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Taxonomy

Discovery of New Genera Challenges the Subtribal Classification of Tok-Tok Beetles (Coleoptera: Tenebrionidae: Sepidiini)

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Abstract

Sepidiini is a speciose tribe of desert-inhabiting darkling beetles, which contains a number of poorly defined taxonomic groups and is in need of revision at all taxonomic levels. In this study, two previously unrecognized lineages were discovered, based on morphological traits, among the extremely speciose genera *Psammodes* Kirby, 1819 (164 species and subspecies) and *Ocnodes* Fåhraeus, 1870 (144 species and subspecies), namely the *Psammodes spinosus* species-group and *Ocnodes humeralis* species-group. In order to test their phylogenetic placement, a phylogeny of the tribe was reconstructed based on analyses of DNA sequences from six nonoverlapping genetic loci (CAD, *wg*, COI JP, COI BC, COII, and 28S) using Bayesian and maximum likelihood inference methods. The aforementioned, morphologically defined, species-groups were recovered as distinct and well-supported lineages within Molurina + Phanerotomeina and are interpreted as independent genera, respectively, *Tibiocnodes* Gearner & Kamiński **gen. nov**. and *Tuberocnodes* Gearner & Kamiński **gen. nov.** A new species, *Tuberocnodes synhimboides* Gearner & Kamiński **sp. nov.**, is also described. Furthermore, as the recovered phylogenetic placement of *Tibiocnodes* and *Tuberocnodes* undermines the monophyly of Molurina and Phanerotomeina, an analysis of the available diagnostic characters for those subtribes is also performed. As a consequence, Phanerotomeina is considered as a synonym of the newly redefined Molurina **sens. nov**. Finally, spectrograms of vibrations produced by substrate tapping of two Molurina species, *Toktokkus vialis* (Burchell, 1822) and *T. synhimboides*, are presented.

Key words: phylogeny, darkling beetle, Pimeliinae, Southern Africa, tapping behavior

Although insects are believed to play crucial roles in many terrestrial ecosystems (e.g., Hanski and Cambefort 1991, Grimaldi and Engel 2005), for many, our understanding of the taxonomy and biology remains fragmentary, even for iconic and culturally important groups (see below). Compared to vertebrates, especially birds and mammals, many insect taxa lack published phylogenetic hypotheses to explore more complex evolutionary problems. As a result, our knowledge concerning many biological processes rely on observations made for a relatively small portion of available taxonomic groups. This is especially disturbing in light of the ongoing global biodiversity crisis (Butchart et al. 2018).

This study focuses on Sepidiini Eschscholtz, 1829, which is a morphologically diverse but understudied tribe of flightless darkling beetles (Tenebrionidae: Pimeliinae). The tribe is distributed throughout Africa, with the majority of taxa residing in the Afrotropical Realm, including Madagascar, and a few species reaching the southern Western Palearctic (Koch 1955, Kamiński et al. 2019). Many members from this tribe, particularly in

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Molurina Solier, 1834, and Phanerotomeina Koch, 1958, perform a behavior called substrate tapping, in which they produce vibrations by tapping their abdomen on the ground, presumably to locate potential mates (Kristensen and Zachariassen 1980; Lighton 1987, 2019, preprint). This form of sexual communication gives them recognition in local culture, as they are believed by the Xhosa people (Southern Africa) to bring good luck. This is reflected in a traditional Xhosa wedding song entitled *Qongqothwane*, which directly translates to 'knock-knock beetle'. This fascinating ethological phenomenon remains poorly investigated due to the lack of reliable taxonomy for sepidiine beetles, with knowledge of the behavior restricted to only a few studies (see Kristensen and Zachariassen 1980; Lighton 1987, 2019, preprint). Furthermore, Phanerotomeina also includes the largest documented tenebrionid species, *Stridulomus sulcicollis* (Péringuey, 1885), measuring ~80.0 mm (Matthews et al. 2010).

Sepidiini currently contains six subtribes: Hypomelina Koch, 1955, Molurina, Oxurina Koch, 1955, Phanerotomeina, Sepidiina Eschscholtz, 1829, and Trachynotina Koch, 1955. A recent phylogenetic study (Kamiński et al. 2021a) supported the monophyly of most subtribes except for Sepidiina, for which no representatives were included. However, due to low taxon sampling in the analysis, further studies are needed to confirm these results, including an examination of morphological data. As noted by Penrith (1986), the morphological concepts supporting the current subtribal classification, and the majority of genera, are ambiguous and in need of additional examination and revision.

One such subtribe is Phanerotomeina (Penrith 1987). Kaminski et al.'s (2021a) phylogenetic analysis of the Sepidiini suggests a close relationship between this subtribe and Molurina; however, the status of these two subtribes as separate lineages is questionable. Characters used by Koch (1955) to separate the two subtribes include margination on the fifth abdominal ventrite, the carinate upper surface of the protibia in Phanerotomeina, and the presence of a pre-episternal suture on the mesoventrite in Molurina (Table 1). However, preliminary investigations have revealed that these features are not universal within either subtribe or are too variable or ambiguous to be reliable. Phanerotomeina is dominated by the large, heterogeneous, and poorly defined genus *Ocnodes* Fåhraeus, 1870, which contains 144 species and subspecies (Kamiński et al. 2019, 2021a,b). The other currently accepted genera in this subtribe are *Tarsocnodes* Gebien, 1920, containing 25 species and subspecies, *Chiliarchum* Koch, 1954, containing 8 species and subspecies, and *Huilamus* Koch, 1953, *Psammorhyssus* Kolbe, 1886, and *Stridulomus* Koch, 1955, each with just 1 species (Kamiński et al. 2019, 2021a). Since its description, *Ocnodes* has never been revised, nor has a set of synapomorphic characters to define the genus been proposed. Hence, *Ocnodes* can currently only be defined based on the absence of specific characters found in other Phanerotomeina genera (Koch 1955). This lack of a clear definition is evident in the tendency of many taxonomists to misidentify species of *Ocnodes* as *Psammodes* Kirby, 1819 (Molurina) and vice versa (O. M. Gearner, personal observations).

As the recently published Sepidiini phylogeny (Kamiński et al. 2021a) mainly targeted Molurina, it does not provide much insight into the intertribal relationships among the other subtribes. Within Phanerotomeina, only three genera were sampled (*Ocnodes*, *Tarsocnodes*, and *Chiliarchum*). Additionally, the included species of *Ocnodes* were relatively monomorphic, so the status of the genus was not strongly challenged. As a result of ongoing taxonomic studies of *Psammodes* and *Ocnodes* by the authors, a few morphologically coherent species-groups were identified within those genera. In order to test the monophyly of these species-groups, as well as their relationship to other species-groups within *Ocnodes* and related genera, a molecular phylogeny based on six genetic loci and 49 taxa was reconstructed.

