The comparison of molecular and morphology-based phylogenies of trichaline net-winged beetles (Coleoptera: Lycidae: Metriorrhynchini) with description of a new subgenus

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Separate morphological and molecular phylogenetic analyses are presented and the classification of trichaline net-winged beetles is revised. The clade, earlier given a subfamily, tribe or subtribe rank, is a terminal lineage in Metriorrhynchina and contains Diatrichalus Kleine, 1926, Eniclases Waterhouse, 1879, Flabellotrichalus Pic, 1921, Lobatang Bocak, 1998, Microtrichalus Pic, 1921, Schizotrichalus Kleine, 1926, and Trichalus Waterhouse, 1877. Maibrius subgen. nov. is proposed in Flabellotrichalus with the type-species Flabellotrichalus (Maibrius) horaki sp. nov. Unlike previous studies, Lobatang is included in the trichaline clade. Further, Spinotrichalus Kazantsev, 2010, stat. nov. is down-ranked to the subgenus in Lobatang Bocak, 1998 and a new combination, Lobatang (Spinotrichalus) telnovi (Kazantsev, 2010) comb. nov., is proposed. The morphology does not provide a sufficient support for robust phylogeny due to the intrageneric variability of most phenotypic traits and the limited number of characters supporting deep relationships. Most morphological generic diagnoses must be based on the shape of male genitalia. Other characters, such as the shapes of pronotum and antennae are commonly variable within genera. The fronto-lateral pronotal ridges of Eniclases + Schizotrichalus resemble the ancestral condition in Metriorrhynchini and they re-evolved in the terminal clade and do not indicate the early split of Eniclases + Schizotrichalus from other trichaline genera. The evolution of morphological traits and the conflict in the morphological and molecular phylogenetic signal are discussed in details. We suggest that the general appearance is affected by the evolution of mimetic complexes, the patterns of elytral costae by their strengthening function, and the presence of flabellate antennae by their role in sexual communication. Then, similar phenotypic traits evolve in unrelated lineages. The results demonstrate that phylogenetic classification must be based on all available information because neither morphological traits nor DNA data robustly support all recovered relationships.
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ABSTRACT

Separate morphological and molecular phylogenetic analyses are presented and the classification of trichaline net-winged beetles is revised. The clade, earlier given a subfamily, tribe or subtribe rank, is a terminal lineage in Metriorrhynchina and contains *Diatrichalus* Kleine, 1926, *Eniclases* Waterhouse, 1879, *Flabellotrichalus* Pic, 1921, *Lobatang* Bocak, 1998, *Microtrichalus* Pic, 1921, *Schizotrichalus* Kleine, 1926, and *Trichalus* Waterhouse, 1877. *Maibrius* subgen. nov. is proposed in *Flabellotrichalus* with the type-species *Flabellotrichalus (Maibrius) horaki* sp. nov. Unlike previous studies, *Lobatang* is included in the trichaline clade. Further, *Spinotrichalus* Kazantsev, 2010, stat. nov. is down-ranked to the subgenus in *Lobatang* Bocak, 1998 and a new combination, *Lobatang (Spinotrichalus) telnovi* (Kazantsev, 2010) comb. nov., is proposed. The morphology does not provide a sufficient support for robust phylogeny due to the intrageneric variability of most phenotypic traits and the limited number of characters supporting deep relationships. Most morphological generic diagnoses must be based on the shape of male genitalia. Other characters, such as the shapes of pronotum and antennae are commonly
variable within genera. The fronto-lateral pronotal ridges of *Eniclases + Schizotrichalus* resemble the ancestral condition in Metriorrhynchini and they re-evolved in the terminal clade and do not indicate the early split of *Eniclases + Schizotrichalus* from other trichaline genera. The evolution of morphological traits and the conflict in the morphological and molecular phylogenetic signal are discussed in details. We suggest that the general appearance is affected by the evolution of mimetic complexes, the patterns of elytral costae by their strengthening function, and the presence of flabellate antennae by their role in sexual communication. Then, similar phenotypic traits evolve in unrelated lineages. The results demonstrate that phylogenetic classification must be based on all available information because neither morphological traits nor DNA data robustly support all recovered relationships.

**INTRODUCTION**

Based on morphological uniqueness, the trichaline genera were given various family-group ranks from the subfamily to subtribe (Kleine, 1928; Kleine, 1933a; Bocak & Bocakova, 1990; Bocak, 2002). The molecular analyses recovered these genera as a terminal lineage in the subtribe Metriorrhynchina and to remedy this, they lost their formal rank (Sklenarova, Kubecek & Bocak, 2014). Although most of them are easily recognizable by a single lanceolate pronotal areola and a shortened elytral costa 1 (Kleine, 1928), the limits of the trichaline clade were questioned once the morphology was studied in detail (Bocak, 1998a; Bocak, 2002). Based on the morphological cladistic analysis, *Leptotrichalus* Kleine, 1925 and *Lobatang* Bocak, 1998a were excluded and *Enylus* Waterhouse, 1879, which is now a part of *Synchonnus* Waterhouse, 1879 (Kusy, Sklenarova & Bocak, 2017), was recovered as a member of Trichalini (Bocak, 2002).
Sklenarova, Kubecek & Bocak (2014) revised the classification of Metriorrhynchini, but only Trichalus Waterhouse, 1877 and Microtrichalus Pic, 1921b were included in their analyses. The trichaline clade contains approximately 230 formally described species and these represent ~20% of Metriorrhynchina diversity. There are high numbers of undescribed taxa in the various regions, as shown by recent studies (Bocak & Bocakova, 1991; Kazantsev, 2010; Bocek & Bocak, 2016; Bocek, 2017; Kusy, 2017). The trichaline species are currently placed in seven genera: Diatrichalus Kleine, 1926, Eniclases Waterhouse, 1879, Flabellotrichalus Pic, 1921b, Microtrichalus, Schizotrichalus Kleine, 1926, Trichalus, and, as shown below, Lobatang.

The high variability of traditionally used phenotypic characters, especially variable general appearance, modifications of elytral costae and diverse morphology of male antennae, led to the description of a large number of genera in this clade (Kleine, 1926; Pic, 1921b; Pic, 1923; Pic, 1926; Pic, 1930; Fig. 1A).

The center of trichaline diversity is located in the wet areas of the Australian region: the eastern coast of Australia (40 spp.), New Guinea (131 spp.), and Wallacea (31 spp.). Only a low number of species reach the Oriental region, mainly the Philippines (9 spp.) and the Greater Sundas (22 spp.). Several Indo-Burman species reach as far as the south of the Palearctic region (Kleine, 1933a; Bocak, 1998b; Bocak, 1999a). The first Australian representatives were already described from specimens brought to Europe in the time of discovery expeditions to the Southern Seas (Fabricius, 1775; Boisduval, 1835). Further species were described in the 19th century, many in other metriorrhynchine genera (Erichson, 1842; Blanchard, 1856; Kirsch, 1875; Macleay, 1886; Macleay, 1887; Fairmaire, 1877; Waterhouse, 1877; Waterhouse, 1878; Waterhouse, 1879; Bourgeois, 1900). A. M. Lea, R. Kleine and M. Pic described over 150 species mainly in 1920's and 1930's (e.g., Lea, 1909; Kleine, 1925; Kleine, 1926; Kleine, 1930;
Kleine, 1936; Kleine, 1939; Pic, 1921a; Pic, 1921b; Pic, 1923; Pic, 1926; Pic, 1930).

*Diatrichalus* and *Microtrichalus* were partly revised in a series of geographically restricted revisions (Bocak & Bocakova, 1991; Bocak, 1998b; Bocak, 1999a; Bocak, 2000; Bocak, 2001).

Later, only a single genus, *Spinotrichalus*, and four trichaline species, were described by Kazantsev (2010).

A growing amount of DNA data is currently available for the molecular phylogeny reconstruction of trichaline genera (Sklenarova, Kubecek & Bocak, 2014; Bocek & Bocak, 2016). The aim of this study is to use morphology and molecular phylogeny for the delimitation of genera and build a hypothesis on their relationships. The generic classification should reflect the best supported phylogenetic hypothesis, include only the monophyletic taxa, and be stable. Simultaneously, the genera should also be reliably identified in practice by the evaluation of phenotypic traits (Vences *et al*., 2013), ideally in the field, or by using simple laboratory equipment. Therefore, we discuss in detail the phenotypic diversification of trichaline genera and the usefulness of various morphological characters for both, phylogenetic inference and diagnostic purposes.

**MATERIAL AND METHODS**

**Sampling, laboratory procedures and sequence handling**

The trichaline net-winged beetles included in current molecular analyses are listed in Table 1. Most terminals in the dataset are identified to the genus level only due to the ambiguous alpha-taxonomy and a high proportion of undescribed species in the dataset. Total DNA was isolated from ethanol-preserved individuals using Wizard SV96 DNA purification system (Promega...
Inc.). All samples were sequenced for three mtDNA markers: \textit{rrnL}+tRNA-Leu+\textit{nad1} (~800 bp), \textit{cox1}+tRNA-Leu+\textit{cox2} (~1100 bp), and \textit{nad5}+tRNAs (~1210 bp; the fragments are further referred as \textit{rrnL}, \textit{cox1}, and \textit{nad5}) using primers reported by Bocak \textit{et al.} (2008) and Sklenarova, Chesters & Bocak (2013). The chromatograms were edited using the Sequencher 4.9 software package (Gene Codes Corp.). The newly reported sequences were submitted to GenBank under Accession Numbers MF288149–557 and MF997538–543 (Table 1). Altogether 21 taxa were chosen from previous publication as outgroups. These represent all known Metriorrhynchina major lineages as identified by Bocak \textit{et al.} (2008), Sklenarova, Chesters & Bocak (2013), and Sklenarova, Kubecek & Bocak (2014). We avoided inclusion of all known ~150 Metriorrhynchini species available in public databases, as we did not intend to repeat the thorough analysis of the Metriorrhynchini published earlier. Additionally, the high number of distantly related taxa may affect the relationships within ingroup and affect its internal topology as demonstrated by Bocak \textit{et al.} (2014).

All voucher specimens, including the type material, are deposited in the voucher collection of the Department of Zoology, Palacky University in Olomouc, Czech Republic (LMBC).

