytra and costae 2 and 3 fused before apex of elytra. Additionally, *Metriorrhynchoides* species are a bright metallic blue with bright yellow body parts unlike Australian *Porrostoma*. All males of *Metriorrhynchoides* also have serrate antennae. I have not found an apomorphic feature defining *Porrostoma*, therefore it is very probable that *Metriorrhynchoides* is a subgroup of *Porrostoma* and will be synonymised with it in the future.

Cladophorus Guérin-Méneville, 1830

Cladophorus Guérin-Méneville, 1830: Plate II, Fig. 9.
Type species. *Cladophorus formosus* Guérin-Méneville, 1830; C. O. Waterhouse, 1878 (by subsequent designation).

Odontocerus Guérin-Méneville, 1830: 72; a homonym of *Odontocerus* Stephens, 1829; C. O. Waterhouse, 1878: 96.
Type species. *Cladophorus formosus* Guérin-Méneville, 1830; Bourgeois, 1892: 495 (by subsequent designation).

Spacekia Strand, 1936; Bocak, 1998c: 247.
Type species. *Cladophorus formosus* Guérin-Méneville, 1830 (*Spacekia* proposed by Strand, 1936 as a nomen novum for *Cladophorus*).

Diagnosis. Body medium sized to large, often brightly coloured. Head without rostrum. Antennae with very long lamellae in male (Figs 44, 51), serrate in female. Maxillary palpi stout, apical palpomere securiform. Pronotum often apparently transverse, with strongly marked seven areoles (Fig. 79). Elytra with entire primary and secondary longitudinal costae. Phallus gradually narrowed to apex, internal sac partly sclerotized. Phallobasal membrane apparently pigmented and additionally margin of phallobase partly sclerotized, with attached membrane. Membrane has a characteristic structure (Fig. 121) and usually reaches halfway along phallus. Ovipositor moderately wide, simple, valvifers slender (Fig. 141). Vagina membranous with short spermaduct and gradually widened spermatheca (Fig.144)

Distribution. Australian Region: New Guinea, Australia. All records outside this region refer to other genera.

Remarks. *Cladophorus* is defined by the form of its phallus and unique shape of phallobasal membrane (Fig. 121), which has not yet been found in other genera of Metriorrhynchinae. At least several dozens of species with this type of aedeagus are known from New Guinea (Kleine, 1926a). On the other hand, most of almost 200 species previously placed in *Cladophorus* are not congeneric with the New Guinean species (all species from the Oriental, Palaearctic and Afrotropical Regions). Kleine classified as *Cladophorus* all species that have slender antennal lamellae (mostly *Cautires*). Pic often used the name *Odontocerus* Guérin-Méneville nec Stephens and these species were transferred to *Cladophorus* by Kleine

(1933). Pic's concept is unclear and his descriptions do not allow identification bellow subfamily level.

Procautires Kleine, 1925

Procautires Kleine, 1925b: 32
Type species. *Procautires toxopei* Kleine, 1925b: 32.

Diagnosis. Body medium sized, moderately robust, parallel-sided. Head without rostrum. Antennae flabellate in male, serrate in female. Maxillary palpi short, apical palpomere securiform, maxillae short, wide, mandibles very slender, curved. Pronotum with strong carinae and seven distinct areoles. Elytra with four strong longitudinal primary costae, secondary costae present on basal fifth and apical two fifths of elytra. Elytral cells minute, rounded to square in basal and apical parts of elytra, strongly transverse in the middle. Male genitalia relatively slender, slightly widened apically, internal sac with sclerotized basal part and primary gonoporus, phallobasal membrane pigmented, structured (Fig. 126). Ovipositor slender, coxites almost as long as valvifers, between coxites triangular sclerite, valvifers slender. Vagina short, small, membranous, reaching two thirds of length of valvifers.

Distribution. Australia Region: Australia, New Guinea and Moluccas. There are several Afrotropical and Oriental species now classified in *Procautires* but they are not congeneric with *Procautires toxopei* and should be classified with *Cautires* or another closely related genus. These species have less conspicuous secondary costae, but do not share other characters with the type species.

Remarks. *Procautires* is characterised by a unique modification of elytral secondary costae. With *Kassemia* and *Cautiromimus* it shares the same shape of phallus and sclerotisation of internal sac and with *Cladophorus* pigmented phallobasal membrane, although it is in this case less extensive and does not have the characteristic structure as in Fig. 121. Additionally, I have found a relatively large sclerite between coxites. Very small structure in similar position is present also in some *Cautiromimus* (Fig. 160). The sclerite between bases of coxites is reminicent of sclerite found in some species of *Xylobanus* (Fig. 154), but unlike in *Xylobanus,* the sclerite is not connected with valvifers and is located between bases of coxites. Therefore I do not consider these structures to be homologous.

Cautiromimus Pic, 1926

Cautiromimus Pic, 1926c: 454
Type species. *Cladophorus reticulatus* Kleine, 1926a: 143 (by monotypy).

Diagnosis. Body medium sized, relatively slender. Head small, without rostrum. Male antennae flabellate, female antennae serrate. Maxillary palpi with almost parallel sided apical palpomere, without papillae. Middle pronotal areola very narrow, deep, attached to the basal margin by very short keel, reaching almost 3/4 of pronotal length, frontolateral carinae very strong, but weak in frontal punctured area, absent in frontal quarter, lateral carinae are not connected with median areola (Fig. 81). Posterior half of pronotum shining, pubescent. Elytra parallel sided, with four primary and five secondary costae extending the whole length, primary costae stronger at humeri, weak in apical fifth. Transverse costae forming quadrate, rounded cells to slightly longitudinal rounded cells. Phallus stout, two plates at base of internal sac, primary gonoporus circular, sclerotized (Figs 122, 123). Vagina very slender, its wall partly stiffened (Fig. 160).