Materials and Methods

Taxonomy

The taxonomic part of this study was based on material from the Ditsong National Museum of Natural History, Pretoria, South Africa (TMNH), Museum and Institute of Zoology of the Polish Academy of Sciences (MIZ PAS), California Academy of Sciences, San Francisco, CA, USA (CASC), Natural History Museum, London, United Kingdom (BMNH), USDA Systematic Entomology Laboratory, Smithsonian Institution, National Museum of Natural History, Washington, DC, USA (USNM), Instituto Argentino de Investigaciones de las Zonas Arida, Mendoza, Argentina (IADIZA), and Purdue University, West Lafayette, IN, USA (Purdue Entomological Research Collection [PERC]). This includes the type specimens of the following species: *Ocnodes argenteofasciatus* (Koch, 1953), *Ocnodes humeralis* (Haag-Rutenberg, 1871), *Ocnodes lanceolatus* (Koch, 1953), *Psammodes lucidus* (Fåhraeus, 1870), *Ocnodes miles* (Péringuey, 1908), *Ocnodes procursus* (Péringuey, 1899), *Ocnodes vaticinus* (Péringuey, 1899), *Ocnodes warmeloi* (Koch, 1953), *Psammodes discrepans* (Péringuey, 1904), and *Psammodes placidus* (Péringuey, 1899). The generic concepts were established by referring to material identified by C. Koch, M.-L. Penrith, and L. Péringuey, with additional verification based on available literature (Koch 1953, 1955). All label data are transcribed verbatim, with each line separated by a backslash (/) and each label separated by quotation marks. Description style and

Table 1. Characters used to separate Molurina and Phanerotomeina (after Koch, 1955)

Character	Phanerotomeina	Molurina
Fifth ventrite of abdomen	Marginate at least basally	Immarginate
Male underside of profemora	Hairy to tomentose	No distinctive characters
Tibiae	Scattered dark bristles	Dense pale bristles
Protibiae	Sharply carinate	Carinate only at apex
Metatibiae	Apex often dilated	Not dilated apically
Metatarsi	Basal segment variable	Basal segment longer than distal
Prosternum	Emarginate	Often collar-like
Elytra	Rarely costate; when costate, primary costa never conceal lateral interval	Often w/ primary costa concealing lateral interval
Mesoventrite	Without distinct pre-episternal suture	Usually with pre-episternal suture or sulcus

morphological terminology follow that of Kamiński et al. (2021a), with additional specialized terms used for the male and female terminalia (Iwan and Kamiński 2016). Images were taken using a Canon 1000D body with accordion bellows and a Canon EF 100-mm macro lens. Scanning electron microscopy images were acquired with a Hitachi S-3400 N in MIZ PAS.

Taxon Sampling: Phylogenetic Analysis

Molecular data generated from 49 specimens of Sepidiini (Fig. 1) was used to reconstruct a phylogeny for the tribe. The same taxa were used as in Kamiński et al. (2021a), with the addition of nine Phanerotomeina specimens (i.e., TB15580, TB14714, TB22656, TB15578, TB22644, TB15574, TB19982, TB22638, TB22657). Label data for the voucher specimens is presented in Supp Table S1 (online only). *Machla setosa* (Asidini) and *Stenocara* sp. (Adesmiini), both members of Pimeliinae (Bouchard et al. 2011), were used as outgroups.

DNA Extraction and Sequencing

DNA was extracted from ethanol-preserved specimens (95% EtOH) using DNeasy Blood & Tissue Kits (Qiagen) following the manufacturer's protocols. Extractions were performed on the soft

