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First insights into the phylogeny of tok-tokkie beetles (Tenebrionidae: Molurina, Phanerotomeina) and examination of the status of the *Psammodes vialis* species-group

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The first molecular phylogeny of the tribe Sepidiini is inferred from analyses of DNA sequence data from the following five loci (*CAD*, *wg*, *COI*, *COII*, 28S rRNA). Bayesian and maximum likelihood analyses were performed on a dataset containing 41 taxa, of which a majority represent Molurina (27) and Phanerotomeina (6). The resulting topologies were used to discuss phylogenetic placement and diagnostic characters of all of the genera representing Molurina. Within the subtribe, the results revealed paraphyly of the genus *Psammodes*. The *P. vialis* species-group, currently classified within *Psammodes*, was recovered as sister to all other Molurina genera. Based on this topology and morphological investigations, a new genus named ***Toktokkus* gen. nov.** is established. Within Phanerotomeina, *Ocnodes* is paraphyletic with regard to *Tarsocnodes*. In order to restore the monophyly of *Ocnodes*, the subgenus ***Chiliarchum* stat. nov.** is elevated to generic level. Finally, as the homology of female terminalia structures has never been fully assessed for Sepidiini, a comparative study of ovipositor morphology was conducted. As a result, this paper presents the first fully annotated ovipositors for tok-tokkie beetles.

ADDITIONAL KEYWORDS: classification – entomology – new taxa – phylogenetic – taxonomy.

INTRODUCTION

Sepidiini Eschscholtz, 1829 (Tenebrionidae: Pimeliinae) is a highly diverse (> 1000 species, 55 genera) tribe of flightless darkling beetles, with the majority of taxa residing in the Afrotropical Realm and a few species reaching the southern Western Palaearctic (Kamiński *et al.*, 2019a). Many members of this tribe, especially representatives of Molurina Solier, 1843 and Phanerotomeina Koch, 1958, are known for their substrate tapping behaviour (Supporting Information, Appendix S1). This specific form of sexual communication gives them the nickname tok-tok beetles (Lighton, 1987, 2019; Matthews *et al.*, 2010). Although Sepidiini species attract the attention of enthusiasts due to their outstanding morphology and behaviour, the group lacks comprehensive revisions at all taxonomic levels (Kamiński *et al.*, 2019a). The tribe is currently subdivided into six subtribes (Hypomelina Koch, 1955, Molurina, Oxurina Koch, 1955, Phanerotomeina, Sepidiina and Trachynotina Koch, 1955), but the monophyly of these subtribes has been questioned several times (e.g. Louw, 1979; Penrith, 1986). Although, representatives of

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Sepidiini have been incidentally included in phylogenetic studies of other groups (Doyen & Tschinkel 1982; Doyen 1994; Kergoat *et al.*, 2014), there are no targeted studies on the tribe available.

The most species-rich genus in Sepidiini is *Psammodes* Kirby, 1819 with 169 currently accepted species and subspecies (Kamiński *et al.*, 2019a). Since its description, no comprehensive revision of the genus has been performed, and the last available identification key dates back to the early 1870s (Haag-Rutenberg, 1871). Despite this, during its 200-year history many species have been placed in the genus without consideration of the synapomorphic characters that define this lineage. As a result, no reliable taxonomic definitions of *Psammodes* currently exist (Koch, 1955). Many authors have postulated the existence of well-defined species groups within the genus. One of the most commonly recognized examples is the *P. vialis* species-group based on *Psammodes vialis* (Burchell, 1822). Morphological distinctiveness of this lineage seems to be evident, as Koch (1955) suggested that it should form its own genus. However, no official nomenclatural act ever followed this opinion (Kamiński *et al.*, 2019a). Furthermore, no diagnostic characters or species composition were ever provided for this species-group.

The main aim of this study is to test the phylogenetic distinctiveness of the *P. vialis* species-group using molecular and morphological methods. Five genetic loci were sequenced from specimens across Sepidiini to determine the placement of the *P. vialis* species-group, and the morphology and composition of this potential new grouping were investigated. Because the phylogenetic analyses conducted here are the first to focus on Sepidiini, the status of several genera is discussed, namely *Dichtha* Haag-Rutenberg, 1871, *Moluris* Latreille, 1802, *Ocnodes* Fåhraeus, 1870, *Psammodes* and *Tarsocnodes* Gebien, 1920.

The revisionary part of this study resulted in the discovery of six new species. During the description process it was noticed that the homology of structures relating to the female terminalia has never been fully assessed for Sepidiini (Doyen & Tschinkel 1982; Doyen 1994). Because the female terminalia structure has proven to be phylogenetically useful for members of darkling beetles (Tschinkel & Doyen, 1980; Doyen & Tschinkel, 1982; Doyen, 1994; Iwan & Kamiński, 2016), an effort was made to incorporate ovipositors of Sepidiini within the nomenclatural system accepted for Tenebrionidae.

MATERIAL AND METHODS

TAXON SAMPLING

Molecular data generated from 39 specimens of Sepidiini (Fig. 1) were used to reconstruct a phylogeny for the tribe. Molurina is represented by 27 specimens (*Amiantus* Fåhraeus, 1870, *Dichtha*, *Moluris*, *Physophrynus* Fairmaire, 1882 and *Psammodes*), including four members of the *P. vialis* species-group and 17 of the genus *Psammodes*, six Phanerotomeina (*Ocnodes*, *Tarsocnodes*), three Trachynotina (*Somaticus* Hope, 1840), two Hypomelina (*Brinckia* Koch, 1962) and a single Oxurina (*Decoriplus* Louw, 1979). *Machla* sp. (Asidini) and *Stenocara* sp. (Adesmiini), both members of Pimeliinae (Bouchard *et al.*, 2011), were used as outgroups. Included terminal taxa were identified by comparison with type and reference material deposited at the museums listed below (Supporting Information, Appendix S2).

DNA EXTRACTION AND SEQUENCING

DNA was extracted from the heads or thoracic soft tissue of specimens preserved in 95% EtOH using DNeasy Blood & Tissue Kits (Qiagen) following the manufacturer's protocols. No cuticle was ground during the extraction process. Voucher specimens are deposited in the Purdue Entomological Research Collection (PERC) at Purdue University (Aaron D. Smith). Six non-overlapping gene regions from five loci were amplified using PCR: nuclear protein-coding genes carbamoyl-phosphate synthetase domain of rudimentary (*CAD*) (810bp), wingless (*wg*) (435 bp), mitochondrial protein-coding cytochrome oxidase subunit I Jerry/Pat (*COI JP*) (828 bp) and barcoding (*COI BC*) (657) fragments, cytochrome *c* oxidase subunit II (*COII*) (681 bp) and nuclear ribosomal 28S (1042 bp). PCRs were performed using ExTaq (Takara) with primers and thermocycler protocols given in Miller *et al.* (2013) and Kanda *et al.* (2015). PCR clean-up, quantification and sequencing were performed by the Genetics Core Facility of the University of Arizona. Cleaned PCR products were sequenced on an Applied Biosystems 3730XL DNA Analyzer. Final sequences are available on GenBank (accessions: 28S: MT241738-MT241775; *COI JP*: MT246505-MT246536; *COI BC*: MT260016-MT260054; *wg*: MT246868-MT246906; *CAD*: MT246907-MT246929; *COII*: MT246930-MT246959).

DNA ANALYSES

Assembly of chromatograms was performed with PHRED v.0.020425.c (Green & Ewing, 2002) and PHRAP v.0.990319 (Green, 1999), implemented in CHROMASEQ v.1.5 package of MESQUITE (Maddison & Maddison, 2018) with subsequent modifications by CHROMASEQ and manual inspection. Protein-coding genes were aligned in MESQUITE 3.61 (Maddison & Maddison, 2019). 28S was aligned with MAFFT