Distribution. Australia Region: New Guinea, Moluccas. At present only *C. reticulatus* is classified here, but several undescribed species exist in collections.

Remarks. *Ditua* is similar to *Cautiromimus* but it differs in serrate male antennae and in the pattern of pronotal carinae. An alpha taxonomic revision of material in collections will clarify of their relationship.

Ditua C. O. Waterhouse, 1879

Ditua C. O. Waterhouse, 1879: 33.
Type species. *Ditua deplanata* C. O. Waterhouse, 1878: 100, 109 (by monotypy).

Invalid designation. *Ditua dichroma* (Boisduval, 1835: 123); Bourgeois, 1891: 345.

Diagnosis. Body medium sized, parallel-sided. Head without rostrum. Antennae serrate in both sexes, antennomeres more acutely triangular in male. Maxillary palpi slender, apical palpomere parallel-sided, slender. Mandibles long, slender, curved. Pronotum transverse, with slightly convex frontal margin. Seven areoles on disc, all carinae very strong (Fig. 80). Elytra with four entire primary and five secondary longitudinal costae, transverse costae dense, reticulate cell minute, quadrate to rounded. Male genitalia with robust phallus, internal sac with basal sclerotized structures and sclerotized primary gonoporus (Fig. 125). Ovipositor slender, vagina membranous.

Distribution. Australian Region: New Guinea. Two species are classified here but several undescribed species exist in collections.

Remarks. *Ditua* is reminiscent of *Cautiromimus* but differs in that male antennae are serrate and in the shape of pronotum. *Ditua deplanata* is a member of a very common lycid Müllerian mimicry complex and I have found in collections several not very closely related species identified as *Ditua dichroma.* The name *D. deplanata* was up to now used as the junior synonym of *Ditua dichroma* along with two other names. The status of the synonyms of *Ditua dichroma* was not checked.

Kassemia Bocak, 1998

Kassemia Bocak, 1998b: 195.
Type species. *Kassemia oculata* Bocak, 1998.

Diagnosis. Body small to medium sized, parallel-sided, all representatives dark brown to brown with humeral quarter to half of elytra light yellow to brown, always distinctly much lighter than the rest of elytra. Head small, without rostrum, mandibles slender, long, three times longer than labrum, apical maxillary palpomere robust, securiform, broad. Antennae strongly compressed, flabellate in males and serrate in females. Pronotum with seven areoles. Elytral secondary costae completely absent, primary costa 1 shortened, costa 2 and 3 sometimes fused

before apex. Legs relatively strong and short, strongly compressed. Male genitalia with relatively short and robust phallus, apical part widely open, internal sac strengthened at base with spine-like structure. Phallobasal membrane never sclerotized. Ovipositor with slender, long valvifers, vagina as long as valvifers, widest at apex, accessory glands inserted laterally.

Distribution. New Guinea, four species known at present (Bocak, 1998b).

Remarks. The combination of seven areoles on the pronotum, complete absence of elytral secondary costae, shape of male genitalia, and shortened primary costa 1 confirm the sure identification of *Kassemia*. The shape of male antennae and shape of male and female genitalia show little assotiation with shortened primary costa 1 in other genera. The shape of phallus indicates a close relationship with genera of the *Cladophorus* - *Ditua* - *Cautiromimus* clade.

Pseudodontocerus Pic, 1921

Pseudodontocerus Pic 1921b: 12, hors texte.
Type species. *Pseudodontocerus pulcher* Pic, 1921b: 12 (by monotypy).

Carathrix Kleine, 1926a: 149, **syn. n.**
Type species. *Carathrix pilosus* Kleine, 1926a: 149 (by original designation).

Diagnosis. Body slender, medium sized. Head without rostrum. Lamellae of male antennae extremely long (Fig. 45). Female antennae flabellate, very slender, antennomeres 2 and 3 with lamella shorter than antennal trunk (Figs 46, 47), lamellae gradually prolonged, and on middle and apical antennomeres clearly longer than trunk. Maxillary palpi long, with slender palpomere 2 and very short palpomeres 1 and 3, apical palpomere broad, with papillae on apical edge (Fig. 18). Labial palpi tiny, with broad apical palpomere and papillae on its margin. Pronotum with seven areoles (Fig. 83), carinae in middle of disc sharp and apparent, more obtuse on margins. Elytra parallel-sided, slightly widened at apex. Four primary and five secondary costae strong over whole elytral length, transverse costae dense, slightly irregular, elytral cells mostly quadrate, often rounded (Figs 52, 54). Legs slender (Fig. 161). Phallus relatively robust, with basal spines and extensively sclerotized internal sac (Figs 127–128). Ovipositor very slender (Fig. 139), vagina constricted, basal part membranous, apical two thirds partly sclerotized (Fig. 143).

Distribution. Australian Region: New Guinea.

Remarks. The flabellate female antennae are the autapomorphy of *Pseudodontocerus* and this character is not present in other Lycidae. *Pseudodontocerus* is characterised by the extremely long antennal lamellae in males, weaker lateral and frontolateral pronotal costae, and a slender body shape. I examined type species of *Carathix* and *Pseudodontocerus* as well as several closely related undescribed species, and have not found any difference supporting their separate generic status. Therefore, *Carathrix* is considered to be a junior subjective synonym of *Pseudodontocerus*.

Oriomum Bocak, 1999

Oriomum Bocak, 1999a: 111.
Type species. *Oriomum femoralis* Bocak, 1999a: 111.

