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Subtribal classification of Metriorrhynchini (Insecta: Coleoptera: Lycidae): an integrative approach using molecular phylogeny and morphology of adults and larvae

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Abstract

The classification of Metriorrhynchini, the most diverse lineage of net-winged beetles (Lycidae) containing ~1400 species, is revised on the basis of three-marker molecular phylogeny of 175 ingroup taxa, and the adult and larval morphology. The study uses the molecular phylogeny for identification of major lineages and critically considers morphology when adult morphology and sparse information of immature stages alone did not provide enough information for building a robust classification. Reconstruction of the ancestral states of morphological characters on the phylogenetic tree recovered from DNA data presents evidence for multiple origins of the four-costae pattern on the elytra, shortened elytral costa 1, patterns of pronotal areolae and flabellate antennae. As a consequence, revised morphological delineations of the subtribes and genera are proposed: three major lineages are defined as Metriorrhynchina Kleine, 1926, Metanoeina subtrib. nov. and Cautirina subtrib. nov. The subtribes Trichalina Kleine, 1928 and Hemiconderina Bocak & Bocakova, 1990 are synonymized with Metriorrhynchina Kleine, 1926. Metanoeina are studied in detail and three genera are placed in the subtribe: *Metanoeus* Waterhouse, 1879, *Xylometanoeus* gen. nov., and *Matsudanoeus* gen. nov., with *Xylometanoeus japonicus* (Bourgeois, 1902) comb. nov. and *Matsudanoeus yuasai* (Nakane, 1969), comb. nov. as type species, respectively. *Xylobanus basivittatus* Nakane, 1970 is transferred to *Xylometanoeus*. The concepts of genera *Cautires* and *Xylobanus* are based on male and female genitalia. Additionally, the molecular hypothesis is supported by morphology of larvae, when newly proposed Cautirina are characterized by entire tergites in contrast to the longitudinally divided meso- and metathoracic tergites of Metanoeina and Metriorrhynchina. Larval characters support the placement of *Xylometanoeus* in Metanoeina and the close relationships of *Matsudanoeus* and *Metanoeus*. The simultaneous consideration of DNA-based phylogeny and morphology of adults and larvae rejects taxa based on diagnostically usable but strongly homoplastic characters and provides a framework for a robust classification of Metriorrhynchini.

Key words

Metriorrhynchina, Cautirina, Metanoeina, classification, new subtribes, new genera, new synonyms, mtDNA.

1. Introduction

Classification based on phylogenetic relationships is an ultimate goal of systematics, which needs integration of extensive data from various sources (Henning 1966; Wheeler et al. 2013). Here, we revise the subtribal classification of the net-winged beetles of the tribe Metriorrhynchini (Lycidae: Lycinae). This is based on the recently published molecular phylogeny used for an investigation of phylogeography (Sklenarova et al. 2013), the present knowledge on metriorrhynchine larvae (Bocak & Matsuda 2003; Levkanicova & Bocak 2009; Zaitsev, unpublished data) and the morphology of adults (e.g. Bocak 2002; Dudkova & Bocak 2010). Neither larval nor adult morphological data have produced a robust phylogeny alone. The previous studies recovered conflicts in the phylogenetic signal provided by adult morphology and additionally, they were limited by scarcity of information on larvae. The molecular data produced a robust phylogenetic hypothesis, which we compare with morphology to test the traditionally held morphological concepts of the subtribes and genera.

The Metriorrhynchini are an Old World lineage of net-winged beetles with ~1400 valid species-group names (Bocak 2002). The recent studies have confirmed their extraordinary diversity in Southeast Asia, Wallacea, and New Guinea (e.g. Bocak 2000, 2007; Dvorak & Bocak 2009; Weiszenstein & Bocak 2011); 223 species occur in the Afrotropical region (Kazantsev 2012); and 203 species in continental Australia (Calder 1998). Metriorrhynchinae/-ini were given subfamily or tribe rank (Kleine 1926, 1933), and later were merged with Trichalini and Cladophorini in a wider concept of Metriorrhynchinae (Bocak & Bocakova 1990). Recently, this Metriorrhynchinae were downranked to Metriorrhynchini, combined with several other lineages, e.g. Platerodini, Calochromini and Erotini, in the redefined Lycinae (Bocak & Bocakova 2008). The latest concept of Metriorrhynchini recognized subtribes Hemiconderina, Trichalina and Metriorrhynchina. The generic classification was morphology-based and used 72 characters in the mouthparts, thorax and genitalia of both sexes along with the pronotal and elytral structures and shape of antennae (Bocak 2002). Despite the relatively high number of characters and dense sampling, the support for deep relationships in Metriorrhynchini was low. Therefore, we intend to compare the phylogenetic hypothesis inferred from the three-gene dataset (the mtDNA fragments from the dataset by Sklenarova et al. 2013 expanded by critical taxa) with morphological data (Bocak 2002; Bocak & Matsuda 2003; Levkanicova & Bocak 2009) to update the classification of the lineage and to investigate in detail the limits of several species-rich taxa. We demonstrate the power of a densely sampled molecular dataset to produce a topology which corresponds with some morphological traits and strongly rejects the previous approach using strongly homoplastic morphological structures.

2. Material and methods

2.1. Sampling

The dataset of *rrnL* + *tRNA-Leu* + *nad1*, *cox1* + *tRNA-Leu* + *cox2* and *nad5* + *tRNA-Phe* + *tRNA-Glu* + *tRNA-Ser* mitochondrial DNA (further referred as *rrnL*, *cox1* and *nad5*) used for the analysis of Metriorrhynchini by Sklenarova et al. (2013) was expanded by newly produced sequences for *Xylometanoeus* gen. nov. and *Matsudanoeus* gen. nov. (Table 1) and by previously obtained sequences from four unidentified larvae (Levkanicova & Bocak 2009). The list of previously published sequences, geographical origins and accession numbers are given in Table ES1 (Electronic Supplement).

Altogether, 17 genera and about 175 species of Metriorrhynchini were represented by 227 terminals. The number of species is estimated for systematic subsets of the sample where assignment of species names is impossible due to the lack of revisionary taxonomic work (mainly concerning genera *Microtrichalus*, *Leptotrichalus*, *Xylobanus* and *Cautires*). In these parts we consider a clade as a species when terminals show low genetic distance and are morphologically different in some character from their closest relatives. Many other taxa included in the analysis were also identified only to the generic level due to poorly known species level taxonomy. The terminals originate from the whole geographic range of the tribe, but the Oriental region, in particular regarding the genera *Metanoeus* Waterhouse, 1879, *Cautires* Waterhouse, 1879, and *Xylobanus* Waterhouse, 1879 was more densely sampled. In addition, 23 species-level taxa (from 9 genera) representing all lycid subfamilies except Dexorinae and all major tribes of Lycinae were sampled as outgroup taxa. The collections of the Natural History Museums in London, Warsaw and Paris were used for the study of the type material and distributions.

2.2. Laboratory methods

The procedures for DNA extraction, PCR amplification, and sequencing were described in detail by Sklenarova et al. (2013). The morphological part of the study is based on adult and larval semaphoronts. Adult bodies were softened in water, the male genitalia dissected, examined and deposited in glycerol, the female genitalia were treated with hot 10% KOH, dissected and subsequently stained in chlorazol black. Larvae were kept in 70% alcohol and observed without any prior treatment. Illustrations were taken by a digital camera attached to a binocular microscope.

2.3. Phylogenetic analysis

The dataset, without the sequences newly added herein but including 18S and 28S rRNA fragments, was thoroughly analyzed by Sklenarova et al. (2013) and therefore the present analysis is limited to a single alignment procedure (Mafft 7.0; Katoh & Standley 2013) and the maximum likelihood analysis as implemented in RAxML

Table 1. List of newly produced sequences.

Species	Voucher number	Genbank accesion numbers		
		rrnL	***cox1***	***nad5***
Xylometanoeus basivittatus	UPOL VK0075	KF652135	KF652115	KF652123
	UPOL LB0222	—	—	KF652128
	UPOL LB0223	—	—	KF652129
Xylometanoeus japonicus	UPOL VK0038	—	KF652116	KF652124
	UPOL VK0039	—	KF652117	KF652125
	UPOL VK0090	—	KF652118	KF652126
	UPOL VK0093	—	KF652119	KF652127
Matsudanoeus yuasai	UPOL VK0248	KF652136	—	KF652130
	UPOL VK0249	KF652137	KF652120	KF652131
	UPOL VK0395	—	—	KF652132

7.2.5. (Belshaw & Katzourakis 2005). The methods of the analysis follow those reported in Sklenarova et al. (2013).

2.4. Evolutionary analysis of morphological characters

The ancestral states and the further evolution of selected morphological characters in Metriorrhynchini were reconstructed using the parsimony criterion and the current molecular phylogeny. Four characters were analyzed:

(A) the shape of male antennae (assessed based on antennomere 6): (1) serrate, (2) flabellate (Figs. 11–14). The serrate antennae are similar in shape to the female antennae illustrated in Fig. 15. We consider the antenna as serrate if the apical process is at most 0.5 × the length of the corresponding stem of the antennomere; with a higher value the antenna is scored as flabellate. Although arbitrary, the value 0.5 × lies between commonly encountered types of antenna and values close to it occur in low frequency. Although antennae with greatly lengthened apical processes are commonly designated as pectinate, we do not discriminate between flabellate and pectinate antennae due to continuous variability in the length of processes. The character states are coded as seen on the specimens, e.g. the type-species of *Metriorrhynchus* has flabellate antennae similar to those of *M. doleschali* (Fig. 13), but *Metriorrhynchus* species included in the analysis have serrate male antennae (Fig. 2).

(B) the number of longitudinal elytral costae (assessed for the humeral part of the elytron): (1) four costae, all similar in strength (Figs. 48–49); (2) nine costae, four strong ones, and five weaker ones located between the former and the elytral margins (Figs. 6–9, 47). The strong costae present in both character states are further called primary costae, the weaker ones only present in state 2 are called secondary costae.

(C) the posterior extension of the elytral primary costa 1 (the one closest to the elytral suture) from the elytral base: (1) reaching the apex of the elytron; (2) reaching at most one third of the elytral length.

(D) the pattern of pronotal areolae: the pronotal carinae delimit a maximum of seven areolae; four areolae are present at the anterior margin of the pronotum and they are separated from each other by a midline carina and a pair of fronto-lateral carinae (FLC); a single lanceolate areola is located along midline in the posterior part of the pronotum, bordered laterally by the postero-lateral areolae; the postero-lateral areolae are separated from the fronto-lateral areolae by the postero-lateral carinae (PLC, Figs. 33, 41, 45–46). We distinguish four character states: (1) the complete pattern of seven areolae is present; (2) five areolae are present due to absence of the postero-lateral carinae; (3) three areolae are present due to absence of the lateral carinae (both FLC and PLC) (i.e. slender areola in the middle part of the pronotum and two lateral areolae are present; Figs. 36–38, 42–43); (4) five areolae are present due to absence of the fronto-lateral carinae (FLC) (Fig. 39; *Wakarumbia* type). (5) No areolae are present due to the absence of all carinae, or of all but the frontal part of midline carina. The categorization can be ambiguous as some carinae can be considerably weakened, but they are still present (Fig. 35); or all carinae are inconspicuous, but the pattern of seven areolae is recognizable (*Metanoeus*, Fig. 40). Nevertheless, most cases can be clearly categorized. The *Wakarumbia* type (state 4) is characterized additionally by sharp and straight carinae and differs from superficially similar arrangements found in some outgroup taxa, e.g. some Dictyopterinae or Lycinae: Conderini and Slipinskiini (Bocak & Bocakova 2008).

The above listed characters have been traditionally used in the taxonomy of Lycidae for delineation of genera and tribes, and therefore they were coded for all taxa included in the molecular analysis (Tables 1, ES1; including outgroup taxa), their ancestral states for Metriorrhynchini were reconstructed using the parsimony approach implemented in the Mesquite 2.7.5 software (Maddison & Maddison 2011) and evaluated using the consistency index counted in PAUP 4.8 (Swofford 2002). Additionally, we used the Bayesian estimation as implemented in the BayesTraits 2.0 software for an alternative ancestral state reconstruction of the patterns of pronotal areolae (Fig. ES1). Nodes to be reconstructed were defined on the best ML topology (Fig. 1) and the same distribution of character states at terminals was used as in the MP analysis. The likelihood of each character state was inferred for nodes of interest using the script published by Sklenarova et al. (2013; freely available at https://sourceforge.net/projects/bayestraits-wrap/).

3. Results

3.1. Sequence variation

The aligned and concatenated *rrnL*, *cox1*, and *nad5* mtDNA fragments for 262 terminals formed an alignment of 3143 homologous positions; 1886/1814 characters were parsimony informative including/excluding outgroup taxa. The aligned *rrnL* fragment had 831 positions (407 parsimony informative characters), *cox1* 1099 positions (623 informative), and *nad5* 1213 positions (856 informative).

3.2. Phylogeny and character evolution

The Metriorrhynchini clade was represented in the current analysis as a monophylum with robust support (bootstrap value = BS 99%). The basal splits consisted of the *Metanoeus* clade (*Xylometanoeus* + (*Matsudanoeus* + *Metanoeus*); orange in Fig. 1), *Cautires* clade (*Xylobanus* + *Cautires*; red in Fig. 1) and *Metriorrhynchus* clade (*Metriorrhynchus*, *Trichalus*, *Wakarumbia* and many other genera; green in Fig. 1). The *Cautires* clade and the *Metanoeus* clade were well supported (BS 98 and 91%, respectively), but the *Metriorrhynchus* clade, although recovered by all analyses here and previously (Sklenarova et al. 2013), had low support (BS 17–68%) and formed an unresolved polytomy with the *Metanoeus* clade in the majority consensus recovered from bootstrap trees.

The evolution of the four characters (A)–(D) (see section 2.4.), which have been commonly used for delineation of genera, was optimized under the MP criterion using the tree in Fig. 1. Altogether 7 steps were needed to explain the distribution of flabellate and serrate antennae (CI 0.167, RI 0.944; Fig. 2); 19 steps for the patterns of pronotal areolae (a five-state character, CI 0.158, RI 0.835; Fig. 5); 7 steps for the presence/absence of the secondary costae on the elytra (CI 0.143, RI 0.920; Fig. 3); and 2 steps for the extension of elytral costa 1 (CI 0.5, RI 0.944; Fig. 4). The ancestral character states recovered by parsimony reconstruction in Mesquite are illustrated in Figs. 2–5 and the calculated likelihoods for origins of pronotal patterns are graphically presented in the supplementary Fig. ES1.

Sequences from four metriorrhynchine larvae published by Levkanicova & Bocak (2009) were included in the dataset and these taxa were identified as *Leptotrichalus atricollis* Pic, 1921 (Voucher UPOL ZL2002) and *Sulabanus lalui* Dvorak & Bocak, 2007 (UPOL ZL2010); the sample UPOL ZL2015 was identified as *Cautires* sp. (Metriorrhynchini gen. spec. by Levkanicova & Bocak 2009) and relationships were inferred more precisely for another sample of *Cautires* sp. (UPOL ZL2009) with the current DNA dataset (Fig. 1).

