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Saprininae: Phylogeny, biogeography and a new classification of the subfamily (Coleoptera: Histeridae)

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Abstract

With 74 genera and subgenera and approximately 740 species, Saprininae represent one of the largest subfamilies of Histeridae (Coleoptera: Histeroidea). Here, we present a phylogenetic hypothesis for Saprininae based on comprehensive taxonomic sampling. This is the first phylogenetic study combining molecular and morphological approaches (cytochrome *c* oxidase subunit 1, 18S ribosomal RNA and 93 morphological characters). As a result, we propose a new classification; five new tribes are erected: **Myrmetini** Portevin **stat. and sens. nov.**; **Euspilotini** Lackner, **trib. nov.**; **Eremosaprinini** Lackner, **trib. nov.**; **Saprinini** Blanchard, **sens. nov.**; and **Hypocaccini** Lackner, **trib. nov**. Additional nomenclatural acts are as follows: *Chelyoxenus* Hubbard is downgraded to a subgenus of *Geomysaprinus* Ross, thus *Geomysaprinus* (*Chelyoxenus*) **stat. nov.**, *Nessus* Reichardt is transferred from a subgenus of *Hypocaccus* C. Thomson to a subgenus of *Hypocacculus* Bickhardt, thus *Hypocacculus* (*Nessus*) **stat. rest.** The following taxa *Paraphilothis* Vienna, *Styphrus* Motschulsky, *Xerosaprinus* Wenzel, *Lophobregmus* Wenzel, *Vastosaprinus* Wenzel, *Auchmosaprinus* Wenzel, *Hemisaprinus* Kryzhanovskij & Reichardt, *Reichardtia* Wenzel and *Australopachylopus* Lackner & Leschen are all downgraded into subgenera of *Saprinus* Erichson. Thus, *Saprinus* (*Paraphilothis*) **stat. nov.**, *Saprinus* (*Styphrus*) **stat. nov.**, *Saprinus* (*Xerosaprinus*) **stat. nov.**, *Saprinus* (*Vastosaprinus*) **stat. nov.**, *Saprinus* (*Auchmosaprinus*) **stat. nov.**, *Saprinus* (*Lophobregmus*) **stat. nov.**, *Saprinus* (*Hemisaprinus*) **stat. rest.**, *Saprinus* (*Reichardtia*) **stat. nov.**, *Saprinus* (*Australopachylopus*) **stat. nov.** A new genus, *Paraxenus* Lackner **gen. nov.**, is proposed for the former South African and Namibian members of the genus *Pholioxenus* Reichardt, with the following new combinations: *Paraxenus diasi* (Vienna) **comb. nov.**; *Paraxenus eremicola* (Thérond) **comb. nov.**; *Paraxenus namibiensis* (Vienna) **comb. nov.**; *Paraxenus oleolus* (Thérond) **comb. nov.**; *Paraxenus therondi* (Olexa) **comb. nov.**; and *Paraxenus uhligi* (Mazur) **comb. nov.** Additionally, based on the analysis of the dispersal patterns, **Myrmetini** appear to be a bipolar (amphitropical) clade, while **Eremosaprinini** appear to be exclusive to the Western Hemisphere. **Euspilotini** are strongly represented in the Western Hemisphere, with only a handful of species known from the Palaearctic/Oriental regions. **Saprinini** and **Hypocaccini** are spread worldwide but are poorly represented in South America. The Holarctic (in particular the Nearctic) Region is proposed as the centre of origin of the subfamily around 80 million years ago (Ma). Inquilinism is hypothesised to be the ancestral state for the group, with several subsequent independent shifts in life histories.

Saprininae cladogenesis occurred mainly during the Palaeogene (66–23.03 Ma) and could be linked to the diversification of mammals.

KEYWORDS
ancestral state reconstruction, biogeography, clown beetles, evolution, inquilinism, integrative taxonomy, morphological characters

INTRODUCTION

Histeridae are commonly known as clown beetles or Stutzkäfer in German—meaning 'truncated' beetles—in both cases due to their highly characteristic body shape. Comprising of more than 4834 described species worldwide in nine extant subfamilies, the family ranks among the more diverse beetle families (Bouchard et al., 2011). Despite a relatively conserved general morphology, histerid lineages have diversified into a remarkable array of highly specialised ecomorphological forms. Many are thought to have convergently evolved across multiple lineages (Kovarik & Caterino, 2016; Lackner et al., 2019), allowing them to inhabit various specific habitats. Based on current knowledge, most histerids are predaceous in their larval and adult stages, preying upon fly larvae, although attacks on adult flies have also been reported (Carlton et al., 1996). Thus, they are important in controlling fly abundance in nature (Kovarik & Caterino, 2016). Additionally, the presence of histerid beetles on corpses may help to estimate the post-mortem interval, making them an interesting group for forensic entomology (Shayya et al., 2018).

The second most species-rich subfamily of Histeridae are the Saprininae (Figure 1), containing currently 739 species in 74 genera and subgenera (Newton, 2022). Saprininae have a worldwide distribution, except in the polar regions. Most species occur in warm, arid regions and avoid mesic, densely forested areas of the tropics and torrid regions alike. Additionally, highly specialised psammophilous (sand-adapted) species occur in the dune systems of large sand bodies worldwide (e.g. the Sahara or the Namib Desert), while other taxa inhabit beach dunes (Lackner et al., 2019). The majority of Saprininae are generalist predators; these beetles are biologically versatile, colonising the burrows and nests of birds, mammals and even tortoises. Furthermore, they can be found in arboreal ant colonies, anthills or termitaria (Lackner, 2014b), but the feeding habits of these specialised taxa remain a mystery, as there is no definite proof of them being predaceous or cleptoparasitic.

Taxonomy and morphology of the Saprininae have received much attention during the past century. Reichardt (e.g. Reichardt, 1926, 1929, 1932) published numerous taxonomic works, including the first attempted monograph of the subfamily, establishing several saprinine genera. Peyerimhoff (1936) provided a critical overview of Reichardt's earlier works. Later, Kryzhanovskij (1959, 1972, 1987), Kryzhanovskij and Reichardt (1976), Wenzel (1962) and Dahlgren (e.g. Dahlgren, 1964) contributed much to the knowledge of the taxonomy of the subfamily. More recently, Olexa (1984, 1990) focused on specialised inquilines and psammophiles. On the other hand, Vienna (e.g. Vienna, 1994, 1995) published mainly on African and Arabian Saprininae. The South American Saprininae have been the focus of works by Arriagada (1987, 2017, 2018). Most of these studies were descriptive in their nature and few (e.g. Peyerimhoff, 1936) tried to pinpoint putative synapomorphies of higher taxa. Traditionally, the presence/absence of frontal stria, or presence/absence of prosternal foveae were used as diagnostic characters; later Lackner (2014b) regarded them as homoplasious. De Marzo and Vienna (1982a) published a morphological study focused on the sensory structures inside antennal club of the Saprininae (so-called 'Reichardt's organ') depicting and describing several morphological manifestations of this structure with hints to its possible phylogenetic implications. The same authors published later that year (De Marzo & Vienna, 1982b) yet another similar study, this time focusing on the spermatheca. The first author of the present article began publishing on the taxonomy of Saprininae approximately 20 years ago and has continued

FIGURE 1 *Saprinus* (*S.*) *amethystinus* Lewis, a member of the subfamily.

this work to date (see e.g. Lackner, 2010 for the summary of Palaearctic higher taxa).

In general, Saprininae classification was built upon the works of Reichardt (1932) and Kryzhanovskij and Reichardt (1976) for the Palaearctic fauna; the Nearctic fauna has been classified based on the work of Wenzel (1962). All three world catalogues of the Histeridae (Mazur, 1984, 1997, 2011) presented a subfamily classification without any phylogenetic backbone. Saprininae were recovered as the sister group to Abraeinae and Dendrophilinae by Ôhara (1994) who presented the first morphology-based phylogeny of the family. Ślipiński and Mazur (1999) who published the second, similarly constructed phylogeny of the Histeridae retrieved similar results, with Abraeinae, Dendrophilinae and Saprininae grouped together in their 'Abraeomorphae'. Caterino and Vogler (2002) were the first to include morphological (larvae and adults) as well as molecular characters in their phylogeny of the superfamily Histeroidea. Their results were similar and suggest that the Dendrophilinae (in part) and Abraeinae are the best contenders for being sister groups to the Saprininae. Based on these results, Lackner (2014b) and Lackner et al. (2019) picked representatives of Abraeinae and Dendrophilinae as outgroups when trying to reconstruct the phylogeny of the subfamily Saprininae—a pattern also followed here.

Phylogenetic hypotheses for the Saprininae have recently been used to better understand the evolution of this group. Saprininae are monophyletic (Lackner, 2014b), with two morphological autapomorphies: the presence of a specialised sensory apparatus on/and in the antennal club (formerly called 'Reichardt's organ') as well as open antennal cavities not covered by the prosternal 'alae'. Their monophyly has recently been confirmed by a molecular phylogenetic analysis (Lackner et al., 2019). Lackner (2014b) suggested multiple ecological shifts in the Saprininae evolution, but those results have not been decisive enough to offer a new classification. The impact of female genitalic characters on the subfamily's evolution has been studied by Lackner and Tarasov (2019). The evolution of sand adaptation (psammophily) has been reviewed by Lackner et al. (2019). A biogeographic synthesis of the group has never been attempted, although Lackner (2010) hinted at the possible Palaearctic origin of the subfamily with 'Out-of-Gondwana' as an alternative scenario.

This article is focused on inferring a phylogeny by combining DNA data and morphological characters based on broad taxonomic and geographic sampling. Further, we investigate the biogeographic origins of saprinine diversity, refine the age of subfamily and its major clades and perform ancestral state of the habitat-shift reconstruction using probabilistic methods. We concentrate on critically evaluating tribal to intergeneric level resolution. New nomenclatural acts are proposed accordingly.

MATERIALS AND METHODS

Taxon sampling, character sampling and morphological analyses

The matrix for inferring phylogenetic relationships was assembled using 107 species/subspecies of Saprininae belonging to 35 genera/subgenera (~50% of the higher taxa globally) from all over the world and combined with three outgroup taxa representing the subfamilies Abraeinae and Dendrophilinae (regarded as Saprininae sister groups, see also above) + *Sphaerites glabratus* (F.) (a representative of the closely related family Sphaeritidae); for more details, see Supporting Information S1. The taxa used in our work originate from all biogeographic regions in which they occur; the majority originate from the Palaearctic Region (42 spp., ~40%), followed by the Nearctic Region (29 spp., or ~27%), Afrotropical Region (14 spp., or ~13%), Australasian Region (11 spp., or ~10%), Neotropical Region (9 spp., or ~8%) and Oriental Region (2 spp., or ~2%). Based on published previous morphological evidence (Lackner, 2010), our sampling covers most of the taxonomic and geographic diversity of the subfamily, and thus can be expected to limit possible biases in biogeographical analyses. Compared to previous studies on the phylogeny of Saprininae, the morphology-based study of Lackner (2014b) contained 72 in-group terminals representing 64 saprinine higher taxa. Lackner (2014b) used mostly type species of each (sub)genus plus eight additional species belonging to heterogeneous (sub)genera, to test their monophyly.

Most of the material used is deposited in the collection of the first author, housed temporarily at ZSM (Munich, Germany). The following institutions were visited and the material was loaned: Santa Barbara Museum of Natural History, Santa Barbara, USA (SBMNH), National Museum of Natural History, Prague, Czech Republic (NMPC), Staatliches Museum Für Naturkunde, Stuttgart, Germany (SMNS) and New Zealand Arthropod Collection (NZAC). All curators of the institutions mentioned above and private persons providing material for this study are mentioned in the Acknowledgements.

Morphological characters represent external and internal structures (male and female genitalia) of all terminals. Morphological techniques followed those of Lackner (2014b), while morphological terminology followed Ôhara (1994) and Lackner (2010). The selection of morphological characters used in the analyses represents a combination of previous studies (Lackner, 2014b; Lackner & Tarasov, 2019) plus several additional characters. After critical consideration, several multi-state or highly variable characters (e.g. the shape of spiculum gastrale) were excluded from the analyses. For the complete list of characters and their states, see Supplementary File S2.

The selection of OTUs (Operational taxonomic unit used in the morphology-based analyses was identical to those found in the molecular part of the study. In total, 93 morphological characters of adults were scored (multi-state coding) and analysed. The characters were treated as non-additive; inapplicable characters were assigned a gap value ('–') and treated as equivalent to missing data ('?'). Data were entered directly into MacClade 4.08 (Maddison & Maddison, 2005). Parsimony analysis was conducted in TNT 1.5 (Goloboff et al., 2008) under implied weighting, at the weighting function $K = 9$, using the 'New Technology' strategy (sectorial search and tree fusing), the consensus was stabilised 10 times with the default factor 75. The character mapping was performed in WinClada v.1.61 (Nixon, 1999–2002); the strict consensus was subsequently visualised and edited in Adobe Illustrator® CS5. Standard bootstrapping (1000 replicates) was also conducted in TNT; trees were annotated in Adobe Illustrator® CS5.

We also analysed the morphological data using IQ-TREE 2 (Minh et al., 2020) under the Mk model (Lewis, 2001) with 1000 Ultrafast Bootstrap support with 95% considered as highly supported (UFboot; Hoang et al., 2018). The complete matrix used for the morphological analyses can be found in Supplementary File S10.