Diagnosis. Body medium-sized, robust. Head rostrate, rostrum reaching to middle coxae. Antennomeres 1 to 5 slender, antennomere 6 of similar shape but slightly serrate, antennomeres 7–9 short, triangular. Bottom side of antennomeres 1 and 3–4 with very long, dense hairs. Pronotum with 7 areoles. Elytra with four primary costae extending whole length, costa 1 weaker in posterior half. Secondary costae distinct in humeral area, weaker on rest of elytra, cells irregular. Legs significantly modified for clasping of female, with long dense pubesce. Femora of fore legs and mid legs with spines basally. Hind legs with bigger, triangular trochanters. Position of hind process of trochanter corresponds with the position of femoral spines on fore and mid legs. Phallus slender, parallel-sided, with exposed, dense pubescence on apical part of internal sac, basal part of internal sac without sclerotisation. Female unknown.

Distribution. Australian Region: New Guinea. Monotypic.

Remarks. *Oriomum* differs from the remaining Metriorrhynchinae genera in the unique shape of its elytra with entire but apically distinctly weaker first primary costa, the presence of spines on hind margins of fore and mid femora, hind legs with acutely projected triangular trochanters and opistognathous head with extremely long rostrum reaching the coxae of the mid legs, and with antennomeres of a very unusual shape. *Oriomum* seems to be closely related to the *Porrostoma* clade, but for the final decision on this a female is necessary.

Cladophorinus Kleine, 1926

Cladophorinus Kleine, 1926a: 149.
Type species. *Cladophorinus cyaneus* Kleine, 1926a: 150 (by original designation).

Diagnosis. Body medium sized, slender, slightly widened in posterior quarter, whole body a shiny metallic blue. Head without rostrum. Male antennae flabellate, lamellae slightly longer than trunk of antennomere, lamellae originate from apical part of antennomere. Maxillary palpi moderately long, apical palpomere securiform. Mandibles curved, sickle-like, long. Pronotum with seven areoles, median areola wide, carinae obtuse, partly less distinct. Scutellum deeply emarginate at apex. Elytra with four entire longitudinal primary and five secondary costae, primary costa 1 weaker. Secondary costae considerably weaker, transverse costae obtuse, irregular. Male genitalia slender, phallus widened apically, internal sac partly sclerotized (Fig. 124). Female unknown.

Distribution. Australian Region: New Guinea. Monotypic.

Remarks. Only the damaged holotype of *Cladophorinus cyanescens* was available for this study. Therefore the genus was not coded into the matrix and is now classified in Metriorrhynchina on the basis of the shape of male genitalia and general appearance. The species is easily

recognisable by its metallic shine, seven pronotal areoles and flabellate antennae.

Mimoxylobanus Pic, 1921

Mimoxylobanus Pic, 1921b: 11, hors texte.
Type species. *Mimoxylobanus angustatus* Pic, 1921b: 11 (by monotypy).

Diagnosis. Body small, slender, almost parallel-sided. Head without rostrum. Male antennae apparently compressed, antennomeres 3–10 parallel-sided. Maxillary palpi short, robust, apical palpomere weakly securiform, short. Pronotum only slightly wider at base than long at midline, lateral margins almost parallel-sided, straight. Seven areoles on disc of pronotum, lateral carinae obtuse (Fig. 86). Elytra with four primary longitudinal costae, secondary costae absent, transverse costae irregular, reticulate cells mostly quadrate. All costae distinct, but low in profile. Male genitalia slender, lanceolate, with protracted apical part of internal sac (Figs 131, 132). Female unknown.

Distribution. Australian Region: Sumbawa. Monotypic.

Remarks. Only the holotype of *Mimoxylobanus angustatus* was available. In general appearance and shape of phallus this species resembles *Xylobanus*. The exact position of this genus within the Metriorrhynchina is because it differs substantially in the structure of internal sac.

Xylobanomimus Kleine, 1926

Xylobanomimus Kleine 1926a: 166.
Type species. *Xylobanomimus papuensis* Kleine, 1926a: 166 [by original designation, mentioned as *X. papuanus* (sic!)]

Diagnosis. Body small, slender, delicate. Head without rostrum. Male antennae flabellate, lamellae slender, up to four times longer than trunk of antennomere, attached to base on basal segment or middle part on more distal antennomeres. Maxillary palpi slender, long, apical palpomere parallel-sided, apex pointed. Pronotum with seven areoles, middle areola large, lateral carinae obtuse. Elytra with four primary costae, vestiges of secondary costae at humeri. Elytral areoles quadrate to longitudinal. Elytra with sparse, long, erect setae. Phallus robust, parallel-sided, with simple sclerotisation of internal sac (as in Fig. 129). Female unknown.

Distribution. Australian Region: New Guinea. Monotypic genus.

Remarks. *Xylobanomimus* has very similar male genitalia, general appearance and structure of elytral cells to *Malacolycus*, but differs in the flabellate male antennae and strong frontolateral carinae on the pronotum. *Malacolycus* can be hypothesised as a sister group of *Xylobanomimus*. *Xylobanomimus* is classified with Metriorrhynchina.

Malacolycus Kleine, 1943

Malacolycus Kleine, 1943: 151
Type species. *Malacolycus paululus* Kleine, 1943: 151 (by monotypy).

Diagnosis. Body small, very slender, only slightly sclerotized. Head small, with convex frons and small, but distinct antennal tubercles. Eyes small, hemispherically prominent. Antennae very slender, compressed (Fig. 48). Palpi slender, apical maxillary palpomere pointed. Pronotum with considerably projected posterior angles. Pronotal carinae absent and only an indistinct median areola (Fig. 84). Elytra narrow, 5.5 times longer than their combined width at humeri. Each elytron with four, slender primary costae, costae weak and hardly distinguishable in apical third. Secondary costae absent, transverse costae sparse, elytral cells mostly longitudinal (Fig. 56). Phallus short, stout, with simple sclerotisation of internal sac (Fig. 129). Female unknown.