4. Discussion

The older morphology-based classification of metriorrhynchine net-winged beetles recognized several family-group taxa of subfamily or tribe ranks (Kleine 1926, 1933). The comparison of morphology (Bocak & Bocakova 1990) and subsequent morphology-based cladistic analysis by Bocak (2002) suggested monophyly of Metriorrhynchini consisting of Hemiconderina, Trichalina, and Metriorrhynchina, the latter containing also the Oriental and Afrotropical genera *Cautires* and *Xylobanus*.

The current molecular phylogeny (Fig. 1) is incongruent with morphological analyses, with three lineages inferred at the basal split; these are here defined as subtribes of Metriorrhynchini (see Taxonomy section):

(1) The *Cautires* + *Xylobanus* clade (subtribe Cautirina) includes all Afrotropical and most Oriental and East Palearctic Metriorrhynchini.

(2) The *Sulabanus* + *Metriorrhynchus* + *Trichalus* + *Wakarumbia* clade (including all related genera as shown in Fig. 1; subtribe Metriorrhynchina) includes Australian lineages, many of them endemic to Australia and New Guinea, but some dispersed in a low number of species to the Oriental region (e.g. Bocak & Yagi 2010).

(3) The *Xylometanoeus* + *Matsudanoeus* + *Metanoeus* clade (subtribe Metanoeina) includes a limited number of Oriental Metriorrhynchini. The enigmatic position of *Metanoeus* (the only genus of this clade defined prior to the present paper) was discussed by Bocak (2002) when the morphological characters did not provide a clear indication of its relationships to *Metriorrhynchus* or *Cautires*, and even the current molecular dataset does not give a robust support for a sister to the *Metanoeus* + *Xylometanoeus* + *Matsudanoeus* clade. Surprisingly, the Japanese species *Xylobanus basivittatus* and *X. japonicus* and several unidentified *Xylobanus* spp. (their classification in *Xylometanoeus* is discussed in the taxonomical part below) are sister to the clade of *Matsudanoeus yuasai* + *Metanoeus* spp. (Fig. 1). The position of these species compromises monophyly of *Cautires* and *Xylobanus* in the traditional sense (Kleine 1933; Bocak 2002; Kazantsev 2012). Therefore, we defined two new genera in Metanoeina for these species (*Matsudanoeus* and *Xylometanoeus*), studied their morphology in detail and compared it with the morphology of *Cautires* and *Xylobanus* (see Taxonomy section for details).

The subtribe Metriorrhynchina, when Cautirina and Metanoeina are defined and excluded from the subtribe, contains several Australian genera (e.g. *Metriorrhynchus*, *Porrostoma*, *Sulabanus*, Fig. 1). These three genera form a clade with *Trichalus* + *Microtrichalus* (former subtribe Trichalina), *Synchonnus* + *Wakarumbia* (former Hemiconderina) and *Leptotrichalus* (classified in Metriorrhynchina by Bocak 2002) The monophyly of these clades is weakly supported or compromised by presence of *Leptotrichalus* in the clade of *Synchonnus* + *Wakarumbia* (Hemiconderina). Therefore, Metriorrhynchina are redefined and include the genera previously classified in Trichalina and Hemiconderina.

We found that the character states used previously for definition of genera (characters (A) – (D) in section 2.4.) are either plesiomorphies, or apomorphies that evolved several times in distantly related lineages. *Xylobanus* and *Cautires* have been defined by having four and nine elytral costae, respectively (Figs. 3, 47 – 49). The origin of the nine-costae pattern in the cautirine ancestor was followed either by three independent origins of the four-costae pattern or the four-costae pattern was present at the root of Cautirina and was followed by a single origin of nine-costae pattern and two reversals (Fig. 3). The *Metanoeus* clade contains two branches: *Xylometanoeus* with the four-costae pattern and the *Matsudanoeus* + *Metanoeus* branch with the nine-costae pattern (Fig. 2).

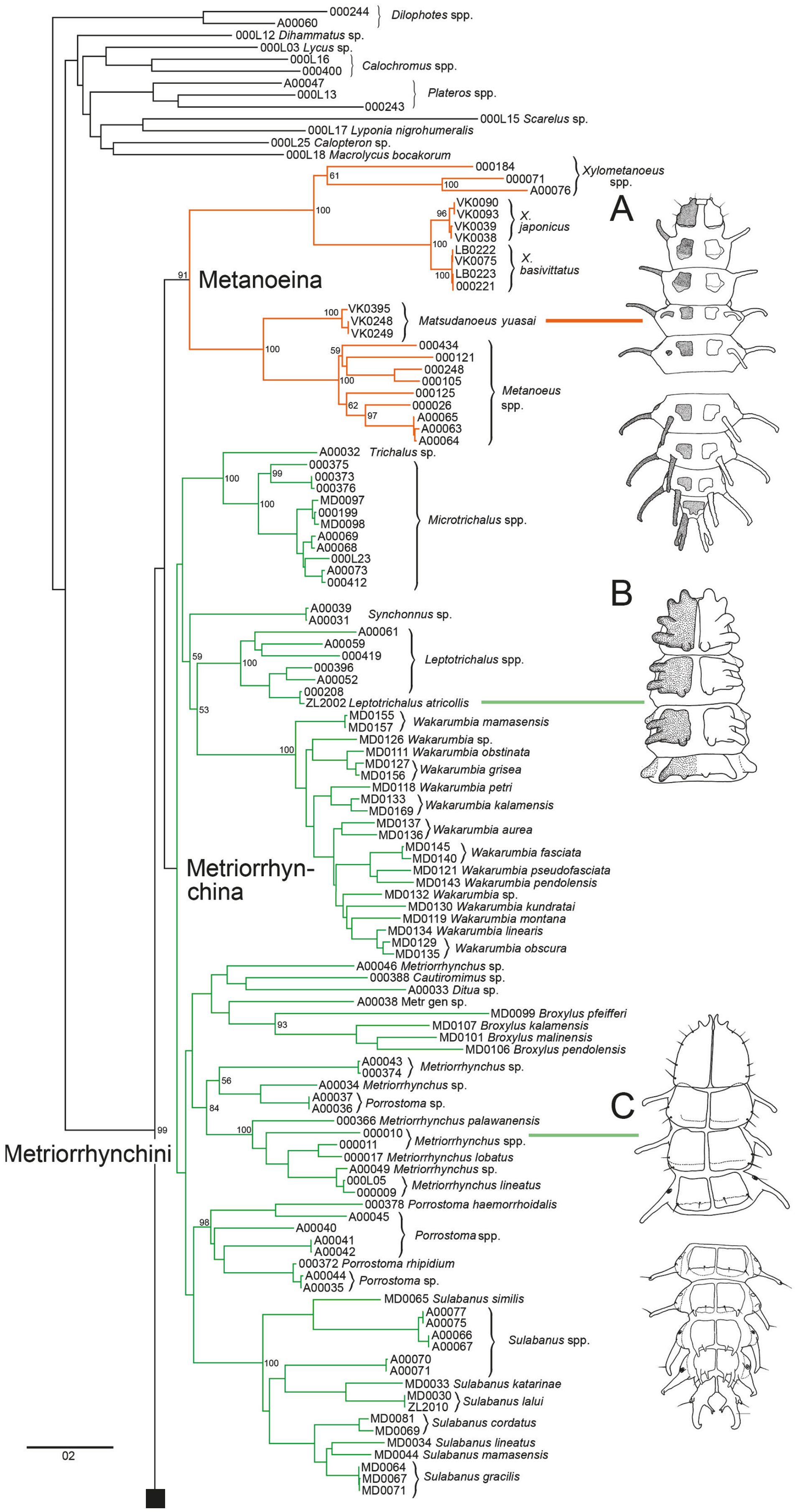
Similarly, the distribution of flabellate antennae suggests multiple origins and our optimization was ambiguous regarding the root of Metriorrhynchini. Therefore, the character should be used with caution in delineation of monophyletic lineages (Fig. 2). We found that *Xylobanus* splits in two sister-clades with flabellate versus serrate antennae; similarly some Australian *Metriorrhynchus*, including the type species, have flabellate antennae but the other, e.g. all species in the Oriental region and Sulawesi, have serrate antennae (Fig. 2). Although the definition of character states “serrate” and “flabellate” by an arbitrary ratio (see Methods) suggests that the changes might be gradual, very few individuals have antennae with a shape of antennomeres close to the given value. We suppose that the flabellate antennae play a role in pheromone communication and therefore, the distribution peaks in serrate and flabellate antennomeres might correspond to the presence/absence of selection for large surface of antennae housing olfactory receptors.

The number of pronotal carinae has been commonly used in systematics of net-winged beetles and the taxa defined based on this character have been accepted since the end of 19th century till recently (e.g. *Bulenides* Waterhouse, 1879, see Dudkova & Bocak 2010). Additionally, new taxa have been based on the number of pronotal areolae recently (e.g. Kazantsev 2012). High likelihood was calculated for the seven-areolae pattern (i.e. for the maximum set of carinae) at the root of Metriorrhynchini (Fig. ES1). Among Lycidae, the seven-areolae pattern only occurs in Metriorrhynchini and it is an autapomorphy of this tribe (while all carinae forming this pattern can also occur in other Lycidae, but not the full set). Subsequently, the various types of reduction of pronotal carinae are recovered in unrelated lineages, and some of them resemble patterns known in other net-winged beetle lineages (Figs. 5, ES1; Dudkova & Bocak 2010). The pattern of absent fronto-lateral carinae (*Wakarumbia* type, state 4; Fig. 39) is similar to those of Dictyopterinae or Conderini and Slipinskiini among Lycinae (Bocak et al. 2008). This pattern of areolae was coded as a single character state also in Conderini (i.e. homology assumption at primary level) in the morphological analysis by Bocak (2002) and as a result Hemiconderini (*Falsolucidota*, *Wakarumbia* and related genera) were recovered as the sister group of all other Metriorrhynchini.

Although with sparse sampling at this moment, we tested the proposal by Bocak (2002) to exclude *Leptotrichalus* from Trichalina and we found that *Leptotrichalus* is closely related to the *Synchonnus* + *Wakarumbia* clade and does not belong to the *Trichalus* + *Microtrichalus* clade (Fig. 1) despite possessing a similarly shortened elytral costa 1 (Fig. 4). Trichalina sensu Bocak (2002) is thus obtained herein as a monophyletic subclade of Metriorrhynchina.

The current analysis provides putative identification for the samples of unknown larvae of Metriorrhynchini reported by Levkanicova & Bocak (2009) and shows the importance of the multi-marker reference database for placement of unidentified samples in the phylogenetic framework as discussed by Bocak et al. (2014). The current sampling enables more precise identification of all four previously unidentified taxa (BS 100%, Fig. 1), although formal identification is unavailable due to the chaotic species-level taxonomy of the group in two cases.

Further, we compared the morphology of larvae of *Matsudanoeus yuasai*, *Metanoeus pendleburyi* (Bocak & Matsuda 2003) and *Xylometanoeus japonicus* (A.A. Zaitsev, unpublished data; Fig. 18) with other Metriorrhynchini. When only morphology was considered, the similarity of larvae of these taxa was noted, but no conclusion on relationships was made (Bocak & Matsuda 2003). The DNA-based association of the Metanoeina (*Metanoeus* + *Xylometanoeus* + *Matsudanoeus* clade) and Metriorrhynchina (Fig. 1) suggests that a midline division of terga is a synapomorphy of these two clades. Similarly, the presence of branched urogomphi supports the relationships of *Matsudanoeus* + *Metanoeus*. Spines at the frontal margin of pronotal hemitergites are ob-