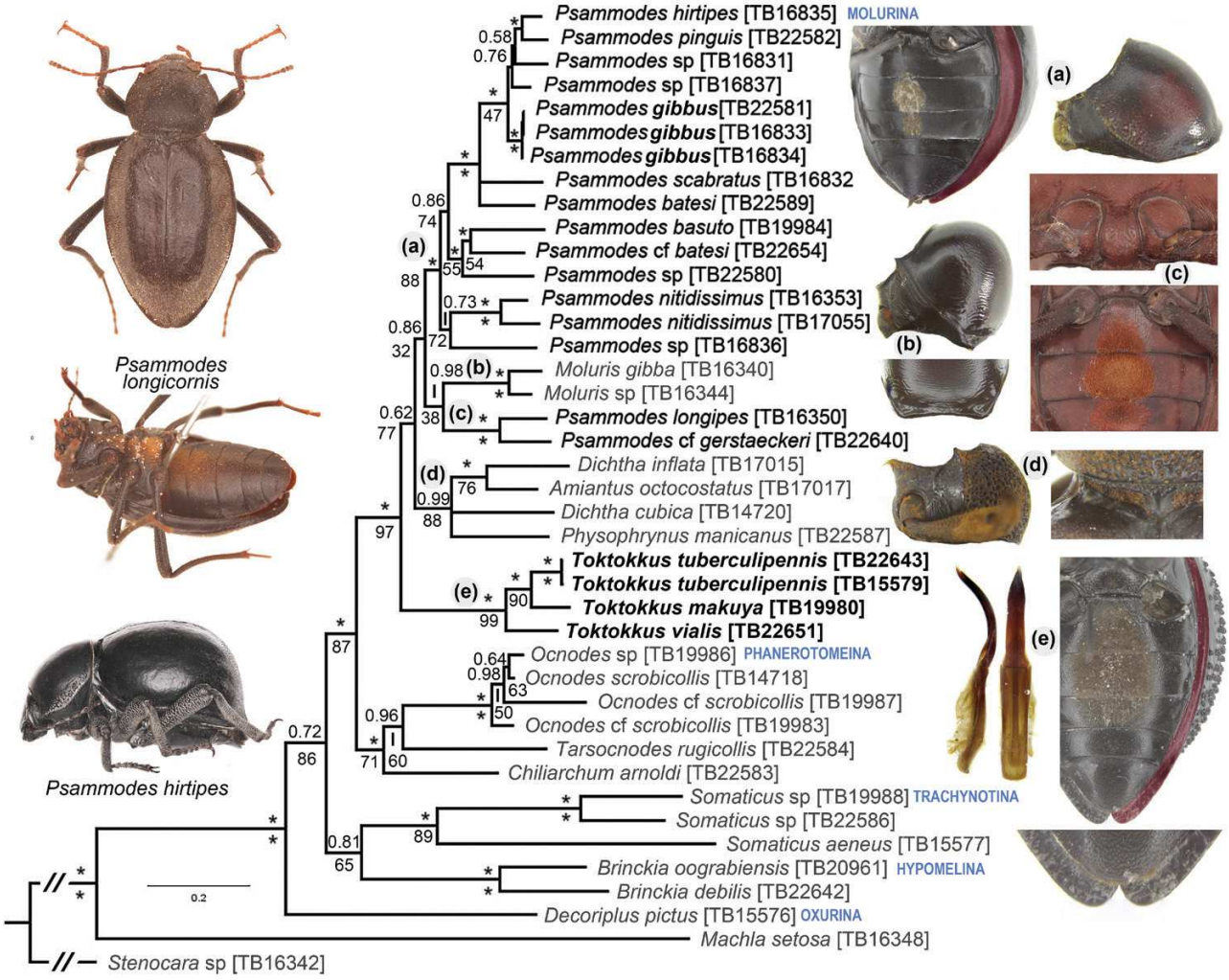

Figure 1. Phylogeny of Sepidiini imposed with new generic classification. Presented topology is the majority rule consensus of post-burn-in trees obtained in Bayesian analysis of the concatenated *CAD*, *wg*, *COI JP*, *COI BC*, *COII*, and 28S matrix. Posterior probabilities are displayed above branches, while the ultrafast IQTree bootstrap values are shown below. Morphological details shown on the right side of the figure corresponds to clades a–e on the tree. Habitus photographs presented on the left illustrates morphological incoherence of the genus *Psammodes*.

v.7.130b (Katoh & Standley, 2013) using the L-INS-i method. All alignments were concatenated into a single matrix (4453 bp) for phylogenetic analyses (Supporting Information, Appendix S3).

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), with the concatenated dataset initially partitioned by gene and codon position (for protein-coding genes). 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 1000 generations. A burn-in fraction of 25% was used, and convergence was checked by visualizing parameters in TRACER v.1.7.1 (Rambaut *et al.*, 2018). Maximum likelihood (ML) analysis was conducted using IQ-TREE v.1.6.10 (Nguyen *et al.*, 2015) on the CIPRES portal. The run was conducted with edge-proportional partition models (–spp). Branch support was estimated using 1000 ultrafast bootstrap replicates (Minh *et al.*, 2013), with the 'bnni' approach to reduce the risk of overestimating support values (Hoang *et al.*, 2018) and an increased value of maximum number of iterations to stop (–nm 10 000). Data partitions and models of sequence evolution for ML analysis were also assessed in IQ-TREE prior to phylogenetic analysis.

In discussing support for obtained relationships, the following abbreviations are used: UFB, ultrafast bootstrap; PP, Bayesian posterior probability. Node support is defined as low/weak (UFB = 70–80, PP = 0.90–0.94), moderate (UFB = 81–95, PP = 0.95–0.97) or strong/high (values above those previously mentioned).

Morphological analysis

The revisionary part of this study was based on material from the Natural History Museum (formerly British Museum of Natural History), London, England (BMNH), California Academy of Sciences, San Francisco, USA (CASC), Ditsong National Museum of Natural History, Pretoria, South Africa (TMNH), Munich Museum Bayerisches Nationalmuseum, Munich, Germany (ZSBS), Museum and Institute of Zoology of the Polish Academy of Sciences (MIZ PAS), Purdue University, West Lafayette, USA (PERC), United States National Museum of Natural, History, Washington DC, USA (USNM) and the personal collections of Kojun Kanda, Ted C. MacRae, Luboš Purchart and T. Keith Philips. The list of the morphologically studied Sepidiini species and the status of investigated specimens is presented in Supporting Information, Appendix S2.

To assess the homology of the ovipositor morphology, additional representatives of Adelostomini (Pimeliinae) were dissected (*Eurychora dilatata* Erichson, 1853 and *Lepidochora kahani* Koch, 1962; Supporting Information, Appendix S2). According to Doyen (1994), species of this tribe share some of the unique features of female terminalia with Sepidiini (e.g. spiculum ventrale with reflexed arms). Terminalia were investigated using standard methodology (see: Iwan & Kamiński, 2016). Morphological measurements were recorded using a filar micrometre. Images were taken using a Canon 1000D (Japan) body with accordion bellows and a Canon Macro Lens EF 100 mm (Japan).

RESULTS

Phylogenetic analysis

Both inference methods (BI, ML) return similar topologies (Fig. 1; Supporting Information, Appendix S4). The only difference is in a shallow clade containing *Psammodes hirtipes* (Laporte, 1840), *P. pinguis* (Solier, 1843), *P. gibbus* (Linnaeus, 1760) and two unidentified *Psammodes* species (see 'clade a' on Fig. 1). Monophyly of Molurina is strongly supported in both analyses (PP: 1.0, UFB: 97), but ML bootstrap support for monophyletic Phanerotomeina is low (UFB: 71). Phanerotomeina and Molurina are recovered sister to each other and support for the clade containing both subtribes is moderate (UFB: 87) to high (PP: 1.00) (Fig. 1). The Molurina + Phanerotomeina clade is recovered sister to Hypomelina (*Brinckia*) + Trachynotina (*Somaticus*), but support for the clade containing representatives of all of these subtribes remains low (PP: 0.72, UFB: 86). The only included representative of Oxurina (*Decoriplus*) recovers sister to all other Sepidiini (Fig. 1).

The *P. vialis* species-group does not cluster with any other *Psammodes* species (see 'clade e' on Fig. 1). The support for monophyly of *P. vialis* species-group remains high regardless of the inference method (PP: 1.00, UFB: 99). According to the recovered topologies, the genus *Psammodes* (without the *P. vialis* group) is paraphyletic with regard to *Moluris* (Fig. 1). However, the support for this clade is weak (PP: 0.86, UFB: 32). Monophyly of *Moluris* is strongly supported (PP: 1.00, UFB: 100), while support for the *Psammodes hirtipes* species-group ('clade a') varies between used inference methods from strong (PP: 1.00) to moderate (UFB: 88). Phylogenetic distinctiveness of the *Psammodes longipes* species-group ('clade c') is highly supported regardless of the approach used (PP: 1.00, UFB: 100), although the strength of support for its inclusion in a clade with *Moluris* is dependent on the analytical approach (PP: 0.98, UFB: 38). Representatives of *Amiantus*, *Dichtha* and *Physophrynus* are recovered in a single clade (PP: 0.99, UFB: 88). Both types of inference methods suggest that the genus *Dichtha* is paraphyletic with regard to *Amiantus*.

Within Phanerotomeina, *Ocnodes* is recovered as paraphyletic with regards to *Tarsocnodes*, with strong support for *Tarsocnodes* + *Ocnodes*, excluding *Chiliarchum* in the BI analysis (PP: 0.96) (Fig. 1).

Revision of the *Psammodes vialis* species-group

The studied specimens revealed a high level of morphological similarity between *Psammodes vialis* and the following species (Fig. 2): *Psammodes kuisup* (Péringuey, 1908), *P. mashunus* (Péringuey, 1896), *P. mulleri* (Péringuey, 1899), *P. schultzei* (Péringuey, 1908), *P. sellatus* Haag-Rutenberg, 1875 and *P. tuberculipennis* (Haag-Rutenberg, 1871). On the other hand, the same conclusion cannot be made for any of the type species of the genera currently included in Molurina and Phanerotomeina. Within the *P. vialis* group, two new synonymies are proposed (see Taxonomy section). No morphological discontinuities were found between *P. sellatus* and *P. vialis*. However, due to their potentially non-overlapping distributions and distinct morphology of the 'typical' forms, both are treated as subspecies of a single species. Furthermore, six new species representing the *P. vialis* species-group