Distribution. Australian Region: New Guinea. Monotypic genus.

Remarks. Only the holotype of *Malacolycus paululus* is known. The pronotal carinae are considerably reduced and simple male genitalia are very similar to those of *Xylobanomimus*. Therefore, *Malacolycus* is placed in the Metriorrhynchina. The body form and structure of elytra resembles that of *Xylobanomorphus*, but they differ in male genitalia (Figs 129, 130).

Xylobanomorphus Kleine, 1935

Xylobanomorphus Kleine, 1935: 316.
Type species. *Xylobanomorphus transformis* Kleine, 1935: 316 (by monotypy).

Diagnosis. Body small, very slender, delicate, covered with erect setae. Head small, without rostrum, eyes very small, their interocular distance 3.2 times longer than maximum diameter. Antennomeres 3–10 slender, parallel-sided. Maxillary palpi slender, apical palpomere pointed. Pronotum with almost parallel-sided lateral margins and projected posterior angles. Only median areola distinct, lateral carinae obtuse, frontolateral carinae absent. Elytra very slender, with four primary longitudinal costae, secondary costae absent. Transverse costae scarce, elytral cells longitudinal (Fig. 56). Male genitalia slender, phallus lanceolate, internal sac extensive with ring-shaped sclerotized structure (Fig. 130). Female unknown.

Distribution. Australian Region: New Guinea.

Remarks. At present, only the holotype of *Xylobanomorphus transformis* is known. This species resembles *Xylobanomimus* and *Malacolycus* in general appearance, but differs in the sclerotisation of the internal sac. Considering its similarity to *Xylobanomimus*, the absent frontolateral pronotal carinae can be hypothesised as secondarily reduced. Several common characters and similarity in general appearance support the affinity of *Malacolycus*, *Xylobanomimus* and *Xylobanomorphus*. All these taxa are known from single specimens of males. Further material is needed for study and provisionally *Xylobanomorphus* is classified incertae sedis in Metriorrhynchina.

Taxon dubium

Falsolucidota Pic, 1921

Falsolucidota Pic, 1921b: 9, hors texte.
Type species. *Falsolucidota testaceicollis* Pic, 1921b: 9 (by monotypy).

Remarks. The identity of the monotypic genus *Falsolucidota* is unknown. The type specimen was not found in Pic's collection in Paris and the original description does not help in the identification of this taxon.