**Phylogenetic analyses of the molecular dataset**

Each DNA fragment was separately aligned with MAFFT 7.017 plug-in (Katoh & Standley, 2013) in Geneious R7.1.9 (Biomatters Inc.) and G-Ins-i algorithm. The alignment of the protein-coding genes \textit{cox1}, \textit{cox2}, \textit{nad1} and \textit{nad5} were checked by amino acid reading frames and manually corrected, if necessary. The concatenated supermatrix was partitioned using PartitionFinder2 for all fragments and codon positions when appropriate (Lanfear \textit{et al.}, 2014; Lanfear \textit{et al.}, 2016). The following partitions and models were proposed for the maximum-
likelihood (ML) and Bayesian analyses. The RAxML best partitioning scheme: 13 subsets; 1 = 1–617, 2 = 618–684, 1592–1651, 3 = 1912–2925\3, 685–808\3; 4 = 686–808\3, 1913–2925\3, 5 = 687–808\3, 6 = 809–1591\3, 7 = 810–1591\3, 8 = 811–1591\3, 9 = 1652–1911\3, 10 = 1653–1911\3, 11 = 1654–1911\3, 12 = 1913–2925\3, 13 = 2926–3184. The model GTR+I+G was proposed for subsets 1–9 and 13 and GTR+G for subsets 10–12. The model GTR+I+G was applied for all subsets in the maximum likelihood analyses as RAxML allows for only a single model of rate heterogeneity in partitioned analyses. I.e., we assigned GTR+I+G as the model providing the most accurate estimation of the DNA evolution (Stamatakis, 2014; Lanfear et al., 2014; Lanfear et al., 2016). The position cited refers to those in the supermatrix provided as the Supplementary File 1, i.e. the aligned DNA dataset used for the ML analysis. The BI best partitioning scheme: 14 subsets; 1 = 1–617, 2 = 618–684, 1592–1651, 3 = 1912–2925\3, 685–808\3, 4 = 686–808\3, 5 = 687–808\3, 6 = 809–1591\3, 7 = 810–1591\3, 8 = 811–1591\3, 9 = 1652–1911\3, 10 = 1653–1911\3, 11 = 1654–1911\3, 12 = 1913–2925\3, 13 = 1914–2925\3, 14 = 2926–3184. The model GTR+I+G was proposed for subsets 1–9, 13–14 and GTR+G for subsets 10–12. The models were applied in the BI analysis as proposed by PartitionFinder2. The position refers to the alignment provided in the Supplementary File 1 as above.

We used the ML criterion and Bayesian interference (BI) for phylogenetic analyses of the partitioned supermatrix (Supplementary File 1). The ML searches were conducted in RAxML 8.2.10 (Stamatakis, 2014) on the CIPRES cluster (Miller, Pfeiffer & Schwartz, 2010) with the partitions described above and the GTR+I+G model identified using PartitionFinder2 as described above. Additionally, we analyzed the dataset with the partition by genes and protein coding positions when appropriate and the GTR+I+G model identified by jModelTest 2.1.7 (Darriba et al., 2012). Bootstrap support values were calculated in both analyses from 1000
pseudoreplicates using the GTR+I+G model proposed by PartitionFinder2 or using the GTRCAT model which enables a time-effective and still sufficiently precise estimation of the bootstrap support in the analysis using partitions by genes (Stamatakis, 2014). The BI analysis was run in MrBayes 3.2.6 (Ronquist et al., 2012) on the CIPRES cluster under the best partitioning scheme suggested by PartitionFinder2 (Lanfear et al., 2014; Lanfear et al., 2016; see above) for $6 \times 10^7$ generations, sampling a single tree every 1,200 generations. The first 5,000 trees were discarded as burn-in after the identification of the stationary phase and the effective sample size in Tracer 1.6 (Rambaut et al., 2014). The same analysis was run with gene partitions and GTR+I+G model as proposed by jModelTest 2.1.7 (Darriba et al., 2012). Posterior probabilities (PP) were calculated from the post-burn-in trees and mapped on the maximum credibility tree. Both trees produced by ML and BI analyses were rooted by Cautires Waterhouse, 1879 (the type genus of the sister subtribe Cautirina, see Bocak et al., 2008; Sklenarova, Chesters & Bocak, 2013; Sklenarova, Kubeczek & Bocak, 2014). The rooting forces Metriorrhynchina to be a clade, but we do not force trichaline genera to be monophyletic and their monophyly can be rigorously re-tested by the current analysis. All trees were visualized in FigTree 1.4.2 (http://tree.bio.ed.ac.uk/software/figtree) and edited in a graphic software.

Morphological phylogeny

Adult semaphoronts were used for morphological descriptions. Male and female genitalia were relaxed and cleared in hot 10% KOH, dissected and stained by chlorazol black when needed. All photographs were taken using a camera on an Olympus SZX-16 binocular microscope. The morphological measurements were taken with the ocular scale.

The characters from earlier published morphological datasets (Bocak, 1998a; Bocak,
2002) and the newly identified characters (Kazantsev, 2010) were compiled in a single dataset of 11 taxa and 28 characters (Table 2, Supplementary File 2). *Metriorrhynchus* was considered as an outgroup when the tree was rooted. The characters in the trichaline clade were polarized by the outgroup criterion. The autapomorphies of genera are based on inspection of all available taxa classified in the respective genus and they are included in the analysis to map their distribution. These characters do not affect the topology. The following characters were coded for all genera of the trichaline clade and taxa representing non-trichaline Metriorrhynchina:

1. **Shape of external mandibular margin in ventral view**: (0) nearly straight; (1) concave.
2. **Shape of mandibles**: (0) slightly curved or sickle-shaped; (1) apical part curved in right angle.
3. **Shape of mandibular incisor**: (0) inner margin twice broken; (1) inner margin continuously curved.
4. **Shape of apical maxillary palpomere**: (0) securiform; (1) parallel-sided, more or less obliquely cut at apex.
5. **Presence of sensillae at apex of terminal palpomere**: (0) absent; (1) present.
6. **Shape of male antennae**: (0) male antennae filiform to serrate; (1) antennomeres 3–10 flabellate.
7. **Shape of pronotum**: (0) approximately as long as wide; (1) much longer than wide.
8. **Pubescence of pronotum**: (0) whole pronotum with pubescence of the same type and density; (1) apparently denser and longer pubescence at lateral and frontal margins.
9. **Strength of hind margin of metascutellum**: (0) hind margin of metascutellum simple; (1) bent, strengthened.
10. Shape of hind margin of metascutellum and presence of the metascutellar keel: (0) hind margin of metascutellum straight, without keel; (1) emarginate, with keel.

11. Arrangement of pronotal carinae: (0) seven pronotal areolae; (1) less than seven pronotal areolae.

12. Number of pronotal areolae: (0) at least five areolae or at least vestiges of frontal and postero-lateral keels present; (1) only a lanceolate median areola present.

13. Strengthened pronotal longitudinal carinae: (0) absent; (1) present.

14. The number of fully developed elytral primary costae in middle part of elytron: (0) four primary costae; (1) three primary costae.

15. Secondary elytral costae: (0) secondary costae present; (1) absent.

16. Split tarsal claws: (0) no; (1) yes.

17. Shape of apical part of phallus: (0) wider or as wide as its middle part, only in apical part open, if apical part slender, then well-sclerotized and internal sac widely exposed; (1) apical part of phallus slender, with cup-shaped apex, only dorsal part sclerotized.

18. Phallus short, robust, sometimes with a ventral process: (0) no; (1) yes.

19. Sickle-shaped thorns at base of internal sac: (0) absent; (1) present.

20. Single keel in dorsal part of phallus: (0) absent; (1) present.

21. Internal sac: 0, membranous or with sclerotized sclerites in apical part; (1) rod-shaped at least in the basal part.

22. Internal sac with y-shaped base: (0) no; 1, yes.

23. Shape of valvifers: (0) valvifers long, slender; (1) valvifers short, fused with coxites.

24. Attachment of lateral vaginal glands: (0) laterally; (1) dorsally.

25. Lateral pockets on vagina: (0) absent; (1) present.
26. **Unpaired slim vaginal gland:** (0) absent; (1) present.

27. **Length of spermatheca:** (0) relatively short, lemon-like; (1) long, slender.

28. **Structure of the basal part of the spermathecal duct:** (0) slim; (1) robust.

The maximum parsimony (MP) analysis was performed using PAUP* 4.0 (Swofford, 2002). Heuristic searches were conducted with 1,000 repetitions and random stepwise additions; all characters were unordered and equally weighted and polymorphic characters were treated as “missing” data. The level of confidence in each node of the MP trees was assessed using bootstrapping based on 1,000 pseudoreplicates, each analysis with 100 random additions.

Further, we estimated morphology-based phylogenetic relationships using Bayesian inference as implemented in BEAST 2 (Bouckaert et al., 2013). The analysis was conducted using Lewis MK substitution model, a lognormal relaxed clock model, and a Birth-Death tree prior. The number of generation was set to $10^7$ and sampling frequency every 1,000 generation. We used Tracer 1.6 (Rambaut et al., 2014) to confirm convergence, and based on this, we discarded the first 25% of generations as burn-in. We used the program TreeAnnotator 2.4.5 (Bouckaert et al., 2013) to produce maximum clade credibility tree with posterior probabilities.

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RESULTS

Molecular analysis

The molecular dataset contained 143 ingroup terminals representing 86 species from the whole range of the trichaline clade. Three markers were sequenced: *rrnL* mtDNA (137 ingroup samples), *cox1*-3' end of mtDNA (137 samples), and *nad5* mtDNA (134 samples). The concatenated dataset consisted of 3184 homologous positions: the alignments of the *rrnL*, *cox1*, and *nad5* fragments contained 808, 1103, and 1273 homologous base pairs, respectively. The phylogenetic trees inferred from the MAFFT alignment using the ML criterion and Bayesian inference were well-resolved and suggested similar relationships. The differences in the applied partitions and models proposed by PartitionFinder2 and jModelTest 2.1.7 did not have any effect on the ML topology and the bootstrap support values inferred in both analyses were highly similar and the topology is shown in Figs 1A and S1. The differences reached up to 2% and can be explained by the stochastic character of bootstrap analyses. The results of analyses based on the jModelTest partitions and models are not shown and they are not discussed further. The BI topology differs only slightly in the outgroup and internal topology of the *Microtrichalus* clade (Fig. S1). However, ambiguities in hypothesized relationships within *Microtrichalus* were expected as all ML and BI analyses recovered low BS and PP values for most internal relationships (Figs 1A, S1). The differences between analyses were limited to re-arrangements in *Microtrichalus* clade and did not include relationships among genera (Fig. 1A). The trichaline
clade was regularly recovered although only with an ambiguous support (BS 44%, PP 0.98).