000244
A00060
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000L12 Dihammatus sp.
000L03 Lycus sp.
000L16
000400
Calochromus spp.
A00047
000L13
000243
Plateros spp.
000L15 Scarelus sp.
000L17 Lyponia nigrohumeralis
000L25 Calopteron sp.
000L18 Macrolycus bocakorum
000184
000071
A00076
Xylometanoeus spp.
A
VK0090
VK0093
VK0039
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X. japonicus
LB0222
VK0075
LB0223
000221
X. basivittatus
Metanoeina
VK0395
VK0248
VK0249
Matsudanoeus yuasai
000434
000121
000248
000105
000125
000026
A00065
A00063
A00064
Metanoeus spp.
A00032 Trichalus sp.
000375
000373
000376
MD0097
000199
MD0098
A00069
A00068
000L23
A00073
000412
Microtrichalus spp.
B
A00039
A00031
Synchonnus sp.
A00061
A00059
000419
000396
A00052
Leptotrichalus spp.
000208
ZL2002 Leptotrichalus atricollis
MD0155
MD0157
Wakarumbia mamasensis
MD0126 Wakarumbia sp.
MD0111 Wakarumbia obstinata
MD0127
MD0156
Wakarumbia grisea
MD0118 Wakarumbia petri
MD0133
MD0169
Wakarumbia kalamensis
MD0137
MD0136
Wakarumbia aurea
MD0145
MD0140
Wakarumbia fasciata
MD0121 Wakarumbia pseudofasciata
MD0143 Wakarumbia pendolensis
Metriorrhyn-china
MD0132 Wakarumbia sp.
MD0130 Wakarumbia kundratai
MD0119 Wakarumbia montana
MD0134 Wakarumbia linearis
MD0129
MD0135
Wakarumbia obscura
A00046 Metriorrhynchus sp.
000388 Cautiromimus sp.
A00033 Ditua sp.
A00038 Metr gen sp.
MD0099 Broxylus pfeifferi
MD0107 Broxylus kalamensis
MD0101 Broxylus malinensis
MD0106 Broxylus pendolensis
A00043
000374
Metriorrhynchus sp.
A00034 Metriorrhynchus sp.
A00037
A00036
Porrostoma sp.
C
000366 Metriorrhynchus palawanensis
000010
000011
Metriorrhynchus spp.
000017 Metriorrhynchus lobatus
A00049 Metriorrhynchus sp.
000L05
000009
Metriorrhynchus lineatus
Metriorrhynchini
000378 Porrostoma haemorrhoidalis
A00045
A00040
A00041
A00042
Porrostoma spp.
000372 Porrostoma rhipidium
A00044
A00035
Porrostoma sp.
MD0065 Sulabanus similis
A00077
A00075
A00066
A00067
A00070
A00071
Sulabanus spp.
MD0033 Sulabanus katarinae
MD0030
ZL2010
Sulabanus lalui
MD0081
MD0069
Sulabanus cordatus
MD0034 Sulabanus lineatus
MD0044 Sulabanus mamasensis
MD0064
MD0067
MD0071
Sulabanus gracilis
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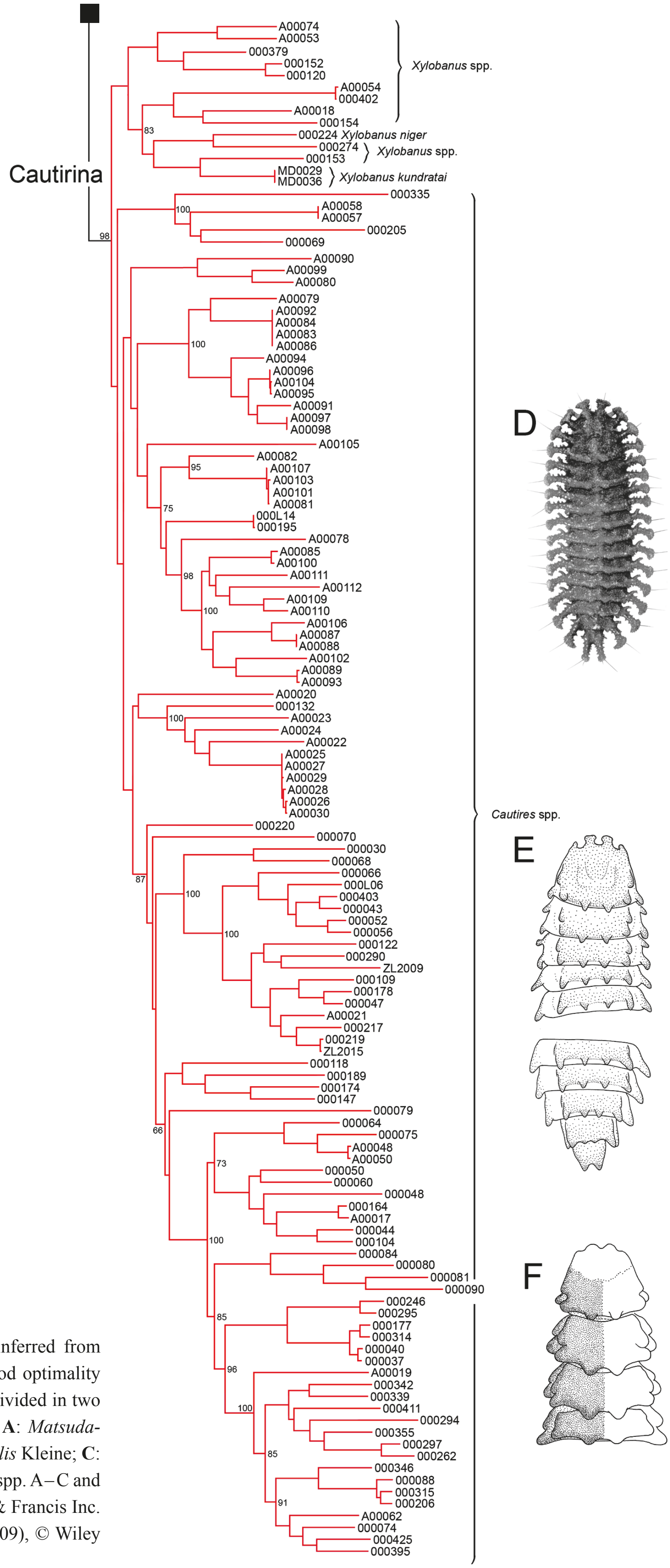
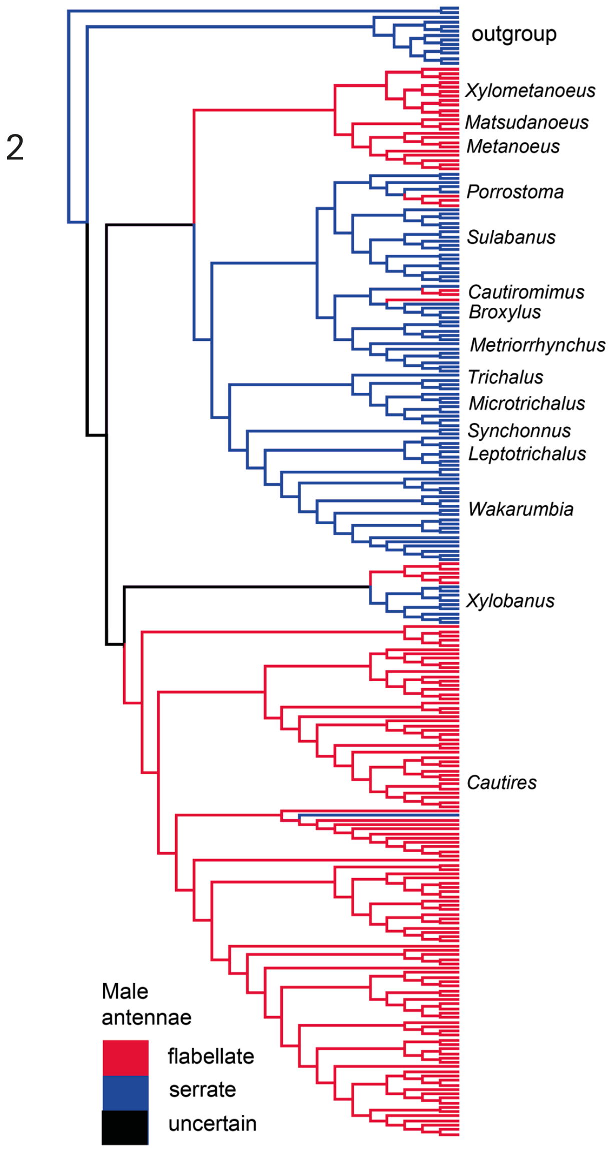
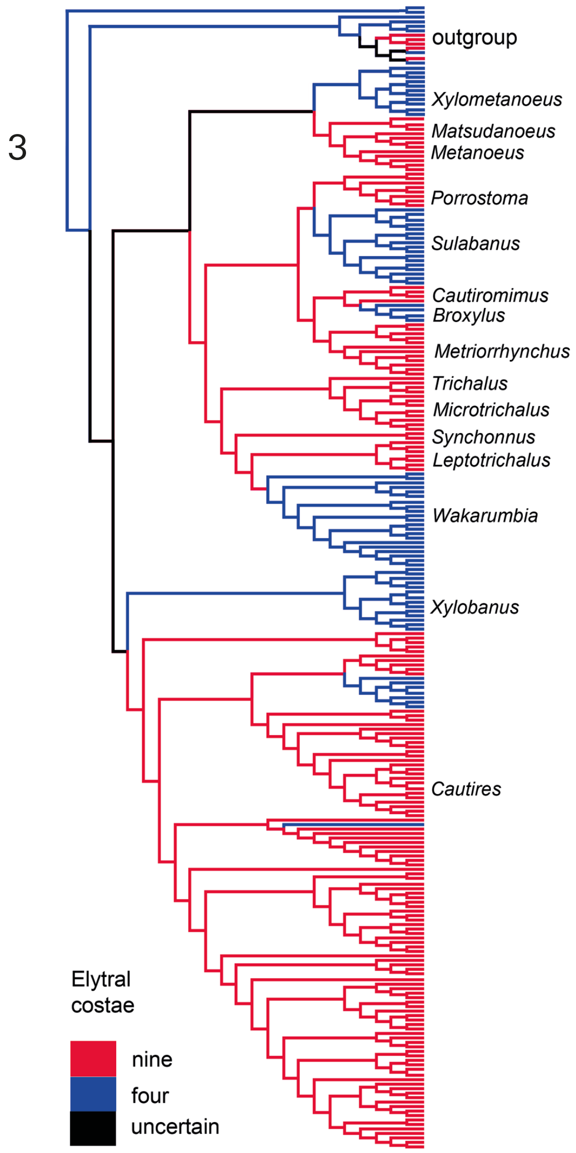


Fig. 1. Phylogenetic tree of Metriorrhynchini inferred from MAFFT alignment using the maximum likelihood optimality criterion; basal part of outgroups omitted. Tree divided in two parts at squares. Larvae, general appearance of **A**: *Matsudanoeus yuasai* (Nakane); **B**: *Leptotrichalus atricollis* Kleine; **C**: *Metriorrhynchus thoracicus* (F.); **D–F**: *Cautires* spp. A–C and E–F from Bocak & Matsuda (2002), © Taylor & Francis Inc. Basingstoke; D from Levkanicova & Bocak (2009), © Wiley & Sons, Inc. Chichester.





Figs. 2–5. Parsimony reconstruction of ancestral character states: **2**: the structure of antennae; **3**: the number of elytral costae; **4**: the length of the elytral costa 1; **5**: the structure of the pronotal areolae.

served in several *Metriorrhynchus* and *Xylometanoeus* and have not been found in any *Xylobanus* or *Cautires*. All these characters support the position of Metanoeina as sister to Metriorrhynchina. The molecular phylogeny supported by some larval and adult morphological characters provides evidence for the newly defined principal lineages.

The consequences of current findings for the taxonomy of Metriorrhynchini are discussed in the taxonomy section below. We show that integration of densely sampled molecular phylogeny with adult and larval morphology provides a strong framework for revised classification with strong explanatory and predictive power. On the other hand, when typologically defined polyphyletic taxa are rejected, and the revised generic and subtribal concepts are defined based on morphology of genitalia or larvae, eventually a combination of several characters must be used for definition of taxa.

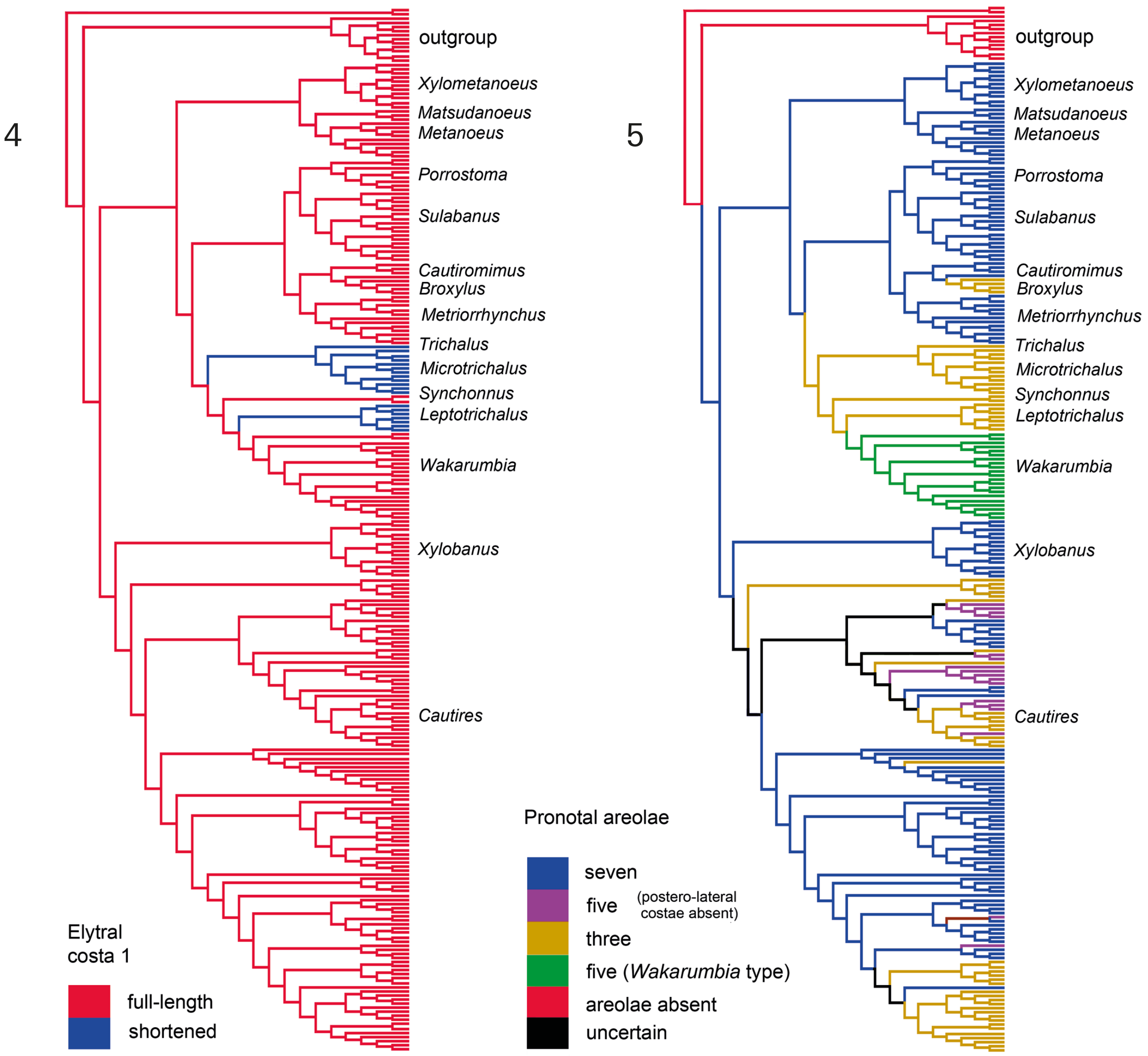
5. Taxonomy

5.1. Tribe Metriorrhynchini Kleine, 1926

Metriorrhynchini Kleine, 1926: 97.

Type genus. *Metriorrhynchus* Gemminger & Harold, 1869.