Key to Metriorrhynchinae genera

1. Elytral primary costa 1 entire and strong in whole length, weaker in apical half or very slightly shortened; always reaching at least beyond half way along elytra 10
– Elytral primary costa 1 considerably shortened, never reaching beyond half way along elytra, typically not longer than one third of elytral length (Fig. 9) 2
2. Pronotum with seven areoles (the same type of arrangement of pronotal carinae as in Figs 69, 71 or 80), only three longitudinal elytral costae (costa 2, 3 and 4) present in the middle of each elytron; costa 1 shortened (as Fig. 9), antennae flabellate (as Fig. 38) ..... ***Kassemia***
– Pronotum with less than seven areoles (as in figs 62–66) .. 3
3. Pair of vaginal glands inserted dorsally, directed apically or laterally (Bocak, 1998b: Figs 68–70), apical part of phallus narrower than middle part, ventrally open, only dorsal part sclerotized (Figs 103–106) 4
– Pair of vaginal glands inserted laterally (Fig. 157), apical part of phallus as wide or wider than the middle (Figs 100–102, 115, 116) 9
4. Pronotum with five areoles (similar to Fig. 70) or with two anteriorly divergent longitudinal carinae (Fig. 66), phallus with pigmented dorsal keel (Figs 105, 106) 5
– Pronotum with one lanceolate longitudinal areola attached to frontal and basal margins of pronotum at one point (Figs 62–65) 6
5. Pronotum with five areoles (similar to Fig. 70) ..... ***Schizotrichalus***
– Pronotum with two anteriorly divergent longitudinal carinae (Fig. 66) ..... ***Eniclases***
6. Male antennae flabellate (similar to Figs 44, 47) ..... ***Flabellotrichalus***
– Male antennae serrate or antennomeres parallel-sided (Figs 34, 35) 7
7. Vagina with two lateral pockets medially and with an unpaired very slim and long gland basally (Bocak, 1998b), valvifers slender, usually free, sometimes connected in basal part ..... ***Microtrichalus***
– Vagina without lateral pockets, unpaired gland absent, valvifers robust, connected subbasally (Bocak, 1998b, Fig. 64) ..... ***Trichalus***
8. Maxillary and labial palpomeres with distinct sensilae, apical palpomeres broad, securiform (similar to Fig. 18), apical part of phallus projected ventrally, internal sac very complex, sclerotized (Figs 100–101) ..... ***Diatrichalus***
– Maxillary and labial palpomeres slender, internal sac mostly without sclerotisation, sometimes completely sclerotized (Figs 115–116) 9
9. Pronotum very slender, longitudinal areola very slender (Fig. 75), internal sac membranous or at most with slender sclerotized rods ..... ***Leptotrichalus***
– Pronotum approximately as wide as long, internal sac completely sclerotized, very slender, basally attached to phallus (Fig. 116) ..... ***Lobatang***
10. Elytral secondary costae absent at least medially (Figs 56, 87, 88, 90) 11
– Elytra with very distinct secondary costae on whole elytra (Figs 44, 45, 48) 21
11. Elytral secondary costae only absent in middle of elytra, present on basal quarter and apical fifth, internal sac with sclerotized circular gonoporus and basal plates (Fig. 126), elytral cells in middle of elytra transverse ... ***Procautires***
– Elytral secondary costae completely absent or at most vestiges present on small area at the base of pronotum 12
12. Pronotum with small, very slender median areola, connected to frontal margin via strong keel, or median areola very obtuse to absent (Fig. 67), frontal margin formed by two strong carinae (Fig. 67), elytral areoles quadrate, with mat, velvet-like bottoms, found only in Madagascar ..... ***Caenioxylobanus***
– Pronotum with different arrangement of carinae (Figs 57, 60, 69, 70, 72, 84), frontal margin of pronotum simple 13
13. Male genitalia with parameres (as in Fig. 91), at most parameres shortened ..... ***Xylobanellus***
– Parameres absent (Figs 92–130) 14
14. Pronotum with five areoles, pronotal carinae slender, straight (as in Fig. 60), phallus very slender with one complex spine at base or in middle part of phallus, apical part often rotated (Fig. 94) ..... ***Wakarumbia***
– Pronotum with differently arranged pronotal carinae, always at last vestiges of frontolateral carinae present (Figs 69–83) or only one unapparent median areola present (Fig. 84), internal sac with two spines in various positions (Figs 107–112, 121–128) or without spines (Fig. 130) 15
15. Most elytral cells distinctly longitudinal (Fig. 56), body very slender, minute, delicate, pronotum costae obtuse, indistinct, pronotum with one inconspicuous areola (Fig. 84) or vestiges of lateral and frontolateral carinae present 16
– Elytral cells quadrate to transverse, body medium sized to moderately large, pronotum always at least with vestiges of frontolateral carinae (Figs 69–83) 18
16. Phallus parallel-sided with rounded apex, internal sac with two sclerotized rods (Fig. 128) 17
– Phallus slender, narrowed to apex, internal sac with ring-shaped sclerotised structure (Fig. 130) ..... ***Xylobanomorphus***
17. Male antennae flabellate, vestiges of pronotal lateral and frontolateral costae present ..... ***Xylobanomimus***
– Male antennomeres parallel-sided (Fig. 48), only indistinct median areola present (Fig. 84) ..... ***Malacolycus***
18. Bottom of elytral cells shiny, apparently concave, quadrate (Fig. 90), elytra more or less dilated, convex, pronotal lateral carinae always indistinct to absent (Fig. 70), male genitalia as in Fig. 111 ..... ***Broxylus***
– Bottom of elytral cells mat, pubescent, elytra parallel-sided to very slightly dilated, flat 19
19. Elytra with three longitudinal primary costae running whole length of elytra ..... ***Prometanoeus part***
– Elytra with four longitudinal primary costae running whole length of elytra 20
20. Pronotum with seven areoles, lateral carinae regularly well developed, seldom lateral carinae more obtuse, internal sac with pair of spines apically, male antennae serrate to flabellate (as in Figs 38, 39) ..... ***Xylobanus***
– Pronotum with seven areoles, lateral carinae obtuse, internal sac without spines, and the internal sac with a very slender apical part (Figs 131–132) ..... ***Mimoxylobanus***
21. Male genitalia with parameres (Fig. 91), unpaired vaginal gland inconspicuous, pronotum as in Fig. 58 .... ***Conderis***
– Male genitalia without parameres (Figs 92–130), unpaired vaginal gland large (Figs 163–159), pronotum with carinae as in Figs 59–86 22
22. Elytra with three longitudinal primary costae running whole length of elytra ..... ***Prometanoeus* part**