*Diatrichalus* marked the deepest node, followed by *Lobatang* and a clade of *Eniclases*, *Trichalus, Flabellotrichalus and Microtrichalus*, further designated as the trichaline clade *sensu stricto*. *Schizotrichalus* was unavailable for molecular analyses. The genus-rank clades obtained mostly robust support >90% and regularly PP ~1.0, except *Diatrichalus* (BS 59%, PP 0.99) and *Trichalus* (BS 42%, PP 0.96). The relationships among these deep nodes remain poorly supported. The sister clade of trichaline genera contains *Leptotrichalus, Synchonnus*, and *Wakarumbia* Bocak, 1999b.

Morphological analysis

The morphological analyses did not support the monophyly of the DNA-based trichaline clade (Figs 1B–C). The relationships of *Schizotrichalus, Eniclases, Flabellotrichalus, Microtrichalus*, and *Trichalus* were satisfactorily resolved only by the BI analysis (Fig. 1B, S2), but the MP analysis recovered three equally parsimonious trees (L = 38, CI = 0.737, RI = 0.714). Their strict consensus and one of the most parsimonious trees were unresolved (Fig. 1C). The deeper relationships were poorly supported. The only synapomorphy which confirms the monophyly of the (*Schizotrichalus, Eniclases, Flabellotrichalus, Microtrichalus, Trichalus*) clade are the dorsally attached lateral vaginal glands (Figs 1A, 6Q). The presence of thorns in the internal sac suggests relationships of *Trichalus* and *Microtrichalus* and the pigmented keel supports relationships of *Eniclases + Schizotrichalus*. All discussed character states, including apomorphies which support individual genera, are mapped on the molecular phylogeny in Fig. 1A.
Taxonomy

Diagnosis of the trichaline clade

Most trichaline genera may be distinguished from other Metriorrhynchini by their general appearance (Figs 2–3) and external characters (Fig. 4). The pronotal carinae are reduced to a single, lanceolate areola in most genera (Figs 4C–J, M–T); two divergent pronotal ridges are present in *Eniclases* and five areolae in *Schizotrichalus* (Figs 4K–L). The first primary elytral costa is shortened in all trichaline genera (Figs 2A–B, F, K, Q; 3A, D–E, H, L), and in some distantly related Metriorrhynchina, e.g., *Leptotrichalus* and *Kassemia* Bocak, 1998 (Bocak, 1998a; Bocak, 2002). Male genitalia are highly variable, either robust with the characteristic sclerites in the internal sac (*Diatrichalus*; Figs 5A–C), the phallus is slender, with a simple sclerotized internal sac (*Lobatang*, Figs 5D–E), robust with the sclerotized base of the internal sac (*Lobatang*, Figs 5G–I), slender with the mostly membranous internal sac with a pair of basal thorns (*Trichalus, Microtrichalus*; Figs 5F, J–L), slender with partly exposed, membranous internal sac (*Flabellotrichalus*; Figs 5N–P) or the phallus is almost completely membranous in the apical half and has a characteristic ventral pigmented keel and small cup-shaped apex (*Eniclases, Schizotrichalus*; Fig. 5M). The genital morphology of each genus is unique within Metriorrhynchini and enables reliable identification. Female genitalia have dorsally attached vaginal glands in *Schizotrichalus, Eniclases, Flabellotrichalus, Microtrichalus*, and *Trichalus* (Fig. 6Q), but the glands are laterally attached in *Diatrichalus* and *Lobatang* (Figs 6B, E), as in other Metriorrhynchini.

Some trichaline net-winged beetles can be reliably identified only by a combination of characters. The pronotal carinae, elytral ridges and genitalia can be similar in distantly related
metriorrhynchine taxa. Therefore, all these structures must simultaneously corroborate the membership in the trichaline clade.

**Redescription**

Body small to medium-sized, 4–20 mm long, dorso-ventrally flattened, elytra parallel-sided or slightly widened backwards (e.g., Figs 2A–B, 3A), body mostly dark brown, seldom yellow, upper side variably colored, often with aposematic color patterns combining yellow and dark colored parts; seldom some parts of pronotum and elytra brightly red colored or upper side metallic blue.

Head hypognathous, small, partly hidden by pronotum, rostrum absent in most species, sometimes moderately long rostrum in *Lobatang*. Cranium slightly dorso-ventrally flattened, with more or less prominent antennal tubercles followed by depression; mouth opening approximately as wide as long. Gula wider than long, with more or less wide process, where postmentum is attached; posterior tentorial pits usually unapparent externally; tentorium mostly membranous, only posterior tentorial arm partly sclerotized. Mandibles relatively stout, short, outer margin covered with dense long setae, sometimes only several short pale setae present.

Labrum wider than long, shallowly emarginate apically, with long dense setae. Labium with robust praementum and much smaller u-shaped postmentum. Labial palpi with three palpomeres, palpomere 2 usually longest. Maxillae with long galea; lacinia smaller, sometimes reduced to limited field of pale short setae. Cardo very small, well-sclerotized, movable, stipes flat, with narrow bent inner margin. Maxillary palpi with four palpomeres, palpomeres 1 and 3 always much shorter than palpomeres 2 and 4. Apical palpomeres distally flattened. Antennae with 11 antennomeres, slightly to strongly flattened, antennomere 1 pear-shaped, robust, antennomere 2
very small, antennomeres 3–10 parallel-sided to acutely serrate in both sexes or flabellate in male and serrate in female, antennomere 11 elliptic; antennomeres 3–11 covered with dense, short pubescence.

Pronotum flat, with pronotal carinae (Figs 4C–T); Diatrichalus, Lobatang, Flabellotrichalus, Trichalus, and Microtrichalus with median lanceolate areola, Eniclases with two divergent longitudinal carinae (Fig. 4L), and Schizotrichalus with three areolae present within the area limited by longitudinal carinae (Fig. 4K). Median areola, if present, either connected with frontal margin by carina or attached directly to frontal and posterior pronotal margins, length of connecting carina variable; sometimes vestigial postero-lateral carinae present close to lateral margins (Figs 4C–T). Pronotal surface roughly punctured at frontal and lateral margins; pronotal pubescence usually short, sparse in most species, denser at lateral margins or very long and dense in some Flabellotrichalus (Figs 4O–P). Prothoracic pleura concave, with strongly elevated margins, similarly structured as pronotal surface. Prothoracic coxal cavities open. Mesosternum transverse, narrow, bridge-like. Scutellum small, apex shallowly emarginate. Metathorax long, robust, metasternum broad and long, with incomplete midline in distal part.

Elytra flat, parallel-sided to slightly widened backwards, each elytron with nine longitudinal costae at base; four costae robust, called primary costae, intermediate secondary costae weak, sometimes irregular. Primary costa 1 robust only in humeral quarter of elytron, then much weaker, similar to secondary costae; secondary costae between suture and primary costa 1 and between primary costae 1 and 2 missing except humeral quarter of elytron (Figs 3A, D–E, L); seldom secondary costae absent (some Diatrichalus; Fig. 2D).

Abdomen flat, free, with eight visible sternites in male and seven in female. Shape of male terminal sternites variable, affected by shape of phallus. Subapical male abdominal sternite
more or less emarginate at hind margin. Last visible tergite long, spoon-like, often with small
sclerotized tergite attached to inner surface, this tergite sometimes membranous, undetectable.
Female terminal abdominal segments variable in shape and most species with short spiculum
gastrale (Figs 6C–D, I–J, L–M, R).

Male genitalia variable in shape (Figs 5A–P). Phallobase circular, subtle, with more or
less extensive membrane, membrane soft to lightly sclerotized. Parameres absent, phallus mostly
slender, with well-sclerotized or partly membranous apical part, open ventrally with exposed
internal sac. Internal sac membranous to sclerotized, with apical complex sclerite or with pair of
slender sickle-like thorns at base.

Ovipositor mostly with long, slender valvifers (Figs 6A, H, K, O–P), sometimes valvifers
connected at their bases by membrane, which can be sclerotized in high degree; seldom valvifers
basally fused with coxites (Fig. 6E). Valvifers robust, connected in basal third in some Trichalus.
Vagina slender, paired glands inserted laterally (Fig. 6B) or dorsally (Fig. 6Q). Bases of
glandular ducts slender, seldom robust (Trichalus), but regularly more sclerotized than terminal
gland, flat unpaired gland in terminal part of vagina, lateral pockets and slender unpaired basal
gland in Microtrichalus (Fig. 6H). Spermatheca long, and slender (Fig. 6B), lemon-shaped, with
spirally coiled spermaduct; y-shaped gland attached to apex of spermatheca (Fig. 6K).

**Diatrichalus Kleine, 1926**

(Figs 2A–E, 4C–E, 5A–C, 6A–D)

*Diatrichalus* Kleine, 1926: 167.
Type species—D. xylobanoides Kleine, 1926, by original designation.

= Mimotrichalus Pic, 1930: 92, hors texte; Bocak, 1998a: 182.

Type species—M. tenimberensis Pic, 1930, by monotypy.

Diagnosis—Pronotum with median, often wide areola, lateral carinae absent or very obtuse (Figs 4C–E), antennae of both sexes more or less acutely serrate to shortly flabellate (Fig. 2C), phallus stout, apical part projected, internal sac more or less sclerotized (Figs 5A–C), vaginal glands inserted laterally, valvifers free, slender, spermatheca long, slim (Figs 6A–B), tarsal claws simple.

Remark—Kleine (1926) restricted Diatrichalus to species with four elytral costae, as in D. xylobanoides (Fig. 2D), and Pic described Mimotrichalus as having additionally obtuse, irregular and commonly interrupted secondary costae. The current concept of Diatrichalus is wide and includes all species with four and nine costae and their intermediate forms (Figs 1A, 2D–E; Bocak, 2001). Our molecular dataset contained only a single species without secondary elytral costae, D. xylobanoides, which is a sister species to other Diatrichalus, included in the analyses. The current results support two clades which correspond with earlier concepts of Diatrichalus and Mimotrichalus, but Bocak (2001) showed that other species without secondary costae have diverse genitalia, and we suppose that if these are included in future phylogenetic analyses they will not form a monophylum. Additionally, there are multiple species with gradual reduction of secondary costae and they can only be arbitrarily assigned to their respective groups. Therefore, we propose to keep Mimotrichalus in the synonymy of Diatrichalus. Although the antennae have
never long lamellae, they are sometimes so acutely serrate that Kleine (1933b) classified *D. salomonensis* (Kleine, 1933b) in *Flabellotrichalus* (Bocak, 2001).

**Lobatang** Bocak, 1998a

(Figs 2F–I, 4F–J, 5D–E, G–I, 6E–G)

*Lobatang* Bocak, 1998a: 190.