SEM micrographs and line drawings

Scanning electron micrographs were taken with a JSM 6301F camera at the laboratory of the Faculty of Agriculture, Hokkaido University, Sapporo, Japan. Digital photographs of male terminalia, mouthparts and antennae were taken with a Nikon 4500 Coolpix camera and edited in Adobe Photoshop® CS5. Based on the photographs or direct observations, the genitalia, mouthparts and antennal structures were drawn on a light-box HAKUBA KLV-7000. All illustrations (except for the male genitalia) were later scanned and elaborated using Adobe Illustrator® CS5.

DNA extraction, PCR amplification and sequencing

Total genomic DNA was extracted from museum specimens using the DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany). The specimens were pierced with a pin in their metathoracic or abdominal area to facilitate thorough tissue lysis. Polymerase chain reactions were carried out in a total volume of 25 µL containing 5 µL Mango Buffer (5× reaction buffer, coloured; Bioline, Luckenwalde, Germany), 2 µL dNTPs (10 mM dNTP Mix; Bioline), 1.25 µL MgCl2 (50 mM; Bioline), 1 µL of each primer (10 mM; Metabion International AG, Planegg, Germany) and 0.5 µL MangoTAQ (5 U/µL; Bioline). For primer sequences and thermocycling conditions, see Supporting Information S3 and S4.

Three fragments from two genes were analysed in this study: the 5′ part and the 3′ part of the mitochondrial cytochrome *c* oxidase subunit 1 (*CO1*) and the partial nuclear 18S rRNA (*18S*) gene. In the alignment of concatenated sequences (2080 bp total length), 805 bp corresponded to the 3′ end of the *CO1* gene, 658 bp to the 5′ end of the *CO1* gene and 617 bp to the partial 18S gene. The rest of the laboratory work follows Lackner et al. (2019).

Phylogenetic and dating analyses

All sequences were aligned using MAFFT 7.2 (Katoh & Standley, 2013) with the Q-INS-I algorithm with default parameters; the protein-coding fragments were checked for correct reading frames and stop codons. To identify ambiguous or random similarity in alignment, we applied Aliscore v.2.076 (Misof & Misof, 2009) with the -e option and default settings and subsequently masked problematic sites using Alicut v.2.3 (Kück et al., 2010; github.com/mptrsen/scripts/blob/master/ALICUT_V2.3.pl). A maximum likelihood analysis was conducted using IQ-TREE 2 (Minh et al., 2013). The substitution models were identified using ModelFinder (Kalyaanamoorthy et al., 2017; see Supporting Information S5) under the Akaike information criterion (AIC). For estimates of support, 1000 replicates of ultrafast bootstrapping, SH-like approximate likelihood ratio tests (SH-aLRT; Guindon et al., 2010) with 80% considered to be highly supported and approximate Bayes tests (aBayes factor, values higher than 0.95 are considered as highly supported; Anisimova et al., 2011) were performed. Finally, we performed a combined analysis of molecular data with the same settings as above, with an additional partition for the morphological data.

Due to the inaccessibility of known fossils classified as Saprininae and/or problematics of Histeridae inter-subfamilial relationships (see e.g. Caterino & Vogler, 2002; Zhou et al., 2020; or Simon-Pražák et al., 2023), we used secondary calibrations to estimate divergence time based on age estimates from a comprehensive phylogenomic study focusing on the evolutionary history of Coleoptera (Zhang et al., 2018). Divergence times at nodes were estimated with BEAST v.1.8.1 (Suchard et al., 2018) using the fixed topology corresponding to the best-scoring tree from the maximum likelihood analysis. The root was set to 113 Ma (first split in Histeridae; Che et al., 2017) with and normal distribution (standard deviation of 5.0), corresponding to 95% time-space interval of 121–104 Ma. The dataset was partitioned according to (A) concatenated *CO1* fragments and (B) *18S* gene, with an unlinked site model and the HKY + I + G substitution model. The tree prior was set to a birth-death speciation process (Gernhard, 2008). The analysis was run for 100 million generations, with a 10,000 sampling frequency. Tracer v.1.7 (Rambaut et al., 2018) was used for checking for the convergence of the run to ensure the ESS (Effective sample size) are all above 200. The maximum credibility tree was estimated using TreeAnnotator v. 1.10 (Suchard et al., 2018) after discarding the initial 30% of trees as burn-in.

Ancestral character state reconstruction and historical biogeography analyses

Joint stochastic character mapping (Huelsenbeck et al., 2003) was performed using the R package *Phytools* v.1.5.1 (Revell, 2012) in R v4.2.2 (R Core Team, 2022) using the dated phylogeny as input after removing the outgroups. The ecology of each species was coded using the following discrete traits: **inquiline** (occurring in nests of other organisms, e.g. termites, ants, reptiles, birds and small mammals), **cavernicolous** (found predominantly in caves on bat guano), **free-living** (found in open spaces mostly on carcass, dung or other decomposing organic matter), **littoral** (found along the coasts mostly under wrack or seaweed), **psammophilous** (living deep in sand of various dune systems, found mostly at the roots of vegetation entombed by sand) or **xerophilous** (found predominantly in arid/sandy regions, but not in deep sand) following Lackner et al. (2019). In contrast to Lackner et al. (2019), we combined their categories 'xerophile' and 'semi-psammophile' into one category, which we labelled 'xerophile' based on the fact that there are several salient morphological features whose clear separation is not straightforward. Our 'psammophilous' category mirrors thus 'ultra psammophile' of Lackner et al. (2019). Three unordered models (equal

rates/ER, symmetric/SYM or all-rates-different/ARD) were tested based on the corrected AIC and implemented with 1000 stochastic character maps using the *make.simmap* function in *Phytools* that were summarised to produce posterior probabilities for each node.

The ancestral range was reconstructed using the same input tree as for the ancestral character state reconstructions. We tested three dispersal models included in BioGeoBEARS v1.1.1 (Matzke, 2013, 2014), which are DEC (Ree & Smith, 2008), DIVALIKE and BAYAREA-LIKE models. The latter two are maximum likelihood adaptations of the original DIVA (Ronquist, 1997) and BAYAREA (Landis et al., 2013) models, respectively. All models were also run with the jump-dispersal parameter (+J), and all six models were compared using the corrected AIC while acknowledging the ongoing debate related to whether the three models and their +J counterparts should be directly compared or not (Matzke, 2022; Ree & Sanmartín, 2018). We divided the biogeographic regions into Afrotropical (A), Australasian (U; Australia, New Zealand and Melanesia), Oriental (O), Neotropical (S), Nearctic (N) and Palaearctic (P) based on Seton et al. (2012). The distribution of each taxon was recovered from the literature (Lackner et al., 2015; Mazur, 2011). An unconstrained analysis and a time-stratified analysis were used to account for continental shifts. For the latter, four time slices (20, 40, 80 and 130 Ma) with differential dispersal rates were added to better account for their connectivity at different geological times, following other global biogeographic studies of other beetle groups (Schwery & O'Meara, 2021; Toussaint et al., 2017). For more details on the time-stratified analysis, see Supplementary File S11.

Regarding the potential limitations associated with sampling in this study that could strongly affect biogeography and the ancestral state reconstruction, the majority of our taxa originate from the Palaearctic Region, followed by the Nearctic Region, Afrotropical Region, Australasian Region, Neotropical Region and Oriental Region (see also above). On the other hand, the bulk of the Saprininae diversity occurs across the Holarctic Region, with Neotropical region as a possible second (because of the possible existence of numerous undescribed species; G. Arriagada, pers. comm. to T. Lackner, 2022). The Afrotropical region follows, while Australasian and Oriental regions are both species-poor compared to the first two. Although we relied on a relatively limited fraction of the total diversity of saprinine taxa (approximately one-seventh of all described species), we believe that our sampling encompasses most of the taxonomic and geographical diversity of the group. In some cases, a taxon can be spread in two or even more regions, but such species are assigned to one region only as additional regions were the result of anthropomorphic events rather than natural distributions.

RESULTS

Morphological analysis

The heuristic search resulted in 72 equally parsimonious trees with a tree length (TL) of 752, a consistency index (CI) of 0.33 and a retention index (RI) of 0.75. The strict consensus of the equally parsimonious trees had the following characteristics: TL: 746, CI = 0.20, RI = 0.67, and was selected as the preferred tree (see Supporting Information S6). Although the strict consensus tree is only mostly resolved, the subfamily is well-supported with a bootstrap support of 90%. Further, most of the recovered splits show much lower support. Saprininae were recovered as monophyletic with three unique changes: antennal insertions hidden under distinct frontal extension (character 2; state 0, Figure 4a–c), presence of antennal cavity (character 31; state 0, Figure 4f) and apical end of spiculum gastrale of male terminalia pointing downwards (character 77; state 0, Figure 5e).

Due to the high amount of homoplasy, only unique changes (full circles) are shown on Supportive Information S6 and discussed (see below). The raw strict consensus tree obtained from the morphological analyses with all mapped characters can be found as a Supplementary File S7. The morphology-only analyses retrieved five clades that were identical to the combined analyses and shown here as the proposed new saprinine classification.

Molecular phylogenetic analyses

Although we only relied on museum samples, sequencing was quite successful, with 86.78%, 69.42% and 76.03% of the samples yielding data for 5′ *CO1*, 3′ *CO1* and *18S*, respectively (see Supporting Information S5). The phylogenetic tree obtained from analyses partitioned by genes can be found in Supplementary File S8. The tribe **Myrmetini** was not retrieved monophyletic on a molecular-only tree (*partbygene* treefile). This lack of monophyly could be driven by missing data, as we did not have *CO1* sequences for *Myrmetes paykulli* Kanaar and only one of the two *CO1* fragments for *Gnathoncus disjunctus suturifer* Reitter.

Phylogenetic analysis of the combined molecular and morphological datasets

The results of the analysis of the combined molecular and morphological datasets (Figure 2) correspond to the best-resolved phylogenetic hypothesis, and are selected here for introducing major taxonomic changes. Yet again, we confirm the monophyly of the Saprininae (100/1.0/100 SH-aLRT, aBayes and UFboot, respectively) as resolved by Lackner (2014b) and Lackner et al. (2019) and present the first suprageneric classification within the subfamily. The backbone of the Saprininae is fully resolved, and we recognise five well-supported major clades, assigning them tribal status. One taxon is left as Saprininae *incertae sedis* (see below). In the following text, we elaborate on each newly erected tribe in detail. When analysing the synapomorphies and diagnostic characters supporting each clade, we present a mix of morphological characters inferred as unique changes supporting clades (in such cases, we always indicate the character number and its state), complemented by characters that we deem diagnostic. Although we illustrate notable

changes herein, some are referenced from other sources given in the Introduction.

Integrative taxonomy

Tribe Myrmetini Portevin, type genus *Myrmetes* Marseul, **stat. nov.** & **sens. nov.** This tribe is well-supported (89.8/1.0/98) and contains small (PEL < 3.50 mm), predominantly non-metallic nondescript taxa, a great majority of which are inquilines of birds, mammals, ants or reptiles. Some are found in caves preying upon arthropods occurring on bat guano. This clade is sister to the rest of the subfamily. For the genera based either on the present research or on the observed morphological characters grouped in the tribe **Myrmetini trib. nov.**, see Table 1.

Morphological synapomorphies and diagnostic characters of **Myrmetini** are: (1) prosternal process terminating in median fovea, which may be variously developed and even split into two (morphological synapomorphy; Figure 4f; barely discernible in several *Gnathoncus* Jacquelin du Val; absent (possibly secondarily lost) in *Myrmetes* and *Erebidus* Reichardt); (2) absence of frontal stria (diagnostic character; Figure 4c); (3) non-metallic dorsum devoid of any macula (diagnostic character; elytra in one Australasian species with faint bluish hue); (4) longitudinally divided tergite IX of the male terminalia (morphological synapomorphy; Figure 5h); (5) sternite and tergite VIII of male genitalia not fused laterally (diagnostic character; Figure 5g, except for *Tomogenius australis* Dahlgren); (6) rather elongate antennal club furnished with slit-like pits or sensory orifices with usually multiple vesicles inside the antennal club (diagnostic character; Figure 3d; but *Tomogenius incisus* (Erichson) as well as *Myrmetes* possess only a single vesicle inside the antennal club) (Lackner, 2014b); (7) doubled marginal epipleural stria (morphological synapomorphy; unambiguous change character 52:2 in the morphological analyses); (8) presence of short, hooked basal appendix of dorsal elytral striae V between stria IV and sutural elytral stria (morphological synapomorphy; absent in *Myrmetes* and at *Tomogenius papuaensis* Gomy); and (9) presence of lacinial hook (diagnostic character; Figure 5b; absent in *Myrmetes*). Within the clade, the relationship of *Myrmetes* and *Gnathoncus* is well-supported (76.1/0.87/98; unambiguous change character 52:2 in the morphological analyses), confirming previous studies. Although we included only one representative of the genus *Gnathoncus*, based on the morphological characters, we suggest that the genus is monophyletic; while *Erebidus* and *Myrmetes*, based on further research, might be possibly synonymised with it, or sunk into subgenera of *Gnathoncus*. *Tomogenius* Dahlgren is likewise monophyletic (99.9/1.0/100); its New Zealand representative is sister to its Australasian congeners (a situation similar to *Saprinus* Erichson, see below). While the results of the morphology-based phylogeny of Lackner (2014b) retrieved *Myrmetes*, *Erebidus*, *Gnathoncus* and *Tomogenius* as a basal 'grade' of the subfamily, results of the molecular phylogeny of Lackner et al. (2019) are more similar to the topology recovered here. Monophyly of *Tomogenius* + *Gnathoncus* received a bootstrap support of 89, while two unambiguous morphological character changes (40:1 presence of median prosternal fovea and 59:0, presence of short, hooked appendix between dorsal elytral stria IV and sutural elytral stria) support their relationship. However, Lackner et al. (2019) in their clade recovered also the Australasian endemic *Saprinodes distinctus* Dégallier (absent from our analyses) and Californian endemic *Aphelosternus interstitialis* (J.L. LeConte) (see below). **Myrmetini** are almost exclusively bipolar (=amphitropical distribution), with only very few *Gnathoncus* recorded from the tropics. Only a single bird-inquiline *Gnathoncus* is known from tropical Africa; the *Gnathoncus* species from Southeast Asia are almost exclusively found inside caves (Lackner, 2020). From the morphological point of view, it is interesting to stress the absence of elytral macula or sash (=band) in the group; in the remaining tribes this macula or sash (usually yellow, orange or red) has evolved in multiple species independently.