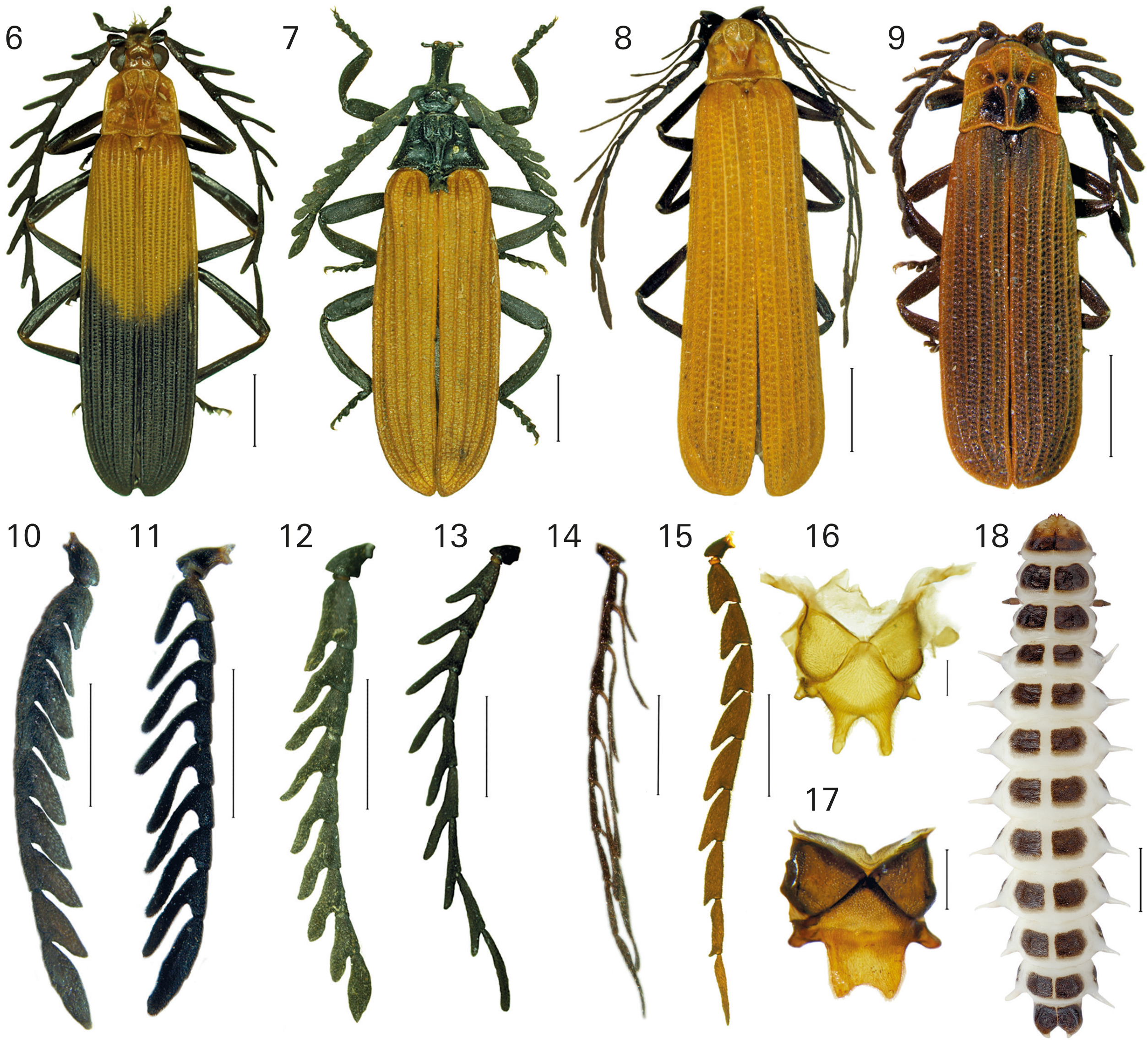
= Cladophorini Kleine, 1928: 222; Bocak & Bocakova 1990: 641.
Type genus. *Cladophorus* Guérin-Méneville, 1930, pl. 2, fig. 9.
= Dilolycinae Kleine, 1926: 186; Bocak & Bocakova 1990: 641.
= Dilolycini: Kleine, 1933: 84.
Type genus. *Dilolycus* Kleine, 1926: 186.



Description. ***Adults***: Body length 2.5–30 mm. Body weakly sclerotized, dorso-ventrally flattened (Figs. 6–9); most species aposematically colored.

Head small (Figs. 6–9), prognathous to hypognathous, partly covered by pronotum; most species without rostrum, flower visiting species rostrate (e.g. *Porrostoma*, *Leptotrichalus*, Figs. 7, 19–21); mouthparts well developed (Figs. 22–32), tiny if head rostrate. Labrum transverse, anterior margin rounded to slightly emarginate (Fig. 26). Mandibles long, slender to robust, shortened in species with rostrum, incisor without teeth (Figs. 23–25). Maxilla with small cardo, stipes plate-like, mala setose. Maxillary palpi 4-segmented. Labium small, without ligula, praementum large, mentum tiny, transverse; labial palpi 3-segmented (Figs. 27–32). Eyes hemispherically prominent. Antennal insertions narrowly separated, antennae 11-segmented, scapus stout, pedicel small, transverse; antennomeres 3–10 serrate to flabellate in males, serrate to shortly flabellate in females (Figs. 10–15).

Pronotum slightly narrower than elytra, flat, with pronotal carinae (Figs. 33–46). Anterior margin convex, anterior angles obtuse, posterior angles projecting. Prosternum transverse (Fig. 44). Mesoscutellum parallel-sided, weakly to deeply emarginate at apex (Figs. 16–17). Metendosternite with simple, robust stalk; arms absent. Elytra subparallel-sided, seldom globular (*Broxylus*); always with longitudinal and regular transverse costae (Figs. 6–9); longitudinal ones in two patterns: (1) four stronger (primary costae) and five weaker ones (secondary costae) (Figs. 6–9, 47, e.g. *Cautires*, *Porrostoma*, *Metriorrhynchus*); (2) only four primary costae present (e.g. *Xylobanus*, *Xylometanoeus*, Figs. 48–49), secondary costae absent; sometimes individual costae reduced in length (*Diatrichalus*, *Leptotrichalus*, etc.). Legs slender, flattened, coxae globular to slightly elongate; trochanters and femora slender; five tarsomeres, tarsomeres 2–4 often with membranous pads. Claws simple (Fig. 84).

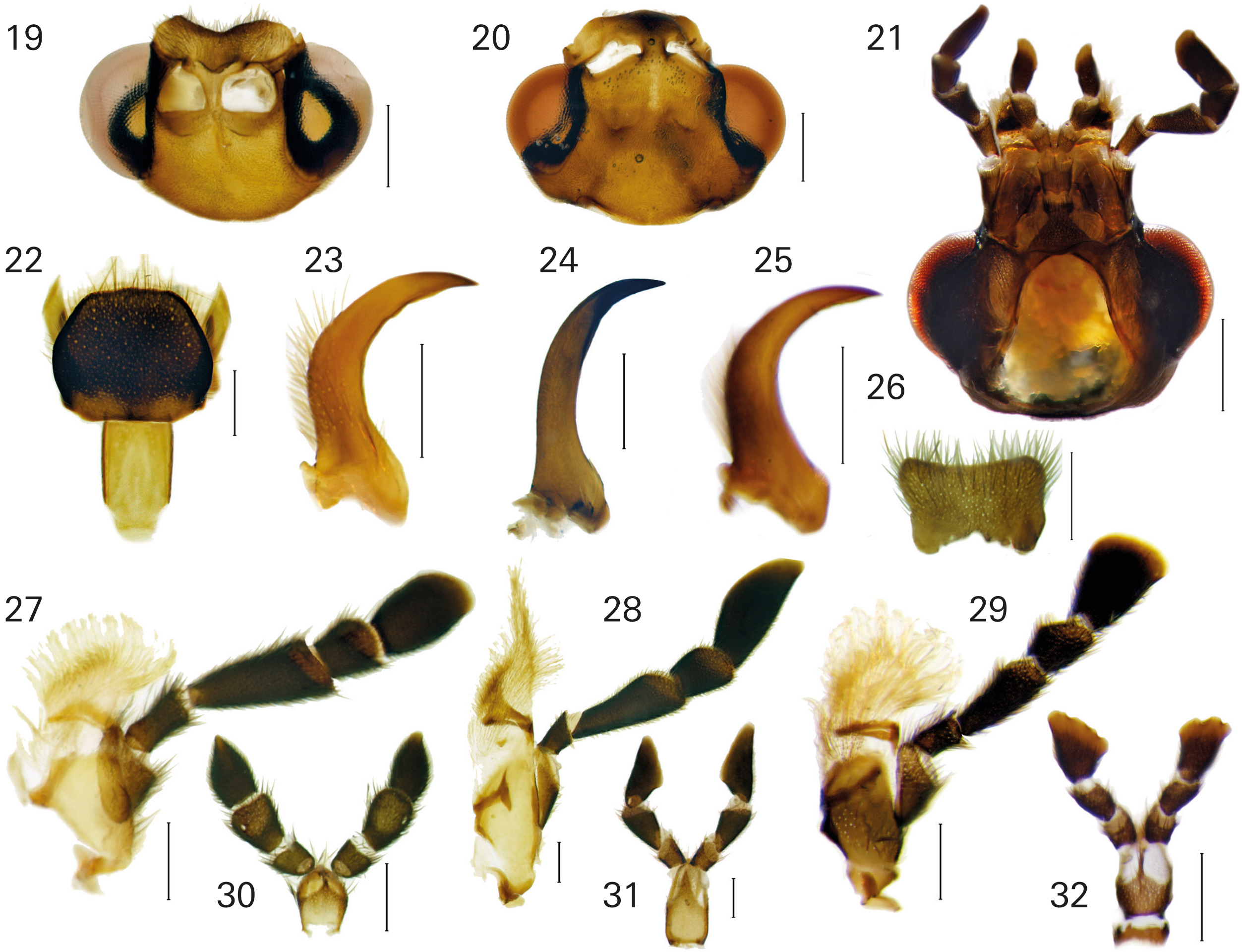


Figs. 6–18. General appearance of **6**: *Metriorrhynchus doleschali* Redtenbacher; **7**: *Porrostoma rhipidium* W. M'Leay; **8**: *Metanoeus bakeri* Kleine; **9**: *Cautires* sp. Antennae of **10**: *Cautires* sp., female; **11**: ditto, male; **12**: *P. rhipidium*, male; **13**: *M. doleschali*, male; **14**: *M. bakeri*, male; **15**: ditto, female. Mesoscutellum of **16**: *M. bakeri*; **17**: *Cautires* sp. Larva, general appearance, of **18**: *Xylometanoeus japonicus*. Scale bars: 2 mm (Figs. 6–15, 18), 0.5 mm (Figs. 16–17).

Abdomen short and much narrower than elytra in most species. Female spiculum gastrale absent. Male genitalia with tubular or partly membranous phallus, circular phallobase, parameres absent (Figs. 50–72). Internal sac regularly with thorns and lamellae (Figs. 50–51, 58–72), seldom completely membranous (*Porrostoma*, Figs. 52–53). Ovipositor with plate-like coxites, either with freely attached rod-like valvifers (Fig. 81) or valvifers reduced (*Metanoeus*, Figs. 73, 79). Styli short, movable (Figs. 73–82). Vagina simple, sac-like, membranous (Figs. 73–82), seldom sclerotized (Fig. 83), with median gland and two lateral accessory glands attached distally. Spermathecal duct short (Figs. 74–75) to very long (*Metanoeus*, Fig. 73). Spermatheca simple, apically bearing y-shaped gland (Figs. 73–83).

Larvae: Only a few genera are known in immature stages (Bocak & Matsuda 2003; Levkanicova & Bocak 2009). The larvae share reduced mala and movable or fixed tergal and pleural processes of variable length. Urogomphi variable in length and shape, long, movable and branched to short and membranous (Figs. 1A,C,D,E, 18).

Diagnosis. The Metriorrhynchini are characterized by several unique characters: Pronotum with carinae usually forming a pattern of four areolae at the anterior margin, single median lanceolate areola in middle and two postero-lateral areolae (unique pattern in Lycidae). However, frequently this set is reduced, in the extreme to a single median areola or only the anterior part of the median carina is present (*Caenioxylobanus*) (Figs. 33–46). Male genitalia with a straight phallus and a circular phallobase, parameres absent (Figs. 50–72). Female genitalia with vagina bearing an unpaired median gland (Figs. 73, 80, 83). Additionally, the Metriorrhynchini are characterized



Figs. 19–32. Head of **19**: *Metanoeus bakeri*; **20**: *Metriorrhynchus doleschali*; **21**: *Cautires* sp. **22**: Labrum and hypopharynx of *M. doleschali*. Mandible of **23**: *M. bakeri*; **24**: *M. doleschali*; **25**: *Cautires* sp. **26**: Labrum of *M. bakeri*. Maxilla of **27**: *M. bakeri*; **28**: *M. doleschali*; **29**: *Cautires* sp. Labium of **30**: *M. bakeri*; **31**: *M. doleschali*; **32**: *Cautires* sp. Scale bars: 0.5 mm (Figs. 19–21), 0.1 mm (Figs. 22–32).

by a pedicel at least four times shorter than antennomere 3 (Figs. 10–15, similar in Lycini and Calopterini) and elytra with longitudinal and transverse costae (similar in Dictyopterini and others, but absent in several lineages such as Lycini, Calochromini etc., Figs. 6–9, 47–49).

Distribution. Afrotropical region including Madagascar, southern part of Arab Peninsula; Oriental region, Australian region including islands of western Pacific (but absent in New Zealand except one introduced species), eastern part of Palearctic region. The dispersal and vicariance history was discussed by Sklenarova et al. (2013).

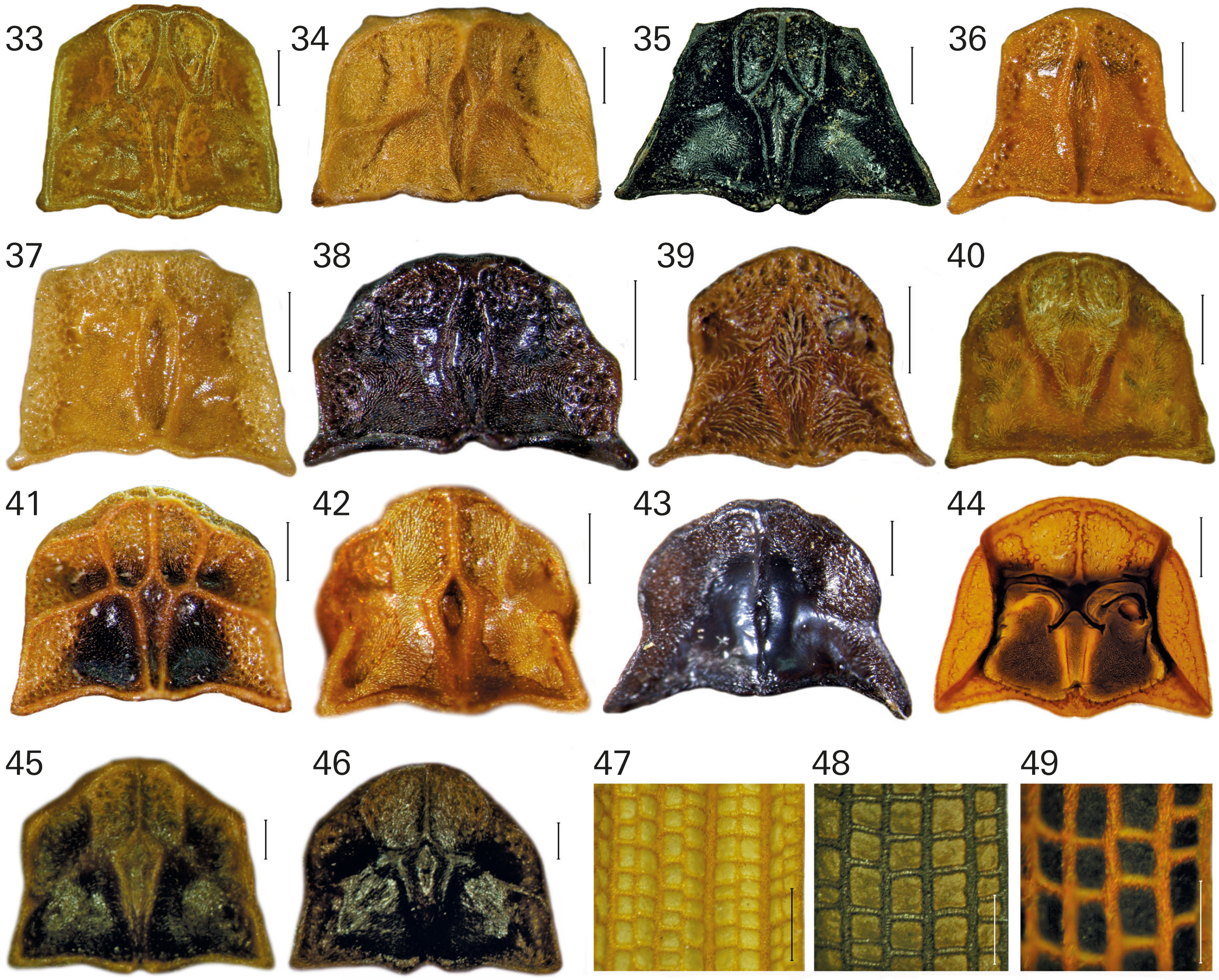
5.2. Subtribe Metriorrhynchina Kleine, 1926

Metriorrhynchini Kleine, 1926: 97.