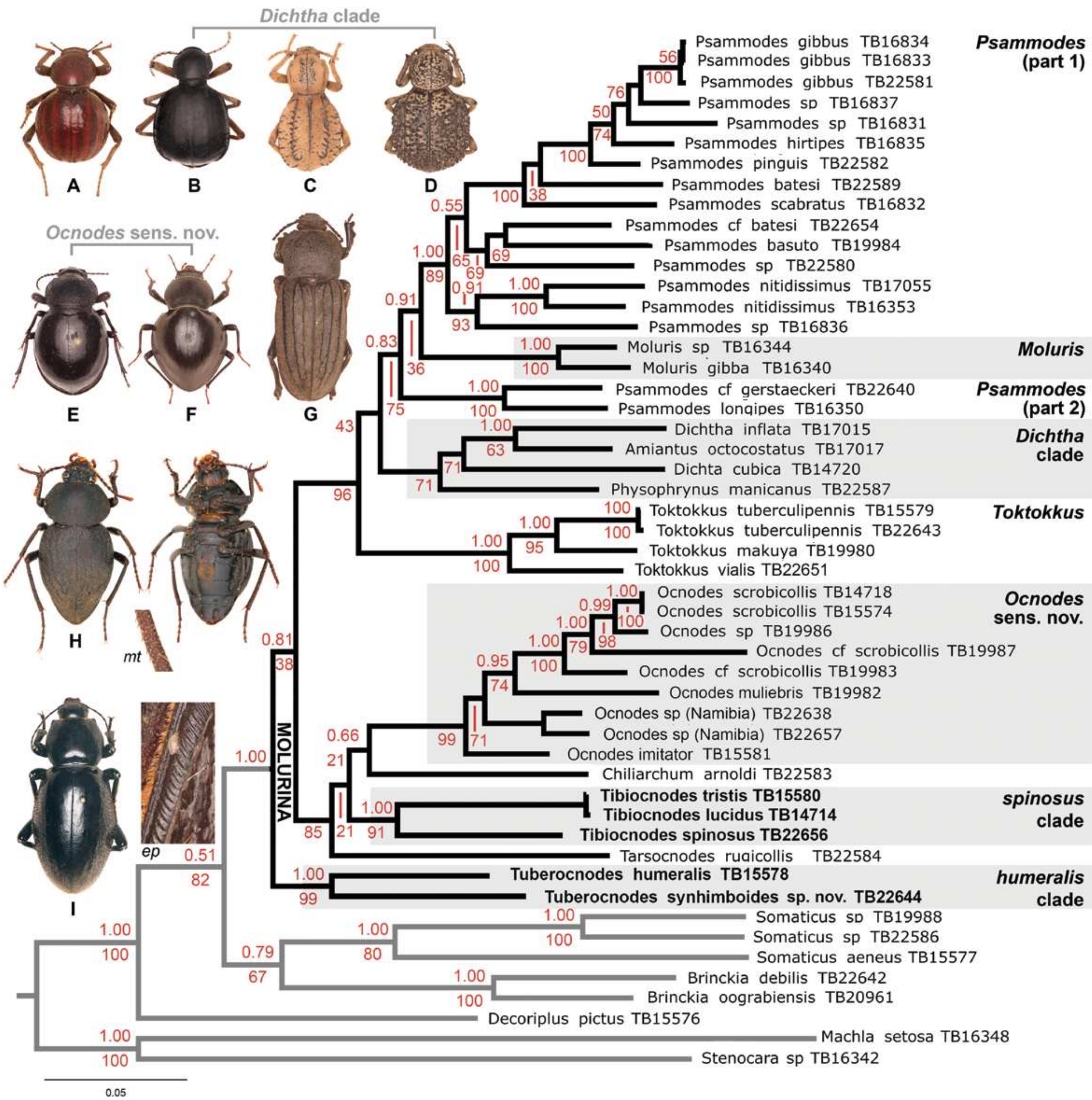

Fig. 1. Phylogeny of Molurina imposed with new generic classification. Maximum likelihood topology from IQ-Tree obtained in the analysis of the concatenated CAD, *wg*, COI JP, COI BC, COII, and 28S matrix. Posterior probabilities are displayed above branches, while the ultrafast IQ-Tree bootstrap values are shown below (black circles indicate a full support of either 1.00 or 100). Representatives of Molurina: (A) *Psammodes pinguis*—holotype; (B) *Dichtha cubica* (voucher TB14720); (C) *Brachyphrynus abyssinicus*—syntype; (D) *Physophrynus burdoi*; (E) *Ocnodes* cf. *scrobricollis* (voucher TB19987); (F) *Ocnodes sericicollis*—paratype; (G) *Psammoryssus titanus*; (H) *Huilamus welwitschi*—*mt*: *metatibia*; (I) *Stridulomus sulcicollis*—*ep*: *epipleuron*.

tissue from the head or thorax; no cuticle was ground during the extraction process. Voucher specimens are deposited in the PERC at Purdue University (Aaron D. Smith). Six nonoverlapping gene regions from five loci were amplified using PCR: nuclear protein-coding gene carbamoyl-phosphate synthetase domain of *rudimentary* (CAD; 810 bp), *wingless* (*wg*; 435 bp), mitochondrial protein-coding cytochrome oxidase subunit I Jerry/Pat (COI JP; 828 bp) and barcoding (COI BC; 657 bp) fragments, cytochrome oxidase subunit II (COII; 681 bp), and nuclear ribosomal 28S (1,042 bp). PCRs were performed using ExTaq (TaKaRa) with primers and thermocycler protocols given in Kanda et al. (2015). PCR cleanup, quantification, and sequencing were performed by the University of Arizona's Genetics Core Facility. Cleaned PCR products were sequenced on an Applied Biosystems 3730XL DNA Analyzer. Final sequences are available on GenBank (accessions MW295916– MW307251).

DNA Analyses

Assembly of chromatograms was performed as described in Kamiński et al. (2021a). All alignments were concatenated into a single matrix (4,453 bp) for phylogenetic analyses (Supp Table S2 [online only]).

Data partitions and models of sequence evolution for Bayesian phylogenetic analyses (BI) were assessed with PartitionFinder v. 2.0 (Lanfear et al. 2017) implemented on CIPRES (Miller et al. 2010). For details, see Kamiński et al. (2021a). Models were compared using greedy searches and the Bayesian information criteria (BIC). Bayesian analyses were conducted through the CIPRES portal using MrBayes (v. 3.2.7a) (Ronquist et al. 2012). Two independent runs were performed, each with four chains. Analyses were run for 20 million generations, and parameters were sampled every 1,000 generations. A burnin fraction of 25% was used, and convergence was determined by the standard deviation of the split frequencies; runs were considered to have converged at <0.01. Maximum likelihood (ML) analysis was conducted using IQ-Tree, v. 1.6.10 (Nguyen et al. 2015) on CIPRES portal. The run was conducted with a setting enabling partitions to have different speeds (–spp). Branch support was estimated using 1,000 ultrafast bootstrap replicates (Minh et al. 2013; for details, see Kamiński et al. 2021a). Data partitions and models of sequence evolution for ML analysis were also assessed in IQ-Tree prior to phylogenetic analysis. When discussing support values, the following abbreviations are used: UFB: ultrafast bootstrap and PP: Bayesian posterior probability. Node support is defined as low/weak (UFB = 90–94, PP = 0.90–0.94), moderate (UFB = 95–97, PP = 0.95–0.97), or strong/high (UFB = 97–100, PP = 0.97–1.0).

Tapping Behavior

Spectrograms were generated using the R language and environment (R Core Team 2013) with tuneR package (Ligges et al. 2018) from available video content for *Tuberocnodes synhimboides* (Supp Movie S1 [online only]) and *Toktokkus vialis* (Kamiński et al. 2021a). In both cases, the recorded beetles were kept in captivity overnight (near the collecting locality) and preserved in 95% EtOH the next morning.

Nomenclature

This paper and the nomenclatural act(s) it contains have been registered in Zoobank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is: urn:lsid:zoobank.org:pub:EEAEC93E-D667-4A07-8C3B-EE33BEA1773C

Results

Morphological Analysis

The morphological study conducted here has revealed the existence of a coherent species-group within *Ocnodes*, which can be distinguished from other Phanerotomeina by the presence of microtubercles on the laterally exposed epipleuron (Fig. 2B). Based on the studied material, the following species are included in this lineage (see also Koch 1953 for '*O. humeralis*-group'): *O. argenteofasciatus* (Koch, 1953), *Ocnodes distinctus* (Haag-Rutenberg, 1871), *Ocnodes heydeni* (Haag-Rutenberg, 1871), *O. humeralis* (Haag-Rutenberg, 1871), *O. lanceolatus* (Koch, 1953), *O. miles* (Péringuey, 1908), *O. procursus* (Péringuey, 1899), *Ocnodes tibialis* (Haag-Rutenberg, 1871), *O. vaticinus* (Péringuey, 1899), *O. warmeloi* (Koch, 1953), and an undescribed species from Namibia (named herein as *T. synhimboides* Gearner & Kamiński **sp. nov.** [new genus is discussed below]). It should be noted that there are strong morphological differences between the *synhimboides* subgroup (i.e., *T. synhimboides*, *O. argenteofasciatus*, *O. warmeloi*) and the remaining species (Figs 2 and 3E–G).

A peculiar lineage was also discovered within *Psammodes*. Based on the analyzed material, the *spinosus* species-group contains *P. discrepans* Péringuey, 1904, *Psammodes herculeanus* Haag-Rutenberg, 1871, *P. lucidus* Fåhraeus, 1870, *P. placidus* Péringuey, 1899, *Psammodes spinosus* Haag-Rutenberg, 1871, *Psammodes tristis* Fåhraeus, 1870, and *Ocnodes badeni* (Haag-Rutenberg, 1871). This species-group possesses more characters associated with Phanerotomeina than Molurina, including a marginated fifth abdominal ventrite and a setal patch on the profemora in males. However, it can be distinguished from other Phanerotomeina by the unique structure of the protibia. The outer tibial ridge, normally present along the entire tibial length in other Phanerotomeina, is confined to the apex, forming a ventrally bent tooth.

