# Phylogeny of the Saprininae reveals interesting ecological shifts in the history of the subfamily (Coleoptera: Histeridae)

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# Phylogeny of the Saprininae reveals interesting ecological shifts in the history of the subfamily (Coleoptera: Histeridae)

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A morphological data set for the histerid beetle subfamily Saprininae comprising 95 adult morphological characters scored (multistate coding) from 72 terminal taxa and four outgroups was developed in order to analyse and determine the relationships amongst the genera and subgenera of the Saprininae subfamily. Cladograms were rooted with exemplars of Dendrophilinae (genus *Dendrophilus*), Bacaniini (genus *Bacanius*), Abraeinae (genus *Chaetabraeus*), and Anapleini (genus *Anapleus*). Parsimony-based phylogenetic analyses were performed based on the type species of each genus and subgenus of the Saprininae occurring around the world, with the exception of three taxa: *Paramyrmetes foveipennis* (type species of the genus *Paramyrmetes*), *Satrapister nitens* (type species of the genus *Satrapister*) and *Xerosaprinus* (*Auchmosaprinus*) *laciniatus* (type species of the subgenus *Auchmosaprinus*) that were not available. In addition, in order to test the monophyly of several questionable genera, multiple exemplars were added in a few cases. The analysis also included an exemplar of an apparently undescribed genus. The results of the analysis confirm the monophyly of the subfamily supported by two unique synapomorphies: (1) presence of sensory structures of the antenna; and (2) presence of the antennal cavity, as well as several other weaker synapomorphies. However, the phylogeny inferred here shows mostly low support for the deeper branches and consequently no major changes in the Saprininae classification are proposed. The presented cladogram is discussed together with its implications for the evolution of the subfamily. The most informative characters and their respective states are outlined. Multiple shifts in lifestyles have evolved during the evolutionary history of the group. Taxa found near the root of the cladogram are mostly nidicolous or myrmecophilous, and inquiliny is presumed to be the plesiomorphic lifestyle of the subfamily. The nidicolous lifestyle has undergone several transformations to other lifestyles and myrmecophily has evolved three times independently during the evolution of the subfamily. Termitoxeny has evolved two times independently in the group whereas ecological adaptation for life in caves has likewise evolved two times independently. The analyses yielded a large clade of predominantly psammophilous taxa; psammophily is thought to have evolved once and has been subsequently lost several times.

## INTRODUCTION

'The task for the future is the development of such a classification for the subfamily, which would cover all zoogeographic regions of the Earth.' O.L. Kryzhanovskij.

Saprininae (Fig. 1) are small to moderately large beetles, usually round or ovoid-shaped and moderately to strongly convex. Their bodies are rigid and compact, often

metallic or with red or yellow cuticular patches, and, as in other histerids, their terminal two abdominal terga are exposed (termed propygidium and pygidium) and their antennae are clubbed. These beetles are unique amongst the Histeridae in having their clubbed antennae adorned by a peculiar sensory apparatus (Fig. 3). With more than 620 described species worldwide, the Saprininae represent the second largest subfamily of the family Histeridae, after the Histerinae (Mazur, 2011). Currently, there are 63 recognized genera and

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and metatibiae. In this respect, several genus-group taxa have seen shifts between generic and subgeneric level (see e.g. Kanaar, 1996; Lackner, 2010, 2013a, c, 2014), and various newly described species have been moved amongst genera; the difficulties with their placement have mostly been because of their convergent characters. For example, a species described by Reitter (1904) as *Saprinus syphax* was moved to *Hypocacculus* by Bickhardt (1916), to *Pachylopus* by Desbordes (1918), to *Exaesiopus* by Reichardt (1926), and ended up in the genus *Paravolvulus*, to where it was moved by Kryzhanovskij (1987). The most likely reason the taxonomic history of this taxon, as well as of many other Saprininae taxa, is so convoluted is that previous authors have been misled or confused by numerous parallelisms that are clearly associated with independent origins of various microhabitat associations.

Across the subfamily, there are apparently unrelated taxa that have been recorded from bat guano inside caves (e.g. genera *Tomogenius*, see Dahlgren, 1976, or *Afroprinus* Lackner, 2013a), have colonized mammal burrows (e.g. *Pholioxenus*, see Olexa, 1984, or *Eremosaprinus*, see Tishechkin & Lackner, 2012; Lackner & Tishechkin, 2014), live in associations with dead (genus *Pilisaprinus*; see Lackner, 2013c) or active (genus *Nannolepidius*; see Reichardt, 1932) termitaria or have been extracted from the debris chambers of leaf-cutter ants (genus *Phoxonotus*; see e.g. Kanaar, 1997). The aims of the present work were to disentangle the inter-relationships (see also below) and elucidate the evolutionary development of the ecologies of these taxa.

Historically, Reichardt (1926, 1932, 1941) was the first to pay serious attention to Saprininae classification, followed by numerous workers who were mainly concerned with problems of a nomenclatural and taxonomical nature (see e.g. Olexa, 1980; Kryzhanovskij, 1987; Vienna, 1994; Tishechkin, 2005; Lackner, 2009a, b, 2010, 2011, 2012, 2013a, 2014). Although ample work on the taxonomy of the Saprininae has been published, only a handful of mostly recent authors have addressed the phylogeny of the group. Chronologically speaking, Peyerimhoff (1936) published a paper on the relationships of the psammophilous taxa of the subfamily; this work can be regarded as the first that tried to address the intricate inter-relationships of the Saprininae genera. DeMarzo & Vienna (1982) used the sensory structures of the antennal club (called the 'Reichardt's organ' in their work) in an attempt to disentangle the inter-relationships of Saprininae genera, and, despite limited taxon selection, found several interesting results; for discussion of their results see Lackner (2010: 20–27) and below. Olexa (1990) tried to disentangle the relationships of the *Philothis* complex of genera based on morphology alone, albeit without



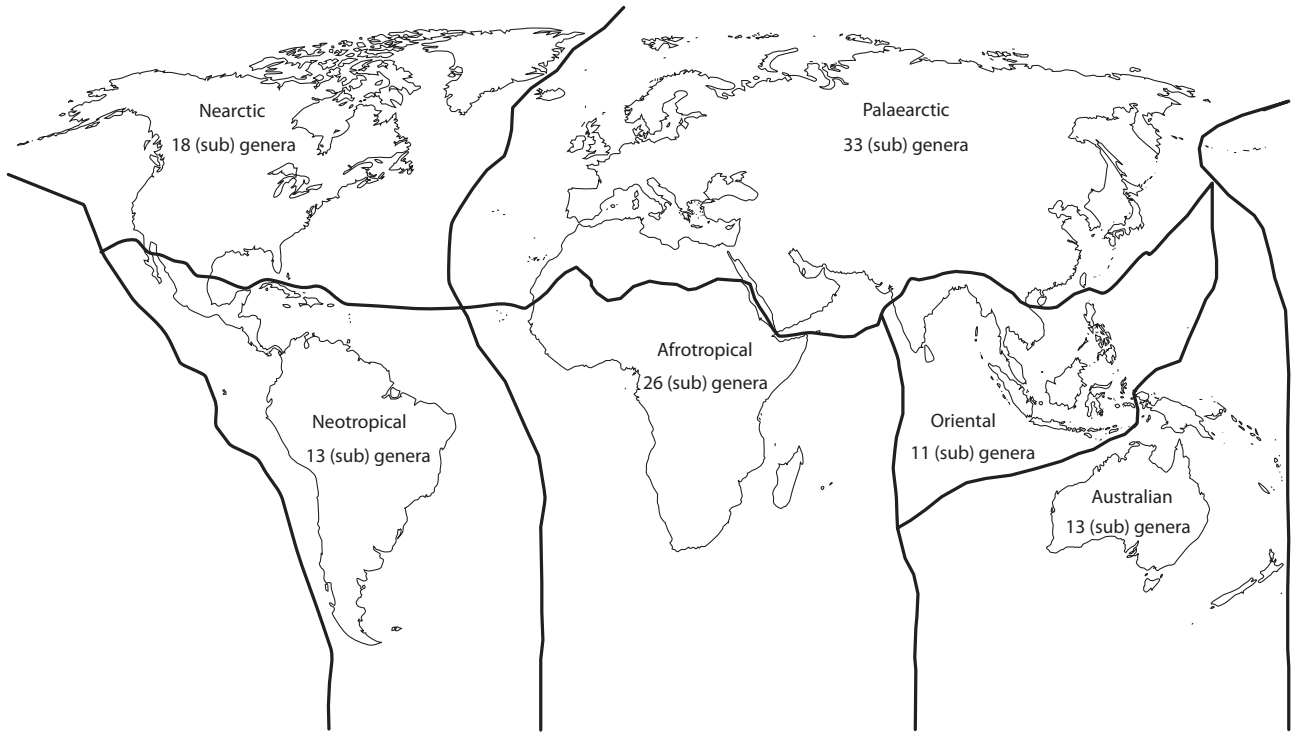**Figure 1.** A Saprininae specimen: *Exaesiopus torvus* Reichardt, 1926 (photo by M.E. Smirnov, Ivanovo, Russia).

subgenera of the Saprininae worldwide (see Lackner, 2010, 2013a, c and Lackner & Gomy 2013 for details). The zoogeographical distribution of the Saprininae genera and subgenera around the world is shown in Figure 2.

All Saprininae are thought to be predators of soft-bodied larvae of flies and other invertebrates (Lackner, 2010 and references therein). Being generalist predators, they have, however, widely varied habits. Most commonly they are found in dung or on carrion, but specialized forms exist (see below). The subfamily comprises a morphologically diverse assemblage of poorly known beetles that have their largest radiations in arid or semiarid regions with a remarkable fondness for psammophily (see e.g. Peyerimhoff, 1936 or Olexa, 1990), unseen amongst other Histeridae. Saprininae, although similar in body shape at glance, upon closer inspection show a range of forms, reflecting mostly their association with psammophily or inquiliny. These adaptations make it rather difficult to find their true generic relationships, as they have resulted in obscuring parallelisms. Many characters used hitherto are in fact homoplasies within unrelated groups, e.g. the ventral vestiture or enlargement of the mesotibiae

**Figure 2.** Distributional map of the Saprininae around the world.

using a cladistic method. More serious studies on the phylogeny of the subfamily have been conducted only recently: Lackner (2010) discussed the monophyly of psammophily of the Palaearctic higher taxa and offered some pointers for future research, and the first phylogeny-based discussions were included in papers by Lackner (2013a, c) and Lackner & Gomy (2013). Work dealing with the higher classification of the subfamily Saprininae using cladistic methods has therefore been long overdue. This study, which formed the core of my PhD studies, was intended to integrate study of taxonomic resolution, ecomorphological adaptation, and character evolution, with the primary purposes: (1) to confirm or refute the monophyly of the group; (2) to establish the first phylogenetic framework of the subfamily in order to give orientation for future research; (3) to focus on resolving Saprininae phylogeny and delineating well-supported groupings of genera; and (4) to focus on interesting ecological shifts that have occurred in the group's evolutionary history. Characters that have proven to be important for disentangling taxonomic relationships will be also discussed. The goal of this study was not to present a complete account of every nuance of the results, especially because the cladogram presented is not fully resolved and the phylogeny presented here is decidedly not the final word.

The knowledge of Saprininae larvae lags far behind that of adults, and this is a particularly acute case of the more general problem of poorly known immature stages in the Histeridae (Kovarik & Caterino, 2005). Only a handful of taxa is known to have their larvae described (see e.g. Reichardt, 1941; Hinton, 1945; Lindner, 1967; Kalashian, 1996), but larval characters might provide highly informative phylogenetic data and so descriptions and comprehensive studies of Saprininae larvae are imperative.

This work is based on the Saprininae classification of Mazur (2011) and the works by Tishechkin & Lackner (2012), Lackner (2013a, c, 2014), and Lackner & Gomy (2013). The classification of the subfamily by Mazur (2011) was arbitrarily developed by the author (S. Mazur, pers. comm. 2011) without any phylogenetic background. The morphology of adults, their biology, and distribution have been reviewed by Lackner (2010) and are therefore not repeated herein.

## MATERIAL AND METHODS

### TAXA EXAMINED

Terminal taxa are exclusively species, but the species richness (more than 620 described species) of Saprininae necessitated a selection. All genus-group taxa,

including subgenera *sensu* Mazur (2011), Lackner (2010, 2013a, c), and Lackner & Gomy, 2013) were included in the analysis, based in most cases on several specimens of the type species of each genus and subgenus of the subfamily (see Taxa included in the phylogenetic analysis below). Three taxa, however, were not available for study: *Satrapister nitens* Bickhardt, 1912 (type species of the genus *Satrapister* Bickhardt, 1912); *Paramyrmetes foveipennis* Bruch, 1929 (type species of the genus *Paramyrmetes* Bruch, 1929); and *Xerosaprinus* (*Auchmosaprinus*) *laciniatus* (Casey, 1916) (type species of the subgenus *Auchmosaprinus* Wenzel in Arnett, 1962). As a result, all (sub)genera included in the analysis are represented by their type species; however, eight additional species belonging to the apparently heterogeneous (sub)genera (*Geomysaprinus*, *Neopachylopus*, *Euspilotus* (*Neosaprinus*), *Pachylopus*, *Paravolvulus*, *Pholioxenus*, and *Reichardtiolus*) were added with the aim of testing the monophyly of these genera. The species in question, those that are non-type species of the respective (sub)genera are: *Geomysaprinus* (subgenus?) *saulnieri* Kovarik & Verity in Kovarik, Verity & Mitchell, 1999, *Neopachylopus lepidulus* (Broun, 1881), *Neopachylopus kochi* (Thérond, 1963), *Euspilotus* (*Neosaprinus*) *perrisi* (Marseul, 1872), *Pachylopus rossi* Kovarik & Verity in Kovarik *et al.*, 1999, *Paravolvulus syphax* (Reitter, 1904), *Pholioxenus oleolus* (Thérond, 1965), and *Reichardtiolus pavlovskii* (Kryzhanovskij, 1959). During the course of the study one apparently undescribed genus was discovered and its prospective type species has likewise been included in the analysis. The description of this taxon is in preparation (T. Lackner & R. Leschen, unpubl. data). Recently, several partial results of this study have been published: a new genus *Afroprinus* Lackner, 2013a, was described based on one undescribed taxon included in the analysis (Lackner, 2013a); a new genus *Malagasyprinus* Lackner & Gomy (2013) has been proposed for the taxon *Saprinus* (*Saprinus*) *caeruleatus*; and, finally, the taxonomic rank of *Pilisaprinus* has been elevated from being a subgenus of the genus *Saprinus* to a fully fledged genus (Lackner, 2013c).

Most of the material used is deposited in the collection of the author, but specimens were also borrowed from the Auckland Institute and Museum (Auckland, New Zealand), Australian National Insect Collection (Canberra, Australia), Natural History Museum (London, United Kingdom), University of Sydney, Macleay Museum (Sydney, Australia), Muséum National d'Histoire Naturelle (Paris, France), Musée Royal de l'Afrique Centrale (Tervuren, Belgium), Netherlands Centre for Biodiversity (Leiden, The Netherlands), Ditsong National Museum of Natural History (Pretoria, South Africa), and Museum für Natürkunde (Berlin, Germany).

## ANALYTICAL METHODS

Cladistic analyses were based on the external structures and male genitalia. In total, 95 morphological characters of adults were scored (multistate coding) and analysed. Adult morphological characters were treated as non-additive; inapplicable characters were assigned a gap value ('–') and treated as equivalent to missing data ('?'). The total number of ingroup taxa was 72; cladograms were rooted with exemplars of Dendrophilinae (genus *Dendrophilus*), Bacaniini (genus *Bacanius*), Abraeinae (genus *Chaetabraeus*), and Anapleini (genus *Anapleus*) so the total number of outgroup taxa was four. The taxa selected as outgroup representatives were selected based on the existing phylogenies of the Histeridae by Ślipiński & Mazur (1999) and Caterino & Vogler (2002), which suggest that representatives of Dendrophilinae and Abraeinae are amongst the best contenders for the Saprininae sister groups.