– Elytra with four longitudinal primary costae running whole length of elytra 23
23. Frontolateral carinae on pronotum absent (Figs 59–60, 68) 24
– Frontolateral carinae on pronotum present (Figs 69–74, 76–83) 28
24. Pronotum with very obtuse frontal angles, distinctly narrowed anteriorly, with one small, slender median areola connected with frontal margin by strong keel, lateral carinae absent (Fig. 68), phallus lanceolate, internal sac with pair of spines (Fig. 107), male antennae flabellate as in Fig. 38 ..... ***Bulenides***
– Pronotum with conspicuous frontal angles, lateral carinae present to vestigial, median areola more extensive (Figs 59–61) 25
25. Lateral carinae apparent, median areola rhomboidal (Figs 59–60), pronotal carinae usually straight, slender, phallus slender as in Fig. 92 or robust (Fig. 95, 96), with paired spines or spines arranged linearly, male genitalia slender, spermatheca bulbous 26
– Lateral carinae vestigial, male genitalia as in Figs 97–99, spermatheca tubular, very long ..... ***Enylus***
26. Elytral primary costa 3 reaching mid way along elytra, spines on internal sac arranged linearly, bases of valvifers with various processes, male antennae as long as body ..... ***Hemiconderis***
– Elytral primary costa 3 reaching beyond middle of elytra, usually complete although weaker apically, spines on internal sac as in Figs 92–96, bases of valvifers without any process, male antennae shorter than body 27
27. Body very slender, fragile, almost parallel-sided, secondary costae very weak, phallus short, slender (Figs 95–96) ..... ***Achras***
– Body small, but moderately robust, widened posteriorly, secondary costae well developed, phallus slender (Figs 92–93) ..... ***Synchonnus***
28. Head with long rostrum (Fig. 10), phallus slender, tubular, internal sac completely membranous (Figs 117–120) .. 29
– Head without rostrum (Fig. 11) or head only slightly protracted, internal sac usually at least partly sclerotized (Figs 107–114, 121–128) 31
29. Elytra considerably widened posteriorly, both ventral and dorsal surface of body a distinctly shiny metallic blue ..... ***Metriorrhynchoides***
– Elytra slender, parallel-sided to slightly widened posteriorly, sometimes only ventral surface of body a shiny metallic blue 30
30. Antennae with slender, long basal antennomeres and short, triangular apical antennomeres, antennae with long, dense setae, fore and mid femora with spines, hind trochanters triangular ..... ***Oriomum***
– Antennae serrate to flabellate, all antennomeres subequal, without long setae, femora without spines, trochanters slender ..... ***Porrostoma***
31. Male antennae with extremely long and very slender, fragile lamellae (Fig. 45), female antennae with short lamellae (Figs 46–47) ..... ***Pseudodontocerus***
– Male antennae serrate to flabellate (Figs 38–43) or with long but moderately slender lamellae (Figs 44, 51), female antennae never flabellate 32
32. Phallus tubular, with completely membranous internal sac, valvifers fused with coxites, lateral and frontolateral pronotal carinae sometimes vestigial ..... ***Stadenus***
– Phallus different, never with completely membranous internal sac, valvifers free, frontolateral and lateral pronotal carinae always distinct 33
33. Phallus lanceolate, internal sac with pair of spines apically (Fig. 108), no body part shiny metallic blue ..... ***Cautires***
– Phallus parallel-sided, tubular, shorter, body often a shiny metallic blue 34
34. Pronotal carinae robust but obtuse, indistinct, male antennae with long, relatively slender lamellae (Fig. 40), male genitalia parallel-sided (Fig. 113) or robust basally, internal sac with several pairs of processes (Fig. 113), ovipositor with considerably shortened valvifers (Fig. 150), lateral glands sometimes attached dorsally and directed upwards, spermaduct often extremely long ..... ***Metanoeus***
– Pronotal carinae moderately strong and well marked, sometimes partly reduced, male genitalia never with apical processes, usually with variously shaped plates or spines, valvifers never considerably shortened (Figs 140, 152, 160), lateral glands attached laterally or lateroventrally, spermaduct moderately long 35
35. Body often large, slender, internal sac of phallus spirally sclerotised (Fig. 114), or with straight sclerotisation and several pairs of adjacent, small, simple spines (Bocak, 1998c, Figs 1, 2), ovipositor very small, lightly sclerotized, partly membranous (Fig. 134), vagina often considerably sclerotized ..... ***Metriorrhynchus***
– Body mostly medium-sized, phallus without any slender, rod-like sclerotized structure (Figs 121–125, 127–128), ovipositor well sclerotized (Figs 140), vagina never strongly sclerotized 36
36. Membrane of phallobase extensive, pigmented, with characteristic structure (Fig. 121), phallus narrowed to apex , male antennae with very long lamellae (Figs 44, 51) ..... ***Cladophorus***
– Phallobasal membrane very soft, small, without any structure (Figs 122–125), never considerably narrowed at apex, male antennae serrate or with short lamellae, lamellae at most twice length of body of antennomere 37
37. Body metallic blue, male antennae flabellate, phallus slender (Fig. 124) ..... ***Cladophorinus***
– Body otherwise coloured, never metallic blue 38
38. Male antennae serrate, male genitalia as in Fig.125 ..... ***Ditua***
– Male antennae flabellate, male genitalia as in Figs 122–123 ..... ***Cautiromimus***

Genus excluded from the subfamily Metriorrhynchinae

Lycoprogenthes Pic, 1915
Lycoprogentes Pic, 1915: 6
Type species. *Lycoprogentes pouilloni* Pic, 1915: 6 (by monotypy).

Pseudosynchonnus Pic, 1922 - **syn. n.**
Pseudosynchonnus Pic, 1922: 13, hors texte.
Type species. *Pseudosynchonnus testaceus* Pic, 1922: 13 (hereby designated).

Parapyropterus Kleine, 1926c: 104 - **syn. n.**
Type species. *Parapyropterus nigrostriatus* Kleine, 1926c: 104 (by monotypy).

Protaphes Kleine, 1926b: 363 - **syn. n.**
Type species. *Protaphes confertus* Kleine, 1926b: 364 (by original designation).

Pseudosynchonnus is here transferred from the Metriorrhynchinae to Erotinae and *Lycoprogenthes* from Calochrominae to Erotinae. I have compared *Pseudosynchonnus*, *Lycoprogenthes*, *Parapyropterus* and *Protaphes* (the last two already sooner classified in Erotinae) and I

have not found any substantial difference between them. Therefore, I consider genera *Pseudosynchonnus*, *Parapyropterus*, and *Protaphes* to be junior synonyms of *Lycoprogenthes*.

Appendix 1: List of type material studied.

Subfamily Metriorrhynchinae Kleine, 1926

Tribe Conderini Bocak et Bocakova, 1990

Conderis C. O. Waterhouse, 1879: 59. *Calopteron signicolle* Kirsch, 1975: Holotype, 1 spec., "Malacca" (SMTD).
=*Pseudoconderis* Pic, 1921a: 8, hors texte. *Pseudoconderis gorhami* Pic, 1921a, Holotype, female, "India, coll. Armitage (MHNP).
Xylobanellus Kleine, 1930b: 171. *Xylobanellus atricolor* Kleine, 1930b: Holotype, female, "Malay. Penin. Selangor, Bukit Kuta" (BMNH).
= *Rossioptera* Kasantsev, 1988: 169. *Eros erythropterus* Baudi, 1871. The type of *E. erythropterus* was not studied.
= *Chuzenjianus* Nakane, 1969: 176. *Conderis tenuis* Kôno, 1932. The type species was not examined.