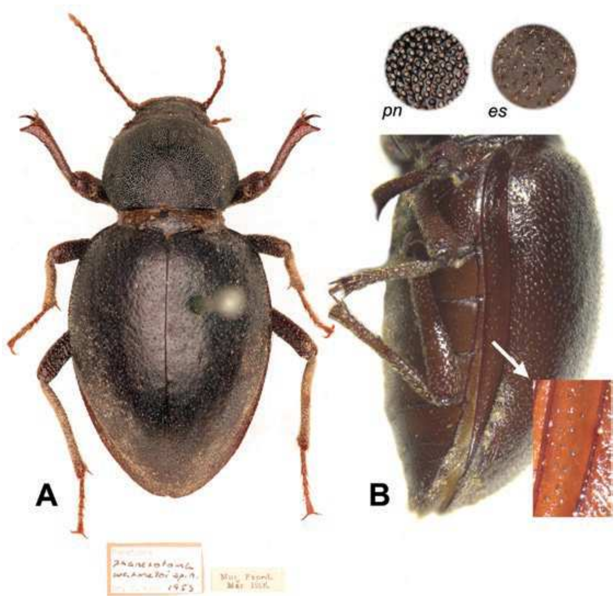

Fig. 2. Morphology of the genus *Tuberocnodes*: (A) paratype of *Tuberocnodes warmeloi* (Koch, 1953) **comb. nov.** (from TMNH); (B) laterally exposed and covered with microtubercles epipleuron of *Tuberocnodes synhimboides*. es, elytral slope; pn, pronotum.

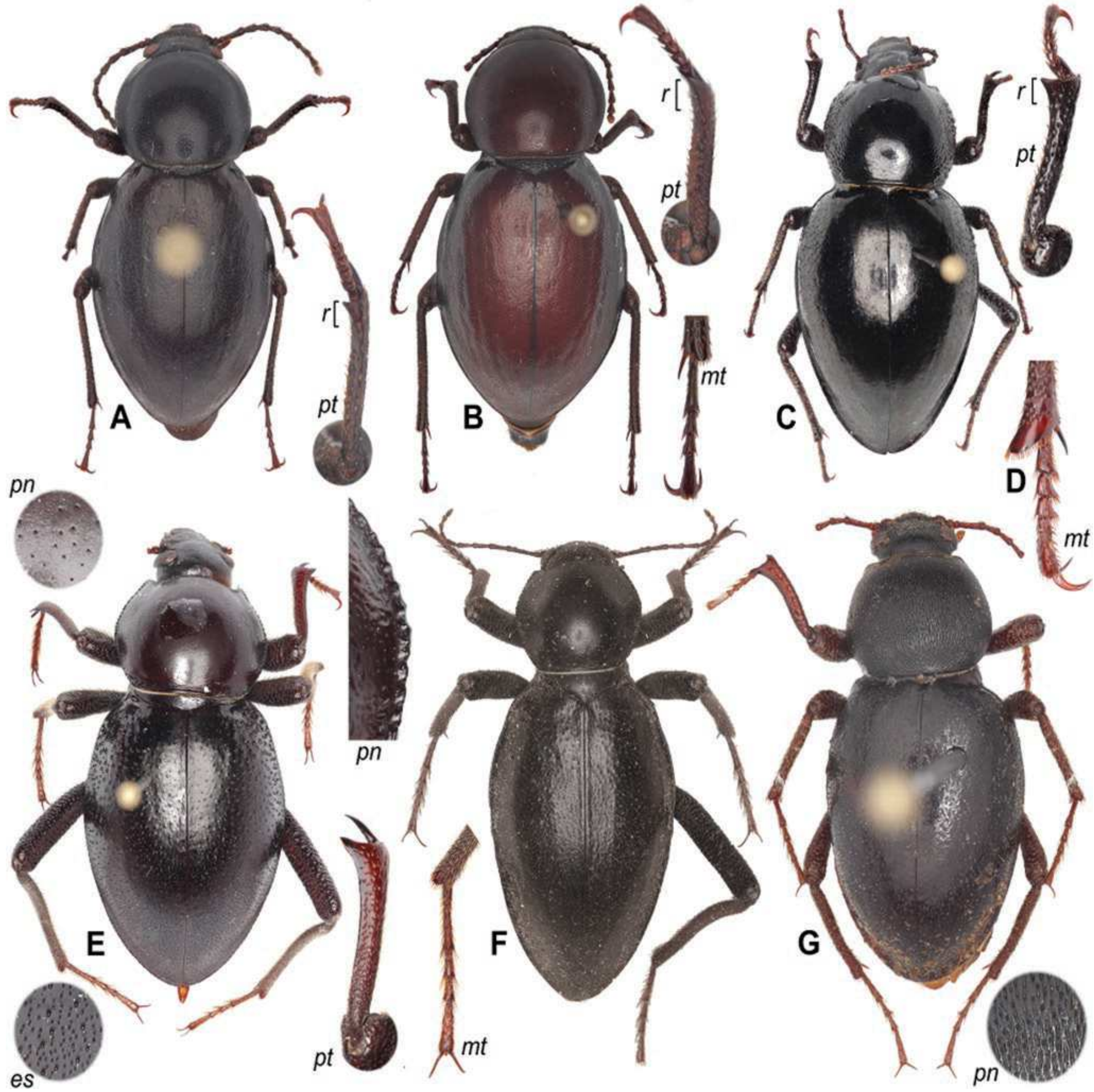

Fig. 3. Dorsal habitus and morphological features of specimens representing the following species: (A) *Tibiocnodes tristis* (Fåhraeus, 1870); (B) *Tibiocnodes lucidus* (Fåhraeus, 1870); (C) *Tibiocnodes spinosus* (Haag-Rutenberg, 1871); (D) *Ocnodes similis* (Péringuey, 1899); (E) *Tuberocnodes humeralis* (Haag-Rutenberg, 1871); (F) *Tuberocnodes procursus* (Péringuey, 1899); (G) *Tuberocnodes synhimboides* **sp. nov.**—paratype. es, elytral slope; mt, metatarsi; pn, pronotum; pt, protibia; r, protibial ridge.

Molecular Analysis

The two independent runs in the Bayesian analyses converged after 605,000 generations. Both inference methods (ML and BI) returned similar topologies (Fig. 1; Supp Fig. S1 [online only]), with a few differences: relationships within the clade containing *Psammodes hirtipes* (Laporte, 1840), *Psammodes pinguis* (Solier, 1843), *Psammodes gibbus* (Linnaeus, 1760), and two unidentified *Psammodes* species are different; in the Bayesian consensus, the *Dichtha* clade is sister to all other Molurina, but in the ML tree, the genus *Toktokkus* Kamiński & Gearner, 2021, is sister to all other Molurina; in the consensus tree, the clade containing *P. spinosus* Haag-Rutenberg, 1871, *P. lucidus* Fåhraeus, 1870, and *P. tristis* Fåhraeus, 1870 is sister to the rest of Phanerotomeina (besides the *O. humeralis* clade) with *Tarsocnodes* sister to *Chiliarchum* + *Ocnodes* clade, while in the ML topology, the positions of *Tarsocnodes* and the *P. spinosus* clade are switched; finally, in the Bayesian tree, *Ocnodes muliebris* is sister to the included Namibian *Ocnodes* species (TB22638, TB22657), while in the ML topology, *O. muliebris* is sister to the rest of the *Ocnodes* clade. Support for many of the deeper nodes of the tree was weak to nonexistent, so few conclusions can be drawn about relationships between major clades (Fig. 1). More loci will need to be sampled in order to clarify relationships at deeper nodes. However, some well-supported lineages were recovered.