Data were entered directly into MACCLADE 4.08 (Msaddison & Maddison, 2005). The most parsimonious trees (MPTs) were searched using PAUP 4.0B10 (Swofford, 2001) with 1000 random addition replicates of tree bisection-reconnection branch swapping. All characters were unordered and equally weighted. Branch support was examined using decay indices (DIs; Bremer, 1994), calculated by the program TreeRot (Sorenson, 1999). Bootstrap (BS) values (Felsenstein, 1985; Sanderson, 1995) were calculated by resampling with 1000 replications using simple searches while holding one tree at each step and swapping on the best tree. Character states were optimized using MACCLADE 4.08 (Maddison & Maddison, 2005); only the unambiguous optimizations are shown on the tree (Fig. 47). The cladogram was graphically depicted using the FIGTREE program (Rambaut, 2007) and subsequently redrawn using ADOBE ILLUSTRATOR CS5. The history of the ecological preference (treated as an unordered character) was reconstructed using the parsimony criterion in MESQUITE, v. 2.7.5 (Maddison & Maddison, 2011) and subsequently mapped on the strict consensus of the MPTs (Fig. 48). As this is the first comprehensive phylogenetic analysis of this group, with some new characters introduced, I had little *a priori* justification for proposing any transformational or polarity assumptions. Consequently, the character state polarity was interpreted in the context of the analysis and no ancestral states were designated. In several cases, however, where I presumed plesiomorphy or apomorphy of the character state I always explicitly indicate it as a working hypothesis. However, I doubt that some of the characters are constant within each genus, particularly for the large genera *Saprinus* and *Euspilotus*.

## MORPHOLOGICAL TECHNIQUES

All dry-mounted specimens were relaxed in warm water for several hours or overnight, depending on body size. After removal from original cards, the beetles were side-mounted on triangular points and observed under a Nikon 102 stereoscopic microscope with diffused light. Some structures were studied using methods described by Ôhara (1994): the head and male genitalia were macerated in a hot 10% KOH solution for about 15 min, cleared in 80% alcohol, macerated in lactic acid with fuchsine, incubated at 60 °C for 2 h, and subsequently transferred into a mixture of glacial acetic acid (one part) and methyl salicylate (one part) heated at 60 °C for 15 min, and cleared in xylene. Specimens were then observed in α-terpineol in a small glass dish. Digital photographs of the male terminalia, male and female mouthparts and antenna were taken by a Nikon 4500 Coolpix camera and edited in ADOBE PHOTOSHOP CS4. Based on the photographs or on direct observations, the genitalia were drawn using a light-box Hakuba klv-7000. Scanning electron microscope (SEM) photographs were taken with a JSM 6301F microscope at the laboratory of Faculty of Agriculture, Hokkaido University, Sapporo, Japan. Beetle terminology follows that of Ôhara (1994) and Lackner (2010).

## LIST OF TAXA USED FOR THE ANALYSIS

*Ingroup taxa*
Taxa marked by an asterisk (*) represent the type species of their respective genera and subgenera, *sensu* Mazur, (2011); Tishechkin & Lackner (2012), Lackner (2013a, c), and Lackner & Gomy (2013).

1. *Afroprinus cavicola** Lackner, 2013a. The genus *Afroprinus* Lackner, 2013, is monotypic, known so far only from Kenya where it was found inside a cave on bat guano (Lackner, 2013a).
2. *Alienocacculus neftensis** (Olexa, 1984). The psammophilous genus *Alienocacculus* Kanaar, 2008, currently contains four species and occurs in the desert zone of northern Africa and the Near East (Lackner, 2011).
3. *Ammostyphrus cerberus** Reichardt, 1924. A monotypic psammophilous genus, *Ammostyphrus* Reichardt, 1924, occurs in the deserts of Middle Asia, and is currently known from Kazakhstan, Turkmenistan, and Uzbekistan (Lackner, 2010).
4. *Aphelosternus interstitialis** (J. L. LeConte, 1851). The North American monotypic genus *Aphelosternus* Wenzel, 1962, is known from California, where it lives as an inquiline inside burrows of ground squirrels of the genus *Spermophilus* Cuvier, 1825 (Kovarik & Caterino, 2005).
5. *Philothis* (*Atavinus*) *atavus** Reichardt, 1931. The strictly psammophilous subgenus *Atavinus* Olexa, 1990, of the genus *Philothis* Reichardt, 1930, currently contains five species known from the deserts of North Africa, Middle Asia, and the Near East (Mazur, 2011).
6. *Axelinus ghilarovi** Kryzhanovskij in Kryzhanovskij & Reichardt, 1976. The monotypic genus *Axelinus* Kryzhanovskij in Kryzhanovskij & Reichardt, 1976, is known from Turkmenistan and Uzbekistan, and is presumably a psammophile (Lackner, 2010).
7. *Hypocaccus* (*Baeckmanniolus*) *dimidiatus dimidiatus** (Illiger, 1807). Members of the psammophilous subgenus *Baeckmanniolus* Reichardt, 1926, of the genus *Hypocaccus* Thomson, 1867, are most commonly found on sandy seashores. Eleven species and three subspecies have been hitherto described, with worldwide distribution (Lackner, 2010; Mazur, 2011).
8. *Hypocacculus* (*Colpellus*) *praecox** (Erichson, 1834). The subgenus *Colpellus* Reichardt, 1932, of the genus *Hypocacculus* Bickhardt, 1914, currently contains seven described species distributed in Afrotropical and Palaearctic regions, with two species reaching as far east as India and Afghanistan and one species entering the Afrotropical region (Mazur, 2011). *Colpellus* species are typically collected on carrion or dung in arid places and fall into the category of generalist predators.
9. *Ctenophilothis chobauti** (Théry, 1900). The genus *Ctenophilothis* Kryzhanovskij, 1987, contains two strictly psammophilous species known from the Moroccan, Algerian, and Egyptian Sahara (Lackner, 2013b).
10. *Dahlgrenius aurosus** (Bickhardt, 1921). Sixty-two species are currently assigned to *Dahlgrenius* Penati & Vienna, 1996; the bulk of them known from Africa (Mazur, 2011). They are predominantly typical generalists attracted to carrion and are often collected in pitfall traps baited with odoriferous substances (T. Lackner, unpubl. data).
11. *Eopachylopus ripae** (Lewis, 1885). *Eopachylopus* Reichardt, 1926, is a monotypic psammophilous genus occurring on beaches under wrack where it probably feeds on wrack-associated dipteran larvae (Lackner, 2010). The taxon is known from Japan, the Russian Far East, South Korea, and Hong-Kong (Mazur, 2011).
12. *Erebidus vlasovi** Reichardt, 1941. Two species are currently assigned to *Erebidus* Reichardt, 1941 – a specialized inquiline of rodents; its distribution is restricted to Kazakhstan, Uzbekistan, and Turkmenistan (Lackner, 2010; Tishechkin & Lackner, 2012).
13. *Eremosaprinus unguiculatus** Ross, 1939. *Eremosaprinus* Ross, 1939, is a strictly nidicolous genus that currently contains ten species in western North America (California, Arizona, Nevada) as well

as in Baja California (Mexico). Beetles are found inside the burrows of kangaroo rats (*Dipodomys* spp.), and presumably also in burrows of pocket gophers (*Thomomys* spp.) (Tishechkin & Lackner, 2012; Lackner & Tishechkin, 2014).

14. *Euspilotus* (*Euspilotus*) *zonalis*\* Lewis, 1907. The nominotypical subgenus *Euspilotus* Lewis, 1907, currently contains 11 species found in the Neotropical region, with the bulk of its species known from Chile and Argentina (Mazur, 2011). Most of the species are typical generalist predators (G. Arriagada, pers. comm. 2014).

15. *Exaesiopus grossipes*\* (Marseul, 1855). Four species and one subspecies of *Exaesiopus* Reichardt, 1926, are described so far from the southern Palaearctic region, with another species known from Somalia (Mazur, 2011). They are typical psammophiles, found across deserts, sandy riverbanks, and (inland) sand dunes, as well as beaches. They are normally found in the rhizosphere of various plants; occasionally they are also collected on carrion (T. Lackner, unpubl. data).

16. *Philothis* (*Farabius*) *hexeris*\* Reichardt, 1930. Two strictly psammophilous species have been described so far from the subgenus *Farabius* Reichardt, 1930, of the genus *Philothis* Reichardt, 1930; both are found in the deserts of Uzbekistan, Turkmenistan, and Kazakhstan (Lackner, 2010).

17. *Geomysaprinus* (*Geomysaprinus*) *goffi*\* Ross, 1940. The nominotypical subgenus *Geomysaprinus* Ross, 1940, contains three described species occurring in North America (Florida, Texas, Manitoba, North Dakota, Illinois, and Nebraska; Mazur, 2011). These beetles are obligate inhabitants of burrows of the eastern pocket gopher (*Geomys* spp.; Kovarik & Caterino, 2005).

18. *Geomysaprinus* (subgenus?) *saulnieri* Kovarik & Verity in Kovarik *et al.*, 1999; a representative of the genus *Geomysaprinus* Ross, 1940, not assigned into a subgenus by its authors. Although Mazur (2011) assigned it to the subgenus *Priscosaprinus* Wenzel, 1962, he did so without any explanation, and the more conservative opinion of Kovarik *et al.* (1999) is upheld here. This species inhabits the burrows of western pocket gophers (*Thomomys* spp.) and occurs in the USA (Arizona, Texas, and California; Kovarik & Caterino, 2005; Mazur, 2011). It was included in the analysis because of its considerable morphological disparity with both of the subgenera of *Geomysaprinus*.

19. *Gnathoncus rotundatus*\* (Kugelann, 1792). *Gnathoncus* Jacquelin-Duval, 1858, currently contains 24 described species, mostly found in the Holarctic region, with a single species known from Congo, another from South-East Asia, and an undescribed species from Madagascar (Mazur, 2011; T. Lackner, unpubl. data). The genus contains species found inside birds' nests (especially those built in hollow trees or in nesting boxes); as well as typical inquilines of rodents. Some species are occasionally also collected on carrion, whereas at least one species is found inside caves. Several species are typical synanthropes and are often collected in pigsties, dovecotes, and chicken coops (Lackner, 2010).

20. *Hemisaprinus subvirescens*\* (Ménétries, 1832). The genus *Hemisaprinus* Kryzhanovskij, in Kryzhanovskij & Reichardt, 1976, contains three described species; two are found in the southern Palaearctic region and one reaches as far east as Burma, India, and China (Mazur, 2011). The biology of one of its species is virtually unknown; the other two are generalists found on carcasses or under decomposing vegetable matter (Lackner, 2011).

21. *Euspilotus* (*Hesperosaprinus*) *assimilis*\* (Paykull, 1811). The subgenus *Hesperosaprinus* Wenzel, 1962, of the genus *Euspilotus* Lewis, 1907, contains the bulk of the species of the genus (55 out of 76 currently described), occurring in the Nearctic and Neotropical regions (Mazur, 2011). Species in this subgenus are typical generalist predators attracted by carrion or dung (Kovarik & Caterino, 2005).

22. *Hypocacculus* (*Hypocacculus*) *metallescens*\* (Erichson, 1834). Eleven species are currently included in the nominotypical subgenus *Hypocacculus* Bickhardt, 1914, all distributed in the Old World; a single species has been introduced into the USA (Mazur, 2011). As far as is known, they are typical generalist predators found on carrion or dung.

23. *Hypocaccus* (*Hypocaccus*) *rugiceps*\* (Duftschmid, 1805). The nominotypical subgenus *Hypocaccus* Thomson, 1867, contains currently 44 psammophilous species and is worldwide in distribution (Mazur, 2011). Its members are found on sandy shores of seas, lakes, and rivers (sometimes also on inland dunes without the presence of water), where they presumably prey on dipteran larvae (Lackner, 2011).

24. *Chalcionellus amoenus*\* (Erichson, 1834). The genus *Chalcionellus* Reichardt, 1932 presently contains 34 described species distributed exclusively in the Old World (Mazur, 2011). Most of its species are normally generalist predators attracted to carrion or dung, with the exception of *Chalcionellus hauseri* (Schmidt, 1894), which is found in desiccating stalks of *Cistanche flava* Fedtschenko & Fedtschenko, 1913, as well as in the sand surrounding its roots, where the beetles prey upon fly larvae of the genus *Eumerus* Meigen, 1822 (Reichardt, 1941).

25. *Chelyoxenus xerobatis*\* Hubbard, 1894. The monotypic genus *Chelyoxenus* Hubbard, 1894, is

known exclusively from Florida, Georgia, and South Carolina in the USA (Mazur, 2011). It is an obligate inquiline of gopher tortoise (*Gopherus polyphemus* Daudin, 1802) (Kovarik & Caterino, 2005).

26. *Chivaenius kryzhanovskii** Olexa, 1980. The genus *Chivaenius* Olexa, 1980 is monotypic, with a single psammophilous species found in sand under *Tamarix* near the city of Khiva, Uzbekistan (Lackner, 2011).

27. *Saprininae* gen. nov. (Australia). A remarkable undescribed monotypic genus from Australia found inside the nests of the meat ant [*Iridiomyrmex purpureus* (Smith, 1858)], being the first obligate Saprininae myrmecophile from the Australasian region (T. Lackner, unpubl. data).

28. *Xerosaprinus* (*Lophobregmus*) *scabriceps** (Casey, 1916). The monotypic subgenus *Lophobregmus* is known from the US states of Nevada and Oregon (Mazur, 2011). Its biology is not sufficiently known, but it is a presumed generalist, usually collected on carrion.

29. *Malagasyprinus caeruleatus** (Lewis, 1899). A recently erected genus containing three species endemic to Madagascar (Lackner & Gomy, 2013). The biology of *Malagasyprinus* Lackner & Gomy, 2013 species is unknown, but individual beetles have been collected by beating bushes as well as in fish-baited pitfall traps.

30. *Microsaprinus therondianus** (Kryzhanovskij in Kryzhanovskij & Reichardt, 1976). *Microsaprinus* Kryzhanovskij, 1976, contains four described species known from the southern Palaearctic; their biology is poorly documented. Although several specimens of *Microsaprinus therondianus* have been collected in the burrows of rodents, it was coded here as of unknown ecology, as specimens have also been collected on flowering *Chondrilla* (Asterceae) and it has been found in a swimming pool (Lackner, 2010; Mazur, 2011).

31. *Monachister californicus** Mazur, 1991. *Monachister* Mazur, 1991, is a monotypic psammophile known only from California (USA) (Mazur, 2011).

32. *Myrmetes paykulli** Kanaar, 1979. The monotypic genus *Myrmetes* Marseul, 1862, is an obligate myrmecophile found in the nests of *Formica* ants across Europe and Siberia (Lackner, 2011).

33. *Nannolepidius braunsi** Bickhardt, 1921. The monotypic genus *Nannolepidius* Reichardt, 1932, is known exclusively from the Cape Province of South Africa and is an obligate termitoxene, found in the nests of *Hodotermes* termites (Bickhardt, 1921).

34. *Neopachylopus sulcifrons** (Mannerheim, 1843). The genus *Neopachylopus* Reichardt, 1926, contains six described species: two species are known from the west coast of the USA, one occurs in New Zealand, one in southern Pakistan, one in Somalia, and one species has been found in Djibouti and Yemen (Mazur, 2011). These beetles are typical psammophiles always found on beaches, where they presumably prey upon larvae of small arthropods associated with coastal wrack (T. Lackner, unpubl. data). Additional representatives, below, were included to test the monophyly of *Neopachylopus*.