Type genus. *Metriorrhynchus* Gemminger & Harold, 1869.

= Hemiconderina Bocak & Bocakova, 1990: 645 – **syn. nov.**
Type genus. *Hemiconderis* Kleine, 1926: 162.
= Trichalinae Kleine, 1928: 222 – **syn. nov.**
= Trichalini: Kleine, 1933: 69.
= Trichalina: Bocak & Bocakova, 1990: 646.
Type genus. *Trichalus* Waterhouse, 1877: 82.

Description. ***Adults:*** Body length 3–30 mm, most species brightly colored, few uniformly black or metallic blue (*Diatrichalus*, Figs. 6–7, 38). Head with rostrum (*Porrostoma*) or without rostrum (Figs. 6–7, 20), antennae flabellate or serrate in males (Figs. 12–13), sometimes pectinate with lamellae extremely long (*Carathrix*), serrate in females. Mandibles moderately long (Fig. 24), very short when rostrum present; palpomeres variable in shape (Figs. 28, 31). Pronotum usually with seven areolae, sometimes lateral carinae weaker to absent (Figs. 33–39). Mesoscutellum parallel-sided, deeply emarginate at apex. Elytra parallel-sided, seldom globular (*Broxylus*), with four or nine longitudinal costae (Figs. 6–7, 47). Male genitalia with tubular, sometimes apically membranous phallus, internal sac armed with thorns (*Metriorrhynchus*) or membranous (e.g., *Porrostoma*,



Figs. 33–49. Pronotum of **33**: *Metriorrhynchus* sp.; **34**: *Cladophorus* sp.; **35**: *Porrostoma rhipidium*; **36**: *Leptotrichalus* sp.; **37**: *Microtrichalus* sp.; **38**: *Diatrichalus* sp.; **39**: *Wakarumbia* sp.; **40**: *Metanoeus* sp.; **41–44**: *Cautires* spp.; **45**: *Matsudanoeus yuasai*; **46**: *Xylometanoeus japonicus*. Structure of elytral costae of **47**: *Cautires* sp. (Cameroon); **48**: *Xylometanoeus basivittatus*; **49**: *Xylometanoeus* sp. (Borneo). Scale bars: 0.5 mm.

Trichalus, Figs. 50–53). Vagina membranous to heavily sclerotized (some Papuan *Metriorrhynchus*), lateral accessory glands attached directly or via partly sclerotized ducts; spermaduct short to moderately long (Fig. 83).

Larvae: Several genera of Metriorrhynchina are known in immature stages: *Porrostoma* spp. from Australia, *Metriorrhynchus* spp. (the Philippines and Great Sundas), *Leptotrichalus* (Java) and *Sulabanus* (Sulawesi). All known larvae share the longitudinally divided meso- and metathoracic terga and many have the spines at the frontal margin of the pronotum. Urogomphi variable in shape, movable or fixed, seldom absent (e.g. *Metriorrhynchus*; Bocak & Matsuda 2003; Levkanicova & Bocak 2009).

Diagnosis. The Metriorrhynchina consist of morphologically diverse genera, which are difficult to collectively define by a unique feature. Most taxa have seven distinct pronotal areolae. Although these are similar to those of Cautirina, many genera have a slightly different shape of the pronotum and areolae: commonly posterior angles of pronotum are rectangular (Figs. 33–34) or lateral areolae are shallow (Fig. 33). Several genera have areolae modified in a way unknown from other subtribes, e.g. *Leptotrichalus*, *Trichalus*, *Synchonnus* and related genera have a long median areola and the lateral carinae are absent (Figs. 36–38), sometimes patterns of areolae resemble those of Conderini or Dictyopterinae (*Falsolucidota*, *Wakarumbia*, Fig. 39). Additionally, some groups of genera have a shortened primary elytral costa 1 (the genera previously placed in Trichalinae/ini by Kleine 1928, 1933). The male genitalia of Metriorrhynchina are very diverse in the shape of the phallus and sclerotization of the internal sac (Figs. 50–53), but they have never a slender, lanceolate phallus and their internal sac does not have a pair of sclerotized thorns as known in Cautirina (Figs. 66–70). Some Metriorrhynchina have the phallobasal membrane modified in a sclerotized structure (e.g. some *Metriorrhynchus*, Figs. 50–51). Morphologically based identification is possible only using a set of various characters and detailed comparison to other taxa.

List of Metriorrhynchina genera. *Achras* Waterhouse, 1879; *Broxylus* Waterhouse, 1878 (= *Samanga* Pic, 1921); *Cautiromimus* Pic, 1926; *Cladophorus* Guérin-Méneville, 1830 (= *Odontocerus* Guérin-Méneville, 1838; = *Spacekia* Strand, 1936); *Cladophorinus* Kleine, 1926; *Diatrichalus* Kleine, 1926 (= *Mimotrichalus* Pic, 1930); *Ditua* Waterhouse, 1879; *Eniclases* Waterhouse, 1879; *Enylus* Waterhouse, 1879; *Falsolucidota* Pic, 1921 (= *Hemiconderis* Kleine, 1926); *Flabellotrichalus* Pic, 1921 (= *Villosotrichalus* Pic, 1921; = *Stereotrichalus* Kleine, 1926); *Kassemia* Bocak, 1998; *Leptotrichalus* Kleine, 1925; *Lobatang* Bocak, 1998; *Malacolycus* Kleine, 1943; *Mangkutanus* Kubecek, Dvorak & Bocak, 2011; *Marena* Kazantsev, 2007; *Metriorrhynchoides* Kleine, 1926; *Metriorrhynchus* Gemminger & Harold, 1869 (= *Metriorhynchus* Guérin-Méneville, 1838; = *Dilolycus* Kleine, 1926; = *Flabelloporrostoma* Pic, 1923); *Mimoxylobanus* Pic, 1921; *Microtrichalus* Pic, 1921 (= *Falsoenylus* Pic, 1926); *Oriomum* Bocak, 1999; *Porrostoma* Castelnau, 1838; *Procautires* Kleine, 1925; *Pseudodontocerus* Pic, 1921; *Schizotrichalus* Kleine, 1926; *Spinotrichalus* Kazantsev, 2010; *Stadenus* Waterhouse, 1879; *Sulabanus* Dvorak & Bocak, 2007; *Synchonnus* Waterhouse, 1879; *Trichalus* Waterhouse, 1877; *Wakarumbia* Bocak, 1999; *Xylobanomimus* Kleine, 1926; *Xylobanomorphus* Kleine, 1935.

Distribution. Australian region including islands of Western Pacific and eastern part of Oriental region (only *Metriorrhynchus* distributed from southeast Asia to Eastern India and Laos, *Microtrichalus* to southernmost Yunnan, *Leptotrichalus* to Vietnam, *Diatrichalus* recorded from the Philippines, Peninsular Malaysia and the Great Sundas, *Cautiromimus* from the Philippines including Palawan and *Sulabanus* from the Philippines, but not from Palawan). Metriorrhynchina are the only subtribe occurring east of the Wallace line except a few species of *Cautires* and *Xylobanus* on Sulawesi.

Remarks. Most morphological diversity of Metriorrhynchini is known from this subtribe and it resulted in a long list of described genera and definitions of subfamilies and tribes (Kleine 1933; Bocak & Bocakova 1990; Bocak 2002). The previously defined tribes were based on clear, diagnostically highly usable characters, which, however, revealed to be either features evolved multiple times or to define just a restricted terminal branch. The taxa based on these characters are unacceptable in a phylogenetic classification.

The former subtribe Trichalina was recovered as a subordinate branch: the *Trichalus* + *Microtrichalus* clade (Fig. 1); therefore Trichalina Kleine, 1928 is synonymized with Metriorrhynchina Kleine, 1926.

Hemiconderina was described as a subtribe of Metriorrhynchini by Bocak & Bocakova (1990) on the basis of the unique pattern of pronotal carinae, shape of genitalia, and weaker elytral primary costae 1 and 3 (Bocak 2002). The morphology-based analysis recovered these genera as one of principal lineages in Metriorrhynchini due to resemblance of their pronotal areolae pattern to that in the outgroup, but molecular data place them in a terminal position within Metriorrhynchina and suggest an independent origin of the hemiconderine rhomboidal areola. Therefore, we propose to synonymize the subtribe Hemiconderina Bocak & Bocakova, 1990 with Metriorrhynchina Kleine, 1926.

5.3. Subtribe Metanoeina subtrib. nov.

Type genus. *Metanoeus* Waterhouse, 1879.

Description. ***Adults****:* Body length 7 – 16 mm, most species brightly colored, seldom uniformly black (Fig. 8). Head without rostrum (Fig. 19), antennae flabellate to pectinate in males, serrate in females (Figs. 12 – 13). Mandibles variable in length (Fig. 23); apical palpomeres slender to pointed (Figs. 27, 30). Pronotum with seven areolae, sometimes carinae obtuse (Figs. 40, 45 – 46). Mesoscutellum parallel-sided, deeply emarginate at apex. Elytra parallel-sided, with four or nine longitudinal costae (Figs. 48 – 49). Phallus variable in shape, internal sac armed with thorns and sclerotized lamellae (Figs. 54 – 55, 58 – 65). Valvifers vestigial (*Metanoeus*, *Matsudanoeus*; Figs. 73, 79, 80) or slender, branched at base (*Xylometanoeus*; Figs. 74, 77); vagina membranous to partly sclerotized, basal parts of lateral glands often sclerotized (Figs. 73 – 75, 80), spermaduct very long (*Metanoeus*) or about as long as coxites and valvifers combined (Figs. 74 – 75, 80).

Larvae*:* The known larvae share the longitudinally divided meso- and metathoracic terga, the spines at the frontal margin of the pronotum (Bocak & Matsuda 2003). The urogomphi are movable and branched (*Metanoeus*, *Matsudanoeus*, Fig. 1A) or vestigial (*Xylometanoeus*).

The larva of *Xylometanoeus japonicus* (Fig. 18) was illustrated in detail by A.A. Zaitsev on flicker (http://farm4.staticflickr.com/3515/4026462633_96ff6ebb02_z.jpg?zz=1, visited on Aug. 21, 2013).

List of Metanoeina genera. *Metanoeus* Waterhouse, 1879; *Xylometanoeus* gen. nov.; *Matsudanoeus* gen. nov.

Diagnosis. The lineage was inferred as a principal metriorrhynchine lineage by Sklenarova et al. (2013) and a re-analysis here (BS 91%, Fig. 1). The only adult morphological synapomorphy supporting their relationships are the short valvifers and wide, short coxites (Figs. 73 – 75, 79 – 80). Further, only a combination of characters can be used for diagnosing Metanoeina: the larvae have longitudinally divided meso- and metathoracic terga (unlike Cautirina but shared with Metriorrhynchina), the pronotal carinae are obtuse and frontal areolae smaller (pronounced in *Metanoeus*, less evident in *Matsudanoeus*, absent in *Xylometanoeus*, Figs. 40, 45 – 46), the lateral margins of the pronotum are not elevated and the frontal margin is simple; the spermathecal duct is extremely long (*Metanoeus*) to moderately long, bases of ducts to lateral glands of vagina sclerotized in most species (Figs. 73 – 75, 80). The male genitalia are variable in

Figs. 50–72. Male genitalia, in lateral and dorsal views, of **50–51**: *Metriorrhynchus doleschali*; **52–53**: *Porrostoma rhipidium*; **54–55**: *Metanoeus bakeri*; **56–57**: *Cautires* sp.; **58–59**: *Matsudanoeus yuasai*; **60–61**: *Xylometanoeus japonicus*; **62–63**: *X. basivittatus*; **64–65**: *Xylometanoeus* sp.; **66–67**: *Cautires* sp. (Madagascar, terminal A00030 in Fig. 1); **68–69**: *Cautires* sp. (Cameroon, terminal A00096, previously classified as *Xylobanus*); **70**: *Cautires* sp. (Cameroon, Voucher A00086); **71–72**: *Xylobanus costifer* (Walker). Scale bars: 0.5 mm.

shape (Figs. 54–55, 58–65), but never lanceolate as in *Xylobanus* and *Cautires* (Figs. 56–57, 66–72).

Distribution. Eastern Oriental region (Laos, the Great Sundas, Peninsular Malaysia, Palawan, the Philippines) and eastern Palearctic Region (China, Japan, Russian Far East).

Remark. The analysis supports a deep position of the clade formed by *Metanoeus*, *Matsudanoeus*, and *Xylometanoeus* (Fig. 1). The larval morphology points strongly to relationships of Metanoeina and Metriorrhynchinae by the shared longitudinally divided thoracic terga and presence of thorns at frontal margin of pronotum in *Xylometanoeus* (Fig. 18). Concerning the morphological and molecular disparity of the lineage we propose a new subtribe Metanoeina for these three genera. *Metanoeus* was thoroughly redescribed by WEISZENSTEIN & BOCAK (2012) and two new genera are described below.

5.3.1. *Xylometanoeus* gen. nov.

Type species. *Xylobanus japonicus* Bourgeois, 1902.

Description. ***Adults****:* Body length 8 – 15 mm, dark reddish brown or brightly colored. Head without rostrum; antennae flabellate in males, serrate in females. Mandibles robust; apical palpomeres parallel-sided. Pronotum with seven areolae (Fig. 46). Elytra parallel-sided, with four longitudinal costae (Figs. 48 – 49). Phallus tubular, short, internal sac with lamellae (Figs. 60 – 65). Ovipositor short and wide, valvifers branched at base, about as long as coxites, vagina membranous (Figs. 74 – 75, 77).