Tribe Metriorrhynchini Kleine, 1926

Subtribe *Hemiconderina* Bocak et Bocakova, 1990

Synchonnus C. O. Waterhouse, 1879: 59. *Porrostoma clientulum* C. O. Waterhouse, 1877: Syntype, male, "Moreton Bai" (BMNH).
Strophicus C. O. Waterhouse, 1879: 73. *Strophicus nigellus* C. O. Waterhouse, 1879: Holotype, female, "Mysool" (BMNH).
Hemiconderis Kleine, 1926a: 162. *Hemiconderis explicatus* Kleine, 1926a: ?Paratype, male, "Mamberamo R., W. G. v. Heuer, 20. xii. - 21. i. Pionierbivak" (MIZW).
Wakarumbia Bocak, 1999b: 166. *Wakarumbia gracilis* Bocak, 1999: Holotype, male, "Sulawesi SE, Buton Island, Wakarumba, 3.-7. ii. 1994, M. Štrba and I. Jeniš lgt." (LMBC).
Achras C.O. Waterhouse, 1879: 61. *Porrostoma limbatum* C. O. Waterhouse, 1877: Holotype, male, "Austral. 73–6" (BMNH)

Subtribe *Trichalina* Kleine, 1928

Enylus C.O. Waterhouse, 1879: 72. *Enylus segregatus* C. O. Waterhouse, 1879: Holotype, female, "Mysool" (BMNH).
Diatrichalus Kleine, 1926a: 167. *Diatrichalus xylobanoides* Kleine, 1926a: Holotype, male, "D.N. Guinea, 285, Hunsteinspitze, 3. iii. 43, Kais. Augustafl. Exp., Bürgers S.G." (NHMB).
= *Mimotrichalus* Pic, 1930: 92, hors texte. *Mimotrichalus tenimberensis*: Holotype, male, "Tenimber Is, Coll. by W. Doherty" (MNHP).
Trichalus C. O. Waterhouse, 1877: 82. *Trichalus flavopictus* C. O. Waterhouse, 1877: Holotype, male, "Port Bowen, 75.22" (BMNH).
= *Xantheros* Fairmaire, 1877: 167. The type of *Xantheros ochreatus* Fairmaire, 1877 was destroyed during the World War II in Hamburg (Bocak, 1998b).
Microtrichalus Pic, 1921b: 9, hors texte. *Microtrichalus singularis* Pic, 1921b: Holotype, male, "?Java" (MHNP).
= *Falsoenylus* Pic, 1926a: 29, hors texte. *Falsoenylus basipennis* Pic, 1926a: Holotype, female, "Baguio, Luzon" (MNHP).
Flabellotrichalus Pic, 1921b: 9, hors texte. *Flabellotrichalus notatithorax* Pic, 1921b: Syntype, male, "Batjan, Aug-Septbr." (MHNP).
= *Villosotrichalus* Pic, 1921b: 9, hors texte. *Villosotrichalus reductus* Pic, 1921b: Syntypes, male, female, "Andai, Nlle Guinée" (MHNP).
Schizotrichalus Kleine, 1926a: 2, p. 183. *Trichalus nigrescens* C.O. Waterhouse, 1879: Holotype, male, "Mysool" (BMNH).
Eniclases C. O. Waterhouse, 1879: 66. *Lycus* (gen. 35) *luteolus* C.O. Waterhouse, 1878: Holotype, male, "Bowring 63.47*" (BMNH).
= *Trichalolus* Pic, 1923: 36, hors texte. *Trichalus (Trichalolus) apertus* Pic, 1923: Holotype, female, "Andai, Nle Guinée" (MNHP).