**Type species**—*Lobatang papuensis* Bocak, 1998a.

**Diagnosis**—Antennomeres 3–10 parallel-sided to serrate (Figs 2H–I), pronotum with median lanceolate areola (Figs 4F–J), male genitalia variable in shape, always with sclerotized base of internal sac (Figs 5G–I) or whole internal sac sclerotized and long (Figs 5D–E), tarsal claws split (Fig. 2G)

**Remark**—The clade *Leptotrichalus* + *Lobatang* was based on the shape of valvifers (Bocak, 1998a; Bocak, 2002), but the molecular phylogeny indicates the distant position of these genera (Fig. 1A, Sklenarova, Kubecek & Bocak, 2014).

**Lobatang s. str.**

**Type species**—*Lobatang papuensis* Bocak, 1998a.
Diagnosis—The nominotypical subgenus differs from Spinotrichalus only in the absence of femoral and tibial thorns in hind legs.

Subgenus Spinotrichalus Kazantsev, 2010, stat. nov.

Spinotrichalus Kazantsev, 2010: 93.

Type species—Spinotrichalus telnovi Kazantsev, 2010, by original designation.

Diagnosis—As the nominotypical subgenus, but hind femora and tibiae with small thorns.

Remark—Kazantsev (2010) described Spinotrichalus, which shares very similarly shaped genitalia and split claws with Lobatang. Besides the body shape and coloration, the type species of Spinotrichalus and Lobatang differ only in the presence of femoral and tibial thorns. This character is the autapomorphy of S. telnovi and Spinotrichalus may be treated as a synonym, if its position renders Lobatang paraphyletic. As the type species of both genera are unavailable for DNA analysis, we prefer to keep Spinotrichalus as a valid name till more data are available. Based on highly similar male genitalia (Figs 5D–E; Kazantsev, 2010), we lower its rank to a subgenus of Lobatang Bocak, 1998a. Consequently, the new combination Lobatang (Spinotrichalus) telnovi (Kazantsev, 2010) is proposed.

Eniclases Waterhouse, 1879

(Figs 2Q–U, 4L, 5M, 6P–R)
**Eniclases** Waterhouse, 1879: 66.

**Type species**—*Lycus* (genus 35) *luteolus* Waterhouse, 1878, by original designation.

= *Trichalolus* Pic, 1923: 36, hors texte; Bocak & Bocakova 1991: 206.

**Type species**—*T. apertus* Pic, 1923, by monotypy.

**Diagnosis**—Pronotum with two longitudinal divergent carinae dividing pronotum in three fields (Fig. 4L), phallus very slender with pigmented dorsal keel, internal sac without thorns; whole internal sac membranous (Fig. 5M); lateral vaginal glands dorsally attached (as in Fig. 6Q).

**Remark**—The *Eniclases* male antennae are highly variable in shape and several species have acutely serrate to flabellate antennae (Figs 2R–U; Bocak & Bocakova, 1991; Bocek & Bocak, 2016). Only one of these species was included in the molecular analysis and it was recovered as a sister to its congeners (Fig. 1A). Other morphological characters and molecular phylogeny indicate that the species with similar antennae are not closely related (Bocek & Bocak, 2016; Bocak & Bocakova, 1991). Therefore, we do not consider this character to be valuable in the delimitation of a genus or subgenus in this clade.

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**Schizotrichalus** Kleine, 1926

(Fig. 4K)

*Schizotrichalus* Kleine, 1926: 167.
Type species—*T. nigrescens* Waterhouse, 1879, by original designation.

**Diagnosis**—Pronotum with five areolae (Fig. 4K), phallus with pigmented dorsal keel, internal sac without thorns; vaginal lateral glands dorsally attached.

**Remark**—*Schizotrichalus* was unavailable for molecular analyses and was inferred as a genus closely related to *Eniclases* in the morphology-based phylogeny (Figs 1B–C; Bocak, 1998a; Bocak, 2002).

*Flabellotrichalus* Pic, 1921b

(Figs 2K–P, 3H–M, 4M–P, 5N–P, 6K–M)

*Flabellotrichalus* Pic, 1921b: 9, hors texte.

**Type species**—*F. notatithorax* Pic, 1921, subsequent designation, Kleine (1936).

= *Stereotrichalus* Kleine, 1926: 183; Kleine, 1930: 330.

**Type species**—*S. evidens* Kleine, 1926, by monotypy.

= *Villosotrichalus* Pic, 1921b: 9, hors texte; Bocak 1998a: 183.

**Type species**—*V. reductus* Pic, 1921b, by monotypy.

**Diagnosis**—Male antennae flabellate (Figs 2M–N) or seldom serrate (Fig. 3K), pronotum with single longitudinal median areola, frontal and lateral margins of pronotum often with dense short to very long pubescence (Figs 4M–P), phallus very slender, internal sac without thorns; whole
internal sac membranous with y-shaped base (Figs 5N–P); lateral vaginal glands attached dorsally.

**Remark**—The molecular phylogeny recovered a species with dense pronotal pubescence in the terminal position (Fig. 1A) which supports the earlier synonymization of *Villosotrichalus* to *Flabellotrichalus* (Bocak, 1998a).

**Subgenus Flabellotrichalus Pic, 1921b**

**Diagnosis**—All diagnostic characters as in the whole genus, but the male antennae are always flabellate (Figs 2M–N).

**Classification and distribution**—*Flabellotrichalus* occur in Australia, New Guinea, and the Moluccas. Nine Australian and New Guinean species were included in current analyses, but none was identified to the species level due to chaotic alpha-taxonomy (Fig. 1). The genus has never been revised and all 15 formally described species are known only from original descriptions. Two species with dense pronotal pubescence were classified originally as *Villosotrichalus* and this genus was synonymized with *Flabellotrichalus* (Bocak, 1998). The species similar to the typical *Villosotrichalus* were inferred in the terminal position within *Flabellotrichalus* in current analyses (Fig. 1A).

**Subgenus Maibrius subgen. nov.**

LSID: urn:lsid:zoobank.org:act:0A2E45FB-72DB-49E7-BD7C-BC792072B106 (Figs 3H–M, 4M, 5N)
Type species—*Flabellotrichalus (Maibrius) horaki* sp. nov.

**Diagnosis**—Male antennae serrate (Fig. 3K), pronotum with single longitudinal median areola, frontal and lateral margins of pronotum with dense short pubescence (Fig. 4M), phallus slender, apically membranous; internal sac without thorns, membranous, with y-shaped base (Fig. 5N); lateral vaginal glands attached dorsally. *Maibrius* subgen. nov. differs from the nominotypical subgenus in the serrate male antennae (Fig. 3K) and shorter, relatively robust phallus (Fig. 5N).

**Remark**—The molecular phylogeny identified *F. (Maibrius) horaki* sp. nov. as a genetically distant sister-lineage to other *Flabellotrichalus* (Fig. 1A). This species cannot be identified as a close relative of *Flabellotrichalus* without dissection of male genitalia or DNA sequencing. The general appearance and morphology of antennae resemble *Trichalus* or *Microtrichalus* and only the male genitalia indicate relationships to *Flabellotrichalus*. This conservative taxonomy keeps *Flabellotrichalus* s. str. morphologically well-defined and reflects the genetic and phenotypic divergence of *F. (Maibrius) horaki* sp. nov. Female remains unknown.

**Etymology**—The subgeneric name is derived from the name 'Maibri', a village in the Arfak mountains where the type species was collected. The genus name is the noun of masculine gender.

*Flabellotrichalus (Maibrius) horaki* sp. nov.

LSID: urn:lsid:zoobank.org:act:86069ACA-BC85-4865-847B-2EB421DC3BC3

(Figs 3H–M, 4M, 5N)
Type material—Holotype. Male, "New Guinea, West Papua prov., Arfak Mts., Maibri vill., 2015, local coll." (GenBank Voucher Number UPOL BM0082; deposited in the collection of the Palacký University in Olomouc, Czech Republic, LMBC).

Diagnosis—Flabellotrichalus (Maibrius) horaki sp. nov. differs from all known Flabellotrichalus in the serrate male antennae (Fig. 3K). Its phallus is slightly more robust than in other Flabellotrichalus (Figs 5N–P). F. (M.) horaki sp. nov. is currently a single trichaline species with white colored humeri.

Description—Male. Body 7.8 mm long, dorso-ventrally flattened, relatively slender, dark brown to black, only basal three fifths of elytra pale yellow to white colored (Fig. 3H). Head small, eyes small-sized, hemispherically prominent, eye diameter 0.64 times interocular distance; antennae serrate (Fig. 3K). Pronotum 1.24 wider than long at midline, trapezoidal, widest at base, anterior angles almost rectangular, well-marked, lateral margins slightly concave, posterior angles sharply prominent; areola wide, connected with anterior margin by short carina, lateral carinae completely absent, disc of pronotum roughly sculptured at frontal and lateral margins, covered with dense, short pubescence (Fig. 4M). Elytra with three primary and four secondary costae in middle part of elytron, elytra 3.7 times longer than width at humeri, rectangular cells dense, irregular, costae covered with dense pubescence (Figs 3L–M). Phallus relatively short, sclerotized and pigmented in basal two fifths, apical part membranous, with a cup-shaped apex held by pair of pigmented keels; internal sac membranous, with y-shaped, pigmented base,
without any thorns (Fig. 5N). Legs flattened, densely pubescent, tarsi wide (Fig. 3I), claws simple (Fig. 3J). Female unknown.

Measurements—Body length 7.8 mm, pronotum length 0.91 mm, pronotum width 1.13 mm, width at humeri 1.75 mm, length of elytron 6.55 mm, eye diameter 0.38 mm, eye distance 0.59 mm, length of phallus 1.14 mm.

Etymology—The specific name is a patronym in honor of Jan Horak, a Czech specialist in Mordellidae.

Distribution—New Guinea, Arfak mountains.

Trichalus Waterhouse, 1877
(Figs 3A–C, 4Q–R, 5F, 6N–O)

Trichalus Waterhouse, 1877: 82.

Type species—T. flavopictus Waterhouse, 1877, subsequent designation, Waterhouse 1878: 103. =Xantheros Fairmaire, 1877: 167; Bourgeois 1891: 347.

Type species—Xantheros ochreatus Fairmaire, 1877.

Diagnosis—Antennae serrate in both sexes, pronotum with single longitudinal median areola, apical part of phallus commonly well-sclerotized (Figs 5F, J–K), internal sac with two thorns;
lateral vaginal glands attached dorsally, valvifers free or connected basally (Fig. 6N) or sub-
basally, forming H-shaped structure in some species, tarsal claws simple, vaginal lateral pockets
and unpaired basal gland absent.