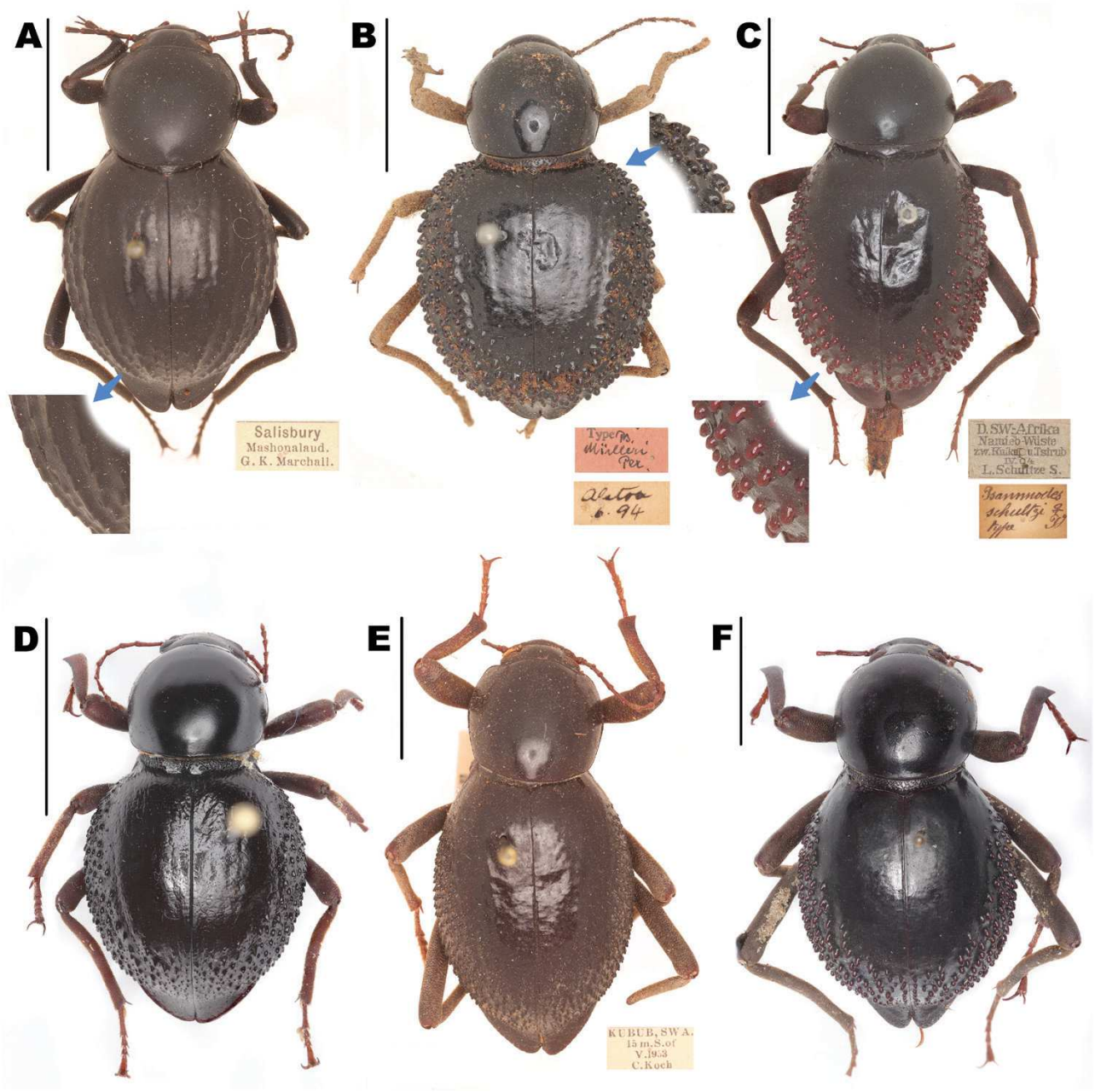

Figure 2. Habitus, morphological details, and labels of species representing *Toktokkus*: A, syntype of *Toktokkus mashunus*; B, syntype of *T. mulleri*; C, holotype of *T. schultzei*; D, specimen of *T. tuberculipennis*; E, specimen (locus typicus) of *T. vialis sellatus*; F, specimen of *T. vialis vialis*. Scale bar = 10.0 mm.

were defined during the present investigation (Fig. 3). Descriptions are given in the Taxonomy section.

Psammodes vialis is the most morphologically variable species within the group. Besides the already mentioned variability reflected in the new intraspecific classification, the representatives of this species seems to differ in overall body size (21.0–34.0 mm), body shape (round to elongate) and tubercle morphology (prominent to obscure tubercles) and arrangement (in some specimens tubercles reaching the elytral humeri). On the other hand, this species is fully diagnosable (see Identification key). Ventral and genital morphology of *P. vialis* and related species is fairly stable (Figs 1E, 6).

Based on molecular and morphological traits, the status of the *P. vialis* species-group is elevated to the genus level (see diagnosis of *Toktokkus*).

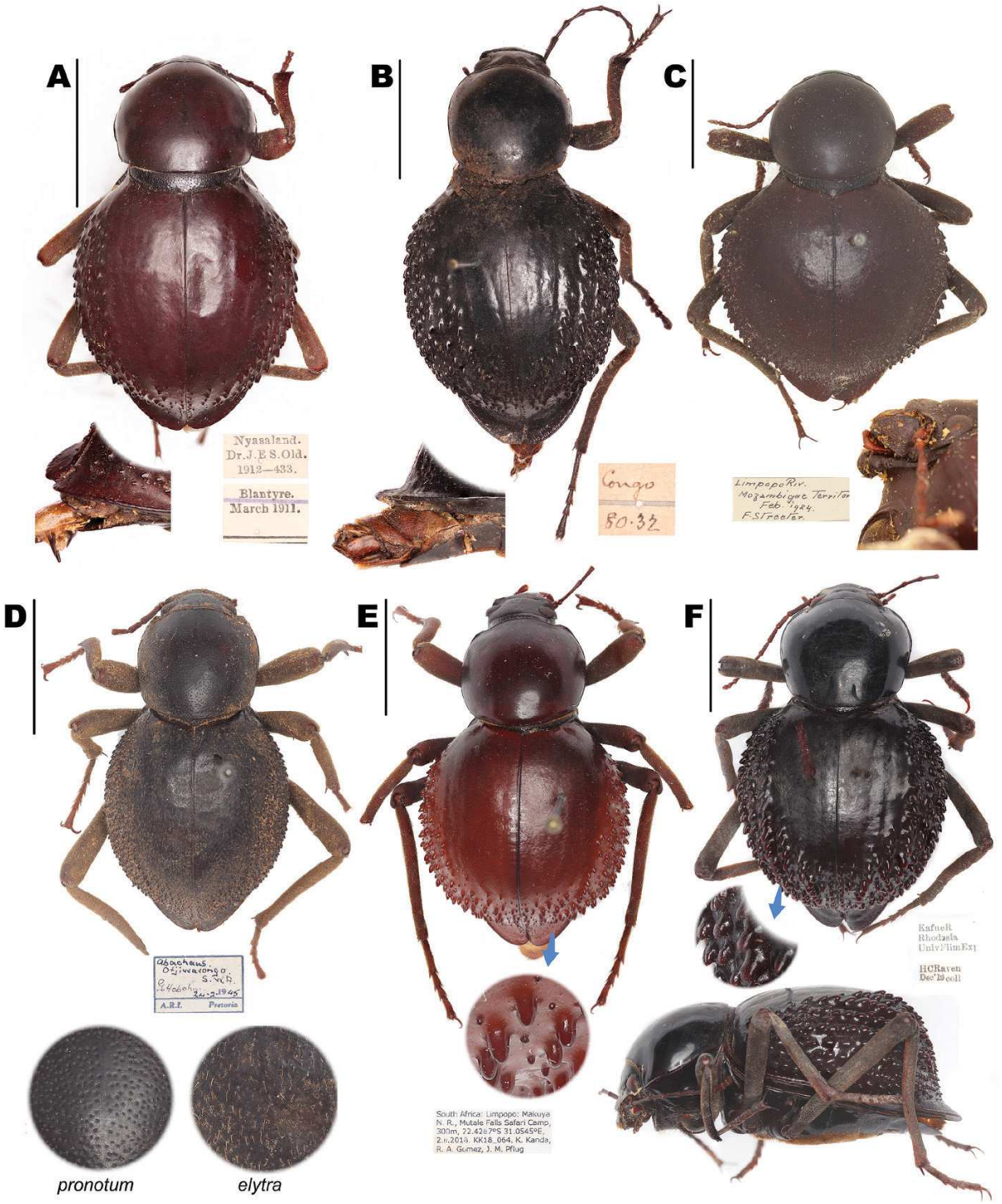

Figure 3. Habitus, morphological details, and labels of the newly discovered species representing *Toktokkus*: A, holotype of *Toktokkus barclayi* Kamiński & Gearner sp. nov.; B, holotype of *T. congolensis* Kamiński & Gearner sp. nov.; C, paratype of *T. tschinkeli* Kamiński & Gearner sp. nov.; D, holotype of *T. herero* Gearner sp. nov.; E, paratype of *T. makuya* Gearner sp. nov.; F, holotype of *T. waclawae* Kamiński sp. nov. Scale bar = 10.0 mm.

Female terminalia

Studied reference material enabled inclusion of Sepidiini ovipositors within the nomenclatural system proposed for other Tenebrionidae (Fig. 6). According to the hereby proposed hypothesis, coxites of Sepidiini are divided into three visible lobes. The basal lobe is composed of the fully fused second and basal (valvifer) plates (Fig. 6A–E, I). The third lobe is located ventrally, with the fourth lobe attached laterally. Morphology of the latter lobe seems to have diagnostic potential, especially at the generic level (Fig. 6C vs. I). However, more taxonomically comprehensive studies are required to fully confirm this statement. Gonostyli were absent in all examined Sepidiini. All ovipositors were equipped with a tuft of setae located at the base of the fourth lobe (Fig. 6C, E) and possess elongate paraprocts, with the inner plate located more apically than the outer one (Fig. 6B). This directly corresponds to the oblique (lateral view) baculus of the coxites. Furthermore, when compared to Adelostomini, females of Sepidiini are equipped with less flattened ovipositors (Fig. 6). Morphology of genital tubes seems to be stable across the tribe. All studied Sepidiini species possess multibranched spermathecae.

DISCUSSION

Phylogeny of tok-tokkie beetles

The phylogeny presented here is the first to illustrate relationships within Sepidiini (Fig. 1). Although both Bayesian and maximum likelihood analyses result in similar topologies, branch support varies between the two methods. Thus, while a complete higher level revision of Sepidiini is premature, the presented molecular analyses, combined with morphological data provides an opportunity to clarify the taxonomic status of at least some taxa.

The monophyly of the *P. vialis* species-group is supported by both inference methods used (Fig. 1). Morphological distinctiveness of this species-group is supported by the specific structure of the epipleuron, which is narrow, straight in the apical part and fully and widely embeds the fifth ventrite; and the presence of large tubercles on the elytral slope and sides (Fig. 1E). None of the currently studied species outside the *P. vialis* species-group displays this combination of characters. Therefore, based on molecular and morphological traits, the *P. vialis* species-group is hereby interpreted as a new genus separate from *Psammodes* (named *Toktokkus*; see Taxonomy section for description and species composition).

Although the distinction of this new genus helps to clarify relations among Molurina, it does not fix the taxonomic definition or phylogenetic status of *Psammodes*, which is recovered as paraphyletic with regards to *Moluris* in both analyses (Fig. 1). The sequenced representatives of *Psammodes* are divided into two groupings. The first one clusters forms that were traditionally interpreted as *Psammodes*: globular beetles with confined abdominal setal patches ('clade a'), while the other one consists of relatively flattened species with a widely distributed/diffuse central abdominal setal patch ('clade c' in Fig. 1). Investigation of the type species of *Psammodes* and its generic synonyms reveal that the morphology of *Psammodes caffra* Fåhraeus, 1870 (type species for *Parmularia* Koch, 1955) is consistent with the representatives of the first clade; while *Psammodes longicornis* Kirby, 1819 (type species of *Psammodes*) is more similar to species from 'clade c' (Fig. 1). However, as the main goal of this paper is to investigate the status of the *P. vialis* group, the number of terminal taxa representing *Psammodes* is insufficient to assess if 'clade c' can represent all non-globular forms within the genus.