35. *Neopachylopus kochi* (Thérond, 1963). This psammophilous species is known from Somalia (Mazur, 2011) and differs from the type species of the genus in several important morphological characters and was therefore included in the analysis to test the monophyly of *Neopachylopus*.

36. *Neopachylopus lepidulus* (Broun, 1881); a psammophilous representative of the genus *Neopachylopus* Reichardt, 1926, from New Zealand (Mazur, 2011) differing from the type species of the genus in several important morphological characters; therefore it was included in the analysis to test the monophyly of *Neopachylopus*.

37. *Euspilotus* (*Neosaprinus*) *perrisi* (Marseul, 1872); a representative of the subgenus *Neosaprinus* Bickhardt, 1909, of the genus *Euspilotus* Lewis, 1907. This taxon is known from the southern Palaearctic region, reaching its northern limit in Slovakia (Lackner, 2010). It inhabits the nests of the European bee-eater (*Merops apiaster* Linnaeus, 1758), but apart from this inquilinous occurrence it has also occasionally been collected on carrion (Lackner, 2010). It was included in the analysis to test the monophyly of the subgenus because it demonstrably morphologically differs from the type species.

38. *Euspilotus* (*Neosaprinus*) *rubriculus** (Marseul, 1855) (= *Saprinus gnathoncoides* Bickhardt, 1909). The subgenus *Neosaprinus* Bickhardt, 1909, of the genus *Euspilotus* Lewis, 1907, occurs chiefly in South America, with a single species described from the southern Palaearctic region and another one from Malaysia (Mazur, 2011). Its members have various ecological preferences: they include an apparent bird inquiline (see above), a noncavernicolous species attracted to bat guano, and a species found inside ant nests, as well as typical generalist predators (Kovarik & Caterino, 2005).

39. *Hypocacculus* (*Nessus*) *rubripes** (Erichson, 1834). The subgenus *Nessus* Reichardt, 1932, of the genus *Hypocaccus* Thomson, 1867, currently contains 53 described species known exclusively from the Old World (Mazur, 2011). Most species are typical generalist predators, but several are apparently psammophiles found in the deserts of Middle Asia (Lackner, 2010).

40. *Notosaprinus irinus** (Marseul, 1862). *Notosaprinus* Kryzhanovskij, 1972, is a monotypic taxon found exclusively in Australia; it is a typical generalist predator attracted to carrion (Mazur, 2011; T. Lackner, unpubl. data).

41. *Pachylopus dispar** Erichson, 1834. *Pachylopus* Erichson, 1834, is a monotypic psammophilous genus found on the beaches of South Africa and Namibia, where it is often found under dead fish or sea molluscs (Mazur, 2011; T. Lackner, unpubl. data).

42. *Pachylopus rossi* Kovarik & Verity in Kovarik *et al*., 1999; a representative of the genus *Pachylopus* Erichson, 1834. This species is found on beaches in Baja California and Sonora (Mexico) and its biology is similar to the type species of the genus (Kovarik *et al*., 1999). As the two species differ in their morphologies, *Pachylopus rossi* was included in the analysis to test the monophyly of the genus.

43. *Parahypocaccus weyerichi** Vienna, 1995. The monotypic genus *Parahypocaccus* Vienna, 1995, is known only from Zimbabwe and its biology remains unknown (Mazur, 2011).

44. *Paraphilothis mirabilis** Vienna, 1994. The monotypic genus *Paraphilothis* Vienna, 1994 is known only from Namibia; its biology is virtually unknown (Mazur, 2011).

45. *Paravolvulus ovillum** (Solskij, 1876). With 11 currently described species, *Paravolvulus* Reichardt, 1932, inhabits steppes or semi-arid regions of Middle Asia and the Middle East, reaching as far west as south-eastern Turkey. The biology of the genus remains poorly documented as beetles are normally not found on carrion and are only sporadically collected (Lackner, 2010).

46. *Paravolvulus syphax* (Reitter, 1904). This species has been repeatedly moved between genera (see above). It occurs in the Sahara and on the Arabian Peninsula (Mazur, 2011) where it is usually found in sand under desiccating vegetation. As its biology (coded here as psammophilous) and morphology differ substantially from the rest of the *Paravolvulus* species (Lackner, 2010), it was included in the present study in order to test its generic affinities.

47. *Saprinus* (*Phaonius*) *pharao** (Marseul, 1855). The subgenus *Phaonius* Reichardt, 1941 of the genus *Saprinus* Erichson, 1834, currently contains two species (Mazur, 2011). One occurs on Madagascar and the Comoros, Seychelles, and Mascarene Islands, and in Somalia; the other is found in the southern Palaearctic (Mazur, 2011). Both are typical generalist predators found mainly on carcasses (T. Lackner, unpubl. data).

48. *Philothis* (*Philothis*) *arcanus** Reichardt, 1930. The nominotypical subgenus *Philothis* Reichardt, 1930, is an obligate psammophile, and, with seven currently described species it is the most species-rich amongst the *Philothis* subgenera (Lackner, 2010). Its members occur in the deserts of Middle Asia as well as the Algerian and Moroccan Sahara (Lackner, 2010, unpubl. data).

49. *Philoxenus desertorum** Mazur, 1991. The monotypic genus *Philoxenus* Mazur, 1991, is a typical psammophile found in dunes of the Sonora Desert (Mexico) as well as California and Arizona (Mazur, 2011; T. Lackner, unpubl. data).

50. *Pholioxenus oleolus* (Thérond, 1965); a representative of the genus *Pholioxenus* Reichardt, 1932. This taxon is found in the Cape Province of South Africa (Mazur, 2011). The type series was collected on sand of the Nossob River (Thérond, 1965). As all Palaearctic representatives of the genus *Pholioxenus* are nidicolous (see below) and *Pholioxenus oleolus* is apparently a free-living generalist predator substantially morphologically different from the Palaearctic taxa, it was included in the analysis to test the monophyly of the genus.

51. *Pholioxenus phoenix** (Reichardt, 1929). *Pholioxenus* Reichardt, 1932, contains 17 Palaearctic species, all strict inquilines of small mammals (Kovarik & Caterino, 2005; Mazur, 2011). However, it also contains eight species, mostly in Namibia or South Africa (with a single species known from northern Sudan) whose lifestyles are poorly known, but do not seem to be associated with inquiliny (Mazur, 2011; T. Lackner, unpubl. data).

52. *Phoxonotus tuberculatus** Marseul, 1862. The attaphilous genus *Phoxonotus* Marseul, 1862, contains five described species and is confined to the forested regions of South America (Mazur, 2011) where it is found inside the debris chambers of leafcutter ants (*Atta* spp.; Kovarik & Caterino, 2005).

53. *Pilisaprinus verschureni** (Thérond, 1959). The monotypic genus *Pilisaprinus* Kanaar, 1996 is found in dead termitaria of *Macrotermes bellicosus* (Smeathman, 1781) and has so far been recorded from the Democratic Republic of Congo, Benin, and the Ivory Coast (Lackner, 2013c).

54. *Euspilotus* (*Platysaprinus*) *latimanus** (Schmidt, 1890). The subgenus *Platysaprinus* Bickhardt, 1916, of the genus *Euspilotus* Lewis, 1907, contains two South American (Brazil and Argentina) described species, both found in association with fungus-growing ants of the genus *Acromyrmex* Mayr, 1865 (Kovarik & Caterino, 2005; Mazur, 2011).

55. *Geomysaprinus* (*Priscosaprinus*) *posthumus** (Marseul, 1855). The subgenus *Priscosaprinus* Wenzel, 1962, of the genus *Geomysaprinus* Ross, 1940, contains the bulk of the species of the genus (25 out of 28) and its members are distributed

mostly in the USA, with several species described also from Central and South America (Mazur, 2011). Its species are also attracted to carrion, but the subgenus contains many species associated with the nests of burrowing owl (*Athene cunicularia hypogea* Bonaparte), inhabiting the nests of *Spermophilus* spp., eastern (*Geomys* spp.) or western (*Thomomys* spp.) pocket gopher, and kangaroo rat (*Dipodomys* spp.) (Kovarik & Caterino, 2005).

56. *Terametopon* (*Psammoprinus*) *namibiensis** Mazur, 1993. *Psammoprinus* Gomy & Vienna, 1996, is a subgenus of the genus *Terametopon* Vienna, 1987, and contains two described psammophilous species found in Namibia and Botswana (Lackner, 2009c).

57. *Reichardtia pedatrix** (Sharp, 1876). The monotypic psammophilous genus *Reichardtia* Wenzel, 1944, is found on beaches in New Zealand preying on small arthropods associated with coastal wrack; specimens are often buried, up to 20 cm deep, under logs (T. Lackner, unpubl. data).

58. *Reichardtiolus duriculus** (Reitter, 1904). The recently revised genus *Reichardtiolus* Kryzhanovskij, 1959, contains five psammophilous species; some have also been found in rodent burrows and under decaying vegetation (Lackner, 2014). Members of *Reichardtiolus* are found in arid regions in Egypt, Jordan, Iran, Saudi Arabia, Tajikistan, Turkmenistan, Kazakhstan, Uzbekistan, and western China (Lackner, 2014).

59. *Reichardtiolus pavlovskii* Kryzhanovskij, 1959; a representative of the genus *Reichardtiolus* Kryzhanovskij, 1959. This psammophilous taxon, known hitherto only from Turkmenistan, is morphologically substantially different from the other members of the genus and was therefore included in the analysis in order to test its affinity with the rest of *Reichardtiolus*.

60. *Saprinillus paromaloides** Kryzhanovskij, 1974. The likewise recently revised genus *Saprinillus* Kryzhanovskij, 1974, contains two species described from Mongolia, one of them found also in Turkmenistan and Kazakhstan (Lackner, 2009a). Their life habits are poorly known; the type series was found in debris under the plant *Kalidium gracile* Fenzl., whereas the specimens from Kazakhstan and Turkmenistan were collected in a burrow of the giant gerbil (*Rhombomys opimus* Lichtenstein, 1823) and in a pitfall trap, respectively (Lackner, 2009a).

61. *Saprinodes falcifer** Lewis, 1891. The two species of *Saprinodes* Lewis, 1891, are known exclusively from New South Wales and Queensland (Australia) and virtually nothing is known about the biology of this highly enigmatic taxon (Mazur, 2011; T. Lackner, unpubl. data).

62. *Saprinus* (*Saprinus*) *semistriatus** (Scriba, 1790). *Saprinus* Erichson, 1834, with 154 currently valid species is the most species-rich genus of the subfamily (Mazur, 2011). Its representatives are found across the globe, on all continents except Antarctica. They normally prefer open xeric landscapes; only a few species prefer mesic biotopes. Although normally typical generalist predators, some species are also attracted to flowers, bird nests, or rotting fungi (Lackner, 2010).

63. *Styphrus corpulentus** Motschulsky, 1845. The monotypic genus *Styphrus* Motschulsky, 1845, is a typical generalist predator of arid regions of southern Russia as well as Middle Asia, occasionally collected also at light (Lackner, 2010, 2011, 2012).

64. *Terametopon* (*Terametopon*) *levissimestriatus** Vienna, 1987. The nominotypical subgenus *Terametopon* Vienna, 1987, contains four described psammophilous species found so far solely in Namibia, predominantly in the Namib Desert (Lackner, 2009c).

65. *Tomogenius incisus** (Erichson, 1842). The Australasian genus *Tomogenius* Marseul, 1862, is found in New Zealand, New Guinea, and Australia and contains seven species, most of them collected inside caves on bat guano (Australian and New Guinean species). The New Zealand species are mostly known from petrel (*Puffinus* spp.) burrows or kaka [*Nestor meridionalis* (Gmelin, 1788)] and kingfisher (Aves: Halcyonidae) nests (T. Lackner, unpubl. data). Occasionally *Tomogenius* are also collected by sifting forest litter (New Zealand species); one Australian species was also collected under sheep carcasses (Mazur, 2011; T. Lackner, unpubl. data).

66. *Hypocacculus* (*Toxometopon*) *rubricatus** (Lewis, 1899) The subgenus *Toxometopon* Reichardt, 1932, of the genus *Hypocacculus* Bickhardt, 1932, contains two described species, both found in southern Africa; one species has been also recorded from Tanzania and the Ivory Coast (Mazur, 2011). Judging from their collection records they appear to be generalist predators of the open African savannah (T. Lackner, unpubl. data).

67. *Turanostyphrus ignoratus** Tishechkin, 2005. The two described species of the genus *Turanostyphrus* Tishechkin, 2005, are confined to Turkmenistan and Uzbekistan, and their ecological preferences are poorly documented. Apparently, one species was collected inside a rodent burrow and another in a pitfall trap (Lackner, 2010).

68. *Xerosaprinus* (*Vastosaprinus*) *ciliatus** (J. L. LeConte, 1851). The subgenus *Vastosaprinus* Wenzel, 1962, of the genus *Xerosaprinus* Wenzel, 1962, contains two described species, both generalist predators known only from the USA (Nevada, Colorado, California) and Mexico (Mazur, 2011).

69. *Xenonychus tridens** (Jacquelin DuVal, 1852). The recently revised genus *Xenonychus* Wollaston, 1864, contains three species found across the sandy regions of the southern Palaearctic; one of the species is known from coastal Somalia. These beetles are typical psammophiles, often found on sand dunes or under carrion, excrement and desiccating plants (Lackner, 2012).

70. *Xenophilothis choumovitchi** (Thérond, in Thérond & Hollande, 1965). The monotypic, strictly psammophilous genus *Xenophilothis* Kryzhanovskij, 1987, is known from the Moroccan and Algerian Sahara as well as the Arabian Desert (Gomy *et al.*, 2011; Mazur, 2011).

71. *Xerosaprinus* (*Xerosaprinus*) *lubricus** (J. L. LeConte, 1851). The nominotypical subgenus *Xerosaprinus* Wenzel, 1962, containa 25 described species found mostly in the Nearctic, and to a lesser degree also in the Neotropical region. Members of the subgenus are typical generalist predators of open landscapes, normally collected on carrion (Kovarik & Caterino, 2005; Mazur, 2011).

72. *Zorius funereus** (Schmidt, 1890). *Zorius* Reichardt, 1932, contains two described species of virtually unknown biology; both species are known from the arid regions of Israel, Palestine, and Jordan (Lackner, 2009b, unpubl. data).

### Outgroup taxa

1. *Anapleus semen* (Lewis, 1884); a representative of the tribe Anapleini Olexa, 1982.
2. *Bacanius* sp.; a representative of the genus *Bacanius* J. L. LeConte, 1853, of the tribe Bacaniini Kryzhanovskij, 1976.
3. *Chaetabraeus bonzicus* (Marseul, 1873); a representative of the subfamily Abraeinae MacLeay, 1819.
4. *Dendrophilus xavieri* Marseul, 1873; a representative of the subfamily Dendrophilinae Reitter, 1909.

### LIST OF CHARACTERS USED FOR THE ANALYSIS

The 95 morphological characters used in this study result from detailed examinations of adult specimens. Many characters and their respective states are illustrated or shown as SEM micrographs. For additional illustrations see Ôhara (1994) and Lackner (2010).

### Head capsule

1. *Antennal insertions*: hidden under distinct frontal extension (for fig. see Lackner, 2010: fig. 750) (0); visible from above (for fig. see Ôhara, 1994: fig. 124F) (1). Antennal insertions are hidden under a distinct frontal extension in all Saprininae; they are likewise hidden in two outgroup taxa: *Bacanius* and *Dendrophilus*. Antennal insertions are visible from above in *Anapleus* and *Chaetabraeus*; consistency index (CI) = 0.50; retention index (RI) = 0.00.