Aphelosternus interstitialis branches off next, sister to all remaining tribes. It is the sporadically collected sole representative of a Californian inquiline *Aphelosternus* Wenzel (found inside the underground nests of ground squirrels; see also Lackner, 2014b). Morphologically, the species lacks the lacinial 'hook', possesses one large pear-shaped vesicle on the internal ventral side and two much smaller pear-shaped vesicles on the dorsal side (for fig. see Lackner, 2014b, figure 9) and lacks inner subhumeral stria. Its prosternum is devoid of foveae; the head lacks frontal and supraorbital striae, while elytra possess dorsal striae I–IV, without a trace of any other stria (or appendix of it). The eighth tergite and sternite of the male genitalia are fused, as is the ninth tergite. Due to its position on the tree and puzzling morphology (most of the above-mentioned morphological characters are shared with other taxa, and none are truly unique to *Aphelosternus*), we treat it here as Saprininae *incertae sedis* pending further studies. In the morphological analysis of Lackner (2014b) *Aphelosternus interstitialis* was recovered as sister to Central-Asian *Turanostyphrus ignoratus* Tishechkin (known only from the holotype and absent from the present study) inside a small clade otherwise containing mainly inquilines from the Western Hemisphere. On the other hand, the results of molecular analysis of Lackner et al. (2019) place *Aphelosternus interstitialis* sister to *Tomogenius*, inside the clade containing all present **Myrmetini** + Australasian endemic *Saprinodes distinctus* (absent from our study).

Euspilotini Lackner, trib. nov., type genus *Euspilotus* Lewis, contain predominantly taxa from the Western Hemisphere, most of which are free-living predators, although the tribe also contains attaphilic (associated with *Atta* leafcutter ants), littoral and even mammal inquiline species (see e.g. Lackner, 2016a or Arriagada & Aballay, 2020). The tribe itself received only moderate support (75.5/0.77/94) and is split into a strongly supported (97.5/1/100) triad containing beach-dwelling *Euspilotus* (*Hesperosaprinus*) *scissus* (J.L. LeConte) + two members of the subgenus *Neosaprinus* Bickhardt of the genus *Euspilotus* sister to the rest of the tribe.

E. (*H.*) *scissus* occurs along the Pacific coast from British Columbia down to Mexico, while the two members of the subgenus *Neosaprinus* included here are the south-Palaearctic *E.* (*N.*) *perrisi* (Marseul), typically an inquiline of European bee-eater (*Merops apiaster* L.), and an undescribed species of the subgenus collected in a cave in Thailand.

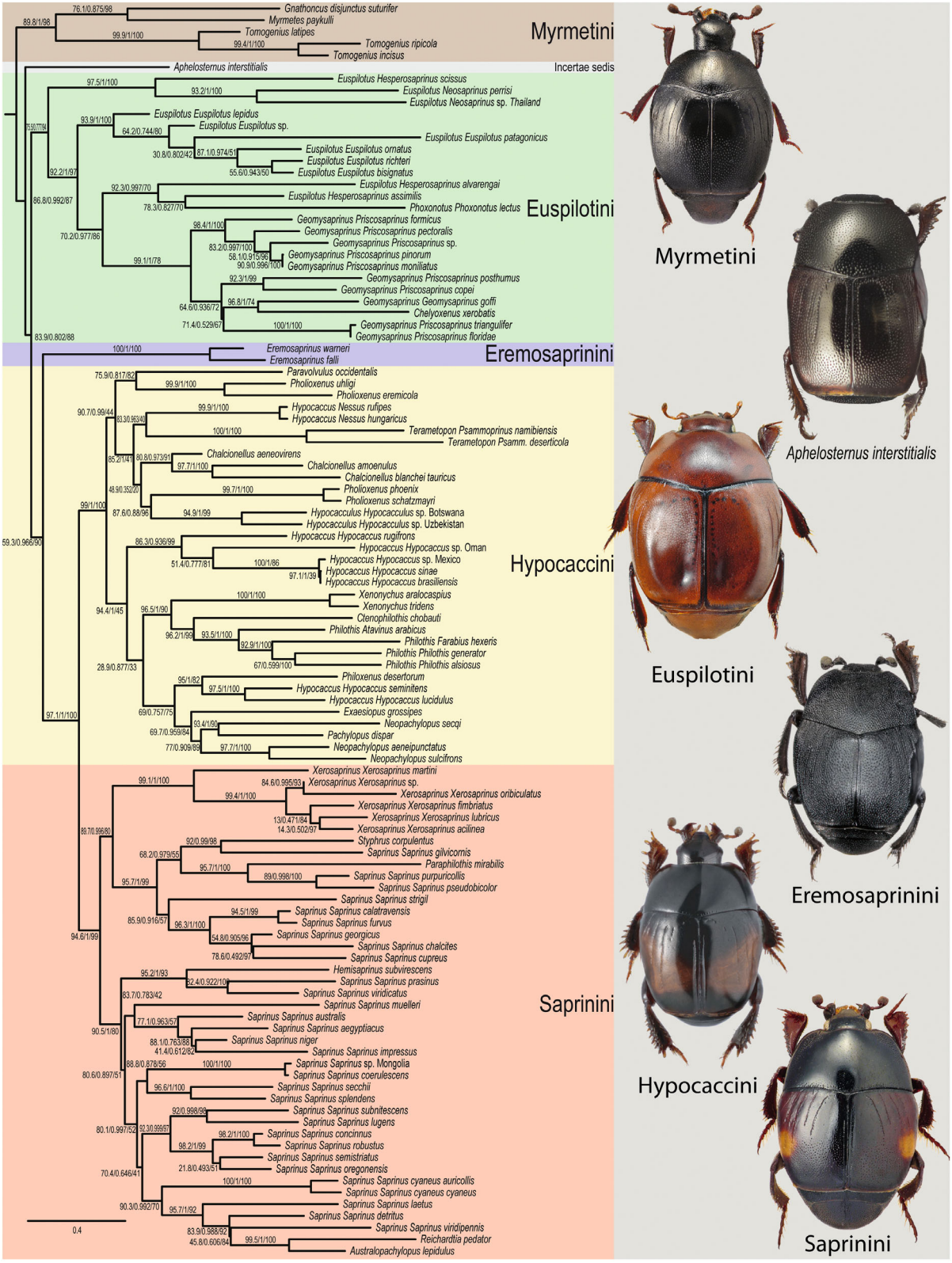

FIGURE 2 Phylogenetic tree presenting the results of combined analyses depicting major changes in the subfamily classification.

The two *Neosaprinus* are morphologically very similar (sharing even pygidial structures in females; unambiguous morphological change 62:1; Figure 5c), and their relationship is strongly supported (93.2/1.0/100). The morphology of *E.* (*H.*) *scissus* differs from the two substantially, for example, by the absence of pygidial structures in female or differently shaped prosternum. The position of *E.* (*H.*)

TABLE 1 New classification of the Saprininae (number of species sensu Newton, 2022).

Tribes	Genera included	# of spp.	Distribution
Myrmetini	*Gnathoncus* Jacquelin du Val, 1857	28 spp.	Holarctic, 1 sp. in Afrotropical, several spp. in Oriental Region
	Tomogenius Marseul, 1862	7 spp.	Australia, New Zealand, Papua New Guinea
	Erebidus Reichardt, 1941	2 sp.	Kazakhstan, Uzbekistan, Turkmenistan
	Myrmetes Marseul, 1862	1 spp.	Palaearctic Region: Europe: Spain to Siberia
Euspilotini	*Euspilotus* Lewis, 1907	85 spp.	Nearctic and Neotropical regions; 1 sp. known also from Palaearctic and 2 sp. from Oriental
	Geomysaprinus Ross, 1940	29 spp.	Nearctic and Neotropical regions
	Phoxonotus Marseul, 1862	5 sp.	Brazil, Peru, Guatemala, Costa Rica, Suriname
	Satrapister Bickhardt, 1912	1 spp.	Peru
	Paramyrmetes Bruch, 1929	1 sp.	Argentina
	Oosaprinus Arriagada, 2017	1 sp.	Argentina
	Paraeuspilotus Arriagada & Aballay, 2020	1 sp.	Argentina
	Tatianella Arriagada, 2019	1 sp.	Brazil, Uruguay, Argentina, French Guiana
Eremosaprinini	*Eremosaprinus* Ross, 1939	10 spp.	USA: Arizona, California, Nevada, New Mexico; Baja California Pen.
Saprinini	*Saprinus* Erichson, 1834	204 spp.	Worldwide
	Microsaprinus Kryzhanovskij, 1976	4 spp.	France, Italy, Spain, North Africa, Iran, Kazakhstan, Mongolia, Uzbekistan, Turkmenistan
	Saprinodes Lewis, 1891	2 sp.	Australia
	Pilisaprinus Kanaar, 1996	1 sp.	Congo, Benin, Ivory Coast
	Notosaprinus Kryzhanovskij, 1972	1 spp.	Australia
	Iridoprinus Lackner & Leschen, 2017	1 sp.	Australia
Hypocaccini	*Hypocacculus* Bickhardt, 1914	76 spp.	Palaearctic, Afrotropical and Oriental regions
	Hypocaccus C. Thomson, 1867	69 spp.	Worldwide; in South America and Australia only 1–2 spp. Otherwise widely distributed taxa
	Dahlgrenius Penati & Vienna, 1996	62 spp.	Afrotropical Region, Algeria, Morocco, Egypt, Iraq, Saudi Arabia
	Chalcionellus Reichardt, 1932	36 spp.	Palaearctic, Afrotropical and Oriental regions; 1 sp. introduced into Australia
	Pholioxenus Reichardt, 1932	20 spp.	Southern Palaearctic Region; Sudan
	Philothis Reichardt, 1930	14 spp.	Algeria, Morocco, Oman, Iran, Kazakhstan, Uzbekistan, Turkmenistan
	Paravolvulus Reichardt, 1932	11 spp.	Northern Africa, Arabian Peninsula, Middle Asia, Turkey, Azerbaijan, Armenia
	Exaesiopus Reichardt, 1926	7 sp.	Southern Palaearctic, Namibia, South Africa
	Terametopon Vienna, 1987	7 spp.	Namibia, Botswana
	Paraxenus Lackner, present paper	7 spp.	Republic of South Africa, Namibia
	Reichardtiolus Kryzhanovskij, 1959	5 spp.	Egypt, Saudi Arabia, Jordan, Iran, Middle Asia
	Neopachylopus Reichardt, 1926	5 spp.	Nearctic, Afrotropical, Oriental, Palaearctic regions
	Alienocacculus Kanaar, 2008	5 spp.	Algeria, Morocco, Tunisia, Libya, Israel, Chad, United Arab Emirates, Saudi Arabia
	Malagasyprinus Lackner & Gomy, 2013	3 spp.	Madagascar
	Xenonychus Wollaston, 1864	3 spp.	Circum-Mediterranean, Sahara, Arab Peninsula, Near East, Middle Asia
	Zorius Reichardt, 1932	2 spp.	Israel, Palestine
	Pachylopus Erichson, 1834	2 spp.	Republic of South Africa, Namibia, Mexico
	Turanostyphrus Tishechkin, 2005	2 spp.	Turkmenistan, Uzbekistan

(Continues)

TABLE 1 (Continued)

Tribes	Genera included	# of spp.	Distribution
	Ctenophilothis Kryzhanovskij, 1987	2 spp.	Algeria, Egypt, Morocco
	Saprinillus Kryzhanovskij, 1972	2 spp.	Kazakhstan, Turkmenistan, Mongolia
	Nannolepidius Reichardt, 1932	1 sp.	Republic of South Africa
	Axelinus Kryzhanovskij, 1976	1 sp.	Uzbekistan
	Chivaenius Olexa, 1980	1 sp.	Uzbekistan
	Parahypocaccus Vienna, 1995	1 sp.	Zimbabwe
	Monachister Mazur, 1991	1 sp.	USA: California
	Afroprinus Lackner, 2013	1 sp.	Kenya
	Philoxenus Mazur, 1991	1 sp.	South-western USA, Mexico
	Eopachylopus Reichardt, 1926	1 sp.	Russia: Far East, Hong Kong, Japan, South Korea
	Ammostyphrus Reichardt, 1926	1 sp.	Kazakhstan, Uzbekistan, Turkmenistan
	Sarandibrinus Lackner & Gomy, 2014	1 sp.	Madagascar
	Xenophilothis Kryzhanovskij, 1987	1 sp.	Algeria, Morocco, Oman, Saudi Arabia, United Arab Emirates
	Orateon Lackner, 2014	1 sp.	Yemen
	Afrosaprinus Vienna, 2015	1 sp.	Kenya

scissus, far removed from other members of the subgenus *Hesperosaprinus* Wenzel of the genus *Euspilotus* on the phylogenetic tree (see also below), confirms the previous assumptions of the non-monophyly of the subgenus (see e.g. Lackner, 2014b, for discussion).