An alternative approach would be to synonymize *Moluris* with *Psammodes* (Fig. 1). However, this solution would create an incoherent grouping of over 150 species (Kamiński *et al.*, 2019a), because *Moluris* is one of the best-defined genera within Molurina (hunchback pronotum; subquadrate pronotal base and scutellum; Fig. 1B), and this would only introduce unnecessary diagnostic disarray to the subtribe. Taking this into account, no taxonomic decisions are hereby made. Future phylogenetic studies should include more non-globular *Psammodes* species, including its type species, *P. longicornis*.

The remaining sampled Molurina cluster in a moderately (UFB: 88) to strongly (PP: 99) supported clade ('clade d' referred here as the *Dichtha* clade). Morphological analysis revealed that this lineage can be clearly defined by the specific structure of the prosternum (elongate and projecting tip of prosternum, in lateral view) and scutellum (often covered by deep punctation; apex with deep transverse grooves) (Fig. 1D). Based on this observation, the following genera, which were not included in the molecular analysis, can be associated with the *Dichtha* clade: *Arturium* Parmularia Koch, *Brachyphrynus* Fairmaire, 1882, *Distretus* Haag-Rutenberg, 1871, *Euphrynus* Fairmaire, 1897, *Glyptophrynus* Fairmaire, 1899, *Melanolophus* Fairmaire, 1882, *Phrynocolus* Lacordaire, 1859 and *Phrynophanes* Koch, 1951. Unlike the morphological definition of the clade itself, the diagnostic characters of the majority of those genera are blurry (Wilke, 1921; Koch, 1951, 1955, 1956, 1962; Mal, 2005). This is also reflected in the recovered paraphyly of *Dichtha* (Fig. 1). Redefinition of all the genera included in the *Dichtha* clade is beyond the scope of this paper, as the estimated diversity of this grouping reaches over 125 species and subspecies

(Kamiński *et al.*, 2019a). However, the molecular and morphological recognition of this phylogenetic lineage creates a firm background for future taxonomic work.

The last two genera of Molurina, not included in the molecular analysis, are *Psammotyria* Koch, 1953 and *Psammophanes* Lesne, 1922 (Fig. 4). In the case of *Psammotyria*, its phylogenetic affiliation can firmly be assessed based on morphological traits (Koch, 1953a). This genus mostly resembles the new genus *Toktokkus* by having straight apical portions of the epipleurae, not elongate and not projecting tip of the prosternum (in lateral view) and the presence of prominent tubercles on the elytral slopes and sides in some of the species, e.g. *Psammotyria attenuata* (Fairmaire, 1887) and

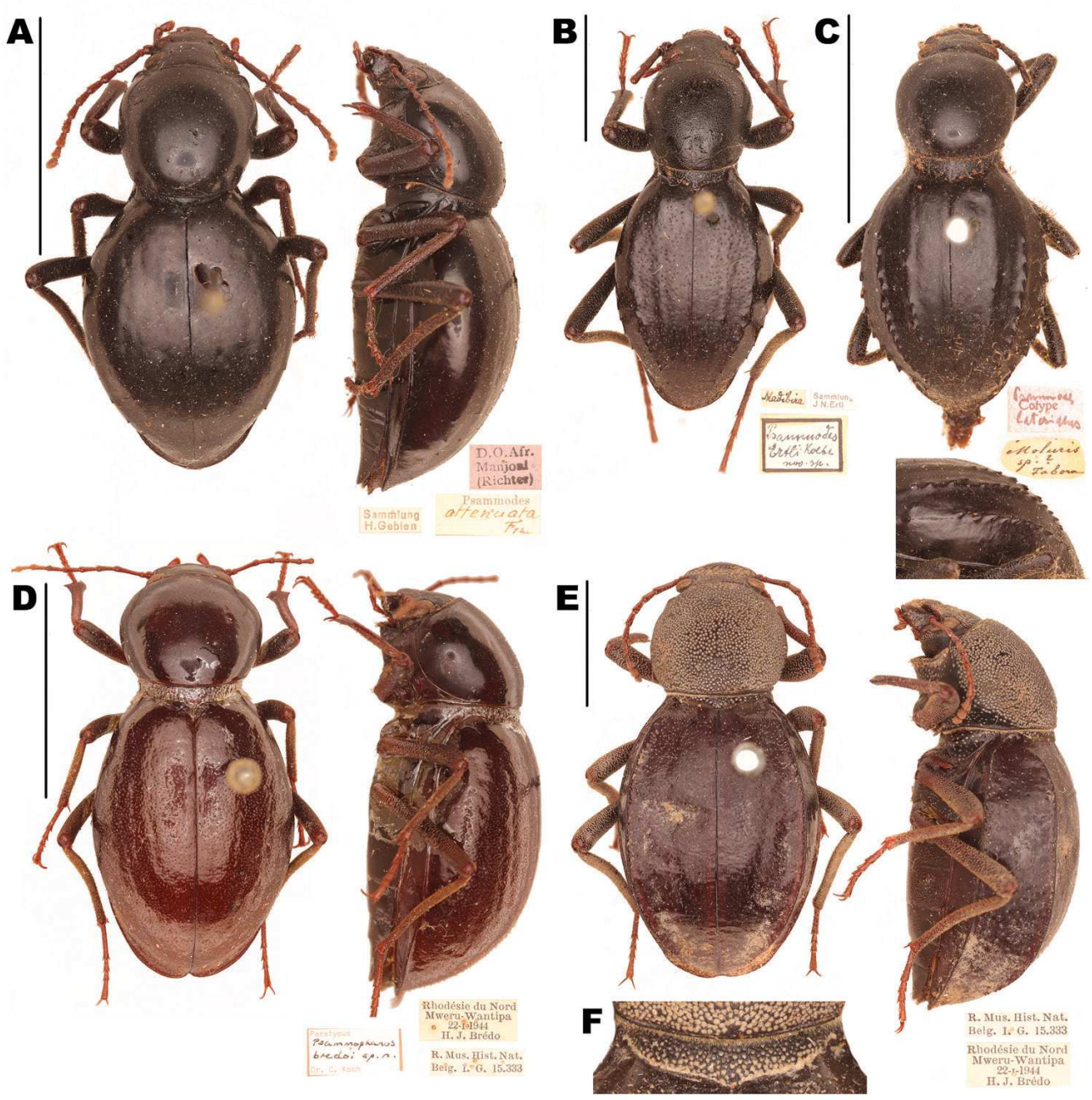

Figure 4. Habitus, morphological details, and labels of species representing Molurina: A, specimen of *Psammotyria attenuatus*; B, syntype of *Psammotyria ertli*; C, holotype of *Psammotyria lateridens*; D, paratype of *Psammophanes* (*Psammotyriopsis*) *bredoi*; E, *Psammophanes* (*Psammostretus*) *prosodoides*; F, scutellum of a syntype of *Psammophanes* (*Psammolophus*) *acuticosta*. Scale bar = 10.0 mm.

the type species *Psammotyria ertli* (Kolbe, 1904). The two genera can be distinguished by a different structure of the epipleural tip (not widely embedding the fifth ventrite in *Psammotyria*). Furthermore, in *Psammotyria* the elytral tubercles, if present, are confined to three narrow rows (Fig. 4C).

The phylogenetic position of *Psammophanes* cannot be easily assessed based on morphological data alone. The genus contains 63 morphologically diverse species and subspecies (Kamiński *et al.*, 2019a). The common feature of the examined species representing *Psammophanes* is the presence of an extremely elongated prosternum in lateral view (Fig. 4D, E). Many species also have the pronotum and scutellum deeply punctured (Fig. 4E, F). This might indicate a close relationship between *Psammophanes* and the *Dichtha* clade. However, unlike the representatives of the *Dichtha* clade, *Psammophanes* lacks apical depressions on the scutellum (Fig. 4E, F). Taking into consideration the large diversity of this genus, its monophyly should be tested by future studies.

Although this paper mostly focuses on Molurina, the analyses also revealed taxonomic issues in Phanerotomeina. *Ocnodes* is recovered as paraphyletic with regard to the Kalaharian genus *Tarsocnodes*. More specifically, *Ocnodes* (*Chiliarchum*) was recovered sister to a strongly supported clade containing *Tarsocnodes* and *Ocnodes s.s.* (Fig. 1). The morphological investigation supported the distinctiveness of *Ocnodes s.s.* with regard to *Tarsocnodes*. These two groups can be distinguished by differing tarsal structure, with tarsi strongly laterally compressed in the latter genus (Koch, 1952; Penrith, 1987). Furthermore, *Ocnodes s.s.* and *Tarsocnodes* differ distinctly from the subgenus *Chiliarchum* based on the characters listed by Koch (1954). As a result, the subgenus *Chiliarchum* is hereby recognized as a genus in Phanerotomeina (Fig. 5). For species composition, characterization and diagnosis, see the Taxonomy section below.

Figure 5. *Chiliarchum bertolonii*, one of the representatives of the newly interpreted genus of Phanerotomeina (Photo by Noël Mal).

Female terminalia

Although the morphology of female terminalia was considered essential for reconstructing phylogenetic relationships within Tenebrionidae (Tschinkel & Doyen, 1980; Doyen & Tschinkel, 1982; Doyen, 1994; Iwan & Kamiński, 2016), this is the first paper to significantly annotate ovipositors for Adelostomini and Sepidiini (Fig. 6). The assessment of homology seems to be extremely problematic in the case of many Pimeliinae tribes, since their representatives possess ovipositors largely different from the general bauplan (plesiomorphic arrangement) described for Tenebrionidae, i.e. coxites composed of four lobes arranged in a single row (Tschinkel & Doyen, 1980, Doyen & Tschinkel, 1982). In order to overcome this obstacle, some authors attempted to develop nomenclatural systems specific to particular phylogenetic groups (e.g. Pérez Vera, 2014) or to concentrate only on evidently homological structures (coxites to paraproct relations), omitting more detailed divisions, such as coxite lobation (e.g. Flores & Pizarro-Araya, 2012; Smith, 2013; Kamiński *et al.*, 2019b). However, these approaches hinder the full exploration of the phylogenetic potential of female terminalia.