2. *Sensory structures of antennal club*: present (Fig. 3) (0); absent (1). Members of the Saprininae possess distinctive sensory apparatus on their antennal club. This apparatus in general consists of the presence and/or combination of the following sensory structures: slit-like pits, sensory areas, and vesicles. These three main sensory structures manifest themselves in several morphological variations, which can differ from each other significantly. The exact function of these organs is unknown, but they most likely serve as olfactory sensors. For more information on the sensory structures of the antenna the reader is referred to the works of DeMarzo & Vienna (1982) and Lackner (2010). Although the dissection of several Saprininae taxa was not permitted, studies indicate that the sensory structures are present in all Saprininae without exception; it is one of the autapomorphies of the subfamily. Antennal clubs of the outgroup taxa lack sensory structures; CI = 1.00; RI = 1.00.

3. *Antennal club, shape*: round (for fig. see Lackner, 2010: fig. 16) (0); compressed and slightly pointed (for fig. see Lackner, 2010: fig. 31) (1); egg-shaped (for fig. see Lackner, 2010: fig. 33) (2); elongate, but not pointed (for fig. see Lackner, 2010: fig. 37) (3); round, but slightly dorsoventrally flattened (Fig. 3) (4); slightly dorsoventrally flattened with pointed tip (for fig. see Lackner, 2010: fig. 35) (5); balloon-shaped (Fig. 4) (6); elongate and pointed (Fig. 5) (7); CI = 0.64; RI = 0.92.

4. *Antennal annuli*: present (Fig. 7) (0); absent (Fig. 4) (1). Amongst the outgroup taxa, antennal annuli are present only in *Dendrophilus* and *Anapleus*. In most of the Saprininae they are absent; however, the slit-like pits present in the antennal clubs of *Pilisaprinus verschureni* and *Saprinus* (*Phaonius*) *pharao*, as well as *Microsaprinus therondianus*, most likely correspond with the antennal annuli found in the outgroup taxa; CI = 0.33; RI = 0.50.

5. *Antennal club, chaetotaxy*: entirely covered with short sensilla intermingled with numerous longer sensilla, especially apically (Fig. 6) (0); entirely covered with short sensilla intermingled with sparse longer sensilla (Fig. 7) (1); approximately lower third of club glabrous, rest covered with sensilla (Fig. 4) (2); more than the lower third (usually up to half of the club) glabrous (for fig. see Lackner, 2010: fig. 183) (3); almost entire club glabrous, no slit-like or oval sensory areas present on the ventral side of the club (for fig. see Lackner, 2010: fig. 734) (4); most of the club glabrous apart from large oval or slit-like sensory areas situated on the ventral side of the club, which are densely covered with
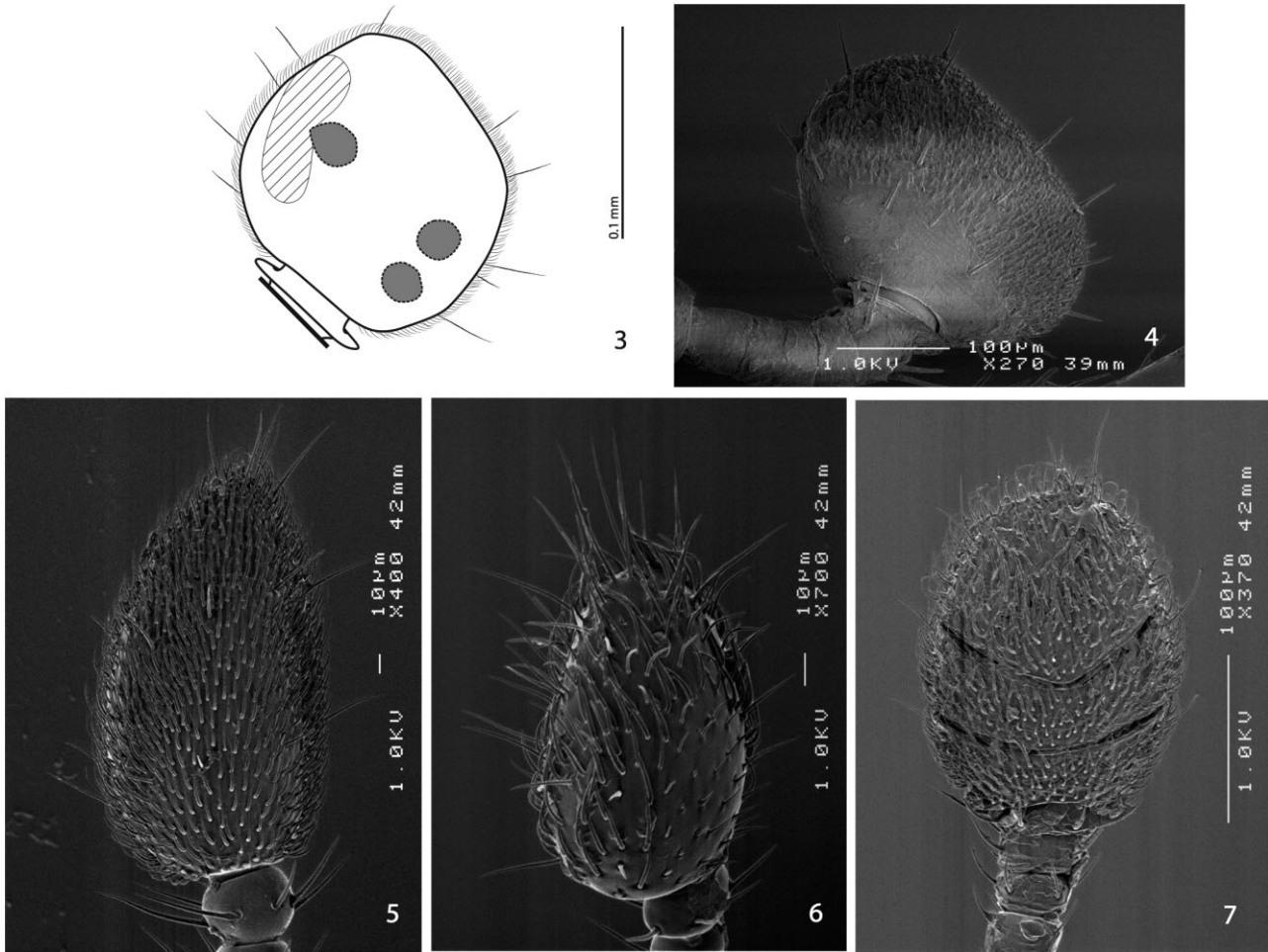
**Figures 3–7.** Figure 3. *Geomysaprinus* (*Priscosaprinus*) *posthumus* (Marseul, 1855), antennal club showing sensory structures of the antenna. Figure 4. New genus of Saprininae (Australia); antennal club. Figure 5. *Chaetabraeus bonzicus* (Marseul, 1873), antennal club ventral view. Figure 6. *Bacanius* sp., (Yayeyama Islands, Japan), antennal club, dorsal view. Figure 7. *Anapleus semen* (Lewis, 1884), antennal club, ventral view.

sensilla (for fig. see Lackner, 2010: fig. 680) (5); CI = 0.45; RI = 0.79.

6. *Antennal scape, shape*: slightly to moderately thickened (for fig. see Lackner, 2010: fig. 681) (0); strongly thickened, pyramidal in shape (for fig. see Lackner, 2010: fig. 184) (1); bulbous (for fig. see Lackner, 2010: fig. 733) (2). This character was not easy to score and therefore I decided to split it into the three well-defined categories listed above. Most of the in- and outgroup taxa have their antennal scape thickened to a varied degree; it is rather difficult to determine when the scape is 'slender' and when it is 'slightly thickened' etc. As a consequence, I lumped all the taxa with their antennal scape not extremely thickened into one category and distinguished two other character states: a strongly thickened, pyramidal antennal scape and a bulbous antennal scape, which is

present in *Xenophilothis choumovitchi*; CI = 0.50; RI = 0.60.

7. *Eighth antennomere, shape*: simple (for fig. see Lackner, 2010: fig. 679) (0); ring-like, resembling a shallow saucer of varied diameter (for fig. see Lackner, 2010: fig. 595) (1); cupuliform (for fig. see Lackner, 2010: fig. 545) (2). Shape of the eighth antennomere varies in Saprininae from a simple ring (found in all outgroup taxa, with the exception of *Dendrophilus xavieri*) to a ring-like shallow saucer that is present in most of the taxa studied. However, several psammophilous Saprininae [*Xenophilothis choumovitchi*, *Terametopon* (*Terametopon*) *levissimestriatus*, *Terametopon* (*Psammoprinus*) *namibiensis*, *Styphrus corpulentus*, and the termitoxenous *Pilisaprinus verschureni*], as well as *Saprinodes falcifer* and *Microsaprinus therondianus* whose biologies are unknown, also
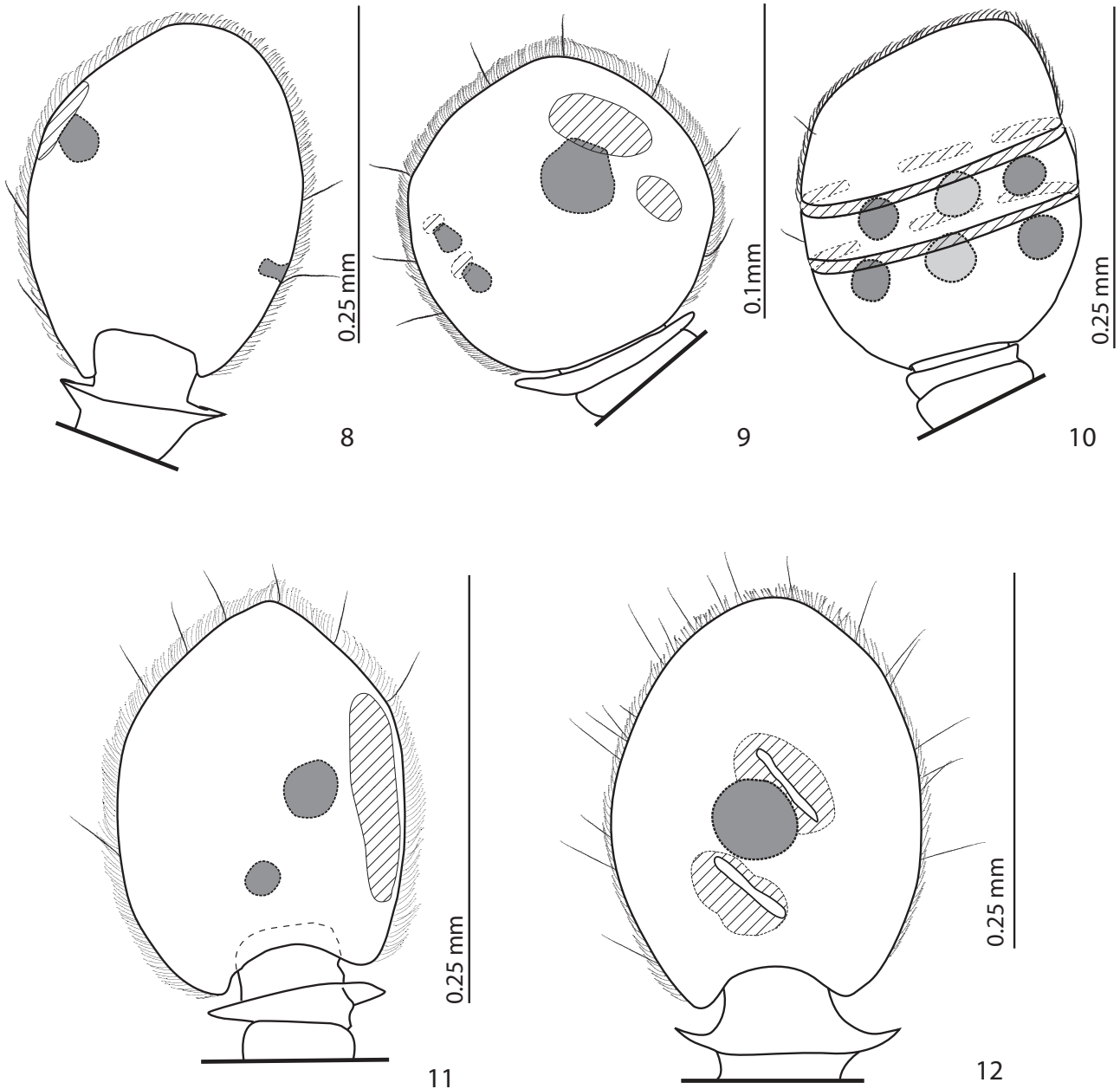
**Figures 8–12.** Sensory structures of the antenna. Figure 8. *Phoxonotus tuberculatus* Marseul, 1862. Figure 9. *Aphelosternus interstitialis* (J.L. LeConte, 1851). Figure 10. *Pilisaprinus verschureni* (Thérond, 1959). Figure 11. *Euspilotus* (*Platysaprinus*) *latimanus* (Schmidt, 1890). Figure 12. *Tomogenius incisus* (Erichson, 1842).

exhibit the (0) character state. Other Saprininae have a cupuliform eighth antennomere that can cover as much as the basal half of the club; for more discussion see Lackner (2010: 19); CI = 0.25; RI = 0.65.

8. *Sensory structures of the antenna, number of vesicles (regardless of their shape, position, and size)*: one (for fig. see Lackner, 2010: fig. 34) (0); two (Fig. 8) (1); three (Fig. 9) (2); four (for fig. see Lackner, 2010:

fig. 38) (3); five (for fig. see Lackner, 2010: fig. 36) (4); six (Fig. 10) (5). Sensory structures of the antennal club are unique to the Saprininae and are absent in all of the outgroup taxa; CI = 0.45; RI = 0.25.

9. *Single (main) vesicle (if possible to determine), position*: internal distal side of the ventral margin of the club (for fig. see Lackner, 2010: fig. 14) (0); under apical surface of the club (for fig. see Lackner, 2010: fig. 33) (1); situated almost in middle of the

club (for fig. see Lackner, 2010: fig. 11) (2). The main vesicle was impossible to determine in taxa that possess several apparently very similar-sized vesicles [e.g. *Saprinus* (*Phaonius*) *pharao*, for fig. see Lackner, 2010: fig. 13]. The main vesicle is usually the only vesicle present in the antennal club; for several of the cases in which there is more than one I chose to label the largest as the main vesicle (for more information see again DeMarzo & Vienna, 1982 and Lackner, 2010); CI = 0.67; RI = 0.93.

10. *Single (main) vesicle (if possible to determine), shape*: pear or stipe-shaped (for fig. see Lackner, 2010: fig. 14) (0); round, ball-shaped (for fig. see Lackner, 2010: fig. 11) (1); CI = 0.50; RI = 0.94.

11. *Two or more vesicles, variation*: four vesicles only on ventral side (for fig. see Lackner, 2010: 38) (0); two vesicles on dorsal side, one on ventral side (Fig. 9) (1); two vesicles on ventral and one vesicle on dorsal side (Fig. 3) (2); two vesicles on dorsal and two on ventral side (for fig. see Lackner, 2010: fig. 35) (3); two vesicles on ventral side (Fig. 8) (4); four vesicles on ventral and two on dorsal side (Fig. 10) (5); one vesicle on ventral and one on dorsal side (Fig. 11) (6). This character applies to taxa for which it either was, or was not, possible to determine the main vesicle. CI = 1.00; RI = 1.00.

12. *Sensory structures of the antenna: sensory areas, shapes and variation*: irregular, mostly round patches, usually one to three in number (Fig. 11) (0); slit-like pits not surrounded by sensilla (for fig. see Lackner, 2010: fig. 38) (1); regular patches, mostly oval and four in number (for fig. see Lackner, 2010: fig. 10) (2); slit-like pits surrounded by sensilla (Fig. 12) (3); CI = 1.00; RI = 1.00.