The aforementioned, morphologically defined, species-groups were rendered as distinct lineages within Molurina and Phanerotomeina, i.e., the clade containing *P. spinosus*, *P. lucidus*, and *P. tristis* (UFB: 91, PP: 0.999), and the clade containing *O. humeralis* and *T. synhimboides* (UFB: 99, PP: 1). The *P. spinosus* species-group was recovered outside *Psammodes*, within a clade containing the majority of included Phanerotomeina (Fig. 1). The placement of this species-group renders Molurina as paraphyletic. On the other hand, representatives of the *O. humeralis*-group were recovered outside the clade containing all other included members of Phanerotomeina. Support for the placement of this species-group as sister to Phanerotomeina + Molurina varied depending on the inference method (UFB: 91, PP: 1.0). Neither inference method showed support for Phanerotomeina + Molurina (UFB: 38, PP: 0.81), casting further doubt on the status of these subtribes as distinct lineages.

New Genera

Based on their phylogenetic and morphological distinctiveness, both *O. humeralis* and *P. spinosus* species-groups are interpreted as independent genera, named, respectively, *Tuberocnodes* **gen. nov.** and *Tibiocnodes* **gen. nov.** (see *Taxonomy* section for further details). These taxonomic acts restore monophyly to *Ocnodes*, with the clade containing *Ocnodes* **sensu nov.** strongly supported. The included species of *Ocnodes* **sensu nov.** are all monomorphic, sharing the following characters (Fig. 4B, C, F, H, J, and K): presence of microtubercles or microsculpturing on the pronotum, smooth elytra, epipleura flat (not visible laterally), frons elevated with respect to the clypeus, and a distinct frontoclypeal suture. Additional morphologically variant species of *Ocnodes* will need to be sampled in future studies in order to verify the stability of these characters. The monophyly of *Psammodes* is not restored due to the existence of the *Psammodes longipes* species-group. However, this problem is beyond the scope of this paper (see Kaminski et al. 2021a for further discussion).

Tapping Behavior

Although the tapping behavior within Sepidiini is widely recognized among entomologists, only a handful of papers were published on this topic (Lighton 1987, 2019, preprint). We assume that the biggest inhibitor for such studies is the lack of reliable species identification tools, including the lack of reference sequences in GenBank for the majority of Sepidiini. The spectrograms presented here are based on extremely short input data and therefore cannot be used for statistical analysis. However, they indicate major differences in tapping behavior between the two analyzed species. Contrary to *To. vialis*, which produces slow individual taps, the recorded individual of *T. synhimboides* produces sound in a series (tap train) of four to five hits (Fig. 5).

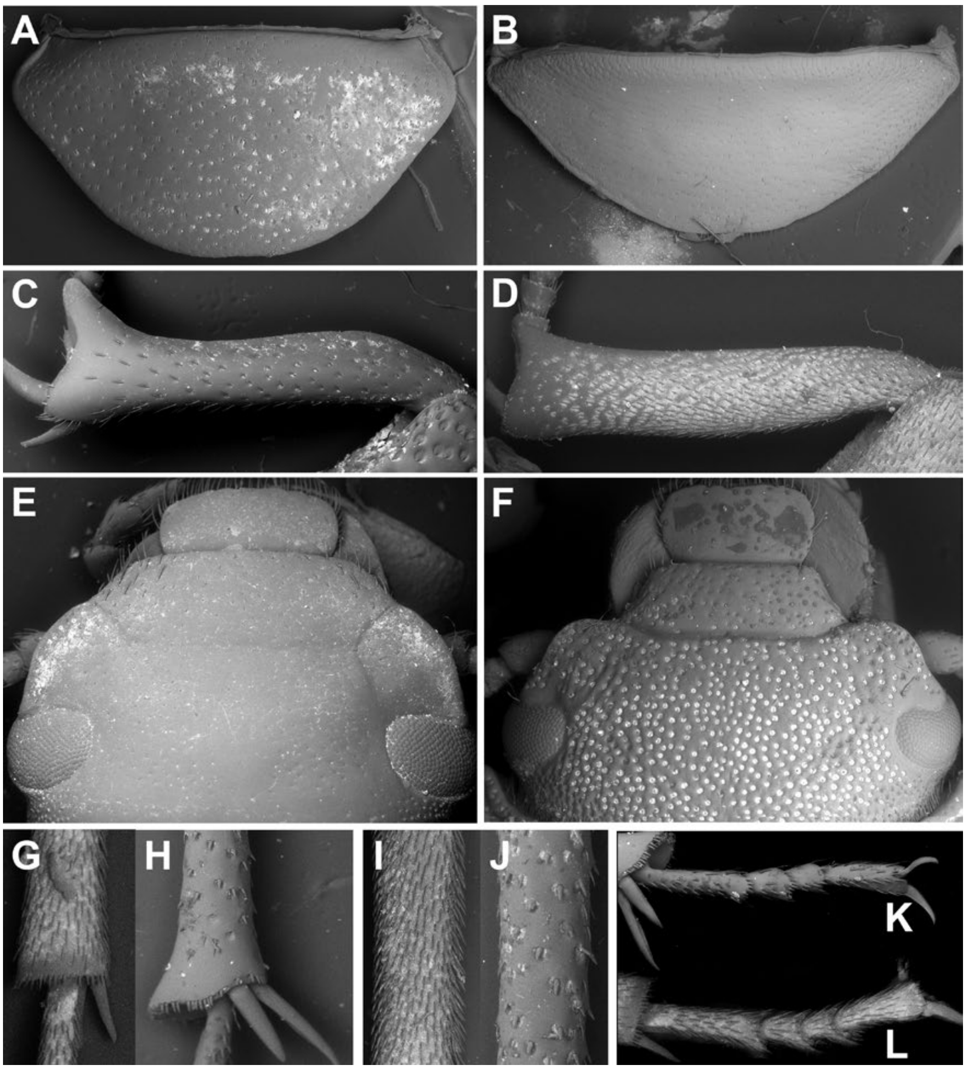

Fig. 4. Examples of morphological characters used by Koch (1955) to separate Molurina and Phanerotomeina. Margination of the fifth ventrite (A: *Distretus amplipennis*; B: *Ocnodes similis*, with margination on only one side of the ventrite); protibia (C: *O. similis*, D: *Toktokkus vialis*); differences in facial structure (O. M. Gearner and M. J. Kamiński, personal observations; note: not used by Koch, 1955) (E: *Psammodes pinguis*, F: *O. similis*); apex of metatibia (G: *P. pinguis*; H: *O. similis*); setation on tibiae (I: *P. pinguis*, J: *O. similis*); metatarsi (K: *O. similis*; L: *P. pinguis*).