Larvae*: Xylometanoeus japonicus*, Fig. 18 (previously unpublished information provided by A.A. Zaitsev): Body parallel-sided, 16 mm long, slightly wider in basal part of abdomen, sclerites brown, small, membranes extensive, yellowish-white. Lateral part of epicranium membranous. Eyes small. Mandibles slender, long, slightly curved. Pronotum T1 extensive, with apparent median longitudinal suture, terga T2 – T3 and A1 – A8 divided in a pair of small hemitergites connected by whitish membrane. Pronotum with small anterior processes; tergites T2 and T3 simple, subquadrate; prosternum small, subtriangular. Sterna T2 and T3 small, less sclerotized. Spiracular plate T2 located in pleural part of mesothorax, small, simple, with spiracular opening in middle of sclerite. Posterior thoracic pleurites present, similar in shape to anterior ones. Abdominal hemi-tergites A1 – A8 transverse, weakly sclerotized, each abdominal segment with long, finger-like, lateral membranous process; upper pleurites with spiracular opening at dorsal margin, lower pleurites much smaller. Segment A9 with pair of narrowly divided tergal sclerites and short membranous urogomphi below their apices.

Included species. Due to chaotic species level classification of the Oriental Metriorrhynchini we are not able to identify the Oriental species to the species level (Fig. 1) and only two Japanese species *X. japonicus* and *X. basivittatus* are formally classified in *Xylometanoeus* at present.

Material examined. 1 larva, Russia, South Kurils, Kunashir island, Cape Alekhino, 19. Aug. 2009, in rotten wood of *Acer*. Det. & leg. A.A. Zaitsev, deposited in Zaitsev coll.

Diagnosis. Adult *Xylometanoeus* differ from other Metanoeina in four elytral costae. The larvae of *Xylometanoeus* resemble other Metanoeina in divided meso-, metathoracic terga and prothoracic spines, but they differ from in short, simple urogomphi, undivided pronotal tergum and divided tergum A9 (Fig. 18).

Distribution. *Xylometanoeus* is widely distributed in the Oriental and the eastern part of the Palearctic region. Confirmed records are available from Japan, Laos, Borneo, and the Philippines.

Name derivation. The generic name is derived from the names *Xylobanus* and *Metanoeus* and points to the presence of the *Xylobanus*-like pattern of elytral costae. Gender masculine.

Remark. The species *Xylometanoeus basivittatus* (Nakane, 1970), comb. nov. and *X. japonicus* (Bourgeois, 1902), comb. nov. are transferred from *Xylobanus* Waterhouse, 1879.

5.3.2. *Matsudanoeus* gen. nov.

Type species. *Cautires yuasai* Nakane, 1969.

Description. ***Adults****:* Body length 8 – 11 mm, dark reddish brown. Head without rostrum; antennae flabellate in males, serrate in females. Mandibles robust; apical palpomeres parallel-sided, obliquely rounded at apex. Pronotum with seven areolae (Fig. 45). Elytra parallel-sided, with nine longitudinal costae. Phallus tubular, short, internal sac with one long and one short thorn (Figs. 58 – 59). Ovipositor short and wide, valvifers short, almost perpendicular to coxites, vagina short and wide, membranous (Figs. 74 – 75, 77).

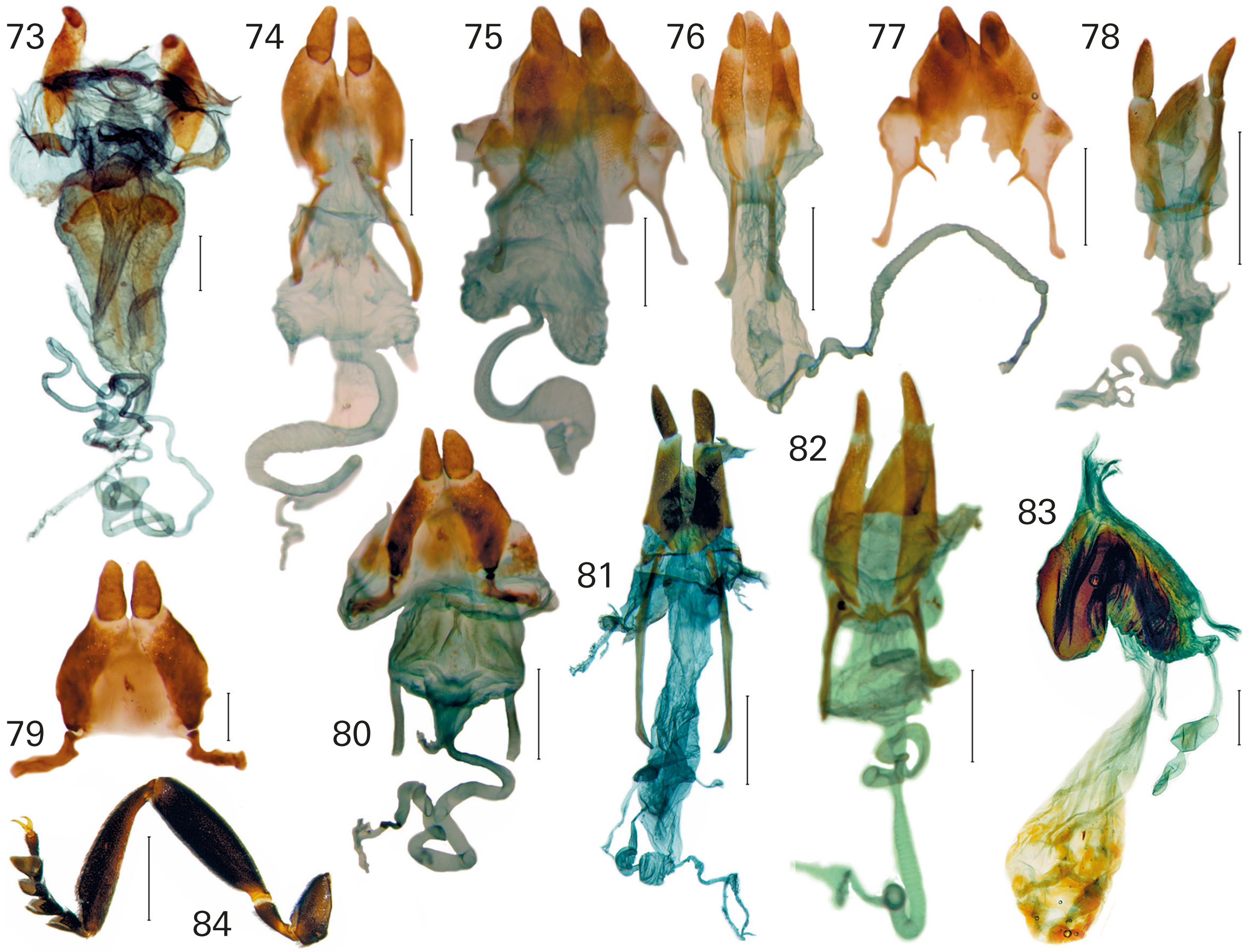
Larvae*:* The larva of *Matsudanoeus yuasai* was described by Bocak & Matsuda (2002) as *Cautires yuasai*. All thoracic and abdominal terga A1 – A8 are divided in two hemitergites, tergite A9 entire, urogomphi movable, branched (Fig. 1A).

Included species. Only the type-species *Matsudanoeus yuasai* (Nakane, 1969), comb. nov. is classified in the genus. It is transferred here from *Cautires* Waterhouse, 1879.

Diagnosis. *Matsudanoeus* gen. nov. resembles in the general appearance *Cautires*, with which it shares the pattern of pronotal areolae and the presence of secondary costae on the elytra. Unlike most *Cautires*, *Matsudanoeus* has a simple frontal margin of the pronotum. Further, the genus differs in the tubular, well sclerotized phallus and unique thorns of the internal sac (Figs. 58 – 59). Female genitalia are characteristic in the very short, laterally directed valvifers, which resemble those of *Metanoeus* (Figs. 79 – 80). Larvae of *M. yuasai* are similar to those of *Metanoeus* and have very long branched urogomphi in contrast to the larvae of *Cautires* (Bocak & Matsuda 2003).

Name derivation. The genus is named in honour of Dr. Kiyoshi Matsuda, Takarazuka, a specialist in Lycidae taxonomy. The name merges his family name and "*noeus*", a part of the name *Metanoeus*. Gender masculine.

Distribution. *Matsudanoeus yuasai* is endemic to Japan. Despite a relatively high number of sequenced species, none species has been recorded from the Oriental Region, where *Metanoeus* occur.



Figs. 73–84. Female genitalia of **73**: *Metanoeus bakeri*; **74**: *Xylometanoeus basivittatus*; **75**, **77**: *X. japonicus*; **76**: *Cautires* sp. (Cameroon, terminal A00104 in Fig. 1); **78**: *Xylobanus* sp.; **79–80**: *Matsudanoeus yuasai*; **81**: *Cautires* sp.; **82**: *Xylobanus costifer* (Walker); **83**: *Metriorrhynchus doleschali*. Hind leg of **84**: *Cautires* sp. Scale bars: 0.5 mm.

5.3.3. Key to identification of Metanoeina genera

1 Each elytron with only four longitudinal costae (Figs. 48–49), male genitalia with short, robust phallus (Figs. 60–65); larva with longitudinally divided hemitergites A1–A9 and very short, membranous urogomphi, abdominal segments A1–A8 with a pair of membranous lateral processes (Fig. 18) .... ***Xylometanoeus* gen. nov.**

1’ Each elytron with four strong and five weak longitudinal costae; larva with entire, transverse tergum A9 and long, branched and sclerotized urogomphi (Fig. 1A), each abdominal segment A1–A8 with two pairs of movable sclerotized processes (Fig. 1A) **2**

2 Pronotal carinae obtuse, male antennae flabellate, branch of antennomere 3 very slender, basally attached, at least 2× as long as stem of antennomere (Fig. 14), male genitalia with more than two thorns in internal sac (Figs. 54–55); movable processes attached to abdominal terga A1–A8 shorter than width of corresponding tergite .... ***Metanoeus* Waterhouse**

2’ Pronotal carinae sharper and more distinct, male antennae flabellate, antennomere 3 with robust branch, which is at most 1.5× as long as stem of antennomere (Fig. 11), male genitalia with internal sac bearing two sclerotized thorns, one of them twice as long as the other (Figs. 58–59); movable processes attached to abdominal terga A1–A8 longer than width of corresponding tergite (Fig. 1) .... ***Matsudanoeus* gen. nov.**

5.4. Subtribe Cautirina subtrib. nov.

Type genus. *Cautires* Waterhouse, 1879.

Description. ***Adults****:* Body length 2.5–21 mm, most species brightly colored, few uniformly black or brown (Fig. 9). Head without rostrum (Figs. 9, 21), antennae flabellate in males, serrate to shortly flabellate in females (Fig. 10). Mandibles moderately long (Fig. 25), palpomeres variable in shape, securiform to pointed at apex (Figs. 29, 32). Pronotum usually with seven areolae, sometimes lateral carinae weaker to absent (Figs. 41–43). Mesoscutellum shallowly emarginate at apex (Fig. 17). Elytra parallel-sided, with four or nine longitudinal costae (Figs. 9, 47). Male genitalia with lanceolate or apically rounded phallus, internal sac armed with two thorns (Figs. 66–72). Valvifers simple, parallel-sided (Fig. 81) seldom fused basally (Fig. 76), short with small sclerite between their bases (*Xylobanus*; Figs. 78, 82); vagina membranous, spermaduct short to moderately long (Figs. 76–77, 81–82).

Larvae: Only several larvae of *Cautires* have been collected and they were described and illustrated by Bocak & Matsuda (2003) and Levkanicova & Bocak (2009). All thoracic terga entire (Fig. 1D,E,F).

Diagnosis. Despite strong support for this clade from molecular data (BS 98%, Fig. 1), the Cautirina are difficult to characterize by the presence of clearly defined morphological characters in the adult stage; only the larvae differ from Metanoeina and Metriorrhynchina in the entire thoracic terga (Fig. 1). Adults share a characteristic shape of the pronotum with elevated lateral margins and seven areolae, but the latter might be reduced to a prominent frontal keel and an obsolete median areola (Figs. 41–44, Dudkova & Bocak 2010). Some Metriorrhynchina have a similar pronotum and then male genitalia must be used for identification. Cautirina have a simple, lanceolate phallus, pointed apically (Figs. 56–57, 66–71) or widely rounded (Figs. 71–72), regularly with a pair of sickle-shaped sclerotized structures in the internal sac or apical lamellae. The Metriorrhynchina and Metanoeina have very variable forms of female genitalia, but never with a similarly slender, finely membranous vagina as found in Cautirina (Figs. 76, 78, 81).

List of Cautirina genera: *Caenioxylobanus* Pic, 1922; *Cautires* Waterhouse, 1879 (= *Bulenides* Waterhouse, 1879); *Paracautires* Kazantsev, 2012; *Prometanoeus* Kleine, 1925 (= *Tapromenoeus* Bocak & Bocakova, 1989); *Spartoides* Kazantsev, 2012; *Tricautires* Kazantsev, 2006; *Xylobanus* Waterhouse, 1879.

Distribution. Afrotropical region including Madagascar and the southernmost part of the Arab Peninsula (Yemen); Oriental region; the eastern part of the Palearctic region (the Himalayas, the eastern slope of the Tibetan Plateau and forest habitats of northeastern China, Japan and Russian Far East), Australian Region: Sulawesi. The ranges of Metriorrhynchina and Cautirina overlap only in a small part of their combined ranges (Sklenarova et al. 2013). A few Cautirina occur in Sulawesi (Kubecek et al. 2011) and none is known east of the Weber's line.

Remarks. The shape of pronotal carinae and elytral costae has been used for definition of genera and higher taxa, both in Cautirina and other Lycidae. The hypothesized phylogeny (Fig. 1) suggests that these structures were often independently modified in unrelated lineages (Figs. 2–5). We suppose that pronotal carinae as well as elytral costae have a strengthening function in the soft-bodied elateroid lineages and are easily modified when the body becomes slender or miniaturized. We hypothesize a multiple origin of the four-costae pattern in Cautirina, which explains the morphological diversity of genitalia in typologically delineated *Xylobanus* as noted by Bocak (2002). The type species, *Xylobanus costifer* (Walker, 1858) was identified as a member of the *Xylobanus* clade in Fig. 1. Other taxa, all with four costae and therefore until now classified as *Xylobanus*, were found in Metanoeina (*X. basivittatus* and *X. japonicus*, Figs. 60–65, herein transferred to *Xylometanoeus*), and in the Afrotropical *Cautires* clade (see distribution of characters in Fig. 3). Further Cautirina species with four-costae pattern are known from Madagascar (e.g. *Caenioxylobanus* Pic, 1922). These species differ from *Xylobanus* in female genitalia and shape of phallus (Figs. 68–72). *Xylobanus* is now defined by the unique shape of the phallus with a rounded apical part, the internal sac bearing lamellae (Figs. 71–72), the female genitalia with valvifers shorter than coxites and a sclerite present between the bases of valvifers (Figs. 78, 82). Males of *Xylobanus* have either serrate or flabellate antennae (Fig. 2). The revised concept of *Cautires* includes taxa with either four or nine elytral costae and most species have flabellate antennae (Figs. 2–3). The male genitalia of *Cautires* have usually a slender, lanceolate phallus (Figs. 56–57, 66–70) and the female genitalia have long slender valvifers without any sclerite between their bases (compare Figs. 81 and 82) or seldom valvifers are short and their bases are connected by a sclerotized bridge (Fig. 76).