13. *Sensory areas, slit-like pits (if present)*: present also on dorsal side of the club (for fig. see Lackner, 2010: fig. 664) (0); absent on dorsal side of the club (for fig. see Lackner, 2010: fig. 474) (1); CI = 1.00; RI = 0.00.

14. *Sensory areas, regular patches (if present), variation*: complemented with an apical sensory cap (for fig. see Lackner, 2010: fig. 12) (0); not complemented with an apical sensory cap, entire club setose (for fig. see Lackner, 2010: fig. 9) (1); CI = 1.00; RI = 1.00.

15. *Sensory areas, irregular patches (if present)*: mohawk-like, criss-crossing the apex of the club (for fig. see Lackner, 2010: fig. 182) (0); irregularly shaped, but mostly round, never criss-crossing the apex of antennal club (Fig. 12) (1); CI = 0.33; RI = 0.00.

16. *Eyes*: convex, well visible from above (for fig. see Lackner, 2010: fig. 646) (0); slightly convex, but visible from above (for fig. see Lackner, 2010: fig. 201) (1); flattened, almost invisible from above (for fig. see Lackner, 2010: fig. 269) (2). Most specialized psammophilous taxa as well as one outgroup taxon (*Bacanius* sp.) have strongly flattened eyes, almost invisible from above. By contrast, most taxa that live inquilinously have large and bulging eyes; this condition probably evolved as a result of the reduced light inside the burrows and nests where these beetles live. However, several free-living taxa also exhibit strongly convex eyes. The rest of the out- and ingroup taxa seem to fall in between, into a category of slightly convex, yet visible eyes, which I coded as (1); CI = 0.11; RI = 0.50.

17. *Clypeus*: margined laterally (for fig. see Lackner, 2010: fig. 420) (0); not margined laterally (for fig. see Lackner, 2010: 581) (1); clypeus and frons with large projection (for fig. see Lackner, 2009c: fig. 4) (2). Most out- and ingroup taxa have their clypeus not margined; the only exceptions that do have a margined clypeus are *Neopachylopus kochi*, *Hypocaccus* (*Nessus*) *rubripes*, *Hypocacculus* (*Toxometopon*) *rubricatus*, *Hypocacculus* (*Colpellus*) *praecox*, and *Pachylopus dispar*; CI = 0.40; RI = 0.00.

18. *Frontal surface*: smooth (for fig. see Lackner, 2010: fig. 546) (0); weakly to moderately strongly punctate (for fig. see Lackner, 2010: fig. 400) (1); very coarsely punctate with minor rugae (for fig. see Lackner, 2010: fig. 218) (2); with longitudinal rugae or chevrons, otherwise smooth (for fig. see Lackner, 2010: fig. 456) (3); punctate and with chevrons (Fig. 13) (4). Degree and coarseness of the frontal punctuation varies greatly within the Saprininae; CI = 0.24; RI = 0.50.

19. *Frontal stria*: complete (Fig. 13) (0); widely interrupted medially, but not prolonged onto clypeus (for fig. see Lackner, 2010: fig. 184) (1); interrupted and prolonged onto clypeus (for fig. see Lackner, 2010: fig. 646) (2); absent (for fig. see Lackner, 2010: fig. 363) (3); clypeus and frons with large projection, presence of frontal stria ambiguous (for fig. see Lackner, 2009c: fig. 4) (4); CI = 0.17; RI = 0.56.

20. *Supraorbital stria*: complete (Fig. 13) (0); absent (for fig. see Lackner, 2010: fig. 302) (1). Kovarik *et al*. (1999) stated that the supraorbital stria of *Geomysaprinus saulnieri* is 'present, but weak'. In the single paratype that I was able to examine it is almost non-existent and I therefore coded it as absent; CI = 0.08; RI = 0.57.

*Mouthparts*

21. *Mandibular mola*: present (Fig. 14) (0); strongly reduced or absent (for fig. see Lackner, 2010: fig. 79) (1). The mola is always strongly reduced to absent in the predatory Saprininae; by contrast, in three presumably nonpredaceous taxa that were selected as outgroups (*Bacanius*, *Chaetabraeus* and
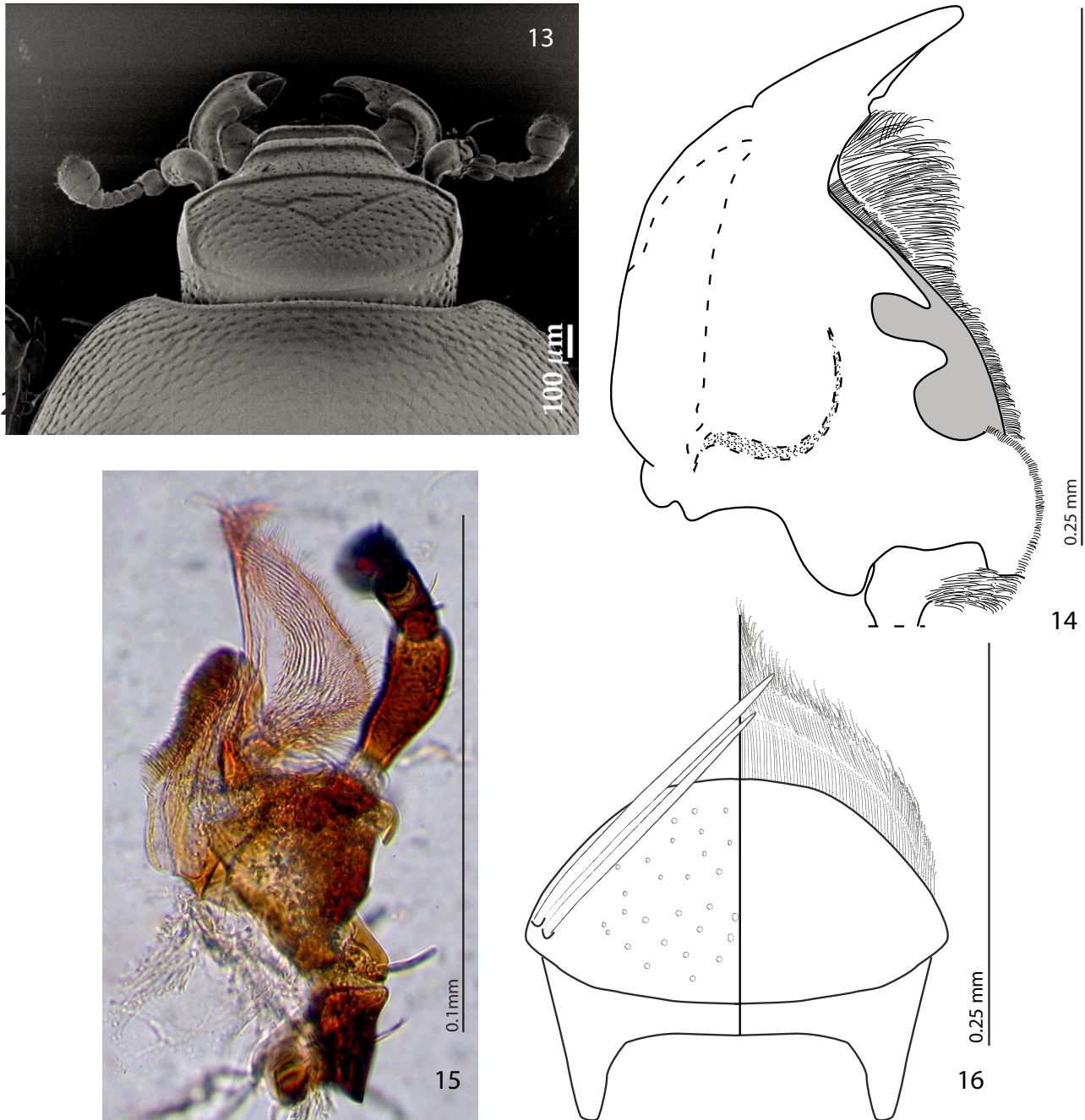
**Figures 13–16.** Figure 13. *Parahypocaccus weyrichi* Vienna, 1995, head, dorsal view. Figure 14. *Chaetabraeus bonzicus* (Marseul, 1873), mandible. Figure 15. *Chaetabraeus bonzicus* (Marseul, 1873), maxilla. Figure 16. *Chaetabraeus bonzicus* (Marseul, 1873), labrum, left half depicting dorsal view; right half depicting ventral view.

*Anapleus*), it is present. The mola is also absent in *Dendrophilus*, which is also predatory. The feeding habits of the outgroup taxa *Bacanius*, *Chaetabraeus*, and *Anapleus* are not known, but based on the presence of the mola it is likely that these beetles are nonpredatory. CI = 1.00; RI = 1.00.

22. *Mandibles, subapical tooth on the left mandible*: large, almost perpendicular (for fig. see Lackner, 2010: fig. 83) (0); extraordinarily small (for fig. see Lackner, 2010: fig. 90) (1); obtuse, not perpendicular (for fig. see Lackner, 2010: fig. 87) (2); rounded (for fig. see Lackner, 2010: fig. 81) (3). A subapical tooth of the left mandible (seen from dorsal view)

is present in almost all studied taxa. See my earlier work for more information concerning the variation in this tooth (Lackner, 2010: fig. 33); CI = 0.16; RI = 0.43.

23. *Lacinia, lacinial hook*: present (for fig. see Lackner, 2010: fig. 144) (0); absent (for fig. see Lackner, 2010: fig. 145) (1). The lacinial hook is a digitiform structure present in almost all outgroup taxa (*Anapleus*, *Bacanius*, and *Dendrophilus*), but absent in *Chaetabraeus*; CI = 0.17; RI = 0.55.

24. *Maxilla, palpal organ*: absent (0); present (for fig. see Lackner, 2010: fig. 144) (1). The palpal organ of the maxilla is situated on the terminal maxillary palpomere and has been observed to be present in all Saprininae. Even though the dissection of the mouthparts of several taxa was not permitted, I presumed it to be present in these as well because my studies indicate that it is present in all Saprininae without exception. However, this organ is weakly developed in inquilinous taxa, often to the degree that it is rather difficult to observe. By contrast, it is rather well developed in the specialized psammophilous taxa, especially those found in desert regions. Except for *Chaetabraeus*, this organ is likewise present in all outgroup taxa; CI = 1.00; RI = 0.00.

25. *Terminal labial palpomere, palpal organ*: absent (0); present (1). This and the previous character (#24) are possibly serial homologies; the palpal organ on the terminal labial palpomere is likewise present in all in- and outgroup taxa (with the sole exception of *Chaetabraeus*); CI = 1.00; RI = 0.00.

26. *Labrum, labral process*: distinct, well developed (for fig. see Lackner, 2010: fig. 39) (0); strongly reduced or absent (for fig. see Lackner, 2010: fig. 41) (1). The labral process (for explanation of the term, and figs see Lackner, 2010: 27, 28) is strongly reduced or absent in all outgroup taxa and many ingroup taxa. As this character is strongly reduced to absent in all of the outgroup as well as most of the ingroup taxa that come out near the root of the tree, the reduced or absent labral process is hypothesized to represent the plesiomorphic condition, and a well-developed and large labral process probably represents the apomorphic condition; CI = 0.50; RI = 0.97.

27. *Penultimate labial palpomere (second)*: with single very long seta (about twice as long as the ultimate labial tarsomere) (0); with up to seven short or moderately long setae (1); with more than 15 long dense setae (2). Most of the studied in- and outgroup taxa have their second labial palpomere adorned with up to seven short or moderately long setae; only *Alienocacculus neftensis*, *Terametopon* (*Terametopon*) *levissimestriatus*, and *Terametopon* (*Psammoprinus*) *namibiensis* share a synapomorphy of a single very long seta, and *Pilisaprinus verschureni*'s labial palpomeres have more than 15 long setae; CI = 0.67; RI = 0.50.

28. *Galea*: predatory type (for fig. see Lackner, 2010: fig. 144) (0); filter-feeding type (Fig. 15) (1). The maxillary galea is of the predatory kind in all Saprininae studied as well as in all outgroup taxa except for *Chaetabraeus*. The maxillary galea of *Chaetabraeus* differs markedly from all ingroup and all other outgroup taxa. It is probably of the filter-feeding type, suggesting that *Chaetabraeus* may suck liquid from mammalian (mostly cow) dung (*sensu* Kovarik, 1994); CI = 1.00; RI = 0.00.

29. *Mandibles near base with a large emargination*: present (Fig. 14) (0), absent (for fig. see Lackner, 2010: fig. 79) (1). The outgroup taxa *Anapleus*, *Chaetabraeus*, and *Dendrophilus* possess a curious large emargination near the base of their mandibles. All ingroup taxa as well as *Bacanius* lack such a structure; CI = 0.50; RI = 0.50.

30. *Epipharynx, position*: Anterad of labrum, detached, completely protruding (Fig. 16) (0); under labrum, protruding only marginally (for fig. see Lackner, 2010: fig. 45) (1). Character state (0) is an autapomorphy of *Chaetabraeus*; in all other taxa the epipharynx is positioned directly under the labrum and only slightly protrudes laterally or anteriorly; CI = 1.00; RI = 0.00.

31. *Labral setae and pits, position (if present)*: growing out from lateral margins (Fig. 16) (0); growing out from dorsal labral surface (for fig. see Lackner, 2010: fig. 45) (1). State (0) is an autapomorphy of *Chaetabraeus*; in all the ingroup and other outgroup taxa the labral setae (if they are present) grow out from the dorsal labral surface; CI = 1.00; RI = 0.00.

32. *Labral setae, if growing out from dorsal labral surface, number*: zero, setae absent (for fig. see Lackner, 2010: fig. 63) (0); two setae present in each labral pit (for fig. see Lackner, 2010: fig. 63) (1); single seta present in each labral pit (for fig. see Lackner, 2010: fig. 63) (2); CI = 0.27; RI = 0.50.

33. *Mentum, shape*: distinctly broadened anteriorly (for fig. see Lackner, 2010: fig. 143) (0); square-shaped or subtrapezoidal (for fig. see Lackner, 2010: fig. 365) (1); anterior margin with a prominent projection (Fig. 17) (2); basally distinctly broader than long (along median line) but without prominent projection on anterior margin (Fig. 18) (3); anterior margin with two deep excavations, apparently for attachment of labial palpus (Fig. 19) (4). Most Saprininae have a uniformly shaped mentum; it is either subtrapezoidal or square-shaped. The sole exception to this pattern is the mentum of *Xenophilothis choumovitchi*, which is distinctly broadened anteriorly. The anterior margin of the mentum of *Anapleus semen* bears a prominent
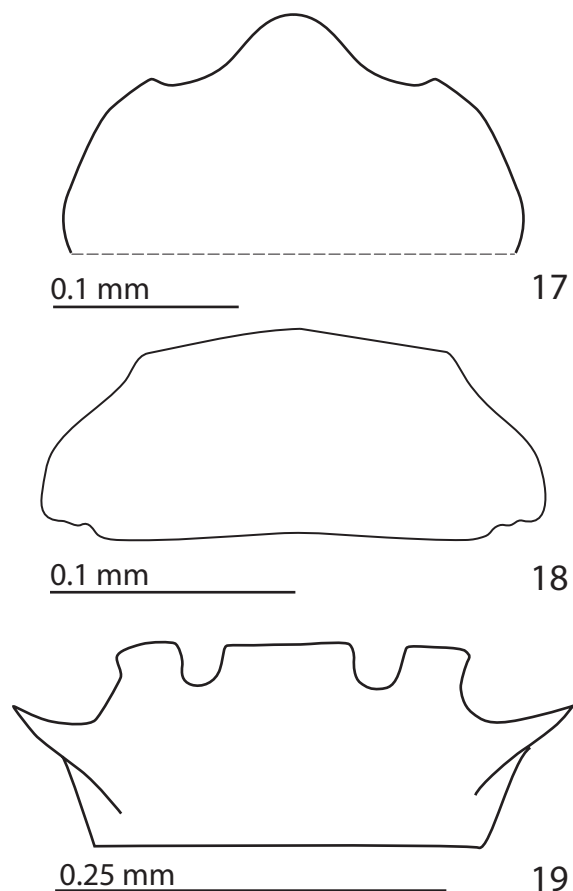
**Figures 17–19.** Mentum outline. Figure 17. *Anapleus semen* (Lewis, 1884). Figure 18. *Dendrophilus xavieri* Marseul, 1873. Figure 19. *Chaetabraeus bonzicus* (Marseul, 1873).

projection; in two outgroup taxa (*Bacanius* and *Chaetabraeus*) the anterior margin of the mentum bears two deep excavations that apparently serve for attachment of the labial palpus. The mentum of *Dendrophilus* is basally distinctly broader than long along the median line, but without a projection on the anterior margin; CI = 1.00; RI = 1.00.