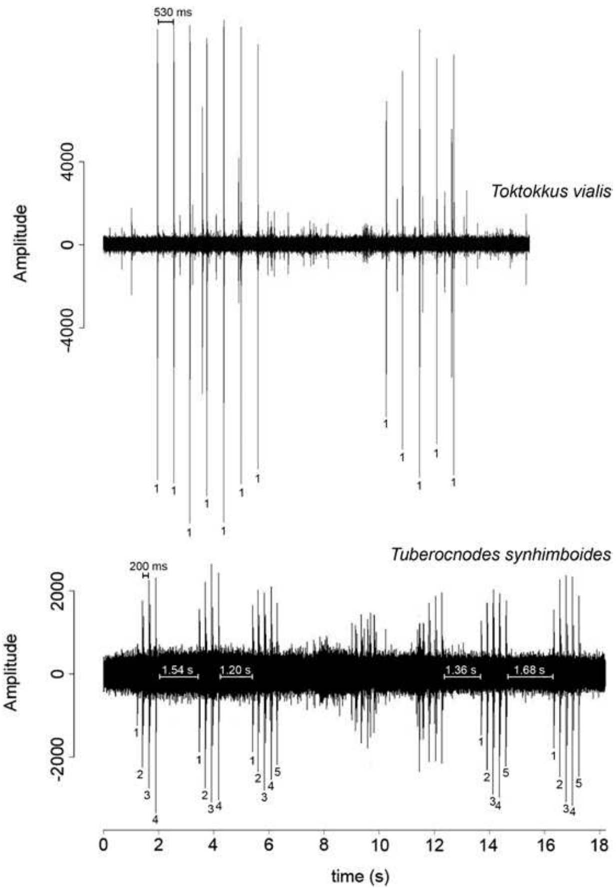

Fig. 5. Spectrograms illustrating differences between two different Molurina species tapping. Both plots were generated based on videos of beetles kept in captivity: *Tuberocnodes synhimboides* (Supp Movie S1 [online only]) and *Toktokkus vialis* (Kamiński et al. 2021a). Sex of the beetles in both cases remain unknown. Contrary to *To. vialis*, the recorded individual of *T. synhimboides* is producing sound in a series of four to five hits.

Discussion

The subtribe Phanerotomeina is paraphyletic with regard to Molurina, due to the clade containing the newly established *Tuberocnodes* **gen. nov.** (Fig. 1). While the clade containing all included Molurina taxa was well supported, nodal support for Phanerotomeina (excluding *Tuberocnodes*) + Molurina was nonexistent. Koch (1955) distinguishes these subtribes based on a number of characters (Table 1); however, upon reexamination, many of these characters were found to be unstable or difficult to use diagnostically.

While the fifth ventrite of the abdomen in Molurina is consistently immarginate (Fig. 4A), some members of Phanerotomeina also lack margination of the fifth abdominal ventrite or the margination is very subtle (Fig. 4B). The density of setae on the tibiae is a fairly consistent character; however, the variability of setal density in these two subtribes does appear to overlap; additionally, setal color (pale vs dark bristles) is variable within the two subtribes and is not a useful character. The use of a carinate protibia to define Phanerotomeina is violated by the new genus *Tibiocnodes* **gen. nov.**, in which the protibia is only carinate at the apex (as in Molurina). Additionally, the dilated apex of the metatibiae in Phanerotomeina is not obvious in many members of this subtribe. The presence of a pre-episternal suture on the mesoventrite was determined not to be useful for distinguishing Molurina, as some members of Phanerotomeina were observed possessing this feature. Two other characters Koch (1955) discussed were the collar-like prosternum and the primary costa concealing the lateral interval in Molurina; however, these characters are only applicable to certain genera within Molurina (e.g., *Dichtha* clade, *Psammophanes*), not to the entire subtribe. Two characters that do seem to hold up well are the dense setal patch on underside of the profemora in males of Phanerotomeina and the basal metatarsomere longer than the distal one in Molurina (Table 1). However, these two characters alone are not sufficient to justify the classification of these two groups as separate subtribes—especially as the phylogenetic analysis did not recover strong support for them as distinct lineages. Even if there are other unexamined characters to sustain the subtribes, our phylogeny suggests that we would need to designate a new monogeneric subtribe for *Tuberocnodes* **gen. nov.** in order to restore monophyly to the subtribes.

Due to the lack of clear characters to delimit the two subtribes, and to restore monophyly to the group, we synonymize Phanerotomeina and Molurina. Koch (1955) outlined a few characters which unite taxa in this group. These include the metanepisternum, which is shiny and punctured and rarely with scattered tubercles; the metanepisternum also with a strong, posteriorly abbreviated episternal suture; in males, abdomen often with a setal patch (sometimes divided into concentric circles as in *Moluris*); pronotum without prominent posterior angles; and elytra never with prominent humeri.

Taxonomy

Subtribe Molurina Solier **sens. nov.**

= Phanerotomeina Koch, 1958 **syn. nov.**

Diagnosis. In addition to the characters listed above, this subtribe can be differentiated from other Sepidiini as follows (see Koch 1955, Louw 1979, and Penrith 1986).

From Sepidiina, it can be differentiated by the mesocoxal trochantin, which is absent or punctiform in Sepidiina, but large in most Molurina. From Oxurina, it can be differentiated by the metanepisternal suture, which is deep and broad (extending from the mes- to metepimeron) in Oxurina but is posteriorly abbreviated in Molurina. Trachynotina are diurnal and have heliotactic eyes with fine, flat corneal facets, and a prosternal apophysis which is narrower than the mentum; Molurina are more often nocturnal with heliophobic eyes which are convex and with larger acinose corneal facets, and with a prosternal apophysis which is rarely narrower than the mentum. Finally, Hypomelina can be differentiated by the pronotum, which is often emarginate basally and often with posterior angles, metanepisterna are dull and densely sculptured, males lack a setal patch on the abdomen but often have conglomerate scales, and elytra often with prominent humeri; in Molurina, the pronotum is not emarginate basally and does not possess posterior angles, metanepisterna are shiny and punctured, males usually have a setal patch on the abdomen, and the elytra never have prominent humeri.

Genera Included (24 Genera, 571 Species and Subspecies). *Amiantus* Fåhreus, 1870, *Arturium* Koch, 1951, *Brachyphrynus* Fairmaire, 1882, *Chiliarchum* Koch, 1954, *Dichtha* Haag-Rutenberg, 1871, *Distretus* Haag-Rutenberg, 1871, *Euphrynus* Fairmaire, 1897, *Glyptophrynus* Fairmaire, 1899, *Huilamus* Koch, 1953, *Melanolophus* Fairmaire, 1882, *Moluris* Latreille, 1802, *Ocnodes*

Fåhreus, 1870, *Phrynocolus* Lacordaire, 1859, *Phrynophanes* Koch, 1951, *Physophrynus* Fairmaire, 1882, *Psammodes* Kirby, 1819, *Psammophanes* Lesne, 1922, *Psammorhyssus* Kolby, 1886, *Psammotyria* Koch, 1953, *Stridulomus* Koch, 1955, *Tarsocnodes* Gebien, 1920, *Toktokkus* Kamiński & Gearner, 2021, *Tibiocnodes* **gen. nov.**, and *Tuberocnodes* **gen. nov.**

Genus *Tuberocnodes* Gearner & Kamiński **gen. nov.**

Type Species. *Psammodes humeralis* Haag-Rutenberg, 1871; here designated.