Remark—The type of *X. ochreatus*, the type species of *Xantheros*, was very probably destroyed
(Bocak, 1998a). The original publication cites "Sydney" as the type locality and although we had
at our disposal the extensive collection of Australian trichaline net-winged beetles from ANIC
(Canberra), we found no specimen whose morphology agrees to the original description and
originates from southern New South Wales. Similar species occur only in northern New South
Wales and in Queensland. As we are not able to designate the neotype, we keep *Xantheros* in
synonymy of *Trichalus* (Kleine, 1933a; Bocak, 1998a; Bocak, 2002).

*Microtrichalus* Pic, 1921b

(Figs 3D–G, 4S–T, 5L, 6H–J)

*Microtrichalus* Pic, 1921b: 9 (hors texte).

Type species—*M. singularis* Pic, 1921b, by monotypy.

= *Falsoenylus* Pic, 1926: 29, hors texte; Bocak, 1998a: 184.

Type species—*F. basipennis* Pic, 1926, by monotypy.

Diagnosis—Antennae weakly serrate in both sexes, pronotum with single longitudinal median
areola, apical part of phallus weakly sclerotized, internal sac with two thorns, lateral vaginal
glands attached dorsally, vagina with two lateral pockets situated in middle of vaginal length and very slim, long, unpaired gland between valvifers (Fig. 6H), valvifers slender, sometimes fused basally.

Key to the genera and subgenera of the trichaline clade

1. Tarsal claws split (Fig. 2G), *Lobatang* Bocak, 1998a ................................. 2
- Tarsal claws simple (Fig. 3J) ................................................................. 3

2. Male hind femora and tibiae without any thorn ........... *Lobatang* (*Lobatang* s. str.)
- Male hind femora and tibiae with small thorns ... *Lobatang* (*Spinotrichalus* Kazantsev, 2010)

3. Apical margins of maxillary and labial palpomeres with sensillae, apical palpomeres securoform, apical part of phallus robust, internal sac complex, partly sclerotized (Figs 5A–C); vaginal glands inserted laterally (Fig. 6B), basal part of spermaduct wide, spermatheca long, slender ................................................. *Diatrichalus* Kleine, 1926
- Apical margins of maxillary and labial palpomeres without sensillae, apical palpomeres variable shaped, apical part of phallus slender, internal sac membranous or with a pair of sickle shaped thorns (Figs 5F, J–P); vaginal glands inserted dorsally (Fig. 6Q), basal part of spermaduct slender, spermatheca bulbous (Figs 6H, K, O–P) ............................................. 4

4. Pronotum with five areolae or with two anteriorly divergent longitudinal carinae (Figs 4K–L), phallus with single pigmented dorsal keel (Fig. 5M) .................................................. 5
- Pronotum with single lanceolate longitudinal areola attached to frontal and basal margin of pronotum at a single point (Figs 4M–T), pigmented dorsal keel absent in most species (Figs 5F, N–P, but compare with Fig. 5J) ................................................................. 6

5. Pronotum with five areolae (Fig. 4K)............................... Schizotrichalus Kleine, 1926

- Pronotum with two divergent longitudinal carinae (Fig. 4L) ...Eniclases Waterhouse, 1879

6. Male antennae flabellate ............................... Flabeliotrichalus (Flabeliotrichalus s. str.)

- Male antennae serrate or antennomeres parallel-sided ........................................ 7

7. Internal sac membranous, without thorns, with pigmented y-shaped basal part (Maibrius females are unknown) ......................... Flabeliotrichalus (Maibrius subgen. nov.)

- Internals sac with two thorns ........................................................................ 8

8. Vagina with two lateral pockets in middle part and with unpaired slim and long basal gland (Fig. 6H), valvifers slender, usually free, sometimes connected basally ....

................................................................. Microtrichalus Pic, 1921b

- Vagina without lateral pockets and unpaired gland, valvifers often robust, connected basally or sub-basally (Fig. 6N) ......................................................... Trichalus Waterhouse, 1877

DISCUSSION

We present the first densely sampled molecular phylogeny and separate morphological analyses of all genera which were traditionally placed in the trichaline clade (Figs 1A–C). The terminal position of the trichaline clade in Metriorrhynchina has already been demonstrated in the molecular analyses of Metriorrhynchini, and trichaline genera lost their formal rank in classification (Sklenarova, Kubecek & Bocak, 2014). Our analyses of the current more extensive
dataset confirm the terminal placement of the trichaline clade within Metriorrhynchina (Fig. 1A).

Metriorrhynchina are well-supported as a monophylum in all previous analyses (Bocak et al., 2008; Sklenarova, Chesters & Bocak, 2013; Sklenarova, Kubecek & Bocak, 2014), therefore, Cautirina were used as an outgroups and Metriorrhynchina, here consisting of trichaline terminals and 17 non-trichaline terminals, were forced by a single outgroup to be monophyletic. Such dataset is fully capable to test if trichaline genera are a sister lineage of other Metiorrhynchina or a terminal lineage within this subtribe as in all earlier analyses (Bocak et al., 2008; Sklenarova, Chesters & Bocak, 2013; Sklenarova, Kubecek & Bocak, 2014).

The (Leptotrichalus, (Synchonnus, Wakarumbia) clade is a sister lineage to trichaline genera in the molecular analyses although with ambiguous support (BS 23%; PP 0.98; Fig. 1A). Leptotrichalus and Synchonnus were earlier placed in the trichaline clade, but Wakarumbia differs substantially in the presence of unique five-areolae in the pronotum, full-length elytral costae, and the morphology of genitalia (Bocak, 2002). Therefore, an expansion of the trichaline clade would be impractical.

Four trichaline genera are included in our molecular analyses for the first time and now six of seven genera are represented in the DNA data set: Diatrichalus and Lobatang are members of the trichaline clade as defined here and they are deeply rooted lineages in close relationships to the earlier narrowly defined trichaline clade (Bocak, 1998a; Bocak, 2002). Eniclases is a sister to the clade ((Flabellotrichalus, Trichalus), Microtrichalus) (Fig. 1A).

The morphological analyses indicate different relationships. They suggest a topology which contains the clades (Synchonnus + Diatrichalus) and (Leptotrichalus + Lobatang) in contrast with molecular analyses (Fig. 1A; Sklenarova, Kubecek & Bocak, 2014). Such relationships are supported by the similar shape of pronotal carinae in trichaline genera,
Synchonnus, and Leptotrichalus and the shortened elytral costa 1 in all genera except Synchonnus. Due to the limited number of other informative phenotypic characters, the homology of these character states cannot be falsified in the current morphological analyses (Figs 1A–C). The single lanceolate areola and the shortened elytral costa 1 were present in the most recent common ancestor of the trichaline clade (Fig. 1A), but similar arrangements of pronotal carinae and elytral costae have been found in several unrelated taxa, e.g. the shortened costa in Kassemia and the similar pronotum in some Cautires (Bocak, 2002; Sklenarova, Kubecek & Bocak, 2014). The high plasticity of pronotal carinae is additionally indicated by a hypothesized reversal in Eniclases and Schizotrichalus (Fig. 1A). Therefore, we consider the phylogenetic signal provided by these external characters to be unreliable and male and female genitalia should be studied to verify recovered relationships.

The molecular topology regularly indicates a deep position of Diatrichalus and Lobatang, but we have not been able to find any phenotypic character which supports their relationships with other trichaline genera, except for the above mentioned lanceolate pronotal areola and the shortened elytral costa 1. Conversely, the monophyly of the restricted trichaline clade i.e., Eniclases + Flabellotrichalus + Trichalus + Microtrichalus is supported by unique, dorsally attached vaginal glands (Fig. 6Q) in the morphological analysis, but their relationships, although simultaneously recovered by molecular analyses, had only a low statistical support (BS 74%, PP 0.48). The internal relationships within this clade were better resolved in the DNA-based topology, which indicates the deeply rooted position for Eniclases with respect to other genera of the restricted trichaline clade (Figs 1A–C). Schizotrichalus was not available for the molecular analyses and its close relationships with Eniclases are based on morphology (Figs 1B–C). Trichalus and Flabellotrichalus form a clade with a low support in molecular analyses (BS 64%,
0.92 PP) and their sister position has never been inferred from morphology (Figs 1A–C). Their relationship is supported by similar pigmented keels at the apex of the phallus in some species, but no other character (Figs 5F, N–P). In contrast, Microtrichalus and Trichalus share sickle-shaped thorns in the basal part of their internal sac (Figs 5F, J–L). Concerning the low bootstrap support, these relationships need further data to be validated. Additionally, Trichalus is not assuredly monophyletic (Fig. 1A) and may split into several clades if more taxa are included in future analyses. The absence of a synapomorphy which supports Trichalus also complicates identification. Some species cannot be reliably identified as Trichalus without information on female genitalia. Microtrichalus has unique pockets in the middle part of the vagina and an unpaired basal vaginal gland (Fig. 6H). Both structures are absent in Trichalus.

For a long time, the phenotypic diagnoses of most trichaline genera were ambiguous. Trichalus served as a basket where most species were placed, and numerous species were later transferred to Diatrichalus, Lobatang, and Microtrichalus (Kleine, 1926; Bocak, 1998a; Bocak, 2000; Bocak, 2001). Now, the generic limits are much better defined than in the original descriptions and concepts applied by M. Pic and R. Kleine (e.g., Kleine, 1926; Pic, 1921b; Pic, 1923; Pic, 1926; Pic, 1930), but even with these revised morphological diagnoses, the evaluation of external phenotypic characters is generally insufficient and dissection of genitalia is needed for reliable generic placement.

Some phenotypic characters are affected by the natural and sexual selection and they can rapidly evolve (Bocek & Bocak, 2016; Frazee & Masly, 2015). Hence, they may provide a misleading phylogenetic signal. Below, we discuss some characters with regard to their diagnostic value and congruence with molecular phylogeny.
The shape of male antennae

Filiform, serrate and flabellate male antennae have been used as diagnostic characters, but their value is questioned by variable morphology in related species (e.g., Cautires; Sklenarova, Kubecek & Bocak, 2014). A high variability in the shape of male antennae was observed in Lobatang (Figs 2H–I) and Eniclases (Figs 2R–U); other genera, such as Microtrichalus, have quite uniform antennae (Figs 3F–G). The present study supports the earlier finding that the serrate and flabellate antennae can evolve repeatedly. Diatrichalus salomonensis (Kleine, 1933b) and some species of Eniclases (Figs 1A, 2R–U) have very acutely serrate to flabellate antennae, unlike the congeneric species. Flabellotrichalus s. str. is well-delimited by the flabellate antennae. We identified a single species, F. (Maibrius) horaki sp. nov., which differs in the serrate male antennae and is also genetically distant from other Flabellotrichalus. It was recovered as a sister to the extensive clade of Flabellotrichalus. The antennae are an olfactory organ and selection for a large surface can be responsible for rapid morphological evolution in some terminal lineages.