Next, the clade is split into two sub-clades whose relationships received strong support (92.2/1.0/97). One contains strongly supported (93.9/1.0/100) South American members of the nominotypical *Euspilotus* s. str. (whose internal branches show low support). The other, moderately supported (70.2/0.97/86) clade contains two members of the subgenus *Hesperosaprinus* of the genus *Euspilotus* + *Phoxonotus* (*Ph.*) *lectus* Lewis, sister to strongly supported (99.1/1.0/78) clade containing members of *Geomysaprinus* Ross (including the tortoise-inquiline *Chelyoxenus xerobatis* Hubbard, see below). *Euspilotus* is a species-rich taxon spread mostly in the Western Hemisphere, containing, apart from the nominotypical subgenus, three subgenera. The monophyly of *Euspilotus*, judged from the morphological point of view, has been questioned before and is refuted in the present study. Its nominotypical subgenus, with 11 described species, is exclusive to the Neotropical region, and its members often bear yellow maculae on their elytra. While another subgenus *Platysaprinus* Bickhardt also occurs solely on the South American continent, members of the other two subgenera (*Hesperosaprinus* and *Neosaprinus*) are also found in the Nearctic, Oriental and Palaearctic regions, respectively. At least one Neosaprinus species has been introduced by humans into Australasian and Afrotropical regions (Mazur, 2011, Lackner & Leschen, 2017). Since we only had a handful of species representing three subgenera (and lacking any member of the subgenus *Platysaprinus*), we refrain from adopting taxonomic changes within the genus, pending further studies on more densely sampled material.

The position of the morphologically quite outstanding attaphilous *Phoxonotus* (the only Saprininae taxon to sport tubercles on its dorsum) on the tree, sister to two members of the subgenus *Hesperosaprinus* would be tempting to implement taxonomical changes. Still, we refrain from doing so since we only sampled two members of the otherwise species-rich *Hesperosaprinus* (55+ species) and only a single *Phoxonotus* species (of five total). *Phoxonotus* was revised recently (Lackner, 2016a, 2016b) and the reader is referred to for its detailed morphology and biology there. Regarding *Euspilotus*, only the subgenus *Platysaprinus* was revised recently (Lackner & Arriagada, 2020); the rest of the members are currently undergoing scrutiny by G. Arriagada (Santiago de Chile, Chile).

The highly supported (99.1/1/78 support values) clade containing *Geomysaprinus* Ross, a largely Nearctic (several species are also known from various South American areas) inquiline genus (two subgenera, 28 spp.), shows the unquestionable monophyly of the taxon. The position of *Chelyoxenus xerobatis* Hubbard, nested deep within *Geomysaprinus*, confirms the previous unpublished assumptions by P. Kovarik based on larval morphology (pers. comm., 2020) that *Chelyoxenus* is a member of *Geomysaprinus*. Based on its phylogenetic position, as well as peculiar biology, we downgrade *Chelyoxenus* into a subgenus of *Geomysaprinus*, thus *Geomysaprinus* (*Chelyoxenus*) **stat. nov.** *Geomysaprinus* is in urgent need for a thorough morphological revision; we were able to include 10 species in our analysis (of the 28 in total, thus more than one third). For the genera that are based either on the present research, or on the observed morphological characters grouped in the tribe **Euspilotini trib. nov.**, see Table 1.

Putative morphological synapomorphies and diagnostic characters supporting **Euspilotini** include: (1) presence of marginal prosternal stria connecting prosternal foveae (diagnostic character; Figure 4d; absent in several taxa); (2) frontal stria absent, or only vestigial (diagnostic character; Figure 4b); and (3) presence of multiple ball-shaped vesicles inside antennal club (diagnostic character; Figure 3c). We have to admit that we are not very familiar with many Neotropical taxa, especially the species-rich genus *Euspilotus*, which contain numerous undescribed species (G. Arriagada, pers. com. 2022). It is,

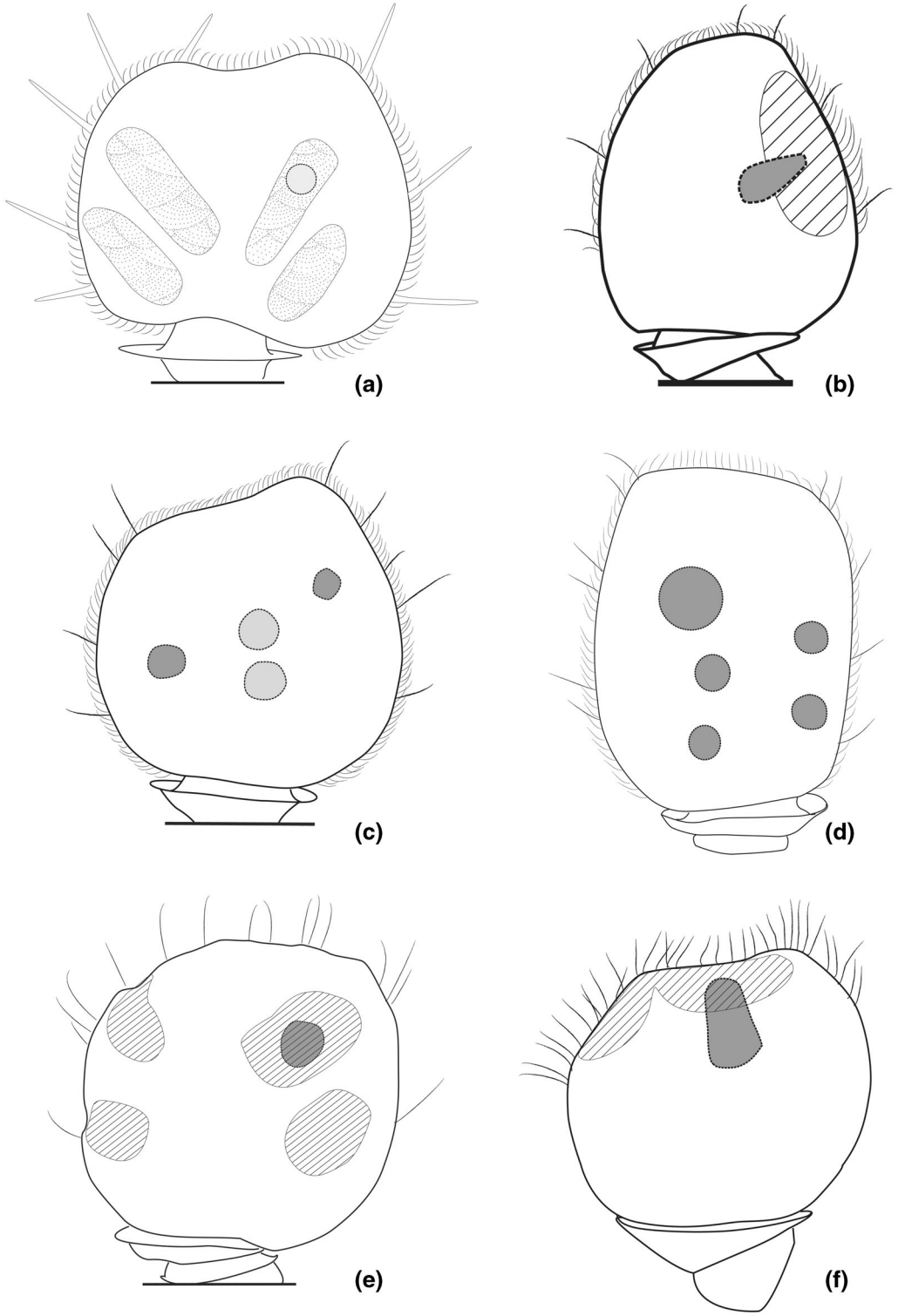

FIGURE 3 Sensory structures of the antennal clubs: a—*Saprinus* (*S.*) *semistriatus*; b—*Ammostyphrus cerberus* Reichardt; c—*Euspilotus* (*E.*) *zonalis* Lewis; d—*Gnathoncus rotundatus* (Kugelann); e—*Saprinus* (*Paraphilothis*) *mirabilis* Vienna; f—*Philothis* (*Ph.*) *arcanus* Reichardt.

however, interesting to note that the 'lacinial hook' or 'uncus' that is present usually in the **Myrmetini** is also present in several **Euspilotini** (e.g. in *Chelyoxenus* or *Phoxonotus*). The morphology-based phylogeny of Lackner (2014b) that contained chiefly only the type specimen of each (sub)genus saw *Euspilotus* as well as *Geomysaprinus* paraphyletic, while the molecular study of Lackner et al. (2019) whose dataset was rather similar to ours rendered *Geomysaprinus* monophyletic and *Euspilotus* paraphyletic. Their clade containing most of the presently studied **Euspilotini** taxa also saw high support; the inclusion of *Phoxonotus* within *Euspilotus* was largely similar to our results here.

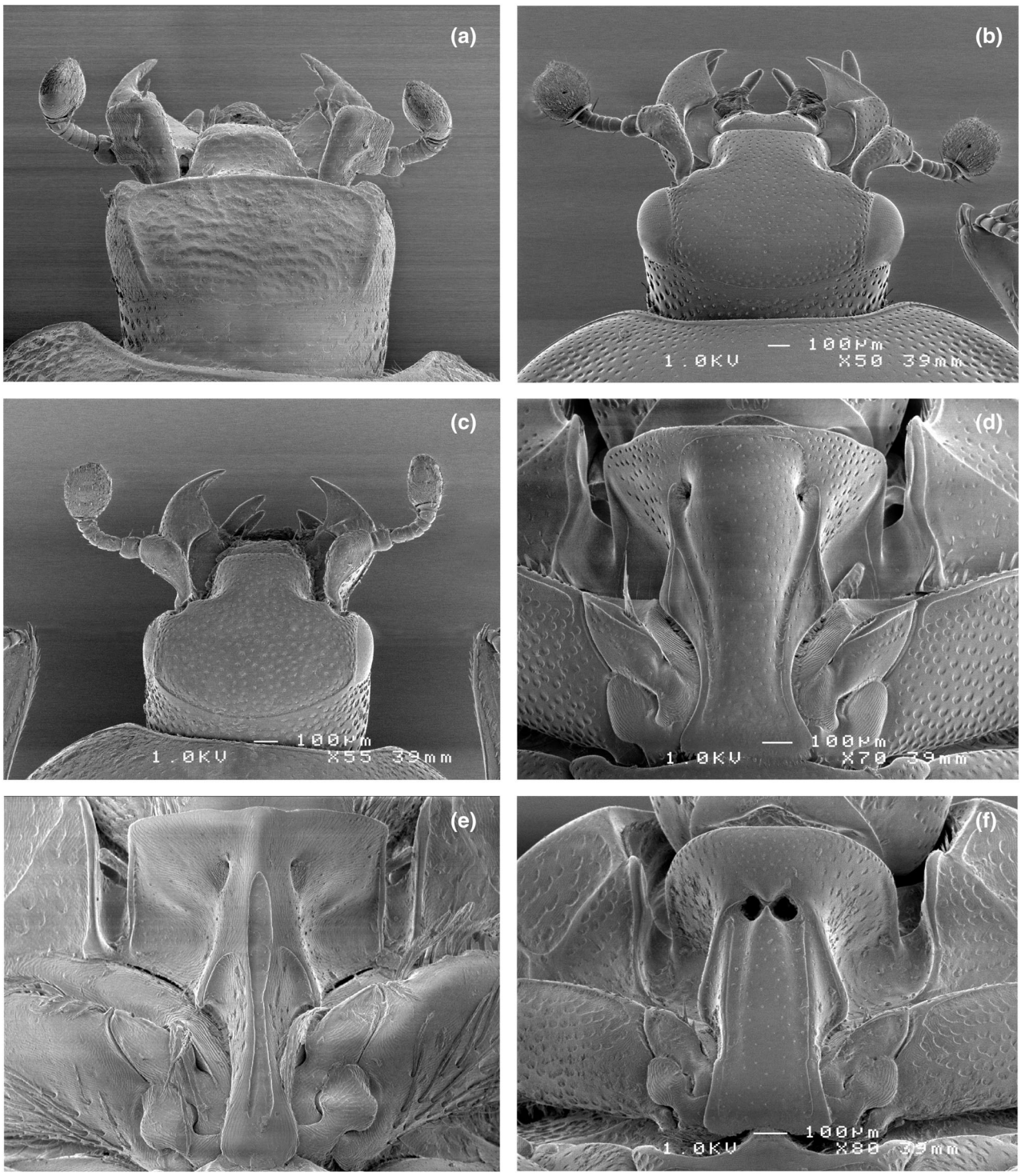

FIGURE 4 External morphology of the Saprininae. a—*Dahlgrenius aurosus* (Bickhardt): head, dorsal view; b—*Euspilotus* (*Hesperosaprinus*) *assimilis* (Paykull, 1811), ditto; c—*Tomogenius motocola* Mazur, ditto; d—*Euspilotus* (*Hesperosaprinus*) *assimilis* (Paykull, 1811), prosternum; e—*Neopachylopus* spec. (Yemen), ditto; f—*Tomogenius motocola* Mazur, ditto.

Euspilotini are sister to the remaining three tribes of the subfamily; the support for this relationship is moderate (83.9/0.80/88).