*Thorax*

34. *Antennal cavity*: present (for fig. see Lackner, 2010: fig. 148) (0); absent (for fig. see Lackner, 2010: fig. 271) (1). Antennal cavity (or impression) is present in almost all studied taxa, with the exception of *Ctenophilothis chobauti* and *Philothis* (*Farabius*) *hexeris*, in which it is presumed to be secondarily lost. This character is weakly developed in *Phoxonotus tuberculatus*, but is coded as present. The antennal cavity is absent in all outgroup taxa; CI = 0.33; RI = 0.60.
35. *Metepisternum*: hidden or fused to the lateral disc of metaventrite (for fig. see Ôhara, 1994: fig. 125A,

B) (0); visible (for fig. see Lackner, 2010: fig. 222) (1). Abraeinae and Bacaniini share a hidden metepisternum, which may be correlated to their small body size. All other out- and ingroup taxa have their metepisternum visible externally. For more discussion see Caterino & Vogler (2002); CI = 1.00; RI = 1.00.

36. *Lateral pronotal stria*: present (for fig. see Lackner, 2010: fig. 198) (0); absent (for fig. see Lackner, 2010: fig. 453) (1). A lateral pronotal stria is absent in all outgroup and almost all ingroup taxa; it is present only in *Ammostyphrus cerberus*; CI = 1.00; RI = 0.00.
37. *Pronotum*: with two bulges near the base (for fig. see Lackner, 2010: fig. 559) (0); without bulges (for fig. see Lackner, 2010: fig. 453) (1); with bulges near base and vague costae medially (Fig. 26) (2). Pronotum lacks bulges in all outgroup and almost all ingroup taxa as well. *Philothis* (*Farabius*) *hexeris* and *Philothis* (*Philothis*) *arcanus* possess two bulges on their pronotum, situated near base and near lateral margins; the taxon *Phoxonotus tuberculatus* supports bulges near base as well as vague costae medially; CI = 1.00; RI = 1.00.
38. *Pronotal surface*: completely smooth, at most there is a row of punctures along pronotal base (for fig. see Lackner, 2010: fig. 453) (0); punctate, at least laterally (for fig. see Lackner, 2010: fig. 318) (1); CI = 0.14; RI = 0.33.
39. *Anterior pronotal angles*: extremely acute, space for head between the angles very narrow (for fig. see Lackner, 2009c: fig. 57) (0); moderately acute to obtuse, space for head not extremely narrow (for fig. see Lackner, 2010: fig. 179) (1). Only three taxa: *Terametopon* (*Psammoprinus*) *namibiensis*, *Terametopon* (*Terametopon*) *levissimestriatus*, and *Xenophilothis choumovitchi* share extremely acute pronotal angles; their heads are concomitantly reduced in size; CI = 1.00; RI = 1.00.
40. *Pronotum*: distinctly depressed laterally, with a median convexity (Fig. 20) (0); even, not depressed laterally (for fig. see Lackner, 2010: fig. 453) (1). State (0) is an autapomorphy of *Malagasyprinus caeruleatus*, a Malagasy endemic of unknown biology; CI = 1.00; RI = 0.00.
41. *Pronotal hypomeron*: asetose (for fig. see Lackner, 2010: fig. 422) (0); setose (for fig. see Lackner, 2010: fig. 271) (1). A setose pronotal hypomeron is present not only in the psammophilous taxa (e.g. *Ammostyphrus cerberus*), but also in apparently free-living volant predators [e.g. *Euspilotus* (*Euspilotus*) *zonalis* and *Xerosaprinus*]; CI = 0.07; RI = 0.60.
42. *Lateral costa of antennal groove*: terminates anterior to the procoxa and does not reach the prosternal process (for fig. see Lackner, 2010: fig. 203) (0);
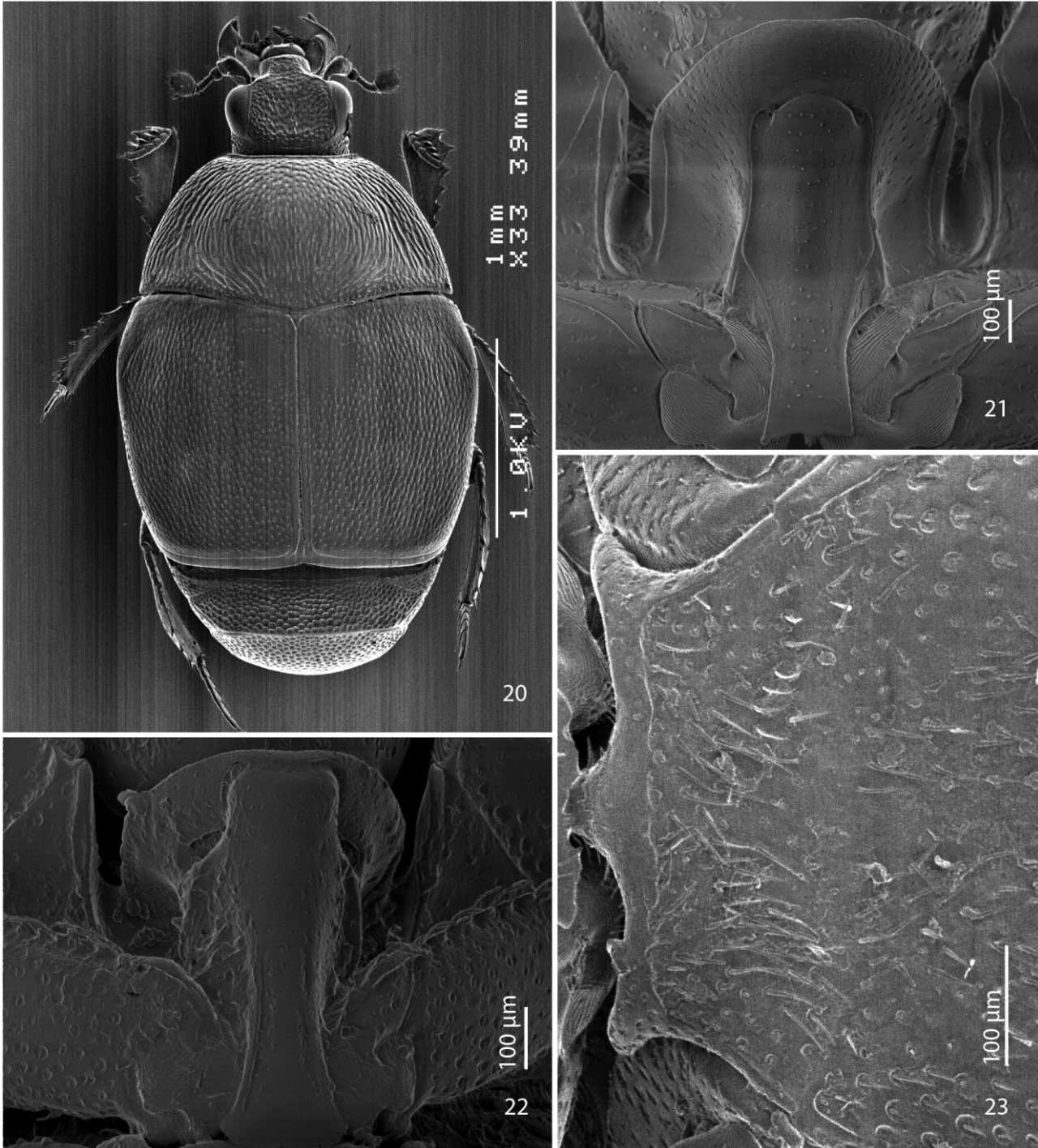
**Figures 20–23.** Figure 20. *Malagasyprinus caeruleatus* (Lewis, 1905), pronotum. Figure 21. *Euspilotus* (*Neosaprinus*) *rubriculus* (Marseul, 1855), prosternum. Figure 22. *Afroprinus cavicola* Lackner, 2013a, prosternum. Figure 23. *Tomogenius incisus* (Erichson, 1842), meso-metaventrite.

costa reaches the prosternal process but its basal part is not distinctly elevated (for fig. see Lackner, 2010: fig. 305) (1); costa reaches the prosternal process and its basal part is distinctly elevated (for fig. see Lackner, 2010: fig. 496) (2); costa strongly reduced, shortened (for fig. see Lackner, 2010: fig. 271) (3). A shortened and strongly reduced lateral costa of the antennal groove is found in the

outgroup (with the exception of *Chaetabraeus* where it was not possible to score it unambiguously) as well as in the following ingroup taxa: *Phoxonotus tuberculatus*, *Philothis* (*Farabius*) *hexeris*, and *Ctenophilothis chobauti*. A distinctly elevated basal part of the lateral costa reaching the prosternal process is found in two Saprininae: *Gnathoncus rotundatus* and *Myrmetes paykulli*, and costa likewise reaching the prosternal process, albeit not distinctly elevated, is found in another two Saprininae: *Erebidus vlasovi* and *Eremosaprinus unguiculatus*. State (0) is present in all other ingroup taxa; CI = 0.38; RI = 0.29.

43. *Prosternum, median fovea(e)*: absent (for fig. see Lackner, 2010: fig. 148) (0); present (for fig. see Lackner, 2010: fig. 149) (1). The prosterna of *Gnathoncus* and *Tomogenius* are not identical and the median fovea in *Tomogenius* is divided into two by the apex of the prosternal process. However, this is hypothesized to be homologous with the median fovea found in *Gnathoncus* and these two taxa are therefore coded similarly; CI = 1.00; RI = 1.00.

44. *Prosternum, pre-apical fovea(e)*: absent (for fig. see Lackner, 2010: fig. 203) (0); present (for fig. see Lackner, 2010: fig. 148) (1). Pre-apical foveae (for more discussion see e.g. Lackner, 2010: fig. 40) are probably homologous within the Saprininae; the foveae present in the prosternum of *Chaetabraeus* are probably not homologous with them and therefore in this taxon they are coded as absent; CI = 0.08; RI = 0.68.

45. *Pre-apical foveae (if present)*: free (for fig. see Lackner, 2010: fig. 148) (0); connected by a sulcus (Fig. 21) (1); connected by marginal prosternal stria (Fig. 22) (2); CI = 0.22; RI = 0.00.

46. *Prosternum, carinal prosternal striae*: absent (for fig. see Lackner, 2010: fig. 549) (0); present (for fig. see Lackner, 2010: fig. 148) (1); CI = 0.09; RI = 0.23.

47. *Prosternum, lateral prosternal striae*: absent (for fig. see Lackner, 2010: fig. 305) (0); present (for fig. see Lackner, 2010: fig. 148) (1); CI = 0.13; RI = 0.30.

48. *Prosternum, setae*: absent (for fig. see Lackner, 2010: fig. 149) (0); present (if the setae are short, coded as setose; for fig. see Lackner, 2010: fig. 685) (1); CI = 0.06; RI = 0.25.

49. *Mesoventrite, setae:* asetose (for fig. see Lackner, 2010: fig. 583; if they are extremely short, mesoventrite is coded as asetose) (0); setose (Fig. 23) (1); CI = 0.14; RI = 0.00.

50. *Metaventrite, disc chaetotaxy*: asetose (for fig. see Lackner, 2010: fig. 649) (0); setose (Fig. 23) (1); CI = 1.00; RI = 0.00.

51. *Lateral disc of metaventrite, chaetotaxy*: asetose (for fig. see Lackner, 2010: fig. 584) (0); setose [for fig. see Lackner, 2010: fig. 565; in the case of extremely short, microscopic setae, state (0) is coded] (1). The lateral disc of the metaventrite is often setose in the Saprininae. As a rule, species that have a setose lateral disc of the metaventrite also have setae on the metepisternum, see below. All outgroup taxa have asetose undersides of their bodies and the setose venter is thus regarded as a derived character state, probably resulting from the convergence in similar lifestyles; CI = 0.11; RI = 0.72.

52. *Metepisternum, chaetotaxy*: asetose (for fig. see Lackner, 2010: fig. 584) (0); setose [for fig. see Lackner, 2010: fig. 565; in the case of extremely short setae, state (0) is scored] (1). This character strongly correlates with the previous one; CI = 0.10; RI = 0.71.

53. *Marginal metepisternal stria*: absent (for fig. see Lackner, 2010: fig. 423) (0); present [for fig. see Lackner, 2010: fig. 324; in the case of presence only on fused metepimeron, state (0) is scored] (1). This stria is often present in the Saprininae; however, it is rarely complete. Often this stria is intermittent and in some cases is limited to the fused metepimeron; CI = 0.06; RI = 0.35.

54. *Metepisternum, groove for reposing mesotarsus*: absent (for fig. see Lackner, 2010: fig. 368) (0); present (Fig. 24) (1); CI = 1.00; RI = 0.00.

55. *Elytral epipleuron, chaetotaxy:* asetose (for fig. see Lackner, 2010: fig. 368) (0); setose (for fig. see Lackner, 2010: fig. 700) (1); CI = 0.20; RI = 0.43.

56. *Elytral epipleuron, marginal epipleural stria*: absent or invisible (for fig. see Ôhara, 1994: fig. 85E) (0); single (for fig. see Lackner, 2010: fig. 629) (1); double (2). The outgroup taxa *Anapleus*, *Bacanius* sp., and *Chaetabraeus* have their marginal epipleural stria absent or invisible; the ingroup taxa *Gnathoncus rotundatus* and *Tomogenius incisus* share a double marginal epipleural stria. All other in- and outgroup taxa have a single marginal epipleural stria (for explanation and fig. see Lackner, 2010: fig. 146); CI = 1.00; RI = 1.00.

57. *Dorsal elytral striae, except sutural stria*: absent (for fig. see Ôhara, 1994: fig. 124A) (0); present (for fig. see Lackner, 2010: fig. 198) (1); CI = 1.00; RI = 1.00.