The shape of the pronotum and pronotal carinae

The shape of the pronotum is commonly used for morphological identification of net-winged beetle genera and some trichaline species can be assigned to a genus using pronotal morphology. The densely pubescent pronotal margins are characteristic for some but not all Flabellotrichalus (Figs 4O–P). Transverse pronota with a large median areola and uniquely shaped lateral margins are characteristic for some Diatrichalus (Fig. 4D), but these traits are inconspicuous in some congeneric species (Figs 4C, E). Similarly, the flat pronotum with the characteristic shape of the frontal margin and almost rectangular anterior angles is typical of some, but not all, Lobatang.
(Figs 4F–J). The shape of the pronotum is affected by the general appearance (e.g. Figs 3D–E).

Net-winged beetles are often associated with mimicry rings and substantially different body sizes, shapes and colorations were identified in recently split sister species, e.g. in *Eniclases* and *Synchonnus* (Bocek & Bocak, 2016; Kusy, Sklenarova & Bocak, 2017). Therefore, these characters, although sometimes useful for quick identification, are generally unreliable, as can be demonstrated by similar pronota in several species of *Lobatang* (Fig. 4F), *Flabellotrichalus* (Fig. 4M), *Trichalus* (Fig. 4R) and *Microtrichalus* (Figs 4S–T).

An earlier study has already demonstrated that the unique arrangement of seven pronotal areoles is an ancestral state in Metriorrhynchina (Fig. 4A; Sklenarova, Kubecek & Bocak, 2014). Although numerous species have the full number of seven areoles (Fig. 4A, *Cautires*, *Metriorrhynchus* Gemminger et Harold, 1869, *Porrostoma* Castelnau, 1838, and others) or their reduction is so limited that the original pattern can easily be recognized (some *Cautires*; Jiruskova, Motyka & Bocak, 2016), there are numerous genera with considerably simplified pronotal carinae. When these reduced patterns are considered to be homologous, they lead to a false phylogenetic placement and classification, as occurred when the monophyly was hypothesized and the genus-rank given to *Bulenides*, now placed in *Cautires* (Fig. 4B; Dudkova & Bocak, 2010) and also when an independent position and high rank were proposed for trichaline genera (Kleine, 1928; Kleine, 1933a; Bocak, 1998a; Bocak, 2002). The earlier defined family-rank taxon for trichaline genera, including *Leptotrichalus* (Kleine, 1928; Kleine, 1933a), was defined by a single areola in most genera: the wide areola in *Diatrichalus* (Figs 4C–D), the very slender areola in *Leptotrichalus*, and a single narrow areola in *Microtrichalus* and *Trichalus* (Figs 4Q–T). A similar single areola has been identified in distantly related net-winged beetles, such as Afrotropical Slipinskiini, which had been considered congeneric with the Australian
metriorrhynchine genus *Stadenus* Waterhouse, 1879 (Kleine, 1933a). Similarly, the arrangement of pronotal carinae in some *Synchonnus*, a genus related to *Falsolucidota* Pic, 1921a and *Wakarumbia*, provided a misleading signal for the placement of an earlier valid *Enylus* into close relationships with the trichaline genera (Figs 1B–C; Bocak, 2002; Kusy, Sklenarova & Bocak, 2017). The complex structures are considered to be better indicators of relationships, but in the case of *Eniclases* and *Schizotrichalus*, unique characteristic pronotal patterns, apparently resembling the complex ancestral arrangement (Figs 4K–L), were recovered in the terminal lineage of the trichaline clade in which all close relatives lost the fronto-lateral pronotal carinae (Figs 1A–C, 4A–T). Our results suggest that variable arrangements of pronotal carinae can evolve through reductions in unrelated lineages and, surprisingly, also through the re-appearance of earlier lost structures. These facts indicate the low explanatory power of this character for phylogenetic inference and generic classification (Fig. 1A).

**Elytral costae**

Elytral costae were traditionally considered to be reliable characters for generic phenotypic diagnoses in net-winged beetles (e.g., Pic, 1923; Pic, 1930; Kleine, 1926). The concept of *Diatrichalus* was originally based on the presence of four longitudinal elytral costae, in contrast with nine costae in other trichaline genera (Kleine, 1926; Pic, 1930). The generic limits of this genus were redefined using genitalia, and the loss of secondary costae is assumed in several unrelated species (Bocak, 2001). The present DNA dataset contains only a single *Diatrichalus* with absent secondary costae (Fig. 1A). A similar loss of secondary costae was identified in some Afrotropical *Cautires* (Sklenarova, Kubecek & Bocak, 2014) and in an undescribed species of *Schizotrichalus*. Net-winged beetles are soft-bodied and therefore the elytral costae apparently
The arrangement of the costae depends on body size and shape. The costae are commonly reduced in species with very slender or small bodies such as in Dilophotes (Lycidae: Dilophotini; Bocak & Bocakova, 2008).

Male genitalia

The limits of most genera are currently based on the morphology of genitalia which is more reliable than external phenotypic characters. Diatrichalus has an exposed and complex internal sac (Figs 5A–C), Lobatang has a rod-shaped basal part of the internal sac (Figs 5D–E, G–I), Eniclases has the characteristic pigmented dorsal keel in the phallus (Fig. 5M) and Flabellotrichalus has the membranous, pigmented internal sac with a y-shaped basal part (Figs 5N–P). These characters were constant in respective genera and enable reliable identification, but they provide no information about deep relationships. Two sickle-like thorns at the base of the internal sac are present in Trichalus and Microtrichalus (Figs 1B–C, 5F, J–K) and the preferred molecular phylogenetic hypothesis indicates their independent origin although with modest support (Fig. 1A). The presence of thorns in the internal sac is the principal character supporting their relationships in morphology-based analyses (Figs 1B–C). Similar thorns are known in some Synchonnus (Kusy, Sklenarova & Bocak, 2017; Kusy, 2017) and various members of distantly related genera of Metriorrhynchini, e.g. Cautires (Jiruskova, Motyka & Bocak, 2016).

Female genitalia

The female genitalia provide additional information consistent with the molecular phylogenetic analyses. The strongest phenotypic character supporting the relationships among some trichaline genera are the dorsally attached lateral glands which define the clade (Eniclases +
Schizotrichalus)((Trichalus, Flabellotrichalus) Microtrichalus)). Other characters define the limits of genera, but do not contribute to the definition of more extensive clades. Diatrichalus has a characteristically long spermatheca (Fig. 6B) and all Microtrichalus have a pair of pockets in the middle part of the vagina and a slim unpaired ventral gland at the base of the vagina (Fig. 6H). With well-defined Microtrichalus, the genus Trichalus is left without any synapomorphy and its monophyly and relationships can be recovered only by molecular analyses (Fig. 1A).

CONCLUSION

The phylogeny of the trichaline clade is separately recovered from morphology and molecular data, but neither analysis robustly solves all relationships. The deepest nodes in our phylogenies remain weakly supported by morphology, and only molecular analyses provide a stable topology with relatively high support for critical nodes (Figs 1A–C). The terminal clade of Eniclases, Schizotrichalus, Trichalus, Flabellotrichalus and Microtrichalus is unambiguously supported by the unique morphology of vaginal glands, but only weakly so by the molecular data. The limits of all genera are congruently supported by morphological synapomorphies and molecular phylogenetic analyses, but their robustness differs. Diatrichalus is well-delimited by several morphological characters but this clade receives only a low statistical support in our molecular analyses. The least supported genus-rank node is Trichalus (Fig. 1A), which is morphologically defined only by the absence of some phenotypic characters when compared with Flabellotrichalus and Microtrichalus. Similarly, this node obtains low statistical support in the molecular analyses (Fig. 1A).

The phenotypic characters can be misleading when similar structures evolve repeatedly or are so simplified that we are unable to identify homologues. Unexpectedly, the anterolateral
pronotal carinae, lost in other trichaline genera, re-evolved in *Eniclases* and *Schizotrichalus*.

Almost all trichaline species are unpalatable and aposematically colored, and due to their memberships in mimetic rings, the unrelated species can have similar body sizes and shapes (Bocak & Yagi, 2010). These homoplasious phenotypes attest to the strength of natural selection (Bocek & Bocak, 2016) and the traditionally used morphological characters, such as pronotal carinae, elytral costae and the shape of pronotum, display high intra-generic variability which might be caused by an independent origin of similar traits due to selective pressure. Further, the molecular phylogeny suggests repeated origins of flabellate antennae, which play a role in sexual communication. To summarize, the evaluation of both molecular and morphological signals is very valuable in net-winged beetles and their congruence should be evaluated whenever possible.

Future studies can refine the trichaline classification, but a large part of the trichaline diversity has already been included in current analyses and we believe that the substantial rearrangements are improbable.

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**Table 1** (on next page)