From the analysed set of ovipositors, the ones dissected from *Lepidochora* (Adelostomini) are the most consistent with the plesiomorphic model described for Tenebrionidae (Fig. 6J, K). The only modifications concern the lateral arrangement of the fourth coxite lobe and the lack of gonostyli (Tschinkel & Doyen, 1980, Doyen & Tschinkel, 1982). The analysis of this morphotype enabled the determination of the following reference features for homological assessment of Sepidiini and *Eurychora* ovipositors (Fig. 6A–I, L, M): (1) longitudinally elongated fourth lobe of coxites, (2) lateral arrangement of the fourth lobe on apex of the third one, (3) base of fourth lobe reaching mid or basal portion of third lobe – never the tip of second coxite lobe, (4) presence of a tuft of setae at the basal portion of fourth lobe (dorsal view) and (5) presence of a shallow depression on the ventral side of the fourth lobe.

Using those reference points, it can be stated that the coxites of the studied Sepidiini species are divided into three visible lobes, where the basal plate is composed of the fused valvifer and second lobe (Fig. 6A–E, I). In the case of *Eurychora*, a similar conclusion can be made (Fig. 6L, M). However, the inner arrangement of fourth lobes, the presence of their shallow dorsal depressions and the ventral orientation of the setal patch, suggest that the coxite part of this ovipositor was rotated 180° in the longitudinal body axis (Fig. 6L). Therefore, the ventrally visible surface of the fourth lobe is homologous to the dorsal surface of the same lobe in the case of Sepidiini and *Lepidochora* (Fig. 6). Furthermore, the ventral surface of the third lobe, in the case of *Eurychora*, is not visible ventrally as it is wrapped in towards the ovipositor – it can be dissected by manual manipulation.

As revealed by Doyen (1994), female terminalia are extremely useful for delimiting Sepidiini from other Pimeliinae. This study supports this assumption and highlights the following features as the most phylogenetically important: (1) oblique baculus of coxites (lateral view), a feature correlated with elevation of the inner plate of the paraproct (Fig. 6A, B). (2) elongated paraprocts (Fig. 6F), (3) coxites not laterally flattened (Fig. 6A, D), (4) strongly sclerotized fourth lobes of coxites (Fig. 6A–I), (5) reflexed arm of spiculum ventrale (Fig. 6G, H), a feature shared with Adelostomini, and (6) multibranched spermatheca. On the other hand, this study revealed the diagnostic potential of ovipositors at the generic level, especially highlighted in the variability of the structure of the third and fourth lobes (Fig. 6B vs. E, C vs. I).

Taxonomy

Genus *Toktokkus* Kamiński & Gearner (Sepidiini: Molurina)

lsid urn:lsid:zoobank.org:act:801D755C-0F10-4F51-B993-9731169ECE33

Type species: Toktokkus tschinkeli Kamiński & Gearner (here designated, described below).

Diagnosis: Toktokkus can be distinguished from other Molurina by the presence of tubercles (without associated setae) on the slope and sides of the elytra (absent on disc) and by the epipleuron, which is expanded and widest at the base, surrounding the fifth ventrite. More specific features differentiating this genus from particular genera of Molurina were presented in the Discussion.

Etymology: The name refers to the common name for Molurina and Phanerotomeina: tok-tokkie beetles, an onomatopoeic name based on the sound these beetles make (gender masculine).

Distribution: Angola, Botswana, Democratic Republic of the Congo (see *T. congolensis*), Malawi, Mozambique, Namibia, South Africa, Zambia, Zimbabwe (Supporting Information, Appendix S2).

Species and subspecies included (13): ***Toktokkus barclayi*** Kamiński & Gearner **sp. nov.**, ***T. congolensis*** Kamiński & Gearner **sp. nov.**, ***T. herero*** Gearner **sp. nov.**, ***T. makuya*** Gearner **sp. nov.**, ***T. mashunus*** (Péringuey, 1896) **comb. nov.**, ***T. mulleri*** (Péringuey, 1899) **comb. nov.**, ***T. schultzei*** (Péringuey, 1908) **comb.**

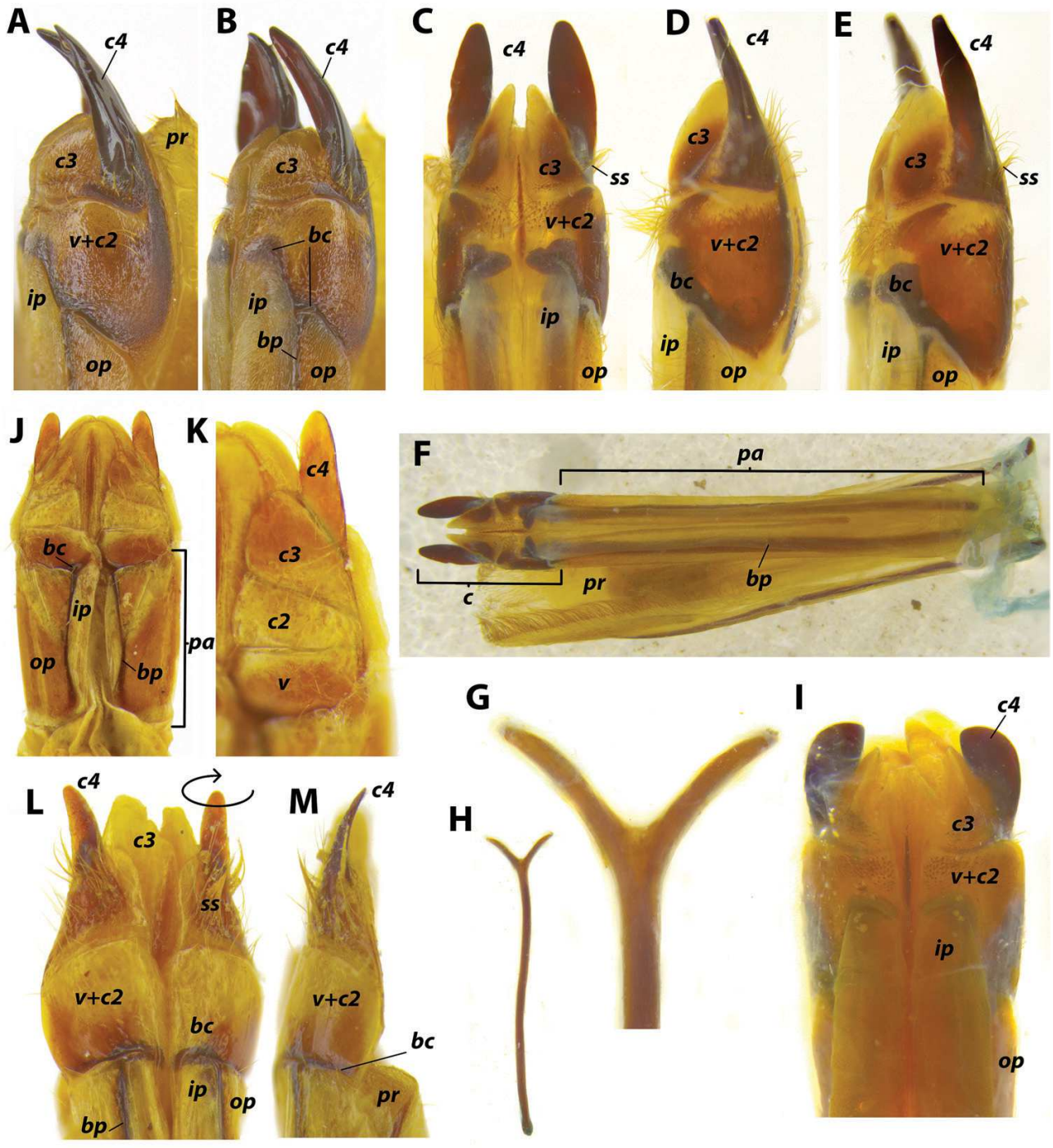

Figure 6. Female terminalia morphology of selected Sepidiini and Adelostomini: A, B, *Toktokkus tuberculipennis*; C–H, *T. waclawae*; I, *Psammodes pinguis*; J, K, *Lepidochora kahani*; L, M, *Eurychora dilatata*. Abbreviations: bc, vacuous of valvifer; bp, vacuous of paraproct;c, coxites; c2–c4, coxite plates 2–4; ip, inner plate of paraproct; op, outer plate of paraproct; pa, paraproct; pr, proctiger; ss, sensory setae; v, valvifer.

nov., ***T. tschinkeli*** Kamiński & Gearner **sp. nov.**, ***T. tuberculipennis*** (Haag-Rutenberg, 1871) **comb. nov.**, ***T. vialis vialis*** (Burchell, 1822) **comb. nov.**, ***T. vialis sellatus*** (Haag-Rutenberg, 1875) **comb. et stat. nov.**, ***T. vialis tuberculifer*** (Haag-Rutenberg) **comb. et stat. nov.**, ***T. waclawae*** Kamiński **sp. nov.**

KEY TO THE SPECIES OF THE GENUS *TOKTOKKUS*

1. Apex of elytra not sloped (dorsal view) and depressed with clear margin (Fig. 3B)..... *T. congolensis*
- Apex of elytra sloped (dorsal view) and flat to slightly convex (e.g. Fig. 3A)..... 2
2. Margin of prosternal collar expanded and folded out into a large lip (Fig. 3C); elytra round, almost heart-shaped (Fig. 3C); declivous portion of elytra with little to no tubercles..... *T. tschinkeli*
- Margin of prosternal collar not expanded, only occasionally folded out; elytra round or elongate; declivous portion of elytra with tuberculate rows..... 3
3. Disc of pronotum with prominent punctures (Fig. 3D); gold setae present on elytra (Fig. 3D)..... *T. herero*
- Disc of pronotum only with micropunctures; elytra not covered with setae..... 4
4. Tubercles on elytral sides round/globular, vertically direct (Fig. 2B, C)..... 5
- Tubercles on elytral sides pointed, directed posteriorly (e.g. Fig. 3F)..... 6
5. Elytral tubercles dense (1.0–1.5 diameters apart), laterally reaching humerus; elytra round (Fig. 2B)..... *T. mulleri*
- Elytral tubercles sparse (2–3 diameters apart), laterally terminating prior to humerus; elytra elongate to round (Fig. 2C)..... *T. schultzei*
6. Elytral tubercles sparse (4–6 lateral rows), deeply angled..... 7
- Elytral tubercles dense (more than 6 lateral rows), slightly angled (Fig. 2B–F)..... 8
7. Elytral tubercles distinct, not confluent, nearly reaching humeri (Fig. 3A)..... *T. barclayi*
- Elytral tubercles small and short, confluent into rows, terminating well before humeri (Fig. 2A)..... *T. mashunus*
8. Microtubercles present between tuberculate rows (e.g. Fig. 3E), tuberculate rows rarely elevated on ridges..... 9
- Elytral tubercles all relatively the same size, no microtubercles present between rows, tuberculate rows often elevated on ridges..... 10
9. Body size fairly small (18.0–23.0 mm); elytral tubercles relatively dense, almost confluent; tubercles relatively short..... *T. tuberculipennis*
- Body size medium to large (28.0–32.0 mm); elytral tubercles less dense, only occasionally confluent; tubercles taller..... *T. makuya*
10. Elytral tubercles large, often confluent (Fig. 3F); tuberculate rows extend over humeri to scutellum; humeri prominent; disk of elytra where smooth often flat (Fig. 3F)..... *T. waclawae*
- Tubercles medium sized (Fig. 2E, F), not confluent; tuberculate rows end at humeri; humeri not prominent; disc of elytra where smooth generally convex..... *T. vialis*