58. *Sutural elytral stria*: absent (Fig. 28) (0); present (Fig. 1) (1). The sutural elytral stria (for explanation and fig. see Lackner, 2010: fig. 146) is truly absent in one outgroup taxon (*Dendrophilus xavieri*), one Palaearctic myrmecophilous taxon (*Myrmetes paykulli*), one South American myrmecophilous member (*Phoxonotus tuberculatus*), and the undescribed myrmecophilous Australian genus (Fig. 28), as well as two psammophilous African taxa: *Terametopon* (*Psammoprinus*) *namibiensis* and *Paraphilothis mirabilis*; CI = 0.20; RI = 0.00.
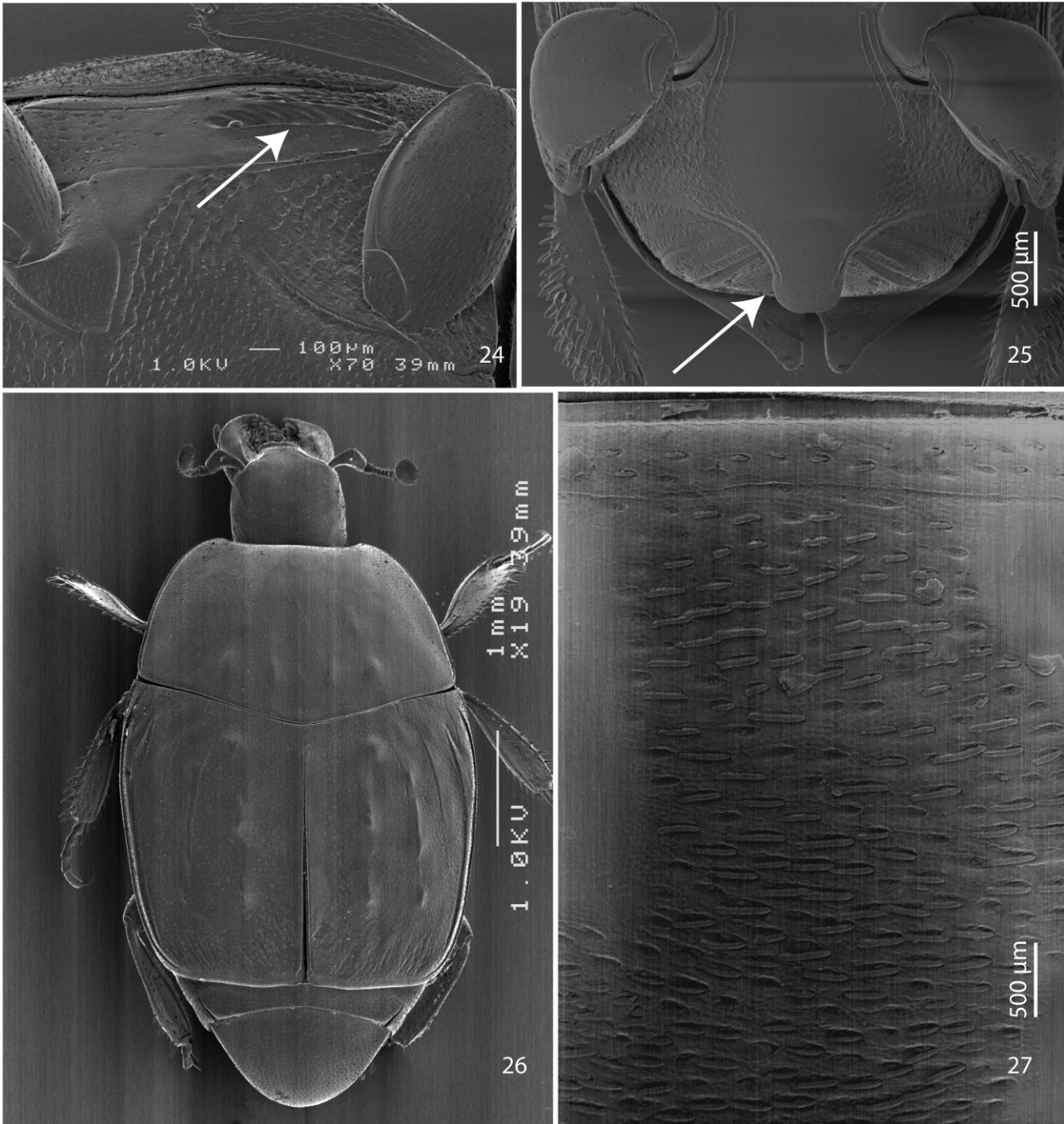
**Figures 24–27.** Figure 24. New genus of Saprininae (Australia), metepisternum depicting the groove for reposing mesotarsus on metepisternum. Figure 25. *Pachylopus dispar* Erichson, 1834, female, first visible abdominal tergite + apex of elytra (ventral view). Figure 26. *Phoxonotus tuberculatus* Marseul, 1862, habitus, dorsal view. Figure 27. *Nannolepidius braunsi* (Bickhardt, 1921), elytral detail.

59. *Apex of elytra sexually dimorphic: apices of elytra in female elongated, overlying pygidium; in male pygidium exposed:* yes (Fig. 25) (0); no (1). *Pachylopus dispar* is the only sexually dimorphic taxon, with females exhibiting elongated apex of the elytra overlying the pygidium, whereas the pygidium of the male is exposed; CI = 1.00; RI = 0.00.

60. *Elytra*: without tubercles (for fig. see Lackner, 2010: fig. 198) (0); with tubercles (Fig. 26) (1). The elytra
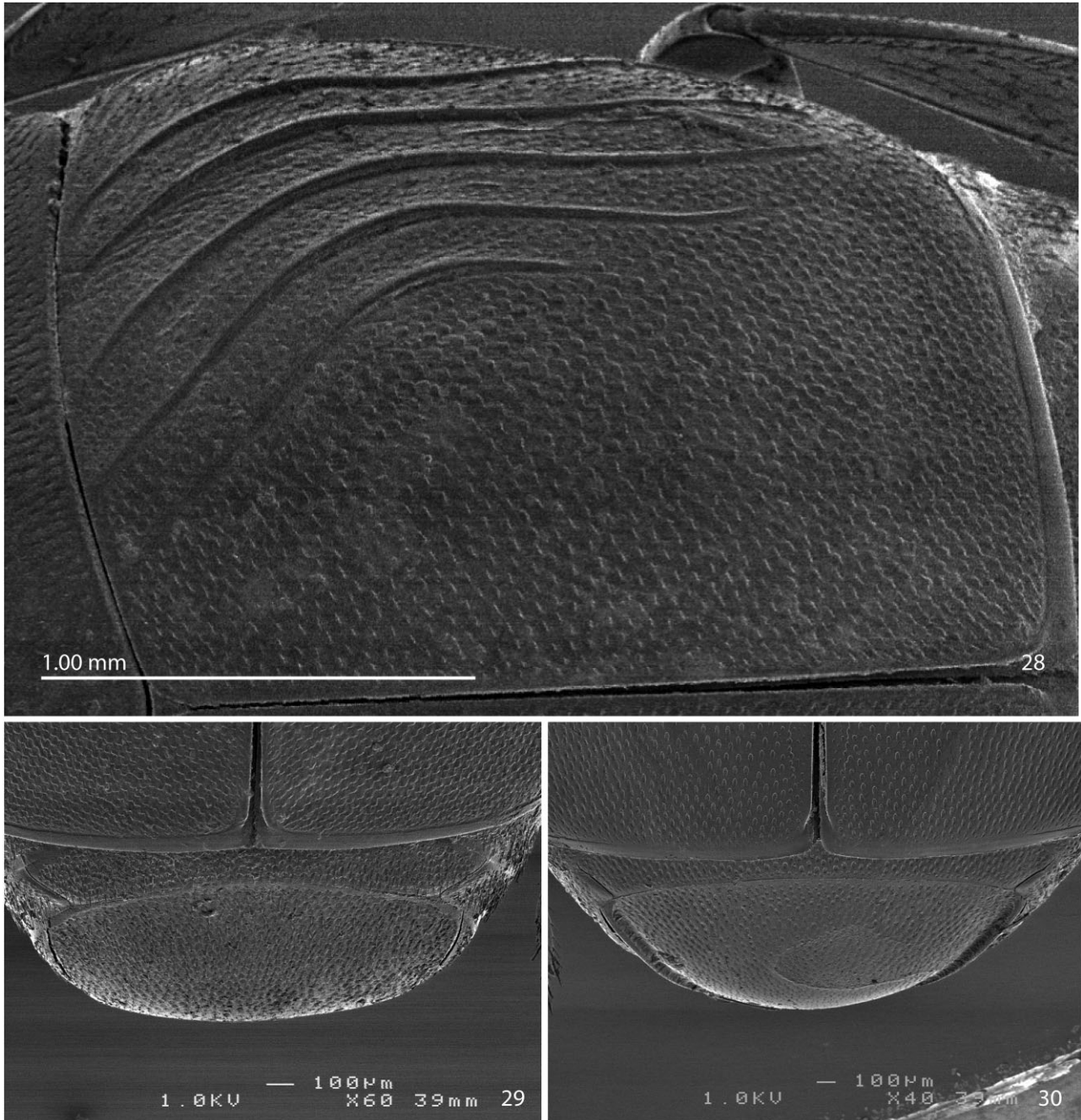
**Figures 28–30.** Figure 28. New genus of Saprininae (Australia), right elytron. Figure 29. New genus of Saprininae (Australia), pygidium. Figure 30. *Euspilotus* (*Platysaprinus*) *latimanus* (Schmidt, 1890), pygidium.

are either punctate or smooth in all out- and ingroup taxa; only *Phoxonotus tuberculatus* has regular tubercles on the elytral disc as well as on the pronotum (see above). CI = 1.00; RI = 0.00.

61. *Elytral flanks*: keel-like, elevated (for fig. see Ôhara, 1994: fig. 88A) (0); not elevated (for fig. see Lackner, 2010: fig. 198) (1). Out of all the out- and ingroup taxa, only *Anapleus semen* and *Euspilotus* (*Platysaprinus*) *latimanus* have keel-like elevated elytral flanks; CI = 0.50; RI = 0.50.

62. *Basal elytral stria*: absent (Fig. 28) (0); present (for. fig. see Lackner, 2010: fig. 559) (1). The basal elytral stria (for more information on this stria see Lackner, 2010: 46) is present only in two psammophilous taxa [*Philothis* (*Farabius*) *hexeris* and *Philothis* (*Philothis*) *arcanus*]; CI = 1.00; RI = 1.00.

63. *Fifth dorsal elytral stria*: absent (for fig. see Lackner, 2010: fig. 198) (0); present (Fig. 28) (1). The fifth dorsal elytral stria is rarely present in the Saprininae [of the taxa included in this study it is present only in *Philothis* (*Atavinus*) *atavus*, *Chelyoxenus xerobatis*, and *Saprininae* gen. nov. (Australia), and in *Afroprinus cavicola* it is present in several specimens]; CI = 0.33; RI = 0.00.

64. *Short, hooked appendix between the fourth dorsal elytral and sutural striae*: present (for fig. see Ôhara, 1994: fig. 130A) (0); absent (for fig. see Lackner, 2010: fig. 198) (1); CI = 1.00; RI = 1.00.

65. *Elytral surface*: covered with dense, short scales (Fig. 27) (0); punctate or smooth, never with scales (for fig. see Lackner, 2010: fig. 198) (1). The elytra being covered with dense, short scales is an autapomorphy of *Nannolepidius braunsi*; CI = 1.00; RI = 0.00.

66. *Dorsal elytral surface*: completely smooth (for fig. see Ôhara, 1994: fig. 159A) (0); punctate or covered with wrinkles (at least partially) (Fig. 1) (1); CI = 0.33; RI = 0.50.

67. *Inner subhumeral stria*: long, originating almost at elytral base and running up to four-fifths of the length of elytra apically (Fig. 26) (0); shortened, usually present as a short median fragment, never originating from elytral base (for fig. see Lackner, 2010: fig. 379) (1); absent (Fig. 28) (2). The inner subhumeral stria can have various modifications; for more details see recent publication by the author (Lackner, 2010: 45); CI = 0.11; RI = 0.56.

*Abdomen (excluding male terminalia and secondary sexual characters)*

68. *Pygidium, pygidial sculpture*: none (for fig. see Lackner, 2010: fig. 254) (0); female with pygidial sulci (for figs see Lackner, 2010: figs 162–167) (1); laterally with sulciform margins (Fig. 30) (2). All outgroup and most of the ingroup taxa have a simple pygidium; state (1) is found only in *Euspilotus* (*Neosaprinus*) *perrisi* and state (2) is found solely in *Euspilotus* (*Platysaprinus*) *latimanus*; CI = 1.00; RI = 0.00.

69. *Surface of propygidium and pygidium*: asetose (for fig. see Lackner, 2010: fig. 254) (0); partly to completely covered with setae (Fig. 29) (1); with exceptionally long, scattered, spine-like setae (for fig. see Ôhara, 1994: fig. 124A) (2). Propygidium and pygidium are partly to completely covered with setae in *Nannolepidius braunsi* and *Saprininae* gen. nov. (Australia). One outgroup taxon (*Chaetabraeus bonzicus*) has long, scattered, spine-like setae on its propygidium and pygidium; CI = 0.67; RI = 0.00.

*Legs*

70. *Meso- and metatibiae, distinct groove for reposing tarsi*: present (for fig. see Ôhara, 1994: fig. 81F, G) (0); absent (for fig. see Lackner, 2010: fig. 258) (1). A distinct groove for receiving the meso- and metatarsi in repose is present only in *Dendrophilus*; CI = 1.00; RI = 0.00.

71. *Protarsus*: absent (for fig. see Lackner, 2010: fig. 551) (0); present, well developed (Fig. 1) (1); present, atrophied (for fig. see Lackner, 2010: fig. 535) (2). Normally, protarsi are well developed in the Histeridae, and Saprininae are no exception. Atrophied protarsi are an adaptation to the psammophilous lifestyle; on the contrary, inquilinous forms have rather long protarsi. Strongly atrophied (but still present) protarsi are found in two psammophiles: *Philothis* (*Farabius*) *hexeris* and *Philothis* (*Philothis*) *arcanus*; the complete absence of protarsi is found in *Philothis* (*Atavinus*) *atavus* and *Ctenophilothis chobauti*, which are likewise forms inhabiting deep sands in the Sahara and Karakum Deserts, respectively; CI = 1.00; RI = 1.00.

72. *Protibial spur*: absent or inconspicuous (for fig. see Ôhara, 1994: fig. 124E) (0); present, growing out from apical protibial margin (not atrophied) (for fig. see Lackner, 2010: fig. 205) (1); present, growing out from apical protibial margin (atrophied) (for fig. see Lackner, 2010: fig. 551) (2); present, growing out from anterior surface of protibia (for fig. see Lackner, 2010: fig. 188) (3); present, massive, forming a spine-like extension of protibia (Fig. 31) (4); CI = 0.31; RI = 0.53.

73. *Protibia, development and number of denticles (for cases in which teeth are absent)*: with numerous short denticles diminishing in size in proximal direction, outer margin not explanate (for fig. see Lackner, 2010: fig. 499) (0); with numerous thin, thorn-like denticles (for fig. see Lackner, 2010: fig. 274) (1); with numerous tiny denticles, outer margin explanate (for fig. see Lackner, 2010: fig. 702) (2); almost without denticles (Fig. 31) (3); CI = 0.75; RI = 0.50.

74. *Protibia, development and number of teeth*: teeth normally developed, usually four to nine in number, gradually diminishing in proximal direction (for fig. see Lackner, 2010: fig. 240) (0); only three (usually large and triangular) teeth present (for fig. see Lackner, 2010: fig. 205) (1); only two large teeth present (for fig. see Lackner, 2010: fig. 551) (2); teeth absent (for fig. see Lackner, 2010: fig. 274) (3); CI = 0.14; RI = 0.53. Both characters 73 and 74 are somewhat ambiguous and rather difficult to score.