Another frequently used character for delineation of genera is the presence of flabellate antennae in males. Similarly to elytral costae or pronotal carinae these evolved frequently in unrelated lineages, e.g. both forms are present in *Xylobanus* and *Cautires* (Fig. 2). The olfactory organs are present on antennae and the expanded surface of antennae might be correlated with more intensive pheromone communication.

Kazantsev (2006, 2012) described three genera: *Tricautires* Kazantsev, 2006, *Paracautires* Kazantsev, 2012 and *Spartoides* Kazantsev, 2012 and based them mostly on the reduction of the number of pronotal areolae and on the shortened elytral costa 3. Additionally, he noted the pointed apical palpomeres in contrast with *Cautires*. The types are deposited in the private collection and unavailable for study (therefore no formal changes are proposed), but we have sequenced a relatively high number of taxa from Cameroon and found that morphologically similar taxa are members of the African *Cautires* clade (Fig. 1) and that this clade has a very diverse shape of apical palpomeres, patterns of pronotal areolae (Fig. 5) and number of elytral costae (Fig. 3). Kazantsev (2012) hypothesized a very old history of Metriorrhynchini in Africa and their restriction to refugia in the African part of the South American-African continent in the Jurassic and Cretaceous, both proposals in deep contrast with the phylogeographic reconstruction by Sklenarova et al. (2013). The supposed ancient origins of African Metriorrhynchini lead him to the proposal of new genera.

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Electronic Supplement Files

at http://www.senckenberg.de/arthropod-systematics (“Contents”)

File: SklenarovaEtAl-LycidaeMetriorrhynchini-ASP2014-ElectronicSupplement.pdf. – Table ES1: Previously published sequences included in the analysis with collecting information, voucher, and GenBank accession numbers. – Fig. ES1: Bayesian estimation of the ancestral patterns of pronotal carinae for selected clades.

Sklenarova, K., Kubecek, V., Bocak, L. Subtribal classification of Metriorrhynchini (Coleoptera: Lycidae): an integrative approach using molecular phylogeny and morphology of adults and larvae.

The list of Supplementary Information

Supplementary Tab. S1. Previously published taxa included in the analysis with collecting information, voucher, and GenBank accession numbers.

Supplementary Fig. S1. Bayesian estimation of the ancestral patterns of pronotal carinae for selected clades.

Supplementary Table S1. Previously published taxa included in the analysis with collecting information, voucher, and GenBank accession numbers.

Species	Voucher number	Geographic origin	*rrnL*	*cox1*	*nad5*
Outgroup					
Libnetis sp.	UPOL 001002	Indonesia	DQ181030	DQ181252	DQ181406
Dilophotes sp.	UPOL 000244	Sabah	DQ180992	DQ181214	DQ181368
Plateros sp.	UPOL 000243	Sabah	DQ180991	DQ181213	DQ181367
Platycis minutus	UPOL 000348	Czechia	DQ180995	DQ181217	DQ181371
Lycoprogenthes sp.	UPOL 000358	Java	DQ180996	DQ181218	DQ181372
Calochromus sp.	UPOL 000400	Palawan	-	KC538321	KC538512
Duliticola sp.	UPOL 000L01	Sabah	DQ180963	DQ181185	DQ181339
Libnetis sp.	UPOL 000L02	Sabah	DQ180964	DQ181186	DQ181340
Lycus sp.	UPOL 000L03	S. Africa	DQ180965	DQ181187	DQ181341
Calopteron sp.	UPOL 000L25	Ecuador	DQ180979	DQ181201	DQ181355
Lyropaeus sp.	UPOL 000L11	Sabah	DQ180968	DQ181190	DQ181344
Dihammatus sp.	UPOL 000L12	Sabah	DQ180969	DQ181191	DQ181345
Plateros sp.	UPOL 000L13	Sabah	DQ180970	DQ181192	DQ181346
Scarelus sp.	UPOL 000L15	Sabah	KC538782	DQ181194	DQ181348
Calochromus sp.	UPOL 000L16	China	DQ180973	DQ181195	DQ181349
Lyponia nigrohumeralis	UPOL 000L17	China	DQ180974	DQ181196	DQ181350
Macrolycus bocakorum	UPOL 000L18	China	DQ180975	DQ181197	DQ181351
Dictyoptera elegans	UPOL 000570	Japan	DQ180999	DQ181221	DQ181375
Pyropterus nigroruber	UPOL 000574	Japan	DQ181003	DQ181225	DQ181379
Lopheros sp.	UPOL 000578	Japan	DQ181007	DQ181229	DQ181383
Lycoprogenthes sp.	UPOL 000801	Sumatra	DQ181021	DQ181243	DQ181397
Plateros sp.	UPOL A00047	Malaysia	-	KC538353	KC538544
Dilophotes sp.	UPOL A00060	Philippines	KC538740	KC538359	KC538552
Ingroup					
Metriorrhynchus lineatus	UPOL 000009	Sumatra	KC538628	DQ904297	DQ904259
Metriorrhynchus sp.	UPOL 000010	Sulawesi	-	DQ144659	DQ144685
Metriorrhynchus sp.	UPOL 000011	Sulawesi	KC538629	DQ144660	DQ144686
Metriorrhynchus lobatus	UPOL 000017	Sulawesi	KC538630	DQ144662	DQ144688
Metanoeus sp.	UPOL 000026	Borneo	KC538631	KC538244	KC538436
Cautires sp.	UPOL 000030	Borneo	KC538632	KC538245	KC538437
Cautires sp.	UPOL 000037	Borneo	KC538633	KC538246	KC538438
Cautires sp.	UPOL 000040	Borneo	KC538634	KC538247	KC538439
Cautires sp.	UPOL 000043	Borneo	KC538635	KC538248	KC538440
Cautires sp.	UPOL 000044	Borneo	KC538636	KC538249	KC538441
Cautires sp.	UPOL 000047	Sumatra	KC538637	KC538250	KC538442
Cautires sp.	UPOL 000048	Sumatra	KC538638	KC538251	KC538443
Cautires sp.	UPOL 000050	Sumatra	KC538639	KC538252	KC538444
Cautires sp.	UPOL 000052	Sumatra	KC538640	KC538253	KC538445
Cautires sp.	UPOL 000056	Sumatra	KC538641	KC538254	KC538446
Cautires sp.	UPOL 000060	Sumatra	KC538642	KC538255	KC538447
Cautires sp.	UPOL 000064	Laos	KC538643	KC538256	KC538448
Cautires sp.	UPOL 000066	Laos	KC538644	KC538257	KC538449
Cautires sp.	UPOL 000068	Borneo	KC538645	KC538258	KC538450
Cautires sp.	UPOL 000069	Borneo	KC538646	KC538259	KC538451
Cautires sp.	UPOL 000070	Malaysia	KC538647	KC538260	KC538452
Xylometanoeus sp.	UPOL 000071	Borneo	KC538648	KC538261	KC538453
Cautires sp.	UPOL 000074	Borneo	KC538649	KC538262	KC538454
Cautires sp.	UPOL 000075	Laos	-	KC538263	KC538455
Cautires sp.	UPOL 000079	Borneo	KC538650	KC538264	KC538456
Cautires sp.	UPOL 000080	Borneo	KC538651	KC538265	KC538457
Cautires sp.	UPOL 000081	Borneo	KC538652	KC538266	KC538458

Cautires sp.	UPOL 000084	Borneo	KC538653	KC538267	KC538459
Cautires sp.	UPOL 000088	Malaysia	KC538654	KC538268	KC538460
Cautires sp.	UPOL 000090	Borneo	KC538655	KC538269	KC538461
Cautires sp.	UPOL 000104	Borneo	KC538656	KC538270	KC538462
Metanoeus sp.	UPOL 000105	Borneo	KC538657	KC538271	KC538463
Cautires sp.	UPOL 000109	Borneo	KC538658	KC538272	KC538464
Xylobanus sp.	UPOL 000120	Laos	KC538659	KC538273	KC538465
Metanoeus sp.	UPOL 000121	Sumatra	KC538660	KC538274	KC538466
Cautires sp.	UPOL 000122	Borneo	KC538661	KC538275	KC538467
Cautires sp.	UPOL 000123	Java	-	KC538276	-
Metanoeus sp.	UPOL 000125	Sumatra	KC538662	KC538277	KC538468
Xylobanus sp.	UPOL 000132	Sumatra	KC538663	HQ456987	HQ457009
Cautires sp.	UPOL 000147	India	KC538664	KC538278	KC538470
Xylobanus sp.	UPOL 000152	Laos	KC538665	KC538279	KC538471
Xylobanus sp.	UPOL 000153	Laos	KC538666	KC538280	KC538472
Xylobanus sp.	UPOL 000154	Laos	-	KC538281	-
Cautires sp.	UPOL 000164	Laos	KC538667	KC538282	KC538473
Cautires sp.	UPOL 000174	Malaysia	-	KC538283	KC538474
Cautires sp.	UPOL 000177	Malaysia	KC538668	KC538284	KC538475
Cautires sp.	UPOL 000178	Malaysia	KC538669	KC538285	KC538476
Xylometanoeus sp.	UPOL 000184	Borneo	KC538670	KC538286	KC538477
Cautires sp.	UPOL 000188	Laos	KC538671	KC538287	KC538478
Cautires sp.	UPOL 000189	Laos	KC538672	KC538288	KC538479
Cautires sp.	UPOL 000195	South Africa	KC538673	KC538289	KC538480
Microtrichalus sp.	UPOL 000199	Sulawesi	KC538674	KC538290	KC538481
Cautires sp.	UPOL 000205	Sumatra	KC538675	KC538291	KC538482
Cautires sp.	UPOL 000206	Sumatra	KC538676	KC538292	KC538483
Leptotrichalus sp.	UPOL 000208	Borneo	KC538677	DQ181212	DQ181366
Cautires sp.	UPOL 000217	Japan	KC538678	KC538293	KC538484
Cautires sp.	UPOL 000219	Japan	KC538679	KC538294	KC538485
Cautires sp.	UPOL 000220	Japan	KC538680	KC538295	KC538486
Xylobanus basivittatus	UPOL 000221	Japan	KC538681	KC538296	KC538487
Xylobanus niger	UPOL 000224	Japan	KC538682	KC538297	KC538488
Cautires sp.	UPOL 000246	Sumatra	KC538683	KC538298	KC538489
Metanoeus sp.	UPOL 000248	Sumatra	KC538684	KC538299	KC538490
Cautires sp.	UPOL 000262	Borneo	KC538685	KC538300	KC538491
Xylobanus sp.	UPOL 000274	Borneo	KC538686	KC538301	KC538492
Cautires sp.	UPOL 000290	Laos	KC538687	KC538302	KC538493
Cautires sp.	UPOL 000294	Sumatra	KC538688	KC538303	KC538494
Cautires sp.	UPOL 000295	Sumatra	KC538689	KC538304	KC538495
Cautires sp.	UPOL 000297	Sumatra	KC538690	KC538305	KC538496
Cautires sp.	UPOL 000314	Sumatra	KC538691	KC538306	KC538497
Cautires sp.	UPOL 000315	Sumatra	KC538692	KC538307	KC538498
Cautires sp.	UPOL 000335	Borneo	KC538693	KC538308	KC538499
Cautires sp.	UPOL 000339	Borneo	KC538694	KC538309	KC538500
Cautires sp.	UPOL 000342	Borneo	KC538695	KC538310	KC538501
Cautires sp.	UPOL 000346	Borneo	KC538696	KC538311	KC538502
Cautires sp.	UPOL 000355	Jawa	KC538697	KC538312	KC538503
Metriorrh. palawensis	UPOL 000366	Palawan	KC538698	DQ144665	DQ144691
Porrostoma rhipidum	UPOL 000372	Australia	KC538699	DQ144678	DQ144702
Microtrichalus sp.	UPOL 000373	Australia	KC538700	KC538313	KC538504
Metriorrhynchus sp.	UPOL 000374	Australia	KC538701	KC538314	KC538505
Microtrichalus sp.	UPOL 000375	Australia	KC538702	KC538315	KC538506
Microtrichalus sp.	UPOL 000376	Australia	KC538703	KC538316	KC538507
Porrost. haemorrhoidalis	UPOL 000378	Australia	KC538704	DQ144679	DQ144703
Xylobanus sp.	UPOL 000379	Palawan	KC538705	KC538317	KC538508
Cautiromimus sp.	UPOL 000388	Palawan	-	KC538318	KC538509
Cautires sp.	UPOL 000395	Palawan	KC538706	KC538319	KC538510