DESCRIPTION OF NEW SPECIES:

TOKTOKKUS BARCLAYI KAMIŃSKI & GEARNER

(FIG. 3A)

lsid urn:lsid:zoobank.org:act:6894F758-CA7B-45F0-8B17-CD4E32967131

Type Material: Holotype (BMNH), female: 'Blantyre. / March 1911', 'Nyasaland. / Dr. J.E.S. Old / 1912--433'. Paratype (BMNH), female: 'Kota Kota, / to Ngara / Nyasaland / Dec. 1910', 'Dr. J.E.S Old / 1914--438'.

Diagnosis: Similar to *mashunus* due to the sparse, deeply angled tubercles. This species can be distinguished from *mashunus* by its more distinct, non-confluent tubercles, which terminate closer to the humerus (Fig. 3A).

Description: Length 25.0 mm, width of pronotum 10.0–11.0 mm and elytra 14.0–16.0 mm. *Head:* Hypognathous. Frons finely punctate (2–5 diameters apart); frontoclypeal suture course, with deep groove in middle; apical clypeal margin broadly shallowly emarginate to non-emarginate; clypeus projected toward front of body; apical margin of labrum shallowly emarginate to non-emarginate medially, little to no punctation, margin of labrum densely covered with yellowish, acuminate setae. Eye comma-shaped, with reduced ventral part, strongly emarginate around epistomal base; with deep groove on temporal side. Mentum trapezoidal, not fully filling buccal cavity; longitudinal groove at middle on ventral surface; anterior margin emarginate at middle. Submentum semicircular, concave basally. Antenna slender, moderately covered in recumbent acuminate goldish setae; antennomere 2 short, equal to 0.2 of antennomere 3 length; antennomere 4 about half of antennomere 3 length; length of antenna roughly equal to pronotal length. *Prothorax:* Pronotal lateral margin rounded, well visible. Pronotum widest just posterior of middle. Disc dull, impunctate; anterior

fully marginated, posterior margin absent at middle, anterior apices strongly produced. Hypomeron convex, without submarginal groove, impunctate but weakly rugulose in places. Prosternal process rounded in lateral view with small projection by coxa, longitudinally depressed in middle (ventral view). Anterior margin of prosternum straight. *Pterothorax:* Scutellum densely covered with microtubercles. Elytra widest at middle to anterior third, slightly rounded; disc impunctate, not covered by tubercles; lateral part (below humerus) covered with tubercles (organized in ~5–6 more or less regular rows on each elytron); declivous portion on each elytron with additional 1–2 tuberculate rows with occasional scattered microtubercles; elytral margin not visible dorsally except in apical quarter, tuberculate rows extend more or less to lateral margin. Elytral slope relatively steep, elytral apex flattened. Epipleura, impunctate, not tuberculate, clearly distinguishable from neighbouring portion of elytra, widely enfolding fifth ventrite. Mesoventrite with deep median groove and elevated sides. Metaventrite impunctate, with scattered setae. Lateral regions of metaventrite (between coxae) extremely short. Metaepisternal suture abbreviated posteriorly. *Legs:* covered with dense, gold setae. Procoxa exposed basally. Apex of protibia with prominent denticle on outer margin, lateral carina terminating at middle to basal third; median spur 0.66 to equal length of outer lateral spur. Spurs on meso- and metatibiae of equal length. Tarsi narrowed laterally. *Abdomen:* Ventrites moderately to weakly punctate and weakly rugulose ventrite 5 with submarginal sulcus at anterior half. *Terminalia:* Due to scarcity of available specimens, terminalia were not dissected; however, the apical part of the coxites is visible externally in one specimen and is identical to that of the other species of this genus (Fig. 6A–H).

Etymology: This species is dedicated to Maxwell V. L. Barclay, Curator and Collections Manager of Coleoptera at the Natural History Museum in London (BMNH).

Toktokkus congolensis Kamiński & Gearner

(Fig. 3B)

lsid urn:lsid:zoobank.org:act:86883CCF-78A5-4DD3-A2C6-0AFA496EB42A

Type material: Holotype (BMNH), male: 'Congo / 80-32'.

Diagnosis: This species is most similar to *T. waclawae* due to its large, dense, confluent tubercles, but can be distinguished by the apex of the elytra, which is straight and depressed with raised margins (Fig. 3B), while in *T. waclawae* this structure is sloped and lacking a depression.

Description: Length 30.0 mm, width of pronotum 9.0 mm and elytra 12.0 mm. *Head:* Hypognathous. Frons finely punctate (2–4 diameters apart) except at middle; frontoclypeal suture course, with deep groove in middle; apical clypeal margin broadly shallowly emarginate to non-emarginate; clypeus projected toward front of body; apical margin of labrum shallowly emarginate medially, scattered punctation in apical half, margin of labrum densely covered with yellowish, acuminate setae. Eye comma-shaped, with reduced ventral part, strongly emarginate around epistomal base; with deep groove on temporal side. Mentum trapezoidal, with straight base, not fully filling buccal cavity; anterior margin not emarginate. Submentum semicircular, concave basally. Antenna slender, moderately covered in recumbent acuminate goldish setae; antennomere 2 short, equal to 0.2 of antennomere 3 length; antennomere 4 about two-thirds of antennomere 3 length; length of antenna equal to or slightly longer than pronotal length. *Prothorax:* Pronotal lateral margin rounded, well visible. Pronotum widest above middle. Disc dull, impunctate; anterior margin complete, basal margin absent at middle, anterior apices strongly produced. Hypomeron convex, without submarginal groove, impunctate. Prosternal process rounded in lateral view, longitudinally depressed in middle (ventral view). Anterior margin of prosternum straight. *Pterothorax:* Scutellum densely covered with microtubercles. Elytra widest in basal third, slightly rounded; disc impunctate, without tubercles in middle; lateral part covered with nearly confluent tubercles organized in rows; declivous portion on each elytron with additional 3–4 tuberculate rows. Elytral slope relatively steep, elytral apex depressed with raised margin. Epipleura, impunctate, not tuberculate, clearly distinguishable from neighbouring portion of elytra, widely enfolding fifth ventrite. Mesoventrite with deep median groove and elevated sides. Metaventrite impunctate, setose. Lateral regions of metaventrite (between coxae) short. Metaepisternal suture abbreviated posteriorly. *Legs:* Covered with goldish setae. Procoxa exposed basally. Apex of protibia with prominent denticle on outer margin, lateral carina terminating at middle to basal third; median spur reduced, about half of outer lateral spur length. Spurs on meso- and metatibiae of equal length. Tarsi narrowed laterally. *Abdomen:* Ventrites 1–4 medially densely covered with goldish setae, weakly punctate and weakly rugulose; ventrite 5 without submarginal sulcus, densely punctured (~0.5 diameters apart), each puncture with single

goldish setae. *Terminalia:* Due to scarcity of available specimens, terminalia were not dissected.

Etymology: Specific epithet is derived from type locality, Congo, an area in Central Africa surrounding the Congo River.

TOKTOKKUS TSCHINKELI KAMIŃSKI & GEARNER

(FIG. 3C)

lsid urn:lsid:zoobank.org:act:61AAB5AF-1529-4D7D-A25C-90FD186FE037

Type material: Holotype (deposited at USNM), male: 'Chiqubo, Mozam. / No. 11–20, II 1964 / Coll. A.L. Moore.'. Paratypes (TMNH): male: 'LimpopoRiv. / Mozambique Territory. / Feb. 1924. / F.Streeter', 'Psammodes / sp? near / tuberculipennis / det. AJH.'; female: same data but lacking the identification label.

Diagnosis: This species can be distinguished from its congeners by having margin of prosternal collar expanded and folded out into a large lip, extremely rounded elytra – almost heart-shaped, and declivous portion of elytra with little to no tubercles (Fig. 3C).

Description: Length 29.0–32.0 mm, width of pronotum 9.0–10.0 mm and elytra 19.0–23.0 mm. *Head:* Hypognathous. Frons finely punctate (3–4 diameters apart); frontoclypeal suture course, with deep groove in middle; apical clypeal margin broadly shallowly emarginate; clypeus projected toward front of body; apical margin of labrum sharply emarginate medially, densely punctate (although punctures fine) in apical half, apical side of labrum densely covered with yellowish, acuminate setae. Eye comma-shaped, with reduced ventral part, strongly emarginate around epistomal base; with deep groove on temporal side. Mentum trapezoidal, with straight base, not fully filling buccal cavity; anterior margin not emarginate; covered with fine setae. Submentum semicircular, concave basally. Antenna slender, moderately covered in recumbent acuminate goldish setae; antennomere 2 short, equal to 0.2 of antennomere 3 length; antennomere 4 about half of antennomere 3 length; length of antenna equal to 0.85 of pronotal length. *Prothorax:* Pronotal lateral margin rounded, well visible. Pronotum widest above middle. Disc dull, impunctate; anterior and basal margins, anterior apices strongly produced. Hypomeron convex, without submarginal groove, impunctate. Prosternal process rounded in lateral view, longitudinally depressed in middle (ventral view). Anterior margin of prosternum labiate, strongly projecting ventrally (lateral view). *Pterothorax:* Scutellum densely covered with microtubercles. Elytra widest in basal third, rounded laterally; disc impunctate, not covered by tubercles; lateral part (below humerus) covered with tubercles (organized in more or less regular rows) and microtubercles (2–4 diameters apart); remaining lateral part of elytra visible only ventrally, impunctate, without tubercles and microtubercles. Elytral slope steep, densely covered with microtubercles (1–4 diameters apart), with sparsely distributed tubercles, elytral apex flattened. Epipleura, impunctate, not tuberculate, clearly distinguishable from neighbouring portion of elytra, widely enfolding fifth ventrite. Mesoventrite with deep, median groove and elevated sides. Metaventrite impunctate, densely setose. Lateral regions of metaventrite (between coxae) extremely short. Metaepisternal suture abbreviated posteriorly. *Legs:* Covered with dense, goldish setae. Procoxa exposed basally. Apex of protibia with prominent denticle on outer margin, lateral carina terminating in basal third; median spur reduced, reaching 0.5 of outer lateral spur length. Spurs on meso- and metatibiae of equal length. Tarsi narrowed laterally. *Abdomen:* Ventrites 1–4 medially densely covered with goldish setae moderately punctate and weakly rugulose; ventrite 5 densely punctate and setose; ventrite 5 without submarginal sulcus, densely punctured (~0.5 diameters apart), each puncture with single goldish setae. *Terminalia:* Due to scarcity of available specimens, terminalia were not dissected.