Eremosaprinini Lackner, **trib. nov.**, type genus *Eremosaprinus* Ross, branches off first, sister to the rest of taxa. The relationship of this newly erected tribe to the two large consecutive clades received low support (59.3/0.96/90), and adding more members of this inquilinous taxon would be very important in future analyses. Strictly inquilinous *Eremosaprinus* (Nearctic; 10 spp.; Lackner & Tishechkin, 2014) is currently the only genus comprising this tribe. It is one of the morphologically enigmatic Saprininae genera, for details see Tishechkin and

Lackner (2012). Our study included two species that form a highly (100/1.0/100) supported clade. As mentioned by Tishechkin and Lackner (2012), the unity of the genus *Eremosaprinus* is dubious since there are substantial disparities regarding the morphology of species (e.g. differences in the antennal sensory structures, presence vs. absence of ventral male secondary characters, etc.). To quote Tishechkin and Lackner (2012), 'such variability makes the validity of *Eremosaprinus* in its current state somewhat questionable'. We, therefore, list here as possible diagnostic characters only the following, rather general characters that can likewise be found across the subfamily: (1) broad, elevated and flattened prosternum, occasionally with prosternal foveae; (2) absent frontal stria; (3) long subparallel carinal prosternal striae; (4) absent lateral prosternal striae; and (5) setose pronotal hypomeron. Although the genus was revised recently by Tishechkin and Lackner (2012), *Eremosaprinus* will require denser sampling and a future phylogenetic study to state the true monophyly of the taxon and disentangling its internal relationships. Lackner's (2014b) morphology-based study retrieved the type of the genus, *Eremosaprinus unguiculatus* (Ross) as a member of the basal 'grade' of the subfamily, while the study of Lackner et al. (2019) did not include any representative of the genus. In the morphology-only analyses the two species came out paraphyletic: one as a member of the **Hypocaccini**, while the other was recovered as a member of **Euspilotini**.

The following highly supported (99/1.0/100 and 94.6/1.0/99, respectively) clades form the two respective new tribes that contain the most species-rich genera of the subfamily (e.g. *Saprinus* and/or *Hypocaccus*) and, indeed, most of saprinine diversity. Their relationship is strongly supported (97.1/1.0/100).

Hypocaccini Lackner, trib. nov., type genus *Hypocaccus* C. Thomson. The strongly supported tribe (99/1.0/100) contains numerous genera and subgenera spread across the Holarctic, Afrotropical and Oriental regions. A modest number of its representatives in South America or Australia is presumed to have invaded the regions from the north. The highest concentration of taxa is across the sub-Saharan Africa, the south Palaearctic steppe and desert belt, with specialised psammophiles or inquilines present in both Holarctic and Afrotropical regions. The interrelationships of **Hypocaccini** were not resolved using morphology-based phylogenetic analyses of Lackner (2014b), and it was hoped that densely sampled molecular phylogeny would shed more light on their internal relationships. Although the sampling used in this work is by no means extensive, based on the present phylogenetic hypothesis the **Hypocaccini** are split into two equally strongly supported (90.7/0.99/44 and 94.4/1.0/45, respectively) subclades. One contains exclusively taxa from the Eastern Hemisphere, while the other one comprises a mix of Eastern Hemisphere and Nearctic taxa. Based on the results of the present research, we propose the following taxonomic and nomenclatural changes:

1. Genus *Pholioxenus* Reichardt (25 spp., Mazur, 2011) is polyphyletic, while *Chalcionellus* Reichardt (34 spp., Mazur, 2011), represented by only three species in our analyses, is rendered monophyletic here. *Chalcionellus* is a free-living, widespread taxon in the Eastern Hemisphere; the bulk of its species occurs in the Palaearctic and Afrotropical regions, with several species also known from the Oriental Region, and one Afrotropical species has been introduced into Australia (Mazur, 2011). The morphological limits of *Chalcionellus* have been notoriously difficult to establish, and its separation from the genus *Hypocacculus* Bickhardt was problematic since its description (see e.g. Lackner, 2010 for discussion). Although we included only three species of the genus, and they form a clade (80.8/0.97/91 support), based on the morphology, we have reasons to suspect this monophyly might not hold pending inclusion of more material. For now, however, we leave the status of *Chalcionellus* unchanged. *Pholioxenus* is a mammal inquiline known from the southern Palaearctic Region (with a single species also known from Sudan: Darfur; enriching thus, technically, also the Afrotropical Region), and a cluster of both inquiline and free-living species from southernmost African countries Namibia and Republic of South Africa. Species included in our phylogeny (two from the Palaearctic Region and two from Namibia) form two respective clades confirming non-monophyly of the genus. Based on the morphology (see below), vast geographical separation and results of the present study we opt for erecting of a new genus ***Paraxenus* Lackner, gen. nov.**; type species *Hypocacculus eremicola* Thérond, for the South African and Namibian members of *Pholioxenus*. The following new combinations are thus proposed: *Paraxenus diasi* (Vienna, 1992) **comb. nov.**; *Paraxenus eremicola* (Thérond, 1965) **comb. nov.**; *Paraxenus namibiensis* (Vienna, 1993) **comb. nov.**; *Paraxenus oleolus* (Thérond, 1965) **comb. nov.**; *Paraxenus therondi* (Olexa, 1984) **comb. nov.;** and *Paraxenus uhligi* (Mazur, 2006) **comb. nov.** The Palaearctic representatives remain in *Pholioxenus*, including the Sudanese *Pholioxenus trichoides* Kapler whose status will need scrutiny pending further research.
2. The monophylies of *Xenonychus* Wollaston (three spp.; southern Palaearctic Region; Newton, 2022; ultrafast bootstrap support of 81%), *Terametopon* Vienna (two subgenera, six spp.; Namibia, Botswana; Lackner, 2009; ultrafast bootstrap support of 100%), *Ctenophilothis* Kryzhanovskij (two spp., Sahara) and *Philothis* Reichardt (three subgenera, 14 spp.; southern Palaearctic Region; Mazur, 2011; ultrafast bootstrap support of 70%) are all confirmed by the present study.
3. Genus *Hypocaccus* (120+ species; three subgenera; predominantly littoral; all regions) is not monophyletic. We included in our analyses two species of the subgenus *Nessus* Reichardt and seven species of the nominotypical subgenus. The two *Nessus* species form a clade far removed from the members of *Hypocaccus* s. str. In his 2011 catalogue of the family Mazur transferred *Nessus* (53 spp.), originally a subgenus of *Hypocacculus* Bickhardt into *Hypocaccus* without any explanation (see also Lackner, 2014b). Members of *Nessus*, when compared to members of the other two *Hypocaccus* subgenera, are generally smaller in size, can have setose pronotal hypomeron and never possess a combination of glabrous frons adorned with chevrons or rugae. On the other hand, *Hypocaccus* (including its subgenus *Baeckmanniolus*) exhibits glabrous pronotal hypomeron, often glabrous frons adorned with chevrons or single or multiple rugae and are larger in size. Based on the tree topology and morphological differences mentioned above, we propose the

transfer of the subgenus *Nessus* from *Hypocaccus* back to *Hypocacculus* thus *Hypocacculus* (*Nessus*) **stat. rest.** *Hypocacculus* thus, in the present sense, contains four subgenera, but apart from the members of *Nessus* we were only able to include two unidentified members of the nominotypical subgenus. Although geographically very separated (one species originates from Uzbekistan and the other from Botswana), they form a strongly supported clade (94.9/1.0/99). We refrain from further taxonomic changes regarding *Hypocacculus* pending inclusion of more material (ideally from all subgenera).

The situation around *Hypocaccus* itself is also rather complicated. Five of the seven species included in the analysis form a well-supported (86.3/0.93/99) clade, while two North American species have been recovered inside a clade containing genera *Philoxenus* Mazur (monotypic, Western USA), *Pachylopus* Erichson (two species, South Africa, Namibia and Mexico), *Neopachylopus* Reichardt (six spp., North America, Horn of Africa, Arabia, Pakistan) and *Exaesiopus* Reichardt (seven spp., Southern Palaearctic, Namibia, South Africa). Genus *Hypocaccus*, without subgenus *Nessus*, includes two subgenera and 69 species (Newton, 2022). Although its monophyly is disputable, we were only able to include seven species belonging to the nominotypical subgenus in our analyses and therefore are not proposing taxonomic changes pending further research. The situation with *Neopachylopus* is similar. Its two included species from North America form a clade, while *Neopachylopus secqi* Kanaar from the Horn of Africa and Arabian Peninsula has been recovered sister to the Afrotropical *Pachylopus dispar* Erichson. The internal relationships are only moderately supported. We therefore refrain from further taxonomic changes keeping the *status quo*.

4. For the genera that are (based either on the present or past research) included in the tribe **Hypocaccini trib. nov.**, see Table 1.

Among the putative morphological synapomorphies and diagnostic characters of **Hypocaccini** can be listed: (1) presence of fronto-clypeal stria or carina (diagnostic character; Figure 4: A; can be interrupted or obliterated in several taxa); (2) presence of prosternal foveae (diagnostic character; Figure 4a; can be microscopic or outright absent = secondarily lost in some taxa); (3) presence of a single pear- or stipe-shaped vesicle inside antennal club with often only a single sensory area (morphological synapomorphy; Figure 3b,f); (4) laterally fused VIII sternite and tergite (diagnostic character; Figure 5f); distinct, well developed labral process (morphological synapomorphy; unambiguous morphological change 23:0; Figure 5a). This last-mentioned character probably represents an autapomorphy of the tribe. Numerous genera of the tribe were taxonomically revised (see e.g. Lackner, 2012, 2014a, 2015), but the taxa with most species, for example, *Dahlgrenius* Penati & Vienna, *Paravolvulus* Reichardt, *Hypocaccus* or *Hypocacculus* are yet awaiting scrutiny. The results of Lackner (2014b) show most of the members of **Hypocaccini** in the analyses included in large, mostly unresolved polytomy (with some taxa, e.g. *Philothis* recovered monophyletic), while the tree topology included in the subsequent paper by Lackner et al. (2019) largely resemble our present results.

Saprinini Blanchard, 1845 sens. nov., type genus *Saprinus* Erichson. **Saprinini**, which contain the majority of saprinine taxa, are placed as sister to **Hypocaccini** and their monophyly is well-supported (94.6/1.0/99). The clade is divided into two large, well-supported sub-clades containing mostly free-living taxa from the Afrotropical, Holarctic and Australasian regions. Most of the species included here belong to *Saprinus*—a genus that occurs in all biogeographic regions. The majority of *Saprinus* species are found in the Holarctic + Afrotropical regions, with only nine species occurring in the Oriental Region, 18 in the Australasian Region and four in the Neotropical Region (Lackner & Leschen, 2017; Mazur, 2011). As our study represents only a fraction of the known *Saprinus* diversity (31 out of the 204 described taxa sensu Newton, 2022), we refrain from interpreting the interrelationships among the species groups pending the inclusion of more material. Based on the position of several taxa on the phylogenetic tree, as well as thorough morphological studies conducted by the first author, however, we suggest the following taxonomic conclusions:

1. The monotypic Namib Desert endemic *Paraphilothis* Vienna contains *Paraphilothis mirabilis* Vienna, and, according to our analysis, is a derived lineage within *Saprinus*, morphologically specialised for life in deep sand. Therefore, based on its phylogenetic placement, nested deep within *Saprinus* and sister to the Afrotropical *Saprinus purpuricollis* Schmidt and *Saprinus pseudobicolor* Marseul, we downgrade it to a subgenus of *Saprinus*. The taxon is biologically (psammophile) and morphologically (elytral disc covered with deep transverse rugae and protibia adorned with dense row of small, almost identical stout denticles—not present in the rest of *Saprinus*; for figs. see Lackner, 2013, figure 31 and 32, respectively) different from the rest of the congeners. The new combination is thus *Saprinus* (*Paraphilothis*) **stat. nov.** The morphology of the sensory structures of the antennal club (Figure 3e) indicates that this taxon does not indeed belong to the rest of the ultra psammophiles, all found within the **Hypocaccini**. As this taxon was not represented in the recent paper by Lackner et al. (2019) where all origins of psammophily are hypothesised to have occurred within the **Hypocaccini**, we can postulate that psammophily had one more independent origin during the evolution of the subfamily and occurred in the **Saprinini** as well.
2. Another monotypic xerophilous genus is *Styphrus* Motschulsky, containing the species *Styphrus corpulentus* Motschulsky. It is distributed in Middle Asia and is recovered nested deep within *Saprinus*, sister to *S*aprinus (*S.*) *gilvicornis* Erichson, (92/0.99/98 support). Both these taxa are found in arid places, at times co-occurring, mostly at least partly buried in sand, well adapted to the life in sand morphologically. Again, since its morphology is rather peculiar (differing from *Saprinus* by impunctate frons and almost straight, thin meso-and metatarsomeral claws), we downgrade it to a subgenus within *Saprinus*, thus *Saprinus* (*Styphrus*) **stat. nov.** It is worth underlining that Kryzhanovskij and Reichardt (1976, p. 186) viewed *Styphrus* as possible xerophilous derivate of *Saprinus*.
3. The sampled members of the predominantly Nearctic *Xerosaprinus* Wenzel (three subgenera, 29 species; 99.1/1.0/100 support)