List of taxa

The list of terminals in the molecular phylogenetic analyses, with voucher and GenBank accession numbers.
| Genus, species | Geographic origin | voucher | mitochondrial DNA fragments |
|----------------|-------------------|---------|-----------------------------|
| **Outgroup**   |                   |         |                             |
| 4 Cautires sp. | Malaysia, Pahang, Tanah Rata | 000088  | KC538654 KC538268 KC538460 |
| 5 Cautires sp. | Sumatra, Jambi, Gn Tujuh | 00206  | KC538676 KC538292 KC538483 |
| 6 Cautires sp. | Borneo, Tenggah, Muara Teweh | 00262  | KC538685 KC538300 KC538491 |
| 7 Cautires sp. | Borneo, Selatan, Loksado | 00342  | KC538695 KC538310 KC538501 |
| 8 Porrostoma sp. | Australia, Queensland, Lamington | A00035  | KC538725 KC538341 KC538532 |
| 9 Porrostoma sp. | Australia, Queensland, Lamington | A00042  | KC538348 KC538539 |
| 10 Lepiotrichalus sp. | Java, Timor, Sodong | A0451  | MF288196 MF288334 MF288457 |
| 11 Metriorrhynchina sp. | Sulawesi, Tenggah, Sappeb | 00001  | KC538629 DQ144660 DQ144686 |
| 12 M. lineatus | Sumatra, South, Danau Ranau | 00009  | KC538628 DQ904297 DQ904259 |
| 13 M. lobatus | Sulawesi, Tenggah, Pendolo | 00017  | KC538630 DQ144662 DQ144688 |
| 14 M. sericans | Laos, Houa Phan, Phou Pan | A00381  | MF288191 MF288329 MF288452 |
| 15 Metriorrhynchina sp. | Australia, Queensland, Lamington | A00043  | KC538732 KC538349 KC538540 |
| 16 Metriorrhynchina sp. | Malaysia, Johor, Kota Tinggi | A00049  | KC538736 KC538354 KC538545 |
| 17 Metriorrhynchina sp. | Australia, Queensland, Bunya Mts. | A00311  | MF288174 MF288312 MF288437 |
| 18 Metriorrhynchina sp. | Australia, Queensland, Lamington | A00348  | MF288183 MF288320 MF288445 |
| 19 Metriorrhynchina sp. | New Guinea, Biak, Korim | A00422  | MF288192 MF288330 MF288453 |
| 20 Metriorrhynchina sp. | New Guinea, Papua, Yiwika | BM0104  | MF288227 MF288351 MF288487 |
| 21 Metriorrhynchina sp. | New Guinea, West Papua, Maibri | BM0083  | MF997538 MF997540 MF997542 |
| 22 Metriorrhynchina sp. | New Guinea, Papau, Yiwika | BM0109  | MF997539 MF997541 MF997543 |
| 23 Synchonnus sp. | Australia, Queensland, Lamington | A0039  | KC538729 KC538345 KC538536 |
| 24 Wakarumbia sp. | Sulawesi, Mamasa | MD0155  | KC538809 KC538432 KC538624 |
| **Ingroup** |                   |         |                             |
| 26 Diatrichalus sp. A | Sulawesi, Selatan, Mamasa | JB0774  | - MF288416 - |
| 27 Diatrichalus sp. B | Malaysia, Kelahar, Kp. Raja | JB0829  | - MF288417 - |
| 28 D. xylobanoides | New Guinea, Crater Mt., Haia | A00118  | - MF288291 MF288419 |
| 29 D. dilatatus | New Guinea, Goroka, Gahavisuka | A00133  | MF288151 - MF288544 |
| 30 D. mancus | Australia, Queensland, Pascoe River | A00298  | MF288172 MF288311 MF288436 |
| 31 D. manokwarensis | New Guinea, West Papua, Maibri | BM0079  | MF288216 MF288343 MF288477 |
| 32 D. mindakensis | New Guinea, Morobe, Mindik | A00184  | MF288160 - MF288427 |
| 33 D. robustus | New Guinea, Papua, Elelim | BM0190  | MF288288 MF288412 MF288555 |
| 34 D. robustus | New Guinea, Papua, Elelim | BM0191  | MF288289 MF288413 MF288556 |
| 35 D. simaticollis | New Guinea, Papua, Bokondini | BM0114  | MF288233 MF288357 MF288550 |
| 36 Diatrichalus sp. C | New Guinea, Papua, Yiwika | BM0113  | MF288232 MF288356 MF288492 |
| 37 Diatrichalus sp. D | New Guinea, Papua, Tikapura | BM0127  | MF288245 MF288369 MF288504 |
| 38 Diatrichalus sp. E | New Guinea, Papua, Elelim | BM0159  | MF288267 MF288391 MF288526 |
| 39 Diatrichalus sp. F | New Guinea, Papua, Elelim | BM0192  | MF288290 MF288414 MF288557 |
| 40 Diatrichalus sp. G | Australia, Queensland, Chilvert | A00208  | MF288163 MF288302 MF288546 |
| 41 Diatrichalus sp. H | Australia, Queensland, Chilvert | A00237  | MF288167 MF288306 MF288547 |
| 42 Diatrichalus sp. I | Australia, Queensland, Garradanga | A00308  | MF288173 - MF288548 |
| 43 Diatrichalus sp. J | Australia, Queensland, Garradanga | A00337  | MF288181 - MF288548 |
| 44 Diatrichalus sp. K | New Guinea, Papua, Tikapura | BM0189  | MF288287 MF288411 MF288554 |
| 45 Diatrichalus sp. L | New Guinea, Papua, Giwika | A00131  | MF288150 - |
| 46 Diatrichalus sp. M | New Guinea, Goroka, Gahavisuka | A00156  | MF288154 MF288295 MF288545 |
| 47 Diatrichalus sp. N | New Guinea, Papua, Tikapura | BM0188  | MF288286 MF288410 MF288553 |
| 48 Diatrichalus sp. O | New Guinea, West Papua, Wasior | JB0772  | - MF288415 - |
| 49 D. tenimerensis | Australia, Queensland, Claudie River | A00366  | MF288190 MF288328 MF288549 |
| 50 Eniclases apertus | New Guinea, Papua, Sentani | BM0018  | MF288201 KT265155 MF288462 |
| 51 E. bicolor | New Guinea, Papua, Elelim | BM0045  | MF288204 KT265166 MF288465 |
| 52 E. bokondinensis | New Guinea, Papua, Bokondini | BM0094  | MF288222 KT265153 MF288482 |
| 53 E. branuccii | New Guinea, Papua, Sentani | BM0005  | MF288199 KT265118 MF288460 |
| 54 E. divaricatus | New Guinea, Papua, Sentani | BM0001  | MF288197 KT265092 MF288458 |
| 55 E. divaricatus | New Guinea, Papua, Elelim | BM0057  | MF288207 KT265098 MF288468 |
| 56 E. elelimesis | New Guinea, Papua, Elelim | BM0051  | MF288206 KT265149 MF288467 |
| 57 E. infuscatus | New Guinea, Papua, Elelim | BM0050  | MF288205 KT265169 MF288466 |
| 58 E. niger | New Guinea, Papua, Bokondini | BM0033  | MF288202 KT265111 MF288463 |
| 59 E. pseudoluteolus | New Guinea, West Papua, Maibri | BM0084  | MF288219 KT265171 MF288480 |
| 60 E. similis | New Guinea, Papua, Sentani | BM0003  | MF288198 KT265099 MF288459 |
| 61 Eniclases apertus | New Guinea, Papua, Bokondini | BM0093  | MF288221 KT265163 MF288481 |
| 62 E. tikapurensis | New Guinea, Papua, Yiwika | BM0039  | MF288203 KT265157 MF288464 |
63 E. variabilis New Guinea, Papua, Sentani BM0008 MF288200 KT265122 MF288461
64 Flabellotrichalus sp. A New Guinea, Crater Mt., Haia A00170 MF288157 MF288298 MF288425
65 Flabellotrichalus sp. B New Guinea, Pindiu, Mongi A00180 MF288159 MF288300 MF288426
66 Flabellotrichalus sp. C New Guinea, Papua, Yiwika BM0103 MF288226 MF288350 MF288486
67 Flabellotrichalus sp. C New Guinea, Papua, Yiwika BM0110 MF288230 MF288354 MF288490
68 Flabellotrichalus sp. C New Guinea, Papua, Yiwika BM0111 MF288231 MF288355 MF288491
69 Flabellotrichalus sp. D New Guinea, Pt. Moresby, Kialaki A00149 MF288153 MF288294 MF288422
70 Flabellotrichalus sp. D New Guinea, Papua, Elelim BM0145 MF288256 MF288381 MF288516
71 Flabellotrichalus sp. D New Guinea, Papua, Elelim BM0149 MF288258 MF288382 MF288517
72 Flabellotrichalus sp. D New Guinea, Papua, Elelim BM0150 MF288259 MF288383 MF288518
73 Flabellotrichalus sp. E New Guinea, Crater Mt., Haia A00172 MF288158 MF288299 -
74 Flabellotrichalus sp. F New Guinea, Crater Mt., Haia A00125 MF288149 MF288292 MF288420
75 Flabellotrichalus sp. F New Guinea, Crater Mt., Haia A00162 MF288155 MF288296 MF288423
76 Flabellotrichalus sp. F New Guinea, Crater Mt., Haia A00169 MF288156 MF288297 MF288424
77 Flabellotrichalus sp. G Australia, Queensland, Chilverton A00211 MF288165 MF288304 MF288430
78 Flabellotrichalus sp. H New Guinea, Papua, Yiwika BM0105 MF288228 MF288352 MF288488
79 Flabellotrichalus sp. I New Guinea, Papua, Elelim BM0151 MF288260 MF288384 MF288519
80 F. (Mairruss) horaki New Guinea, West Papua, Mailri BM0082 MF288218 MF288345 MF288479
81 Lobatang sp. A New Guinea, Papua, Sentani BM0162 MF288269 MF288393 MF288528
82 Lobatang sp. A New Guinea, Papua, Sentani BM0168 MF288274 MF288398 MF288533
83 Lobatang sp. B Australia, Queensland, Claudie River A00363 MF288187 MF288325 MF288450
84 Lobatang sp. B Australia, Queensland, Claudie River A00365 MF288189 MF288327 -
85 Lobatang sp. C Molucass, Buru isl., Remaja Mt. BM0071 MF288208 MF288335 MF288469
86 Lobatang sp. C Molucass, Buru isl., Remaja Mt. BM0072 MF288209 MF288336 MF288470
87 Lobatang sp. C Molucass, Buru isl., Remaja Mt. BM0073 MF288210 MF288337 MF288471
88 Lobatang sp. Molucass, Buru isl., Remaja Mt. BM0074 MF288211 MF288338 MF288472
89 Lobatang sp. D New Guinea, West Papua, Mailri BM0075 MF288212 MF288339 MF288473
90 Lobatang sp. D New Guinea, West Papua, Mailri BM0076 MF288213 MF288340 MF288474
91 Lobatang sp. D New Guinea, Papua, Elelim BM0145 MF288254 MF288378 MF288513
92 Lobatang sp. D New Guinea, Papua, Elelim BM0146 MF288255 MF288379 MF288514
93 Lobatang sp. D New Guinea, Papua, Sentani BM0165 MF288271 MF288395 MF288530
94 Lobatang sp. D New Guinea, Papua, Sentani BM0166 MF288272 MF288396 MF288531
95 Microtrichalus sp. A New Guinea, Papua, Sentani BM0175 MF288277 MF288401 MF288551
96 Microtrichalus sp. A New Guinea, Papua, Sentani BM0180 MF288281 MF288405 MF288552
97 Microtrichalus sp. B New Guinea, Papua, Sentani BM0178 MF288279 MF288403 MF288537
98 Microtrichalus sp. B New Guinea, Papua, Sentani BM0179 MF288280 MF288404 MF288538
99 Microtrichalus sp. B Australia, Queensland, Claudie River A00356 - MF288322 MF288447
100 Microtrichalus sp. C Australia, Queensland, Claudie River A00364 MF288188 MF288326 MF288451
101 Microtrichalus sp. D New Guinea, Papua, Elelim BM0158 MF288266 MF288390 MF288525
102 Microtrichalus sp. E New Guinea, Papua, Tikapura BM0134 MF288247 MF288371 MF288506
103 Microtrichalus sp. F New Guinea, Papua, Bokondini BM0117 MF288236 MF288360 MF288495
104 Microtrichalus sp. F New Guinea, Papua, Tikapura BM0135 MF288248 MF288372 MF288507
105 Microtrichalus sp. G New Guinea, Papua, Yiwika BM0102 MF288225 MF288349 MF288485
106 Microtrichalus sp. G New Guinea, Papua, Tikapura BM0126 MF288244 MF288368 MF288503
107 Microtrichalus sp. H New Guinea, West Papua, Mailri BM0077 MF288214 MF288341 MF288475
108 Microtrichalus sp. H New Guinea, West Papua, Mailri BM0085 MF288220 MF288346 -
109 Microtrichalus sp. I New Guinea, Papua, Bokondini BM0122 MF288241 MF288365 MF288500
110 Microtrichalus sp. I New Guinea, Papua, Bokondini BM0123 MF288242 MF288366 MF288501
111 Microtrichalus sp. I New Guinea, Papua, Elelim BM0152 MF288261 MF288385 MF288520
112 Microtrichalus sp. I New Guinea, Papua, Elelim BM0153 MF288262 MF288386 MF288521
113 Microtrichalus sp. J Australia, Queensland, Chilverton A00239 MF288168 MF288307 MF288432
114 Microtrichalus sp. J Australia, Queensland, Chilverton A00243 MF288169 MF288308 MF288433
115 Microtrichalus sp. K New Guinea, Papua, Sentani BM0160 MF288268 MF288392 MF288527
116 Microtrichalus sp. K New Guinea, Papua, Sentani BM0164 MF288270 MF288394 MF288529
117 Microtrichalus sp. K New Guinea, Papua, Sentani BM0167 MF288273 MF288397 MF288532
118 Microtrichalus sp. K New Guinea, Papua, Sentani BM0169 MF288275 MF288399 MF288534
119 Microtrichalus sp. L New Guinea, Papua, Elelim BM0147 MF288256 MF288380 MF288515
120 Microtrichalus sp. M Australia, Queensland, Claudie River A00353 MF288184 MF288321 MF288446
121 Microtrichalus sp. N New Guinea, Papua, Bokondini BM0119 MF288238 MF288362 MF288497
122 Microtrichalus sp. O New Guinea, Papua, Napua BM0185 MF288283 MF288407 MF288540
123 Microtrichalus sp. O New Guinea, Papua, Tikapura BM0141 MF288253 MF288377 MF288512
124 Microtrichalus sp. P Australia, Queensland, Mt. Molloy 000375 KC38702 KC38315 KC38506
Microtrichalus sp. P Australia, Queensland, Pascoe River A00314 MF288176 MF288314 MF288439
Microtrichalus sp. P Australia, Queensland, Pascoe River A00315 MF288177 MF288315 MF288440
Microtrichalus sp. Q Australia, Queensland, Chilverton A00316 MF288178 MF288316 MF288441
Microtrichalus sp. R New Guinea, Papua, Sentani BM0183 MF288282 MF288406 MF288539
Microtrichalus sp. S New Guinea, Papua, Bokondini BM0120 MF288239 MF288363 MF288498
Microtrichalus sp. T Australia, Queensland, Chilverton A00317 MF288179 MF288317 MF288442
Microtrichalus sp. U New Guinea, Papua, Yiwika BM0177 MF288278 MF288402 MF288536
Microtrichalus sp. U New Guinea, Papua, Yiwika BM0178 MF288279 MF288403 MF288537
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Microtrichalus sp. Y New Guinea, Papua, Bokondini BM0124 MF288243 MF288367 MF288502
Microtrichalus sp. Y New Guinea, Papua, Bokondini BM0125 MF288244 MF288368 MF288503
Microtrichalus sp. Y New Guinea, Papua, Bokondini BM0126 MF288245 MF288369 MF288504
Microtrichalus sp. Y New Guinea, Papua, Bokondini BM0127 MF288246 MF288370 MF288505
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Microtrichalus sp. Y New Guinea, Papua, Bokondini BM0131 MF288250 MF288374 MF288509
Microtrichalus sp. Y New Guinea, Papua, Bokondini BM0132 MF288251 MF288375 MF288510