Diagnosis. Modified from Koch (1953) for the '*humeralis*-group': base of pronotum either with duplicated margination or its edge forming a transverse, narrow, shiny, horizontal to slightly oblique marginal edge, more or less grown together with the foraminal carina, and without perpendicular and below concave articulation face. Prosternal apophysis inermous, simply bent towards foramen. This genus shares the following characters with related genera like *Ocnodes*: margination of the fifth ventrite and underside of the profemora in males with a tomentose patch. *Tuberocnodes* can be also differentiated from other related genera by the presence of microtubercles on the laterally exposed epipleuron as well as the presence of tubercles on the elytra, slender and elongate antennae and tarsomeres, and the meso- and metatarsomeres, in which the first and last tarsomeres are around two to three times longer than the other tarsomeres. Further diagnosis is provided below.

Etymology. Name refers to the most prominent diagnostic character of the newly described genus. Gender masculine.

Species Included (11). *Tuberocnodes argenteofasciatus* (Koch, 1953) **comb. nov.**, *Tuberocnodes distinctus* (Haag-Rutenberg, 1871) **comb. nov.**, *Tuberocnodes heydeni* (Haag-Rutenberg, 1871) **comb. nov.**, *Tuberocnodes humeralis* (Haag-Rutenberg, 1871) **comb. nov.**, *Tuberocnodes lanceolatus* (Koch, 1953) **comb. nov.**, *Tuberocnodes miles* (Péringuey, 1908) **comb. nov.**, *Tuberocnodes procursus* (Péringuey, 1899) **comb. nov.**, *Tuberocnodes synhimboides* Gearner & Kamiński **sp. nov.**, *Tuberocnodes tibialis* (Haag-Rutenberg, 1871) **comb. nov.**, *Tuberocnodes vaticinus* (Péringuey, 1899) **comb. nov.**, and *Tuberocnodes warmeloi* (Koch, 1953) **comb. nov**.

Tuberocnodes synhimboides Gearner and Kamiński **sp. nov.**

Figs 2B, 3G, and 6E–G

Type Material. Holotype (PERC): male, 'NAMIBIA: Khomas Region/Eagle Rock Lodge, ~32 km W Windhoek, −22.58, 16.761/ El. 1,808 m, Nam2019#02/31.XII.2018, ADSmith'; *Paratypes*: 15 specimens (7 PERC, 4 British Museum, and 4 MIZ PAS), same data as holotype; 9 specimens (Kanda, private collection), 'NAMIBIA: Khomas Region, Eagle Rock Lodge, 25 km W. of Windhoek −22.5799, 16.7617, 1,800 m, 31.xii.2018–1.i.2019, KK19_001, CCW19_001, Nam2019 #02'; one female (USNM), same data but with 'Tenebrionid Base/Aaron D. Smith/Catalog# 22644' (DNA voucher specimen); one specimen (IADIZA) 'NAMIBIA: Khomas Eagle Rock/Guest Farm 40 Km NW/Windhaek 1,814 m/22.57988S 16.7610E/01-I-2019 Coll. G. Flores'.

Diagnosis. This species can be distinguished from most other species in the genus (*T. distinctus*, *T. heydeni*, *T. humeralis*, *T. lanceolatus*, *T. miles*, *T. procursus*, *T. tibialis*, *T. vaticinus*) by punctation on the pronotal disc, which is dense and coarse in *T. synhimboides*, but fine and scattered in the other species listed (Fig. 3E–G). Two species which also have dense, coarse punctation on the pronotum are *T. argenteofasciatus* and *T. warmeloi* (Fig. 2A); *T. argenteofasciatus* can be easily recognized by the presence of 'stripes' of white setae on the elytra (three dorsally and one laterally on each elytron). *Tuberocnodes warmeloi* can be differentiated from *T. synhimboides* by the punctures on the pronotum; in *T. synhimboides*, these punctures are very confluent and appear to look like microsculpturing, while in *T. warmeloi*, the punctures are only minorly confluent and are generally more separate and distinct (Figs 2 and 3G).

Description. Length 11.0–13.0 mm, width of pronotum 3.0–4.0 mm and elytra 4.0–5.0 mm. ***Head***: Prognathous. Frons with microsculpturing and scattered microtubercles; frontoclypeal suture shallow; clypeus with microsculpturing and scattered punctures, extending well beyond the epistomal ridges; labrum with scattered punctures, margin densely covered with yellowish, acuminate setae. Eyes comma-shaped, with reduced ventral part, strongly emarginate around epistomal base. Mentum trapezoidal, not fully filling buccal cavity. Antenna slender, moderately covered in recumbent acuminate goldish setae; antennomere 2 short, equal to approximately one-fourth of antennomere 3 length; antenna slightly longer than pronotum. ***Prothorax***: Pronotal lateral margin rounded, barely visible in dorsal view. Pronotum widest at middle. Disc with microsculpturing and micropunctures; anterior and basal pronotal margins complete, anterior apices not strongly produced. Hypomeron glabrous, convex, without submarginal groove, with scattered punctures. Prosternal process rounded in lateral view, slightly convex. ***Pterothorax***: Scutellum densely covered with microtubercles. Elytra elongate; widest in basal third; covered in microtubercles. Elytra extending slightly laterally at epipleura, such that margin is visible dorsally. Epipleura with scattered microtubercles; concave and angled laterally. Mesoventrite depressed at anterior half. Metanepisternal suture fairly distinct, abbreviated posteriorly. ***Legs***: with scattered microtubercles. Procoxa exposed basally. Tibiae with scattered goldish setae, apex of protibia with prominent denticle on outer margin, lateral carina present on apical three-fourth of protibia; median spur reduced, reaching half to three-fourth length of outer lateral spur. Spurs on meso- and metatibiae of equal length. ***Abdomen***: Ventrites 1–3 medially densely covered with goldish setae (males). ***Terminalia***: Ovipositor as in Fig. 6E and F, spiculum ventrale with short, reflexed arms (Fig. 6G), apex of proctiger with three evenly sized lobes, as in Fig. 6D.

Etymology. Name is highlighting the superficial resemblance of this new species to the representatives of the genus *Synhimba* Koch, 1952 (Sepidiini: Oxurina Koch, 1955).

Tapping Behavior. The observed male produced sound in a series of four to five taps.

Genus *Tibiocnodes* Gearner & Kamiński **gen. nov.**

Type Species. *Psammodes lucidus* Fåhraeus, 1870; here designated.

Diagnosis. This genus can be differentiated from related genera, such as *Ocnodes*, by the protibial ridge, which is reduced to a 'tooth' at the apex of the tibia (Fig. 3A–C). Some larger species in this genus also have tubercles on the lateral sides of the pronotum. Finally, this genus can be distinguished by the unusually long arms of the spiculum ventrale (Fig. 6C), as compared to other members of the tribe. Further diagnosis provided below.