Subtribe Metriorrhynchina Kleine, 1926

Bulenides C.O. Waterhouse, 1879: 34: *Lycus* (gen. 21) *obsoletus* C. O. Waterhouse, 1878: Holotype, female, "Java" (BMNH).
Caenioxylobanus Pic, 1922: 13, hors texte. *Caenioxylobanus ater* Pic, 1922: Holotype, female, "Madagascar, collection Le Moult, Janvier" (MHNP).
Cautires C.O. Waterhouse, 1879: 36. *Lycus* (gen. 22) *excellens* C. O. Waterhouse, 1878: Holotype, male, "Sar." (= Sarawak) (BMNH).
Prometanoeus Kleine, 1925c: 133. *Prometanoeus ochraceus* Kleine, 1926b: Holotype, male, "Ceylon, G. Lewis, 1910–320; Dikoya, 3800-4200ft, 6. xii. 81–16. i. 82" (BMNH)
Tapromenoeus Bocak et Bocakova, 1989: 327. *Xylobanus hirtus* Kleine, 1928: 234. Paratype, male, "Dikoya, Ceylon" (MIZW).
Broxylus C.O. Waterhouse, 1879: 20. *Calopteron pfeifferi* C. O. Waterhouse, 1878: Holotype, male, "Celebes, Wallace" (BMNH).
= *Samanga* Pic, 1921b: 9, hors texte. *Samanga fenestrata* Pic, 1921b: Holotype, male, "Samanga, S. Celebes, Nov. 1895, H. Fruhstorfer" (MHNP).
Xylobanus C. O. Waterhouse, 1879: 38. *Lycus costifer* Walker, 1858: Holotype, male, "Ceylon" (BMNH).
Mimoxylobanus Pic, 1921b: 11, hors texte. *Mimoxylobanus angustatus* Pic, 1921b: Holotype, male, "Sumbawa, Doherty" (MHNP).
Metriorrhynchus Gemminger et Harold, 1869: 1629. The type of *Metriorhynchus parallelus* Guérin-Méneville, 1838 was not found in either Brussels or Paris Museums and was very probably destroyed during a fire in the Brussels Museum (L. Baert, pers. comm.).
= *Metriorhynchus* Guérin-Méneville, 1838: 72 (unavailable senior objective synonym of *Metriorrhynchus* Gemminger et Harold.
= *Flabelloporrostoma* Pic, 1923: 35, hors-texte. *Porrostoma* (*Flabelloporrostoma*) *mirabilis* Pic, 1923: Holotype, female, "N. S. Wales" (MHNP).
Leptotrichalus Kleine, 1925a: 296. *Metriorrhynchus cyaniventris* Kirsch, 1875: Holotype, female, "Malacca" (SMTD).
Lobatang Bocak, 1998b: 190. *Lobatang papuensis* Bocak, 1998b: Holotype, male, "Irian Jaya: Jayawijaya, Bime, 1600–1900 m, 11. 9. 1993, leg. A. Riedel" (SMNS).
Metanoeus C.O. Waterhouse, 1879: 73. *Lycus* (gen. 37) *conformis* C.O. Waterhouse, 1878: Holotype, male, "Borneo" (BMNH).
Stadenus C.O. Waterhouse, 1879: 61. *Porrostoma dichroum* C. O. Waterhouse, 1977: Holotype, female, "K. George's Pound, 75–36" (BMNH).
Porrostoma Castelnau, 1838: 26. *Porrostoma rufipennis* Fabricius, 1801: The specimen compared with Fabricius' type was available for study (O. Martin, pers. comm.).
Metriorrhynchoides Kleine, 1926a: 118. *Metriorrhynchoides helleri* Kleine, 1926a: Paratype, male, "K. Wilhelmland, Bongu" (MIZW).
Oriomum Bocak, 1999a: 111. *Oriomum femoralis* Bocak, 1999c: Holotype, male, "New Guinea: Papua, W. District Govt. Sta. 26.-28. x. 1960, J. L. Gressitt Collector" (BPBM).

Cladophorus Guérin-Méneville, 1830: Plate II, Fig. 9. The type of *Cladophorus formosus* Guérin-Méneville, 1830 was not found in the Brussels or Paris Museums and was very probably destroyed during a fire in the Brussels Museum (L. Baert, pers. comm.).
= *Odontocerus* Guérin-Méneville, 1838: 72 (a homonym of *Odontocerus* Stephens, 1829 (Trichoptera)).
=*Spacekia* Strand, 1936: 169; Bocak, 1998c: 247 (a objective synonym of *Metriorrhynchus* Guérin-Méneville, 1830).
Cladophorinus Kleine, 1926a: 149. *Cladophorinus cyanescens* Kleine, 1926a: Holotype, male, D. N. Guinea, Schradenbg., 5.-13.vi. 13, Kais. August. Exp., Bürgers S. C. (MIZW).
Cautiromimus Pic, 1926c: 454. *Cautiromimus reticulatus* Kleine, 1926a: Holotype, female, "Batjan, Aug-Septbr. ex coll. H. Fruhstorfer" (DEIE).
Procautires Kleine, 1925b: 32. *Procautires toxopei* Kleine, 1925: Paratype, female, "Buru Stn. 13, Toxopeus" (MIZW).
Ditua C.O. Waterhouse, 1879: 33. *Lycus* (gen. 20) *deplanatus* C.O. Waterhouse, 1878: Holotype, male, "59.58, Dory, New Guinea" (BMNH).
Kassemia Bocak, 1998b: 195. *Kassemia oculata* Bocak, 1998b: Holotype, male, "New Guinea, NE Wau, 1200–1300 m, 22. x.1965, J. Sedlacek Collector Bishop Mus." (BPBM).
Pseudodontocerus Pic, 1921b: 12, hors texte. *Pseudodontocerus pulcher* Pic, 1921b: Holotype, female, "Humboldt Bay, N. Guinea, Doherty" (MHNP).
=*Carathrix* Kleine, 1926a: 149. *Carathrix pilosus* Kleine, 1926a: Holotype, male, Paumonu Riv. ix. - xii. 92" (MSNG).
Xylobanomimus Kleine, 1926a: 166. *Xylobanomimus papuensis* Kleine, 1926a, Holotype, male, "N. Guinea, Dilo, Loria, vi-vii 90" (MSNG).
Xylobanomorphus Kleine, 1935: 316. *Xylobanomorphus transformis* Kleine, 1935: Holotype, male, "Papua: Mt. Tafa, 8500ft, ii. 1934, L. E. Cheesman, B. M. 1934–244" (BMNH).
Malacolycus Kleine, 1943: 151. *Malacolycus paululus* Kleine, 1943: Holotype, male, "N. Guinea, Biró, 901, Friedrich-Wilh.-hafen" (HNHM).
Dilolycus Kleine, 1926a: 186. *Dilolycus lamellatus* Kleine, 1926a: Holotype, male, "N. Guinea, Dilo, Loria, vi-vii 90" (MSNG).

Genera classified outside the Metriorrhynchinae

Lycoprogentes Pic, 1915: 6. *Lycoprogenthes* Pic, 1915: 6. *Lycoprogenthes pouilloni* Pic, 1915: Holotype, female, "Darjeling, Pouillon" (MNHP).
= *Pseudosynchonnus* Pic, 1922: 13. *Pseudosynchonnus testaceus* Pic, 1922: 13: Holotype, male, "Perak" (MHNP).
= *Protaphes* Kleine, 1926b: 363. *Protaphes confertus* Kleine, 1926b: 364: Holotype, male, "Mindanao, Surigao" (MIZW).

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