Leptotrichalus sp.	UPOL 000396	Palawan	KC538707	KC538320	KC538511
Xylobanus sp.	UPOL 000402	Palawan	KC538708	KC538322	KC538513
Cautires sp.	UPOL 000403	Palawan	KC538709	KC538323	KC538514
Cautires sp.	UPOL 000411	Palawan	KC538710	KC538324	KC538515
Microtrichalus sp.	UPOL 000412	Palawan	KC538711	KC538325	KC538516
Leptotrichalus sp.	UPOL 000419	Palawan	KC538712	KC538326	KC538517
Cautires sp.	UPOL 000425	Palawan	KC538713	KC538327	KC538518
Metanoeus sp.	UPOL 000434	Palawan	KC538714	KC538328	KC538519
Xylobanus sp.	UPOL A00018	Taiwan	HQ456946	HQ456964	HQ456988
Cautires sp.	UPOL A00019	Taiwan	KC538715	KC538329	KC538520
Cautires sp.	UPOL A00021	Taiwan	HQ456947	HQ456965	-
Cautires sp.	UPOL A00022	Madagascar	KC538716	HQ456966	HQ456986
Cautires sp.	UPOL A00023	Madagascar	KC538717	KC538330	KC538521
Cautires sp.	UPOL A00024	Madagascar	KC538718	KC538331	KC538522
Cautires sp.	UPOL A00025	Madagascar	KC538719	KC538332	KC538523
Cautires sp.	UPOL A00026	Madagascar	-	KC538333	KC538524
Cautires sp.	UPOL A00027	Madagascar	-	KC538334	KC538525
Cautires sp.	UPOL A00028	Madagascar	-	KC538335	-
Cautires sp.	UPOL A00029	Madagascar	-	KC538336	KC538526
Cautires sp.	UPOL A00030	Madagascar	KC538720	KC538337	KC538527
Synchonnus sp.	UPOL A00031	Australia	KC538721	KC538338	KC538528
Trichalus sp.	UPOL A00032	Australia	KC538722	KC538339	KC538529
Ditua sp.	UPOL A00033	Australia	KC538723	-	KC538530
Metriorrhynchus sp.	UPOL A00034	Australia	KC538724	KC538340	KC538531
Porrostoma sp.	UPOL A00035	Australia	KC538725	KC538341	KC538532
Porrostoma sp.	UPOL A00036	Australia	KC538726	KC538342	KC538533
Porrostoma sp.	UPOL A00037	Australia	KC538727	KC538343	KC538534
Metriorrhynchus sp.	UPOL A00038	Australia	KC538728	KC538344	KC538535
Metriorrhynchus sp.	UPOL A00039	Australia	KC538729	KC538345	KC538536
Porrostoma sp.	UPOL A00040	Australia	KC538730	KC538346	KC538537
Porrostoma sp.	UPOL A00041	Australia	KC538731	KC538347	KC538538
Porrostoma sp.	UPOL A00042	Australia	-	KC538348	KC538539
Metriorrhynchus sp.	UPOL A00043	Australia	KC538732	KC538349	KC538540
Porrostoma sp.	UPOL A00044	Australia	KC538733	KC538350	KC538541
Porrostoma sp.	UPOL A00045	Australia	KC538734	KC538351	KC538542
Metriorrhynchus sp.	UPOL A00046	Australia	KC538735	KC538352	KC538543
Cautires sp.	UPOL A00048	Malaysia	HQ456948	HQ456967	HQ456990
Metriorrhynchus sp.	UPOL A00049	Malaysia	KC538736	KC538354	KC538545
Cautires sp.	UPOL A00050	Malaysia	-	-	KC538546
Leptotrichalus sp.	UPOL A00052	Philippines	HQ456949	HQ456968	HQ456991
Xylobanus sp.	UPOL A00053	Palawan	KC538737	KC538355	KC538547
Xylobanus sp.	UPOL A00054	Palawan	KC538738	-	KC538548
Cautires sp.	UPOL A00057	Philippines	-	KC538356	KC538549
Cautires sp.	UPOL A00058	Philippines	-	KC538357	KC538550
Leptotrichalus sp.	UPOL A00059	Philippines	KC538739	KC538358	KC538551
Leptotrichalus sp.	UPOL A00061	Philippines	KC538741	KC538360	KC538553
Cautires sp.	UPOL A00062	Philippines	KC538742	KC538361	KC538554
Metanoeus sp.	UPOL A00063	Philippines	-	KC538362	KC538555
Metanoeus sp.	UPOL A00064	Philippines	-	KC538363	KC538556
Metanoeus sp.	UPOL A00065	Philippines	-	KC538364	KC538557
Sulabanus sp.	UPOL A00066	Philippines	KC538743	KC538365	KC538558
Sulabanus sp.	UPOL A00067	Philippines	KC538744	KC538366	KC538559
Microtrichalus sp.	UPOL A00068	Philippines	KC538745	KC538367	KC538560
Microtrichalus sp.	UPOL A00069	Philippines	KC538746	KC538368	KC538561
Sulabanus sp.	UPOL A00070	Philippines	KC538747	KC538369	KC538562
Sulabanus sp.	UPOL A00071	Philippines	KC538748	KC538370	KC538563
Microtrichalus sp.	UPOL A00073	Philippines	KC538749	KC538371	-
Xylobanus sp.	UPOL A00074	Philippines	KC538750	-	-

Sulabanus sp.	UPOL A00075	Philippines	KC538751	KC538372	KC538564
Xylometanoeus sp.	UPOL 00A076	Philippines	KC538752	KC538373	KC538565
Sulabanus sp.	UPOL A00077	Philippines	KC538753	KC538374	KC538566
Cautires sp.	UPOL A00078	Cameroon	KC538754	KC538375	KC538567
Cautires sp.	UPOL A00079	Cameroon	KC538755	KC538376	KC538568
Cautires sp.	UPOL A00080	Cameroon	HQ456950	HQ456969	HQ456992
Cautires sp.	UPOL A00081	Cameroon	KC538756	KC538377	KC538569
Cautires sp.	UPOL A00082	Cameroon	KC538757	KC538378	-
Cautires sp.	UPOL A00083	Cameroon	KC538758	KC538379	KC538570
Cautires sp.	UPOL A00084	Cameroon	KC538759	KC538380	KC538571
Cautires sp.	UPOL 00A085	Cameroon	KC538760	KC538381	KC538572
Cautires sp.	UPOL A00086	Cameroon	KC538761	KC538382	KC538573
Cautires sp.	UPOL A00087	Cameroon	KC538762	KC538383	KC538574
Cautires sp.	UPOL A00088	Cameroon	KC538763	KC538384	KC538575
Cautires sp.	UPOL A00089	Cameroon	KC538764	KC538385	KC538576
Cautires sp.	UPOL A00090	Cameroon	KC538765	KC538386	KC538577
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Cautires sp.	UPOL A00094	Cameroon	KC538768	KC538390	KC538581
Cautires sp.	UPOL A00095	Cameroon	KC538769	-	KC538582
Cautires sp.	UPOL A00096	Cameroon	KC538770	-	KC538583
Cautires sp.	UPOL A00097	Cameroon	KC538771	KC538391	KC538584
Cautires sp.	UPOL A00098	Cameroon	KC538772	KC538392	KC538585
Cautires sp.	UPOL A00099	Cameroon	KC538773	KC538393	KC538586
Cautires sp.	UPOL A00100	Cameroon	KC538774	KC538394	KC538587
Cautires sp.	UPOL A00101	Cameroon	-	KC538395	-
Cautires sp.	UPOL A00102	Cameroon	-	KC538396	KC538588
Cautires sp.	UPOL A00103	Cameroon	-	KC538397	-
Cautires sp.	UPOL A00104	Cameroon	KC538775	-	KC538589
Cautires sp.	UPOL A00105	Cameroon	KC538776	-	KC538590
Cautires sp.	UPOL A00106	Cameroon	KC538777	KC538398	KC538591
Cautires sp.	UPOL A00107	Cameroon	-	KC538399	-
Cautires sp.	UPOL A00109	Cameroon	KC538778	KC538400	KC538592
Cautires sp.	UPOL A00110	Cameroon	KC538779	-	KC538593
Cautires sp.	UPOL A00111	Cameroon	KC538780	KC538401	KC538594
Cautires sp.	UPOL A00112	Cameroon	KC538781	KC538402	KC538595
Metriorrhynchus lineatus	UPOL 000L05	Malaysia	DQ180966	DQ181188	DQ181342
Cautires sp.	UPOL 000L06	Malaysia	DQ180967	DQ181189	DQ181343
Cautires sp.	UPOL 000L14	South Africa	DQ180971	DQ181193	DQ181347
Microtrichalus sp.	UPOL 000L23	Malaysia	DQ180978	DQ181200	DQ181354
Xylobanus kundratai	UPOL MD0029	Sulawesi	-	HQ456972	HQ456994
Sulabanus lalui	UPOL MD0030	Sulawesi	-	KC538403	KC538596
Sulabanus katarinae	UPOL MD0033	Sulawesi	KC538783	KC538404	KC538597
Sulabanus lineatus	UPOL MD0034	Sulawesi	KC538784	KC538405	KC538598
Xylobanus kundratai	UPOL MD0036	Sulawesi	-	HQ456973	HQ456995
Sulabanus mamasensis	UPOL MD0044	Sulawesi	KC538785	KC538406	KC538599
Sulabanus gracilis	UPOL MD0064	Sulawesi	KC538786	KC538407	KC538600
Sulabanus similis	UPOL MD0065	Sulawesi	-	KC538408	KC538601
Sulabanus gracilis	UPOL MD0067	Sulawesi	KC538787	KC538409	KC538602
Sulabanus cordatus	UPOL MD0069	Sulawesi	KC538788	KC538410	KC538603
Sulabanus gracilis	UPOL MD0071	Sulawesi	KC538789	KC538411	KC538604
Sulabanus cordatus	UPOL MD0081	Sulawesi	KC538790	KC538412	KC538605
Microtrichalus sp.	UPOL MD0097	Sulawesi	KC538791	HQ456978	HQ457000
Microtrichalus sp.	UPOL MD0098	Sulawesi	HQ456956	HQ456979	HQ457001
Broxylus pfeifferi	UPOL MD0099	Sulawesi	HQ456957	HQ456980	HQ457002
Broxylus malinensis	UPOL MD0101	Sulawesi	HQ456958	HQ456981	HQ457003
Broxylus pendolensis	UPOL MD0106	Sulawesi	KC538792	KC538413	KC538606

Broxylus kalamensis	UPOL MD0107	Sulawesi	KC538793	KC538414	KC538607
Wakarumbia obstinata	UPOL MD0111	Sulawesi	KC538795	KC538416	KC538609
Wakarumbia petri	UPOL MD0118	Sulawesi	HQ456960	HQ456983	HQ457005
Wakarumbia montana	UPOL MD0119	Sulawesi	HQ456961	HQ456984	HQ457006
Wak. pseudofasciata	UPOL MD0121	Sulawesi	KC538796	KC538418	KC538610
Wakarumbia sp.	UPOL MD0126	Sulawesi	KC538797	KC538419	KC538611
Wakarumbia grisea	UPOL MD0127	Sulawesi	-	KC538420	KC538612
Wakarumbia obscura	UPOL MD0129	Sulawesi	KC538798	KC538421	KC538613
Wakarumbia kundratai	UPOL MD0130	Sulawesi	KC538799	KC538422	KC538614
Wakarumbia sp.	UPOL MD0132	Sulawesi	KC538800	KC538423	KC538615
Wakarumbia kalamensis	UPOL MD0133	Sulawesi	KC538801	KC538424	KC538616
Wakarumbia linearis	UPOL MD0134	Sulawesi	KC538802	KC538425	KC538617
Wakarumbia obscura	UPOL MD0135	Sulawesi	KC538803	KC538426	KC538618
Wakarumbia aurea	UPOL MD0136	Sulawesi	KC538804	KC538427	KC538619
Wakarumbia aurea	UPOL MD0137	Sulawesi	KC538805	KC538428	KC538620
Wakarumbia fasciata	UPOL MD0140	Sulawesi	KC538806	KC538429	KC538621
Wakarumbia pendolensis	UPOL MD0143	Sulawesi	KC538807	KC538430	KC538622
Wakarumbia fasciata	UPOL MD0145	Sulawesi	KC538808	KC538431	KC538623
Wakarumbia mamasensis	UPOL MD0155	Sulawesi	KC538809	KC538432	KC538624
Wakarumbia grisea	UPOL MD0156	Sulawesi	KC538810	KC538433	KC538625
Wakarumbia mamasensis	UPOL MD0157	Sulawesi	KC538811	KC538434	KC538626
Wakarumbia kalamensis	UPOL MD0169	Sulawesi	KC538812	KC538435	KC538627
Leptotrichalus atricollis	UPOL ZL2002	Jawa	EF143215	EF143230	EF143244
Cautires sp.	UPOL ZL2009	Sumatra	EF143219	EF143234	EF143248
Sulabanus lalui	UPOL ZL2010	Sulawesi	EF143220	EF143235	EF143249
Cautires sp.	UPOL ZL2015	Japan	EF143224	EF143239	-

The voucher specimens are deposited in the Laboratory of Molecular Systematics, Department of Zoology, Palacky University, Olomouc, Czech Republic.

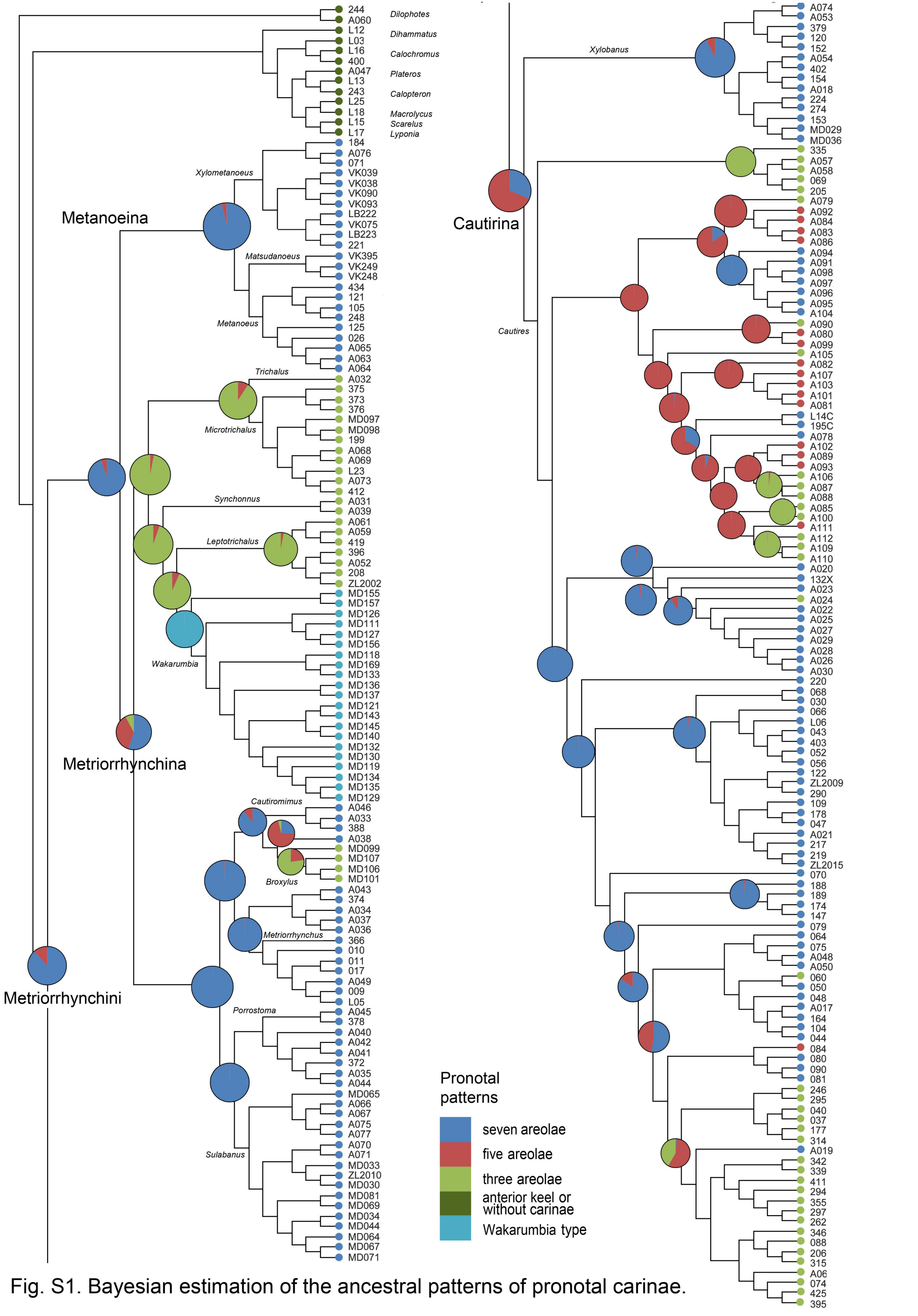

Fig. S1. Bayesian estimation of the ancestral patterns of pronotal carinae.