Etymology: Named in honour of Dr Walter R. Tschinkel (Florida State University), an internationally renowned entomologist, for his outstanding contributions to darkling beetle systematics.

TOKTOKKUS HERERO GEARNER

lsid urn:lsid:zoobank.org:act:DE95E0D8-39B9-4555-AF0C-77AEDD599E20

Type material: Holotype (deposited at USNM), male: 'Abachaus./ Otjiwarongo/ S.W.A/ G. Hobohm/ 24-2-1945', 'Psammodes/ tuberculipennis/ Haag/ det. Penrith'.

Diagnosis: This species is the only known species in this genus with macroscopic punctation on the pronotum and setae on the elytra (Fig. 3D). This species can be further differentiated from *T. mashunus*, *T. mulleri*, *T. schultzei*, *T. vialis* and *T. waclawae* by the presence of microtubercles between tuberculate rows on the elytra. This species, while round, is much more elongate than *T. tschinkeli* and lacks the lip-like margin of the prosternum characteristic of *T. tschinkeli.* The tubercles in this species are smaller and less prominent than those of *T. tuberculipennis* and *T. makuya*.

Description: Length 25.0 mm, width of pronotum 8.0 mm and elytra 12.0 mm. *Head:* Hypognathous. Frons coarsely punctate (1–2 diameters apart); frontoclypeal suture course, with deep groove in middle; apical clypeal margin broadly shallowly emarginate; clypeus projected anterioventrally; apical margin of labrum emarginate medially, sparsely punctate in apical half, margin of labrum densely covered with yellowish, acuminate setae. Eye comma-shaped, with reduced ventral part, strongly emarginate around epistomal base; with deep groove on temporal side. Mentum trapezoidal, with straight base, not fully filling buccal cavity; anterior margin not emarginate; covered with fine setae. Submentum semicircular, concave basally. Antenna slender, moderately covered in recumbent acuminate goldish setae; antennomere 2 short, ~0.1–0.2 of antennomere 3 length; antennomere 4 less than half of antennomere 3 length. *Prothorax:* Pronotal lateral margin rounded, 'flared' at anterior third, well visible. Pronotum widest above middle. Disc dull, with dense punctation; anterior fully marginate, posterior margin absent at middle, anterior apices strongly produced. Hypomeron convex, without submarginal groove, rugulose and occasionally punctate. Prosternal process rounded in lateral view with small projection by coxa, longitudinally depressed in middle (ventral view) between procoxae. Anterior margin of prosternum straight, with gold setae. *Pterothorax:* Scutellum densely covered with microtubercles. Elytra widest in basal third, slightly rounded, covered in scattered gold setae; disc impunctate, with scattered microtubercles; lateral half at and below humerus and declivous portion (apical third) with alternating rows of tubercles and microtubercles (larger than those on the disc); elytral margin not visible dorsally except in apical quarter, tuberculate rows extend to lateral margin. Elytral slope relatively steep, elytral apex flattened. Epipleura impunctate, not tuberculate, clearly distinguishable from neighbouring portion of elytra, widely enfolding fifth ventrite. Mesoventrite with deep median groove and elevated sides. Metaventrite impunctate, densely setose. Lateral regions of metaventrite (between coxae) extremely short. Metaepisternal suture abbreviated posteriorly. *Legs:* Covered with dense gold setae. Procoxa exposed basally. Apex of protibia with prominent denticle on outer margin, lateral carina terminating in basal third; median spur reduced, reaching 0.5 of outer lateral spur length. Spurs on meso- and metatibiae of equal length. Tarsi narrowed laterally. *Abdomen:* Ventrites 1–3 medially densely covered with goldish setae moderately punctate and weakly rugulose; ventrite 5 densely punctate, each puncture with single gold seta (~0.5 diameters apart); ventrite 5 with submarginal sulcus only at base. *Terminalia:* Due to scarcity of available specimens, terminalia were not dissected.

Etymology: Named in honour of the Herero people of Namibia, where this species occurs.

Toktokkus makuya Gearner

lsid urn:lsid:zoobank.org:act:7265FD25-E2AF-49BD-947A-A4C6D80E0C97

Type material: Holotype (USNM), male: 'South Africa: Limpopo: Makuya / N.R., Mutale Falls Safari Camp, / 300m, 22.42°S 31.05°E, / 2.ii.2018. KK18_064. K. Kanda, / R. A. Gomez, J. M. Pflug'. *Paratypes***:** Four males and three females (Kojun Kanda): same data as holotype; male (PERC): same data but with: 'Tenebrionid Base / Aaron D Smith / Catalog # 22651'; female (CASC): 'MOZAMBIQUE / Lourenco Marques', 'ii 1957 **/** NLHKrauss'; male (CASC): '28°E18°S, Rhodesia / Hostes Nicolle Inst. / Wildlife Res. Jan. / 1974 M. B. Fenton'; male and three females (T. Keith Philips): 'SO. AFRICA: Northern Prov. just NW of Sukses, Madikela / Game Res., 12–14.III.1999 / Philips, Gerofsky, and Kryger / S24°05', E28°18"; male (CASC): 'S. AFRICA / Bechuanaland / Tsuagara / Jan. 7, 1965 / John W. Neal'; male (CASC): 'Naawpoort; / Pbg 21-11-21 / G. V. Son', 'PSAMMODES / vialis / Burchell / det. Dr. C. Koch'; three females (Luboš Purchart): 'AFRICA, MOZAMBIQUE / S 22°04.963'; E 33°55.577' / camp site / 3–4. iii. 2011', 'R. Blažek lgt.'; male (BMNH): 'Naauwpoort, / Petersburg / distr. / 25/x.1928 / G.V.Son'; male (BMNH): 'Naauwpoort, / Petersburg Distr. / 25/xii. 27. / G. van Son'; female (BMNH): 'Lake / Nigami'; male (BMNH): 'P. vialis Burchell / = pierreti Amyot / det. K.G.Blair.', 'Psammodes tuberculipennis', 'L. M. / 20-1-09', 'Pres. by / Imp. Bur. Ent. / Brit. Mus. 1925–93.', 'Lourenco Marques: / 20.1.1909 / Howard Coll.'; female (BMNH): 'ZAMBIA 1147m / Lukwakwa, West Lunga N.P. / S12°39'40", E24°26'13" / 28–29.iv.14. Light Trap / leg. Smith, R., Takano, H., / Chmurova, L, & Smith, L.', 'Psammodes / vialis / E. Ruzzier det. 2015'; male (BMNH): 'Damara Land', 'F. Bates / 81–19'; male and two females (Ted MacRae): 'R.S. Africa Northern Prov. / waterberg, Goelhoutbosh / 24°22'34" S, 27°33' 64" E', '29.xi.1999, T.C. MacRae / Nocturnally in sandy / ground in open woodland'; male (MIZ PAS): same data; three females (PERC): same data; female (XXX): 'SOUTH AFRICA 1965 / Bechuanaland 5 IV / Ngamiland Nokaneng'; two males and a female (CASC): 'SW Africa / 19° 14'S / 20° 14'E', 'CO Handley Jr / XI. 28, 1952'.

Diagnosis: The presence of microtubercles between the tuberculate rows on the elytra of this species distinguishes it from the following species: *T. mashunus*, *T. mulleri*, *T. schultzei*, *T. vialis* and *T. waclawae*. This species can be differentiated from *T. tschinkeli* by the lack of a prominent lip-like structure on the margin of the prosternum, and the elytra, while round, are more elongate than *T. tschinkeli.* The

tubercles in this species are taller and less dense than those of *T. tuberculipennis* and *T. herero*, with those of *T. tuberculipennis* being nearly confluent at times.

Description: Length 28.0–33.0 mm, width of pronotum 10.0–13.0 mm and elytra 17.0–22.0 mm. *Head:* Hypognathous. Frons finely punctate (2–4 diameters apart); frontoclypeal suture course, with deep groove in middle; apical clypeal margin broadly shallowly emarginate to non-emarginate; clypeus projected toward front of body; apical margin of labrum shallowly to sharply emarginate medially, densely punctate (although punctures often fine) in apical half, margin of labrum densely covered with yellowish, acuminate setae. Eye comma-shaped, with reduced ventral part, strongly emarginate around epistomal base; with deep groove on temporal side. Mentum trapezoidal, with straight base, not fully filling buccal cavity; anterior margin not emarginate. Submentum semicircular, concave basally. Antenna slender, moderately covered in recumbent acuminate goldish setae; antennomere 2 short, equal to 0.1–0.2 of antennomere 3 length; antennomere 4 about half of antennomere 3 length; length of antenna slightly longer than pronotal length. *Prothorax:* Pronotal lateral margin rounded, well visible. Pronotum widest at middle. Disc dull, impunctate; anterior fully marginate, posterior margin occasionally absent at middle, anterior apices strongly produced. Hypomeron convex, without submarginal groove, impunctate but weakly rugulose in places. Prosternal process rounded in lateral view with small projection by coxa, longitudinally depressed in middle (ventral view). Anterior margin of prosternum straight to slightly projecting ventrally (lateral view). *Pterothorax:* Scutellum densely covered with microtubercles. Elytra widest at middle, slightly rounded; disc impunctate, not covered by tubercles; lateral part (below humerus) covered with tubercles (organized in ~7–8 more or less regular rows on each elytron), with microtubercles scattered between rows; declivous portion on each elytron with additional 3–4 tuberculate rows with microtubercles in between; elytral margin not visible dorsally except in apical quarter, tuberculate rows extend more or less to lateral margin. Elytral slope relatively steep, elytral apex flattened. Epipleura, impunctate, not tuberculate, clearly distinguishable from neighbouring portion of elytra, widely enfolding fifth ventrite. Mesoventrite with deep median groove and elevated sides. Metaventrite impunctate, often densely setose (in males). Lateral regions of metaventrite (between coxae) short. Metaepisternal suture abbreviated posteriorly. *Legs:* Covered with dense gold setae. Procoxa exposed basally. Apex of protibia with prominent denticle on outer margin, lateral carina terminating at middle to basal third; median spur reduced, reaching 0.5 of outer lateral spur length. Spurs on meso- and metatibiae of equal length. Tarsi narrowed laterally. *Abdomen:* Ventrites 1–3 medially densely covered with goldish setae (males), moderately punctate and weakly rugulose; ventrite 5 densely punctate; ventrite 5 without submarginal sulcus. *Terminalia:* Aedeagus as in Figure 1E. Ovipositor similar to others in the genus (Fig. 6A–H).