Trichalus sp. A Australia, Queensland, Lamington A00032 KC538722 KC538339 KC538529
Trichalus sp. A Australia, Queensland, Lamington A00033 KC538723 KC538340 KC538530
Trichalus sp. A Australia, Queensland, Lamington A00034 KC538724 KC538341 KC538531
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Trichalus sp. A Australia, Queensland, Lamington A00036 KC538726 KC538343 KC538533
Trichalus sp. A Australia, Queensland, Lamington A00037 KC538727 KC538344 KC538534
Trichalus sp. A Australia, Queensland, Lamington A00038 KC538728 KC538345 KC538535
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Trichalus sp. A Australia, Queensland, Lamington A00040 KC538730 KC538347 KC538537
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Trichalus sp. A Australia, Queensland, Lamington A00063 KC538753 KC538370 KC538560
Trichalus sp. A Australia, Queensland, Lamington A00064 KC538754 KC538371 KC538561
Table 2 (on next page)

Morphological dataset

The description of character states is provided in the text.
| Characters | 0000000001111111111222222222 |
|------------|-------------------------------|
| Taxa       | 1234567890123456789012345678 |
| Metriorrhynchus | 00000-0000000000000000000000000000 |
| Kassemia   | 01001000000001100000000000010 |
| Synchonnus | 0110000000110000010000000010 |
| Diatrichalus | 01101000011101-001000000011 |
| Leptotrichalus | 000100100011010000000100000 |
| Lobatang   | 0000000000110101001010000100-0 |
| Schizotrichalus | 01010000101001-010010001000 |
| Eniclases  | 11010-001010110010010001000 |
| Flabellotrichalus | 110101010011010010001010000 |
| Trichalus  | 1100000001110100101-0001000 |
| Microtrichalus | 110100000111010010000111000 |
Figure 1

Phylogenetic hypotheses

Figure 1: (A) Molecular phylogenetic reconstruction of trichaline relationships using Maximum Likelihood; (B) Bayesian phylogenetic reconstruction of trichaline morphological relationships, the maximum clade credibility tree with posterior probabilities mapped; (C) Phylogenetic reconstruction of trichaline relationships inferred from morphology using the parsimony criterion. The topologies in Figs 1B and 1C were inferred from morphological dataset shown in Tab. 1. The numbers at branches show bootstrap support values (Figs 1A, values before slash and 1C) and posterior probabilities (Figs 1A, values after slash, 1B). Only values over 50% shown in Fig. 1C. Voucher numbers at branch tips identify the samples listed in Tab. 1.
Manuscript to be reviewed
Figure 2

General appearance (1)

General appearance, basal male antennomeres, and the posterior part of the right elytron. (A) *Diatrichalus* sp.; (B) *Diatrichalus aeneus* Bocak; (C) *Diatrichalus* sp.; (D) *D. cerberus* (Bourgeois), (E) *D. sinuaticollis* (Pic); (F) *Lobatang* sp.; (G) *L. papuensis* Bocak, hind tarsus claws; (H-J) *Lobatang* spp.; (K) *Flabellotrichalus* sp.; (L) *Flabellotrichalus* sp., female basal antennomeres, (M-N) *Flabellotrichalus* spp., male antennae; (O-P) *Flabellotrichalus* spp.; (Q) *Eniclases divaricatus* Kleine, female; *Eniclases* spp., male antennae: (R) *Eniclases* sp., (S) *E. divaricatus* Kleine; (T) *E. bicolor* Bocek et Bocak, (U) *E. similis* Bocak & Bocakova. Scales 1 mm (Figs A-B, F, K, Q), 0.5 mm (other figures).
Figure 3

General appearance (2)

General appearance, basal male antennomeres, and the posterior part of right elytron. (A–C) *Trichalus flavopictus*; (D) *Microtrichalus* sp., male; (E) *Microtrichalus* sp., female; (F–G) *Microtrichalus* spp.; (H) *Flabellotrichalus* (*Maibrius*) horaki sp. nov.: (H) general appearance, (I) tarsus, (J) claws, (K) male antenna, (L) humeral part of elytron, (M) middle part of elytron. Scales 1 mm (Figs A, D–E, H), 0.5 mm (Figs B–C, F–G, I, K–M), 0.1 mm (Fig. J).
Figure 4

Pronota

Pronotum. (A) *Metriorrhynchus inaequalis* (F.); (B) *Bulenides* sp.; (C) *Diatrichalus* sp.; (D) *D. mancus* (Kleine); (E) *D. aeneus* Bocak; (F) *Lobatang papuensis* Bocak; (G–J) *Lobatang* spp.; (K) *Schizotrichalus* sp.; (L) *Eniclases divaricatus* Kleine; (M–P) *Flabellotrichalus* spp.; (Q) *Trichalus flavopictus* Waterhouse; (R) *T. communis* Waterhouse; (S–T) *Microtrichalus* spp. Scales 0.5 mm.
Figure 5

Male genitalia

Male genitalia and terminal abdominal sclerites. (A–C) *Diatrichalus* sp.; (D–E) *Lobatang* sp.; (F) *Trichalus flavopictus* Waterhouse; (G–I) *Lobatang* sp.; (J–K) *Trichalus* sp.; (L) *Microtrichalus* sp.; (M) *Eniclases* sp.; (N) *Flabellotrichalus* (*Maibrius* horaki) sp. nov.; (O–P) *Flabellotrichalus* sp.; (Q–R) *Lobatang* sp., male terminal abdominal sclerites, ventrally and dorsally. Scales 0.5 mm.
Figure 6

Female genitalia and terminal abdominal sclerites. *Diatrichalus* sp. (A) ovipositor, (B) female genitalia, (C) terminal tergite, (D) terminal sternite; *Lobatang* sp. (E) ovipositor and female genitalia, (F) terminal sternite, (G) terminal tergite; *Microtrichalus* sp. (H) ovipositor and female genitalia, (I) terminal tergite, (J) terminal sternite; *Flabellotrichalus* sp. (K) ovipositor and female genitalia, (L) terminal sternite, (M) terminal tergite; *Trichalus* sp. (N) ovipositor, (O) female genitalia; *Eniclases divaricatus* Kleine (P) ovipositor, (Q) vagina, dorsally, (R) terminal sternite; uvg – unpaired gland; lvp – lateral vaginal pocket. Scales 0.5 mm.