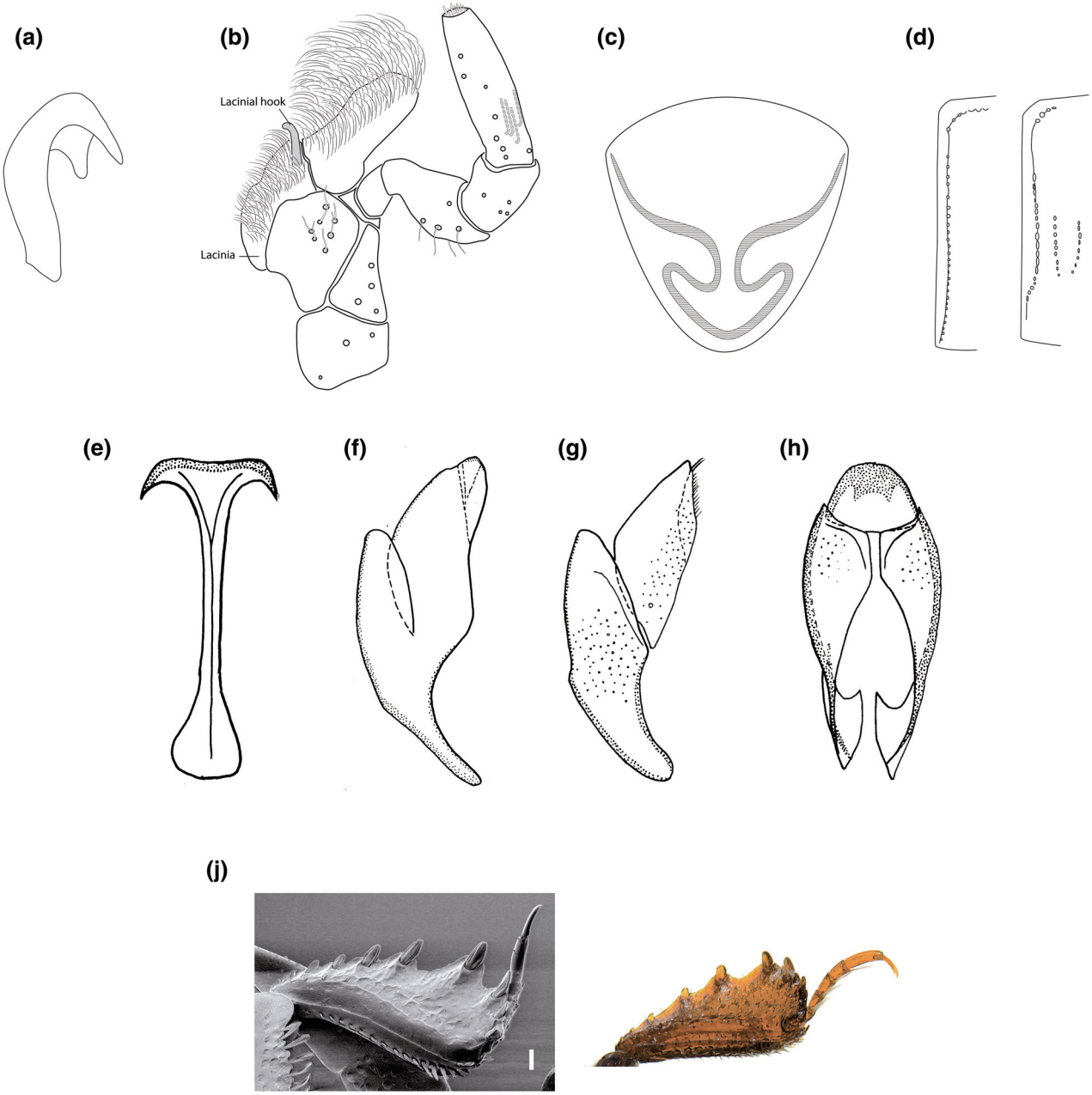

FIGURE 5 Internal and external morphology of the Saprininae. a—*Ctenophilothis chobauti* (Théry), labrum, schematic, lateral view; b—*Erebidus vlasovi* (Reichardt), maxilla; c—*Euspilotus* (*Neosaprinus*) *perrisi* (Marseul), female pygidial structures; d—*Pholioxenus normandi* Olexa and *Ph. quedenfelfti* (Schmidt), sutural region of the right elytron; e—*Alienocacculus neftensis* (Olexa), spiculum gastrale; f—*Axelinus ghilarovi* Kryzhanovskij, 1976, eighth sternite + tergite of male terminalia, lateral view; g—*Tomogenius incisus* (Erichson), ditto; h—*Tomogenius incisus* (Erichson) ninth and tenth tergite of male terminalia, dorsal view; i—*Pholioxenus phoenix* (Reichardt), protibia, ventral view; *Paraxenus eremicola* **comb. nov.**, ditto.

constitute a single clade, recovered within *Saprinus* in our phylogenetic analysis. Based on its position, we propose to downgrade its rank and those of its respective subgenera *Auchmosaprinus* Wenzel, *Vastosaprinus* Wenzel and *Lophobregmus* Wenzel to subgenera of *Saprinus*, thus *Saprinus* (*Xerosaprinus*) **stat. nov.**, *Saprinus* (*Auchmosaprinus*) **stat. nov.**, *Saprinus* (*Vastosaprinus*) **stat. nov.** and *Saprinus* (*Lophobregmus*) **stat. nov.** We admit that we are rather unfamiliar with members of *Xerosaprinus* and had no chance to include members of their respective subgenera in our analyses (in fact, we included only six species out of the 29 total), but, according to W. B. Warner (Phoenix, USA; pers. comm. 2022), who is an authority on the group, the former subgenera of *Xerosaprinus* are morphologically well defined. That said, *Xerosaprinus* would undoubtedly benefit from a thorough taxonomic revision in the future.

4. The predominantly Southern Palaearctic genus *Hemisaprinus* Kryzhanovskij (three spp.; Lackner, 2014c) is, based on its position on the tree, nested within *Saprinus*, downgraded to a subgenus of

Saprinus, thus *Saprinus* (*Hemisaprinus*) **stat. rest.** *Hemisaprinus* is well defined morphologically by the presence of prosternal foveae, which is an apomorphic condition, otherwise absent in all other **Saprinini**.

5. The New Zealand Saprininae: Hitherto, New Zealand proper (including the surrounding islands, e.g. Chatham Islands, etc.) has had four autochthonous genera of Saprininae (*Saprinus*; three species, *Tomogenius*; three species, *Reichardtia*; monotypic and *Australopachylopus*; monotypic; Lackner & Leschen, 2017). Apart from *Tomogenius*, which is a member of **Myrmetini**, both monotypic genera *Australopachylopus* Lackner and Leschen and *Reichardtia* Wenzel are herein, based on their phylogenetic position, downgraded into subgenera of *Saprinus* and regarded as its mere beach-dwelling derivates with rather peculiar morphologies. Thus *Saprinus* (*Reichardtia*) **stat. nov.** and *Saprinus* (*Australopachylopus*) **stat. nov.** When studying female genitalia, Lackner and Tarasov (2019) already stated: 'by the shape and configuration of their spermathecae these New Zealand endemics (*Reichardtia* and *Australopachylopus*) thus resemble species of *Saprinus* or *Hemisaprinus*'. These two taxa probably evolved in isolation and adapted morphologically to life in sand. In fact, their morphological features, which are thought to be the result of selective pressure, have puzzled previous researchers assigning them separate generic statuses. Their cases probably best represent the amount of rampant homoplasy that occurred in the subfamily that kept blurring the picture until the molecular analyses started clarifying phylogenetic patterns.
6. Australasian *Saprinus*: Our molecular phylogeny argues against the single origin of Australasian *Saprinus*, confirming previous assumptions of Lackner and Leschen (2017) (see also discussion therein). Although most of the Australasian *Saprinus* form a well-supported clade, one species, *S.* (*S.*) *australis* (Boisduval) was recovered rather removed from the rest. We admit that we would have liked to include more Australasian species to test this. For the genera that are based either on the present research or on the observed morphological characters grouped in the tribe **Saprinini**, see Table 1.

Putative morphological synapomorphies and diagnostic characters of the **Saprinini** include: (1) frontal stria largely interrupted (diagnostic character; can also be seldom present) to absent; (2) lack of prosternal foveae (a putative morphological synapomorphy, albeit present in subgenera *Hemisaprinus* and *Xerosaprinus*); (3) dorso-ventrally flattened, mostly circular antennal club furnished with sensory plaques or slit-like orifices and single ball-shaped vesicle (morphological synapomorphy; Figure 3a,e; except for *Microsaprinus*, *Pilisaprinus*, *Saprinus* (*Phaonius*) *pharao* Marseul where up to six vesicles are present). Interestingly Australasian *Saprinus* often bear tiny setae on the aedeagal apex; this feature can, however, be found also in other *Saprinus* and at least one species of *Xerosaprinus* (Lackner, pers. observ.). The morphology-based analysis by Lackner (2014b) included most type species of each respective Saprininae taxon, and most of the taxa grouped in the newly erected tribe Saprinini formed a clade. The work of Lackner et al. (2019) contained a similar dataset; overall, their results were similar to ours, with several exceptions. Several **Saprinini** genera have not been sampled and their future taxonomic status is therefore uncertain. With the exception of the free-living Australasian *Notosaprinus* Kryzhanovskij, the not-sampled taxa are inquilines of ants (Australasian *Iridoprinus* Lackner & Leschen), termites (Afrotropical *Pilisaprinus* Kanaar) or ground-dwelling mammals (Palaearctic *Microsaprinus* Kryzhanovskij) and are very rare in the collections. One, likewise unsampled **Saprinini** taxon, *Saprinodes* Lewis is of unknown biology. Based on the previous analyses (Lackner, 2014b) and thorough morphological examinations we expect most of them (perhaps apart from *Microsaprinus*) to be downgraded to subgenera of *Saprinus* as well.

FIGURE 6 *Paraxenus eremicola* **comb. nov.**, habitus, dorsal view.

Paraxenus Lackner, new genus

Type species: *Hypocacculus* (*Nessus*) *eremicola* Thérond, 1965 (Figure 6).

Diagnosis

Small (PEL <2.50 mm) oval, non-metallic saprinine beetles; cuticle castaneous brown to black, in most cases shining, at least in one species (*Paraxenus oleolus* (Thérond)) with matte appearance. Frons sparsely and finely punctate, frontal and supraorbital striae complete, eyes large, bulging. Pronotal hypomeron setose; pronotum at times with anterior marginal pronotal stria. Elytra finely punctate, all dorsal elytral striae I–IV present, carinate, thin, reaching approximately ¾ of elytral length apically; stria V present at least in one species; inner

TABLE 2 Genus *Paraxenus* Lackner, gen. nov.

Taxon	Distribution	Biology
Paraxenus diasi (Vienna, 1992) **comb. nov.**	Republic of South Africa, Namibia	Unknown; collected inside cave entrance, on bat guano
Paraxenus endroedyi (Vienna, 1988) **comb. nov.**	Namibia	Unknown; collected by pitfall traps
Paraxenus eremicola (Thérond, 1965) **comb. nov.**	Republic of South Africa, Western Cape; Namibia	Lives inside burrows of Cape ground squirrel, found also outside of burrows
Paraxenus namibiensis (Vienna, 1993) **comb. nov.**	Namibia	Unknown; collected by pitfall traps
Paraxenus oleolus (Thérond, 1965) **comb. nov.**	Republic of South Africa: Western Cape	Unknown, collected in the sand on riverbank
Paraxenus therondi (Olexa, 1984) **comb. nov.**	Namibia	Unknown, collected by pitfall traps as well as by a trap at the mouth of mammal burrow
Paraxenus uhligi (Mazur, 2006) **comb. nov.**	Republic of South Africa: Western Cape, Namibia	Unknown; collected by pitfall traps

TABLE 3 Stem and crown ages for major clades within Saprininae. Median age and 95% highest probable density (min and max) of ages are given in million years ago (Ma).

	Stem (Ma)			Crown (Ma)		
Clade	**Min**	**Max**	**Median**	**Min**	**Max**	**Median**
Saprininae	94.63	119.42	107.03	66.29	93.36	79.83
Myrmetini	66.29	93.36	79.83	61.82	99.95	80.89
Euspilotini	66.29	93.36	79.83	65.56	92.3	78.93
Eremosaprinini	63.61	90.13	76.87	32.19	57.31	44.75
Hypocaccini	50.04	80.67	65.36	51.4	74.85	63.13
Saprinini	50.04	80.67	65.36	50.96	73.08	62.02

subhumeral stria long; sutural elytral stria often complete. Prosternum with both sets of striae present, at times anterior marginal prosternal stria likewise present connecting prosternal foveae; these may be occasionally absent. Apical third of prosternal process in some species convex. Protibia with up to seven short teeth topped by denticle, gradually diminishing in size in the proximal direction. Male genitalia similar to other members of **Hypocaccini**. The rest of the body characters generally similar to those of *Pholioxenus*.

Differential diagnosis

Members of *Paraxenus* differ from those of *Pholioxenus* chiefly by the setose pronotal hypomeron, which is otherwise present only with *Pholioxenus orion* Reichardt from Inner Mongolia (China), *Pholioxenus schawalleri* Mazur from Morocco and *Ph. trichoides* Kapler from Sudan. Furthermore, elytral striae of *Pholioxenus* often bear tiny beads on their carinate margins; rows of beads are occasionally present also on the fourth elytral interval (Figure 5d). Elytral striae of *Paraxenus* never exhibit this condition. Another distinguishing character between the two respective genera is the differently shaped protibia, which in *Pholioxenus* is typically dilated bearing two or three larger teeth topped by short denticle followed by several tiny denticles, while in *Paraxenus* it is not dilated, bearing up to seven short teeth topped by tiny denticle (teeth are becoming progressively smaller proximally; compare Figures I & J of Figure 5). *Paraxenus* differs from *Pholioxenus* also in its biology: members of *Pholioxenus* are exclusive inquilines of small mammals, whereas those of *Paraxenus* are mostly free-living, but occasionally also present in mammal burrows and cave entrances alike.