Etymology: Named after the locality from which the holotype was collected and is also the name of a tribe in the Limpopo province of South Africa.

Toktokkus waclawae Kamiński

lsid urn:lsid:zoobank.org:act:CCA6EFFB-401D-40AF-9341-AB40107E2698

Type material: Holotype (MIZ PAS), male: 'N Rhodesia / 8 I 1942 / Dr W. Eichler', '42', 'Psammodes / pierreti Amyot'. Paratypes (MIZ PAS): male and female: 'N Rhodesia / 10 I 1942 / Dr W. Eichler'; male: 'KafueR / Rhodesia / UnivFilmEx', 'HCRaven / Dec`19 col'; male: 'Victoria Falls / Zimbabwe /??? 11–89'; female: 'Psammodes Pierreti / Solier / Zamberer', 'Sammlung / Schroeder'; female: 'ZIMBABWE Victoria / Falls, 17°56'S 25°50'E / 19–22 Dec 1995 / W.J. Pulawski collector'; male and five females (Luboš Purchart): 'AFRICA, S ZAMBIA / Victoria falls env. (Livingstone) / 26.–30.xii.1993 / leg. J. Moravec'.

Diagnosis: Similar to *T. vialis* due to the lack of microtubercles between the lateral tubercles, and presence of longitudinal ridges on elytral sides and slope. Both species can be distinguished by different morphology (larger and often confluent in *T. waclawae*) and arrangement (rows extend over humeri to scutellum in *T. waclawae*) of tubercles; and elytral disc (almost flat in lateral view in *T. waclawae*) (Fig. 3F).

Description: Length 29.0–30.0 mm, width of pronotum 9.0–10.0 mm and elytra 19.0–20.0 mm. *Head:* Hypognathous. Frons finely punctate (3–4 diameters apart); frontoclypeal suture course, with deep groove in middle; apical clypeal margin broadly shallowly emarginate; clypeus projected toward front of body; apical margin of labrum sharply emarginate medially, densely punctate (although punctures fine) in apical half, apical side of labrum densely covered with yellowish, acuminate setae. Eye comma-shaped, with reduced ventral part, strongly emarginate around epistomal base; with deep groove on temporal side. Mentum trapezoidal, with straight base, not fully filling buccal cavity; anterior margin not emarginate; covered with fine setae. Submentum semicircular, concave basally. Antenna slender, moderately covered in recumbent acuminate goldish setae; antennomere 2 short, equal to 0.2 of antennomere 3 length;

antennomere 4 about half of antennomere 3 length; length of antenna equal to 0.85 of pronotal length. *Prothorax:* Pronotal lateral margin rounded, well visible. Pronotum widest above middle. Disc dull, impunctate; anterior and basal margins, anterior apices strongly produced. Hypomeron convex, without submarginal groove, impunctate. Prosternal process rounded in lateral view, longitudinally depressed in middle (ventral view). Anterior margin of prosternum labiate, strongly projecting ventrally (lateral view). *Pterothorax:* Scutellum densely covered with microtubercles. Elytra widest in basal third, rounded laterally; disc impunctate, not covered by tubercles; lateral part (below humerus) covered with tubercles (organized in more or less regular rows) and microtubercles (2–4 diameters apart); remaining lateral part of elytra visible only ventrally, impunctate, without tubercles and microtubercles. Elytral slope steep, densely covered with microtubercles (1–4 diameters apart), with sparsely distributed tubercles, elytral apex flattened. Epipleura, impunctate, not tuberculate, clearly distinguishable from neighbouring portion of elytra, widely enfolding fifth ventrite. Mesoventrite with deep median groove and elevated sides. Metaventrite impunctate, densely setose. Lateral regions of metaventrite (between coxae) extremely short. Metaepisternal suture abbreviated posteriorly. *Legs:* Covered with dense, goldish setae. Procoxa exposed basally. Apex of protibia with prominent denticle on outer margin, lateral carina terminating in basal third; median spur reduced, reaching 0.5 of outer lateral spur length. Spurs on meso- and metatibiae of equal length. Tarsi narrowed laterally. *Abdomen:* Ventrites 1–4 medially densely covered with goldish setae moderately punctate and weakly rugulose; ventrite 5 densely punctate and setose; ventrite 5 without submarginal sulcus, densely punctured (~0.5 diameters apart), each puncture with single goldish setae. *Terminalia:* Aedeagus as in Figure 1E. Ovipositor as in Figure 6C–H.

Etymology: This new species is dedicated to the memory of the first author's grandmother, Wacława Kamińska (born on 5 November 1927 in Bartniki, Poland, died on 29 September 2010, in Warsaw, Poland).

Synonymy notes:

Toktokkus vialis sellatus (Haag-Rutenberg)

= *Psammodes kuisup* Péringuey, 1908, synon. nov. (as *P. 'kuisip'* in Gebien, 1937 and Kaminski *et al.*, 2019a).
= *Psammodes sellatus uriai* Koch, synon. nov.
Justification: When describing *Psammmodes kuisup* (in erratum, referred to in the description as *Psammodes tuberculipennis*), Péringuey (1908) was apparently unaware of *Psammodes sellatus* Haag-Rutenberg and, therefore, did not provide diagnosable characters to differentiate the two species. Examination of specimens, including the *P. sellatus* holotype and a specimen collected at the type locality and determined by Koch as *P. kuisup*, and comparison of the species descriptions, reveal no easily diagnosable characters between these two species.

Koch (1953b) described the subspecies *P. sellatus uriai* as differing from *P. sellatus sellatus* by the following characters: a more elongate body, a slenderer pronotum with less prominent punctation and tubercles less dense and organized in rows (as opposed to denser and more irregular in *sellatus*). However, when comparing specimens, these differences appear minor and not sufficient to justify classifying these as separate subspecies.

Notes on Phanerotomeina:

Genus *Chiliarchum* Koch (Sepidiini: Phanerotomeina)

lsid urn:lsid:zoobank.org:act:CB712371-B604-4D1B-93A2-1258C6920572
Type species: Moluris (*Phanerotoma*) *bertolonii* Guérin-Méneville (by original designation).

Diagnosis: From Koch (1954): submarginal area of the sides of the pronotum, and often that of the elytra, with either a broad stripe of white to yellow subtomentose hairs along the lateral carina or with densely conglomerated micropunctation or granulation with associated scattered short, fine, squamulated bristles; pronotum with two prebasilar impressions at or near the posterior angles, filled with pale subtomentose hairs or densely micropunctured with scattered short, fine bristles; males with a reddish brown brush of hairs on the outer edge of the upper surface of the mesotibiae, sometimes extending to the tibial base.

Species and subspecies included (8): ***Chiliarchum arnoldi arnoldi*** (Koch, 1952) **comb. nov.**, ***C. arnoldi sabianus*** (Koch, 1952) **comb. nov.**, ***C. bertolonii*** (Guérin-Méneville, 1844) **comb. nov.**, ***C. freyi*** (Koch, 1952) **comb. nov.**, ***C. guerini guerini*** (Haag-Rutenberg, 1871) **comb. nov.**, ***C. guerini lawrencii*** (Koch, 1954) **comb. nov.**, ***C. guerini mancus*** (Koch, 1954) **comb. nov.**, ***C. junodi*** (Péringuey, 1899) **comb. nov.**

CONCLUSIONS

From the phylogenetic analysis of 39 taxa representing Sepidiini and a supplementary morphological investigation, the following conclusions can be drawn:

1. Results from the phylogenetic analysis highlight the need for a taxonomic revision of several genera representing Molurina and Phanerotomeina (e.g. *Dichtha*, *Psammodes*, *Ocnodes*).
2. In its previous systematic concept, *Psammodes* remained paraphyletic with respect to the *Dichtha* clade and the genus *Moluris*. Designation of the *P. vialis* species-group as a separate genus (named herein *Toktokkus*) partially clarifies the taxonomic status of *Psammodes*.
3. *Toktokkus* encompasses 11 southern and central African species, which all can be easily distinguished from other Molurina by the specific structure of epipleuron (apex widely embedding fifth ventrite) and elytra (presence of tubercles).
4. The genus *Ocnodes* is recovered paraphyletic with respect to *Tarsocnodes*, but the establishment of *Chiliarchum* at the genus level has restored its monophyly.
5. The results of the performed comparative analysis of the female terminalia morphology enabled the assessment of homology of the ovipositors within Sepidiini (and partly in Adelostomini).

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Mention 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 USDA. The USDA is an equal opportunity provider and employer.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Tapping behaviour displayed by *Toktokkus vialis* (Namibia).
Appendix S2. Additional data on studied material.
Appendix S3. Nexus-format matrix of molecular data spanning six non-overlapping gene regions from five loci (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) fragments, cytochrome oxidase subunit II (*COII*) (681 bp), and nuclear ribosomal 28S (1042 bp)) for sampled taxa ($N = 41$).
Appendix S4. Maximum likelihood topology obtained in IQ-Tree analysis.