Etymology. Name refers to the most prominent diagnostic character of the newly described genus. Gender masculine.

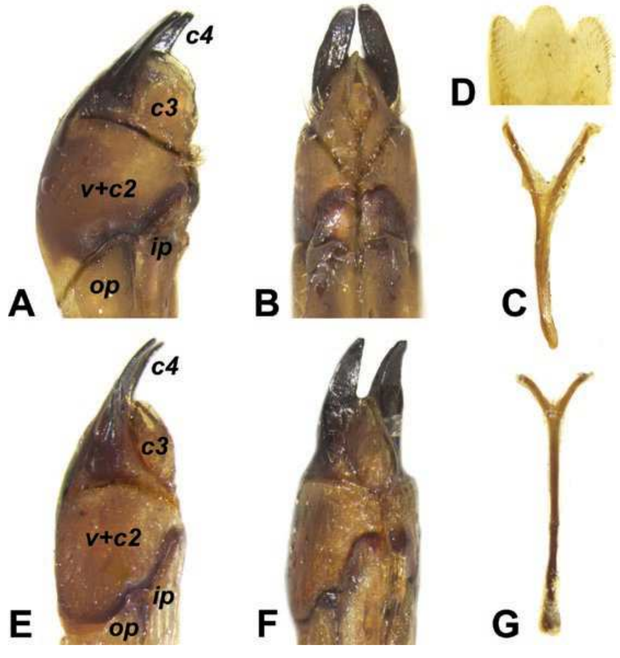

Fig. 6. Female terminalia of species representing newly established genera. (A–D) *Tibiocnodes lucidus*; (E–G) *Tuberocnodes synhimboides*. (A, B) Ovipositor; (C, G) spiculum ventrale; (D) proctiger. c, coxites; c2–c4, coxite plates 2–4; ip, inner plate of paraproct; op, outer plate of paraproct; v, valvifer.

Species Included (7). *Tibiocnodes badeni* (Haag-Rutenberg, 1871) **comb. nov.**, *Tibiocnodes herculeanus* (Haag-Rutenberg, 1871) **comb. nov.**, *Tibiocnodes discrepans* (Péringuey, 1904) **comb. nov.**, *Tibiocnodes lucidus* (Fåhraeus, 1870) **comb. nov.**, *Tibiocnodes placidus* (Péringuey, 1899) **comb. nov.**, *Tibiocnodes spinosus* (Haag-Rutenberg, 1871) **comb. nov.**, and *Tibiocnodes tristis* (Fåhraeus, 1870) **comb. nov.**

Note. It should also be noted that based on our phylogeny and apparent lack of morphological differences, except the body size, *Ti. tristis* and *Ti. lucidus* are likely synonyms; however, due to lack of access to type materials for *Ti. tristis*, we are refraining from formally synonymizing them at this time.

Full Differential Diagnosis of *Tuberocnodes* **gen. nov.** and *Tibiocnodes* **gen. nov.**

Tuberocnodes and *Tibiocnodes* can be differentiated from *Ocnodes*, *Tarsocnodes*, and *Psammorhyssus* by the protibial ridge, which is present on the apical three-fourth of the tibia in *Tuberocnodes* and is less pronounced than in *Ocnodes*, and is absent except for the apical denticle in *Tibiocnodes* (Figs. 3 and 4C). These genera can be further distinguished from *Ocnodes* and *Tarsocnodes* by the clypeus, which is on the same plane as the frons and lacks an obvious frontoclypeal suture; in the latter genera, the frons is elevated relative to the clypeus, with a well-defined suture dividing them (Fig. 4F). *Chiliarchum* also shares this facial structure lacking a frontoclypeal suture, but can be easily recognized by the submarginal area of the pronotum, which has either a broad stripe of white to yellow subtomentose hairs along the lateral carina or densely conglomerated micropunctation or granulation with associated scattered short, fine, squamulated bristles (Kamiński et al. 2021a).

Both newly described genera are easily differentiated from *Stridulomus*, which possesses a stridulatory surface on the outer edge of the epipleuron and a ridge on the hind femora for stridulation, as well as a longitudinal median depression at the base of the pronotum (Fig. 1I). *Tibiocnodes* and *Tarsocnodes* lack these characters. *Huilamus* can be easily differentiated by the flat, transverse pronotum and the distinctive abdominal setal patch in males (Fig. 1H).

Tibiocnodes is distinguished from *Psammotyria* and *Toktokkus* by the presence of tubercles on the elytra in the latter genera, which are absent in *Tibiocnodes*. *Tuberocnodes* also has tubercles on the elytra; however, in *Toktokkus* and *Psammotyria*, tubercles are present only on the slope and sides of the elytra (Koch 1955, Kamiński et al. 2021a).

Both genera can be differentiated from members of the *Dichtha* clade (*Amiantus*, *Arturium*, *Brachyphrynus*, *Dichtha*, *Distretus*, *Euphrynus*, *Glyptophrynus*, *Melanolophus*, *Phrynocolus*, *Phyrnophanes*, *Physophrynus*) by the prosternal collar and deeply punctured scutellum with a deep transverse groove which define this genus group and are lacking in the new genera. The genus *Psammophanes* also possesses an elongate prosternum, differentiating it from *Tibiocnodes* and *Tuberocnodes* (Kamiński et al. 2021a).

Moluris is also easy to distinguish from these two genera, as it lacks margination of the fifth abdominal ventrite, and has an epipleuron which is widened and rounded in the middle and an extremely convex pronotum. *Psammodes* is a large, heterogenous genus, with few consistent morphological characters (Kamiński et al. 2021a). However, there are a few characters which can generally be used to differentiate it from the new genera. Members of *Psammodes* tend to have dense setation on the legs (whereas setae are more scattered in *Tibiocnodes* and *Tuberocnodes*), lack margination on the fifth abdominal ventrite, and often possess a distinct frontoclypeal suture. Additionally, males of *Tibiocnodes* and *Tuberocnodes* usually possess a dense patch of setae on the profemora (which is lacking in *Psammodes*). Finally, *Psammodes* can be further differentiated from *Tibiocnodes* by its first and last tarsomeres on the metatibia, which are significantly longer than the other tarsomeres; and *Tuberocnodes* can be distinguished from *Psammodes* by the carina on the profemora which is lacking in *Psammodes*.

Supplementary Data

Supplementary data are available at *Insect Systematics and Diversity* online.

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of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture (USDA). The USDA is an equal opportunity provider and employer.

Author Contributions

OMG: Conceptualization; Formal analysis; Investigation; Writing – original draft; Writing – review & editing. MJK: Conceptualization; Formal analysis; Investigation; Supervision; Visualization; Writing – original draft; Writing – review & editing. KK: Investigation; Methodology; Resources; Writing – review & editing. KS: Investigation. ADS: Funding acquisition; Methodology; Resources; Supervision; Writing – review & editing.

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