Biology

Paraxenus includes apparently free-living and nidicolous species alike. At least one species (*Paraxenus. eremicola*) lives inside burrows of the Cape ground squirrel (*Xerus inauris* (Zimmerman)), occasionally collected also outside of them (Thérond, 1965; Lackner pers. observ., 2018).

Distribution

The genus is so far known only from the Republic of South Africa and Namibia (see Table 2).

Etymology

The generic epithet of the newly proposed genus originates from the Greek adjective paraxenos (παράξενος), which is a compound of the prefix 'para-' (παρα−/παρά) and adjective 'xenos' (ξένος). We chose 'xenos' to demonstrate its relationship to *Pholioxenus*, which itself is a compound of two roots: 'pholeos' (φολεος; meaning hole, cave) and 'xenos' (meaning stranger, foreigner). The adjective paraxenos means 'strange' or 'counterfeit' and the prefix para- can also be

interpreted as strange—hence the name *Paraxenus* being 'strange' or 'counterfeit' *Pholioxenus*.

Comments

The Sudanese species *Pholioxenus trichoides* is known from a single female collected in northern Darfur (=Shamal Darfur), and nothing is known about its biology. Northern Darfur lies in western Sudan, near Chadian and Libyan borders—right on the border between Palaearctic and Afrotropical realms. We decided to keep its taxonomic status unchanged pending the collection of further specimens.

Dating analyses

The divergence times of the Saprininae were estimated based on the analyses of the two-gene fragment dataset, using a tree obtained from the ML analysis (see Figure S8). According to the results of BEAST analyses (Table 3; the divergence dating tree can be found in the Supplementary File S12), the Saprininae likely originated in the early Cretaceous during the Albian age (median age of 107 Ma for the MRCA of the subfamily). The first inferred split and diversification event in the Saprininae beetle clade occurred in the late Cretaceous about 80 Ma. All tribes evolved shortly after. Their origins are estimated to have occurred during the Campanian and Maastrichtian ages (83.6–72.1 and 72.1–66 Ma, respectively; Walker & Geissman, 2022), which has seen most of the cladogenesis of the subfamily. If we contrast these dates with the ones inferred in Zhou et al. (2020) we can state that according to their analyses, Saprininae likely originated in the Lower Cretaceous during the Aptian age about 120 Ma, while the first split and diversification occurred earlier than our results suggested, during the Albian age about 103 Ma. Zhou et al. (2020), however, used only four Saprininae taxa in their analyses, namely *Euspilotus* (*Hesperosaprinus*) *scissus* (**Euspilotini**), *Saprinus* (*S.*) *splendens* (**Saprinini**) and two members of the **Hypocaccini** (*Philothis* (*Atavinus*) *arabicus* and *Hypocaccus* (*H.*) *lucidulus*)—all of which are also included in this study. The general sequence of splits suggests a gradual diversification without clear shifts in the tempo of the evolution.

Ancestral character state reconstruction and historical biogeography analyses

The ancestral lifestyle of the Saprininae (Figure 7) was recovered as inquilinous based on the best model (ER), with subsequent shifts in natural histories. Inquilinism has given rise to several life strategies, spawning free-living, cavernicolous, xerophilous, littoral and psammophilous lineages. According to our analyses, free-living has evolved at least twice within the subfamily, with subsequent shifts to littoral, inquilinous, psammophilous or xerophilous lifestyles. Cavernicolous habits have evolved at least twice in the history of the subfamily, littoral habits as well as psammophily at least three times, while xerophilous life mode has evolved at least four times. These findings are in accordance with the work of Lackner (2014b), who likewise suggested the

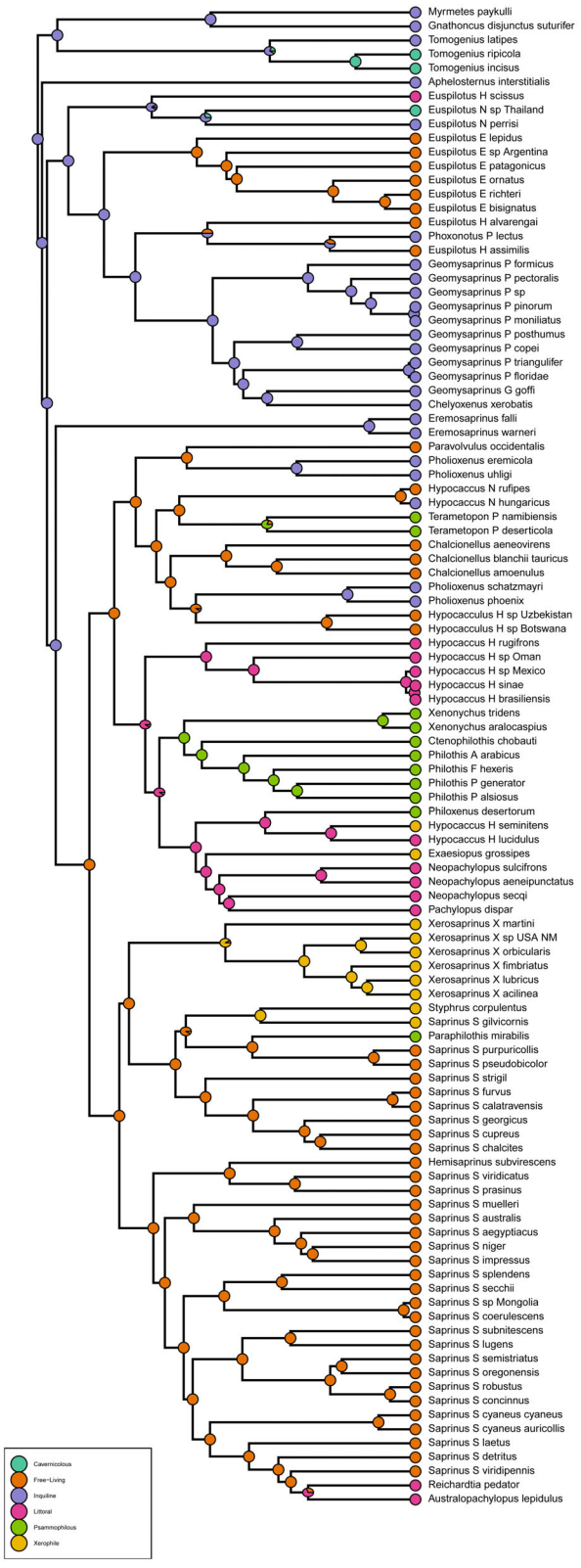

FIGURE 7 Ancestral character state reconstruction of the general ecology of the Saprininae subfamily under equal-rates model.

inquiline lifestyle as a plesiomorphic lifestyle for the group. We agree with Lackner (2014b)'s conclusions that 'multiple shifts in lifestyles have evolved during the evolutionary history of the group'.

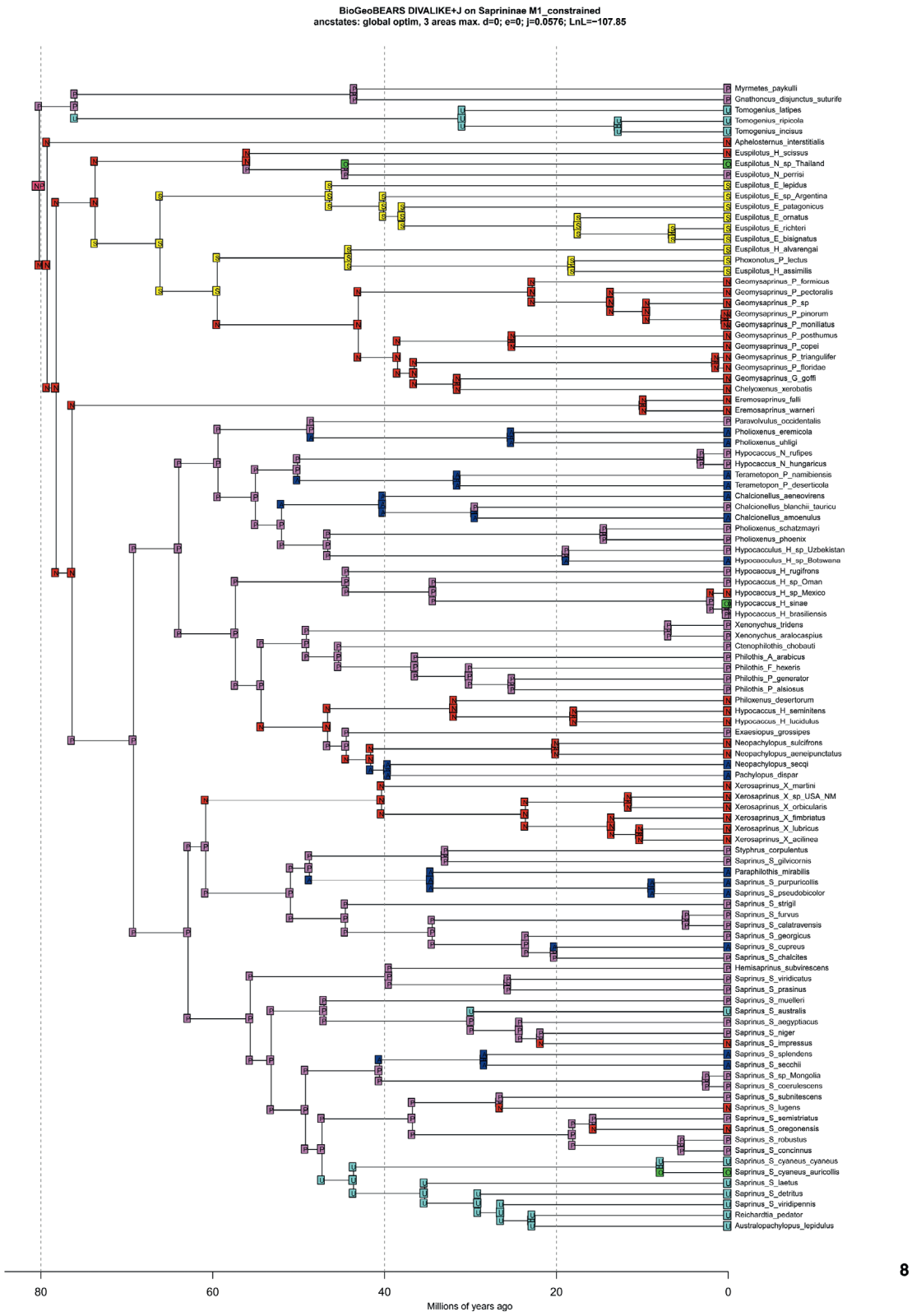

FIGURE 8 Historical biogeography of the Saprininae subfamily under the DIVALIKE+J time-stratified model. Acronyms for the biogeographic regions are Afrotropical (A), Australasian (U), Oriental (O), Neotropical (S), Nearctic (N) and Palaearctic (P).

The ancestral historical origin of Saprininae selected DIVALIKE +J as the best model for both unconstrained and the time-stratified analyses (see Supplementary File S9), although the DEC + J and BAYAREA +J also had relatively similar AIC scores. Both unconstrained and time-stratified models recovered nearly identical results, with the only exception being the origin of **Myrmetini** in the unconstrained

analysis as Holarctic + Australia, but only as Holarctic in the time-stratified analysis. Given the more conservative results recovered by the time-stratified analysis, we chose this model as our preferred interpretation (Figure 8). DIVALIKE was also selected as the best model among the three models without the +J parameter, and both the unconstrained and time-stratified models results were identical to that of the +J counterparts.

DISCUSSION

Saprininae classification

The present study represents the first phylogenetic arrangement of the Saprininae subfamily based on molecular data and morphological characters. We propose five new tribes: **Eremosaprinini**, **Euspilotini**, **Hypocaccini**, **Myrmetini** and **Saprinini**, supported by morphological features. Although our selection of morphological characters was rather broad, we were confident in establishing only several key unique changes. The problems with rampant homoplasy among the subfamily are well-known since the morphology-based phylogeny of Lackner (2014b), where the morphological discussion stressed that only a few of the character pool showed qualities to bear meaningful phylogenetic signals. The results of Lackner (2014b) mirror the present ones: internal branches depict low support, while more terminal branches depict higher support. A similar pattern with low support for intermediate divergences was found in dung beetles (Tarasov & Genier, 2015). Lackner (2014b), referring to the multiple homoplasies and reversals found in the Saprininae, together with several 'hyperdiverse' characters (e.g. shape of spiculum gastrale; dropped from the analysis here) advocated the involvement of the molecular methods to present an unambiguous Saprininae classification presented here. Despite all efforts, we have to conclude that Saprininae phylogenies based on morphological traits are poorly supported, with ambiguous phylogenetic signals and unstable inferred trees. We believe that the selection pressures linked with the biology of these insects are behind a large amount of homoplasy within saprinine morphology. Along these lines, we find only several characters bearing strong phylogenetic signals. In accordance with previous studies (Lackner, 2014b; Lackner & Tarasov, 2019) these are found either inside the antennal club, mouthparts or in male/female terminalia.

In the morphological analyses tribes **Myrmetini**, **Saprinini**, **Euspilotini** and **Hypocaccini** were retained. On the other hand, **Eremosaprinini** were recovered as paraphyletic, with *Eremosaprinus falli* joining **Hypocaccini** and *Eremosaprinus warneri* being a member of **Euspilotini**. In addition, the taxon *Aphelosternus interstitialis* that was in the combined analyses recovered as sister to most of the subfamily (without **Myrmetini**); alternatively this taxon was recovered as a member of **Euspilotini** in the morphology-based analysis, where the bulk of the subfamily is instead sister to *Phoxonotus* (*Ph.*) *lectus* (a member of **Euspilotini** in the combined analyses). In the combined analyses, the situation was different, with **Hypocaccini** and **Saprinini** forming sister clades. Numerous discrepancies exist in the clades recovered by morphological-only analyses when compared with the combined analyses. Still, due to the low support of the branches, these are not elaborated on here. Molecular analyses also recovered tree topology similar to the combined analyses, but **Myrmetini** and **Euspilotini** were rendered paraphyletic, while **Eremosaprinini** were recovered sister to **Euspilotini** (part; see also above).

Although we are still far from reaching a comprehensive phylogeny of the subfamily, we can posit that the picture is becoming clearer after combining morphological and molecular characters. The establishment of five new tribes, rather well-supported, provides a stable scaffold upon which to build future research. We have included 48% of the described higher taxa (35 out of 74 in total), yet several noteworthy taxa have not been procured. Apart from those mentioned above (e.g. *Microsaprinus*), our study lacks any representative of species-rich genus *Dahlgrenius*. Among other, similarly absent taxa (which we consider intriguing due to their morphologies), we advocate including in future studies: (1) *Pilisaprinus verschureni* (Thérond); its number of vesicles inside the antennal club is six—highest in the subfamily, contrasting strongly with a single vesicle present in most *Saprinus*; (2) *Satrapister nitens* Bickhardt (Peruvian endemic of minute size and unusual cylindrical body shape); (3) any representative of *Zorius* Reichardt (combination of **Saprinini** and **Hypocaccini** characters); (4) *Paravolvulus syphax* (Reitter); its species were moved several times between genera; (5) *Neopachylopus pakistanicus* Lackner (this taxon has been only tentatively included into *Neopachylopus*, as its morphology did not allow it to be properly included in any known genus); (6) *Pachylopus rossi* Kovarik & Verity (the monophyly of *Pachylopus*, containing one species from southern Africa and another from Mexico is doubtful at best and should be tested by molecular analysis); (7) any member of the subgenus *Terametopon* Vienna (the present study contains two members of the subgenus *Psammoprinus* Gomy & Vienna—the two subgenera differ substantially morphologically); (8) *Xenophilothis choumovitchi* (Thérond)—this taxon is morphologically most different from the rest of the subfamily, especially by the shape of mentum, densely pilose antennal scape, the shape of protibia, etc., see Lackner, 2010 for discussion)); and (9) any autochthonous Malagasy Saprininae (*Saprinus* (*S.*) *fulgidicollis* Marseul, *Malagasyprinus* Lackner & Gomy or *Sarandibrinus* Lackner & Gomy)—for elucidating the origin(s) of the Malagasy fauna. This phylogeny likewise provides a framework for this group's badly needed taxonomic inventory. In particular, revisions of the genera *Saprinus*, *Euspilotus*, *Hypocaccus*, *Hypocacculus*, *Chalcionellus*, *Geomysaprinus* or *Dahlgrenius* are most needed. Future studies aimed at elucidating the relationships should focus on a multiple-gene approach and target a richer pool of taxa. Our present problems lie in the weak support of several crucial deep nodes—especially the support for the **Eremosaprinini** + (**Hypocaccini** + **Saprinini**), or **Euspilotini**. This study makes biodiversity research on this subfamily tractable and accessible, thus setting the stage for future works addressing other evolutionary and ecological trends.

Evolutionary history of Saprininae

Lackner (2010) was the first to have hypothesised that the Palaearctic Region could have been the origin of the subfamily since it 'harbours the greatest number of the extant genera, is probably the most ecologically suitable region and circumscribes the greatest morphological diversity for the group, together with the greatest number of "advanced" forms' (Lackner, 2010). The same author presented an alternative scenario for the Saprininae origin—the ancient continent of Gondwana. Here, we hypothesise that the Holarctic Region (especially its Nearctic part), which at the time of the subfamily origin (ca. 80 Ma) was almost an interconnected vast area, has been the origin of the subfamily, with the subsequent colonisation of the globe southwards by dispersal. The Holarctic is a vast biogeographic realm embracing several terrestrial biomes of North America and Eurasia and is characterised by a rich and diverse biota with many genera and even some species, mainly arctic and subarctic, shared between both continents (Hansen et al., 2023). Although there is a substantial deal of literature with large datasets and narratives available on the subject (summarised e.g. in Hansen et al., 2023), unresolved questions (e.g. precise timing of the opening of the Bering Strait as a dispersal barrier) remain. According to Seton et al. (2012), in the time of the subfamily origin (ca. 80 Ma), Eurasia existed as a huge continent that showed close proximity to (or was even connected with) North America. India separated from Madagascar and was drifting upwards; South America and Africa, while closer to each other than today, occupied positions rather similar to the present. Based on our research, the largest amount of Saprininae cladogenesis occurred in the Palaeogene (66–23.03 Ma). During the Palaeogene, mammals diversified from relatively small, simple forms into a large group of diverse animals in the wake of the Cretaceous-Palaeogene extinction event that ended the preceding Cretaceous Period (Meredith et al., 2011). Saprininae evolution could thus be linked to the unambiguous ordinal diversification of placental mammals in the Paleocene/Eocene (Álvarez-Carretero et al., 2021). We can hypothesise that with the onset of (large) mammals, Saprininae found suitable niches for their food (mammalian dung, carcasses, underground nests) where their prey (maggots and other larvae of Arthropods) would develop.

Myrmetini present some intriguing biogeographical patterns. They are presumed to have originated in the Palaearctic Region approximately 81 Ma, but colonised the Australasian Region much later, approximately 35 Ma, presumably from the north, using islands of proto-Indonesia and proto-Melanesia as possible stepping stones in their dispersal. Indeed, their present distributions are difficult to reconcile with the arrangement of landmasses at the time without invoking regional extinction. While some of the Holarctic members of *Gnathoncus* adapted to the free-living lifestyle, others remain inquilines of mammals and birds. *Gnathoncus* went almost extinct in the Oriental Region, leaving several cave-adapted taxa and one bird inquiline in Africa (Lackner, 2020). Other extant members of the tribe, *Erebidus* and *Myrmetes* are inquilines of small mammals and ants, respectively, while Australasian *Tomogenius* represent similar lifestyles with the combination of free-living, cave adapted and inquilinous taxa. The ancestor of New Zealand *Tomogenius* is presumed to have arrived from Australia before the Oligocene drowning of New Zealand (~25 Ma) and the genus speciated in situ approximately 30 Ma and later.

Euspilotini according to our analyses originated ~77 Ma in the Nearctic, but colonised South America much later, approximately 45–40 Ma, possibly via land connection between North and South America and diversified in situ. The presumed ancestor of **Euspilotini** was recovered as inquiline and the tribe then underwent rampant radiation and speciation in South America, switching between free-living (majority of extant *Euspilotus*) to inquiline (*Paramyrmetes*, *Satrapister*, *Phoxonotus*, some *Euspilotus*, etc.) and even littoral (*E.* (*H.*) *scissus*, *Tatianella*, *Oosaprinus*—not represented in our analyses) lifestyles. It is interesting to note here that the origin and diversification of *Geomysaprinus*, many of which are Nearctic obligate pocket-gopher (Rodentia: Geomyidae) dwellers occurred in the middle Eocene (Lutetian), which had been before the origin and diversification of their hosts. Geomyidae, based on their fossil record, appeared approximately in the Oligocene (33.7–28.5 Ma; Jiménez-Hildago et al., 2018). However, Kovarik and Caterino (2016) note numerous exceptions to *Geomysaprinus*-pocket gopher relationships, with beetles being inquilines of very distant hosts like owls or tortoises. Therefore, not knowing the phylogeny of host use precludes any meaningful statements about its evolution. The origin and occurrence of several extant members of subgenus *Neosaprinus* (Palaearctic *E.* (*N.*) *perrisi*; Oriental *E.* (*N.*) *loebli* Mazur and an undescribed Thai species used in our work) is puzzling and can either be explained by long-distance dispersal or represent (inquilinous) remains of once widely spread taxon that underwent vast regional extinctions.

Although the Nearctic origin of **Eremosaprinini** can be traced back to almost 80 Ma, they seem to have colonised their mammal hosts much later, in the past ~7 Ma. By that time their mammal hosts would be well underway in North America.

Hypocaccini and **Saprinini** show both Palaearctic origin at around 77 Ma, their ancestor split about 10 million years (Myrs) later into two large clades that underwent massive radiation approximately 50 Ma that continued to the recent times. According to our research, the ancestor of **Hypocaccini** was free-living, and conquered niches as different as deep sand, mammal nests and world beaches, preying upon fly larvae developing in coastal wrack dispersing across Holarctic, Afrotropical and Oriental regions. **Hypocaccini** were apparently unable to cross into Southern America; a few taxa that are present there today are shared with Central America. At least in one case (*Nannolepidius braunsi* (Bickhardt)), they were able to bypass the chemical defences of *Hodotermes* termites and became obligate hosts. It is interesting to note that **Hypocaccini** have no inquiline members in the Western Hemisphere. Although in general much more successful in conquering sand systems, beaches and open space, only a limited number of the tribe became obligate dwellers of mammal burrows (*Pholioxenus*, *Paraxenus*, *Hypocacculus* (*Nessus*) *hungaricus*), and none really established itself in bird or ant nests (except for the

above-mentioned termite inquiline from the Republic of South Africa).

Finally, **Saprinini**, with their free-living ancestor, underwent a large radiation between 50 and 20 Ma, with most extant taxa retaining the ancestral (free-living) lifestyle having conquered and dominated all regions, except South America. In the Holarctic Region they switched to xerophilous landscapes, evolving morphological features for their lifestyles (ventral vestiture, etc.), while in the dune systems of Namib Desert they spawned a true psammophile, strongly morphologically adapted for life in deep sand and collectable only by using rather laborious methods (*S.* (*Paraphilothis*) *mirabilis*; Lackner pers. obs., 2018). Probably the most interesting biological strategies occurred in Saprinini taxa that we were not fortunate to have sampled. Among them is an obligate inhabitant of African termitaria (*Pilisaprinus verschureni*), possible inquilines of small mammals (Palaearctic *Microsaprinus*), Australasian termitophile *Iridoprinus* as well as its morphologically puzzling, enigmatic compatriot *Saprinodes*. Australasian **Saprinini** seem to have colonised the continent presumably from the north, about 50 Ma, with the subsequent colonisation of New Zealand, similar to that of members of **Myrmetini**.

CONCLUSIONS

- The results of our phylogenetic analyses indicate that Saprininae are undoubtedly monophyletic, supporting previous studies (Lackner, 2014b; Lackner et al., 2019).
- Five new tribes **Eremosaprinini Lackner, trib. nov.**; **Euspilotini Lackner, trib. nov.**; **Hypocaccini Lackner, trib. nov.**; **Myrmetini Portevin, stat. nov. & sens. nov.**; and **Saprinini Blanchard, sens. nov.** are established; the taxon *Aphelosternus interstitialis* is not included in either tribe and is treated here as species *incertae sedis*.
- **Myrmetini** appear to be a geographically bipolar tribe, with very few representatives in the tropics.
- **Euspilotini** are a tribe found almost exclusively in the Western Hemisphere, with a single origin.
- **Saprinini** appear to have spread worldwide but are limited in number in South America and Australia. The Australasian **Saprinini** probably have an origin that can be explained by multiple colonisations from the north. The **Saprinini** of New Zealand are also sister to the Australasian taxa.
- **Hypocaccini** are mainly absent from the Neotropical or Australasian regions, and their presence in these regions is thought to be a by-product of a relatively recent colonisation from the north.
- Ancestral character state reconstructions indicate that inquilinism is the most probable ancestral state for the subfamily with multiple subsequent shifts in life history. This result is in accordance with a previous study (Lackner, 2014b).
- The origin of the subfamily is deemed to be the Holarctic (Nearctic in particular) realm, with subsequent southward radiation via dispersal. This result slightly contrasts with the earlier hypothesis of Lackner (2010), who postulated the hypothesis of the Palaearctic Region as the origin.
- Saprininae diversification occurred mainly in the Palaeogene and could be linked to the diversification of mammals, which probably provided numerous niches suitable for their feeding and development.
- Our study reveals at least one independent origin of psammophily (sand association) within the subfamily (*Saprinus* (*Paraphilothis*) *mirabilis* **comb. nov.**; Namibia)—a member of **Saprinini**.
- A single new genus *Paraxenus* Lackner, **gen. nov.** (**Hypocaccini**) is erected to accommodate the former South African and Namibian members of the genus *Pholioxenus*, and new combinations are proposed accordingly.
- The inclusion of several intriguing taxa absent from our datasets and the use of a larger set of molecular markers should be among the main objectives of future studies of the subfamily.

AUTHOR CONTRIBUTIONS

Tomáš Lackner: Conceptualization; investigation; funding acquisition; writing – original draft; writing – review and editing; methodology; formal analysis; data curation; supervision. **Yuanmeng Miles Zhang:** Writing – review and editing; methodology; software; formal analysis; writing – original draft; visualization. **Carolin Kindler:** Methodology; formal analysis. **Michal Motyka:** Methodology; writing – review and editing; software; formal analysis; writing – original draft; visualization. **Michael Balke:** Supervision; writing – review and editing; validation; methodology; resources.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All new sequences generated for this study have been deposited at the NCBI GenBank accession numbers OR196584-OR196683 (cox1-3'), OR179664-OR179755 (cox1-5'), and OR179929-OR180022 (18S). All tree and data analysis input files for this study have been deposited at the Mendeley Data Repository https://doi.org/10.17632/wpj5pmcgym.1

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Supporting Information.

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