75. *Mesotibia, outer margin*: with a single row of denticles (for figs see Lackner, 2010: figs 160, 161)
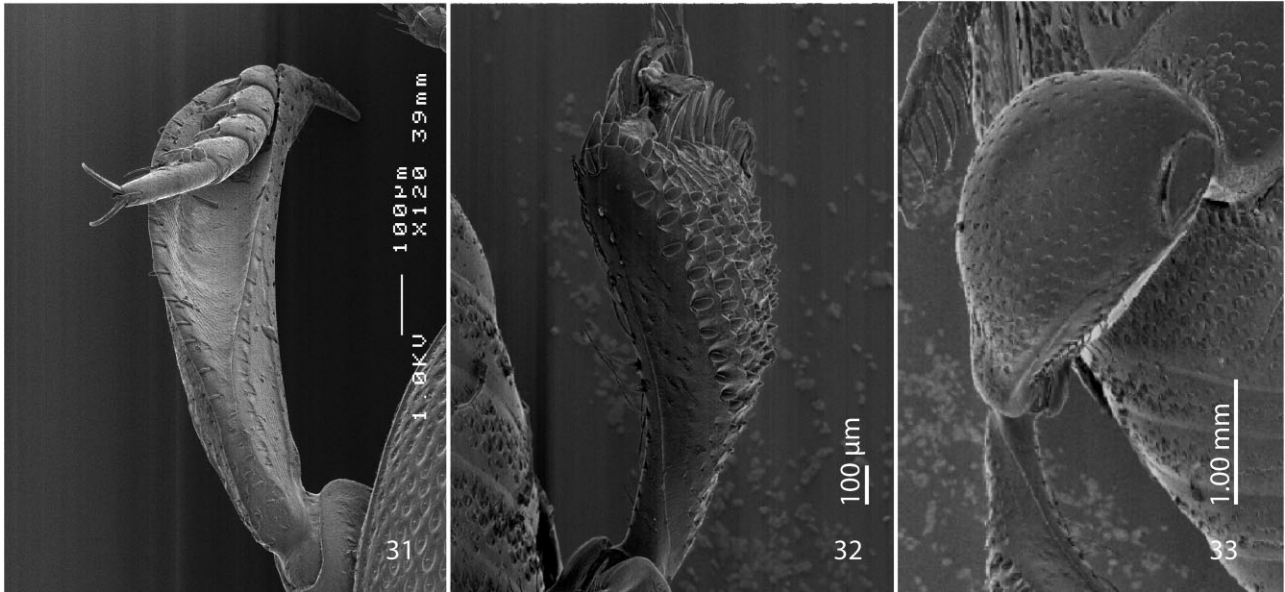
**Figures 31–33.** Figure 31. *Saprinodes falcifer* Lewis, 1891, protibia, dorsal view. Figure 32. *Reichardtiolus pavlovskii* (Kryzhanovskij, 1959), metatibia, ventral view. Figure 33. *Reichardtiolus pavlovskii* (Kryzhanovskij, 1959), hind femur, ventral view.

(0); with two rows of denticles (for fig. see Lackner, 2010: fig. 223) (1); with three rows of denticles (for fig. see Lackner, 2010: fig. 350) (2); with four rows of denticles (for fig. see Ôhara, 1994: fig. 160D) (3). The outer margin of the mesotibia exhibits a single row of denticles in all outgroup taxa; however, this state is also found in *Myrmetes paykulli*, *Styphrus corpulentus*, *Paraphilothis mirabilis*, and likewise in *Saprinodes falcifer*. Most of the ingroup taxa have two rows of denticles on their mesotibia. Several littoral taxa [*Hypocaccus* (*Baeckmanniolus*) *dimidiatus*, *Exaesiopus grossipes*, *Neopachylopus sulcifrons*, *Reichardtia pedatrix*] have three rows of denticles on their outer margin. Yet, other taxa (*Eopachylopus ripae* and *Reichardtiolus pavlovskii*) have four rows of denticles on the outer margin of their mesotibia. *Reichardtiolus pavlovskii* is not a true littoral taxon; it has been found in the inland sands in eastern Turkmenistan; CI = 0.60; RI = 0.85.

76. *Metatibia, shape*: slender, elongate (for fig. see Ôhara, 1994: fig. 124A) (0); normal, not particularly thickened or dilated (for fig. see Lackner, 2010: fig. 186) (1); thickened, swollen, dilated (Fig. 32) (2). This character seems to vary greatly in the Saprininae as well as in the outgroup and is probably homoplastic. In general, however, inquilinous taxa seem to have slender, elongate metatibiae and littoral and psammophilous taxa usually exhibit thickened and swollen metatibiae. The free-living generalist forms fall into state (1); CI = 0.11; RI = 0.38.

77. *Metatibia, denticles (for cases in which two or more rows are present)*: closely abutting each other (Fig. 32) (0); creating free space between the rows (for fig. see Lackner, 2010: fig. 477) (1); rows markedly shifted from each other, outer row only observable from ventral view (for fig. see Lackner, 2010: fig. 206) (2); metatibia explanate, both rows on anterior face of metatibia (for fig. see Lackner, 2010: fig. 704) (3). This character is probably a serial homology with character 75; however, in the Saprininae there are more variations on the metatibia than on the mesotibia. In most Saprininae the denticles on the metatibia either closely abut each other, or create a free space between themselves. In several psammophilous taxa [*Philothis* (*Atavinus*) *atavus*, *Philothis* (*Farabius*) *hexeris*, *Philothis* (*Philothis*) *arcanus*; (*Reichardtiolus duriculus* and *Ammostyphrus cerberus* can be regarded as transitional forms and are scored as '1/2')], however, the two rows of the denticles are markedly shifted from each other and the outer row is only observable from ventral view. In one single taxon of unknown biology (*Turanostyphrus ignoratus*), the metatibia is explanate and both of its rows are situated on the anterior face of the metatibia; CI = 0.38; RI = 0.81.

78. *Metatibia, outer margin*: with a single row of denticles (for fig. see Ôhara, 1994: fig. 81G) (0); with two rows of denticles (for fig. see Lackner, 2010: fig. 406) (1); with three rows of denticles (for fig. see Lackner, 2010: fig. 206) (2); with four or

more rows of denticles (Fig. 32) (3). This character may be serially homologous with character 74; however, in the Saprininae the metatibia can be even more strongly dilated and thickened than the mesotibia; CI = 0.38; RI = 0.72.

79. *Hind femora*: not swollen (for fig. see Lackner, 2010: fig. 300) (0); swollen (Fig. 33) (1). All outgroup and most of the ingroup taxa do not have their hind femora swollen, which is hypothesized to be the plesiomorphic state. Most of the taxa with swollen femora burrow in damp sand and it is believed that swollen femora help accommodate a large number of shorter muscle bundles, which are needed to offset the loss in length (R. Wenzel, unpubl. data); CI = 0.20; RI = 0.67.

*Genitalia*

80. *Basal piece of aedeagus*: not fused into a complete ring (for fig. see Ôhara, 1994: fig. 89B) (0); fused into a complete ring (strongly sclerotized and never fused with the tegmen; for fig. see Lackner, 2010: fig. 194) (1); fused with the tegmen (for fig. see Ôhara, 1994: fig. 126A) (2); weakly sclerotized, but present (3). Basal piece of aedeagus of all ingroup taxa is a strongly sclerotized, complete ring. *Anapleus* is the sole studied taxon whose basal piece of aedeagus is not fused into a complete ring; the basal piece of the aedeagus of *Chaetabraeus* is solidly fused with the tegmen. Although Caterino & Vogler (2002) stated that the basal piece of the aedeagus of *Bacanius* is not visible, either fused with tegmen or lost, I was able to observe it as present, albeit weakly sclerotized, on the exemplars of that genus belonging to an unidentified species from the Iriomote Island in the Yayeyama Islands, southern Japan; CI = 1.00; RI = 0.00.

81. *Male genitalia, ninth tergite*: divided longitudinally (for fig. see Ôhara, 1994: fig. 82F) (0); undivided (for fig. see Lackner, 2010: fig. 354) (1). The outgroup taxa *Anapleus semen*, *Chaetabraeus bonzicus*, and *Dendrophilus xavieri* have the ninth tergite of their male terminalia longitudinally divided, which is hypothesized to be the plesiomorphic character state. The same state has been scored for four ingroup taxa: *Erebidus vlasovi*, *Gnathoncus rotundatus*, *Tomogenius incisus*, and *Myrmetes paykulli*. All other ingroup taxa have their ninth tergite longitudinally fused medially; CI = 1.00; RI = 1.00.

82. *Male genitalia, tenth tergite*: with two setae (for fig. see Lackner, 2010: fig. 504) (0); without setae (for fig. see Lackner, 2010: fig. 354) (1); with four setae (Fig. 34) (2). The tenth tergite is without setae in most of the ingroup as well all of the outgroup taxa. Three Saprininae (*Myrmetes paykulli*, *Erebidus vlasovi*, and *Geomysaprinus saulnieri*) possess two setae on their ninth tergite; and *Euspilotus* (*Euspilotus*) *zonalis* possesses four setae; CI = 0.33; RI = 0.00.

83. *Male genitalia, spiculum gastrale, anterior (basal end)*: thin, not expanded, resembling a stick (Fig. 35) (0); widely expanded, rounded, spoon-like (Fig. 36) (1); cordate, inwardly arcuate (for fig. see Lackner, 2010: fig. 469) (2); shovel-like (for fig. see Lackner, 2010: fig. 314) (3); parallel-sided (for fig. see Ôhara, 1994: fig. 126E) (4); thin, resembling a stick, but expanded posteriorly (for fig. see Lackner, 2010: fig. 337) (5); thickened, widely emarginated medially (Fig. 37) (6); triangular (Fig. 38) (7); cordate and posteriorly expanded (Fig. 39) (8); not particularly expanded (for fig. see Lackner, 2010: fig. 489) (9). The anterior end of the spiculum gastrale (ninth sternite) is likewise highly variable within the Saprininae; the character states were not easy to score unambiguously; CI = 0.47; RI = 0.62.

84. *Eighth sternite and tergite of male terminalia*: completely separated (for fig. see Lackner, 2010: fig. 503) (0); fused (for fig. see Lackner, 2010: fig. 538) (1); almost fused, narrowly connected (for fig. see Lackner, 2010: fig. 191) (2). I scored the eighth sternite and tergite as completely separated [character state (0)] when the two can unambiguously be considered as apart; CI = 0.13; RI = 0.61.

85. *Apical third of eighth sternite of male terminalia*: asetose (for fig. see Lackner, 2010: fig. 568) (0); with several (few) setae (for fig. see Lackner, 2010: fig. 552) (1); with dense setae (for fig. see Lackner, 2010: fig. 620) (2). This is yet another highly variable character that was not easy to score unambiguously. It must be also stressed that this character may vary within a genus and its phylogenetic validity is therefore questionable; CI = 0.09; RI = 0.32.

86. *Eighth sternite of male terminalia*: without two tiny sclerites in the membrane (for fig. see Lackner, 2010: fig. 620) (0); with two tiny sclerites in the membrane (Fig. 40) (1). Only the North American taxon *Chelyoxenus xerobatis* possesses two tiny sclerites in the apical membrane; CI = 1.00; RI = 0.00.

87. *Spiculum gastrale, apical half*: parallel-sided to near apex, where it is abruptly dilated (Fig. 36) (0); gradually dilated in most of apical half, thence divided into two arms (for fig. see Lackner, 2010: fig. 314) (1); gradually dilated in most of apical half, thence undivided (for fig. see Ôhara, 1994: fig. 89G) (2); amorphous (for fig. see Ôhara, 1994: fig. 126E) (3). The neck of the spiculum gastrale in the Saprininae varies slightly less than its basal end; CI = 0.23; RI = 0.60.
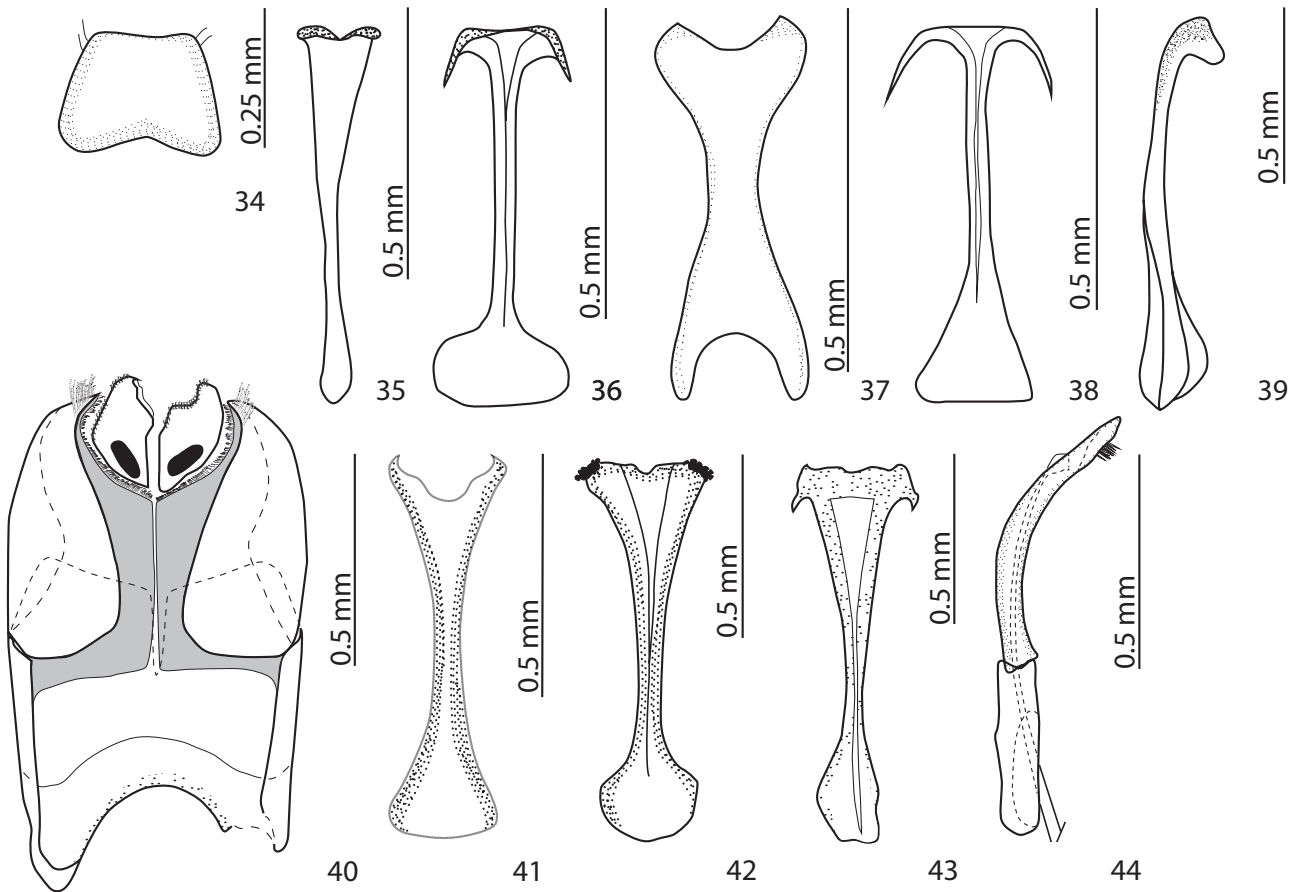
**Figures 34–44.** Figure 34. *Euspilotus* (*Euspilotus*) *zonalis* Lewis, 1907, tenth tergite, dorsal view. Figure 35. *Saprinodes falcifer* Lewis, 1891, spiculum gastrale, ventral view. Figure 36. *Afroprinus cavicola* Lackner, 2013a, spiculum gastrale, ventral view. Figure 37. *Paraphilothis mirabilis* Vienna, 1994, spiculum gastrale, ventral view. Figure 38. *Philoxenus desertorum* Mazur, 1991, spiculum gastrale, ventral view. Figure 39. *Chelyoxenus xerobatis* Hubbard, 1894, spiculum gastrale, lateral view. Figure 40. *Chelyoxenus xerobatis* Hubbard, 1894, eighth sternite and tergite, ventral view. Figure 41. *Xerosaprinus* (*Lophobregmus*) *scabriceps* (Casey, 1916), spiculum gastrale, ventral view. Figure 42. New genus of Saprininae (Australia), spiculum gastrale, ventral view. Figure 43. *Chelyoxenus xerobatis* Hubbard, 1894, spiculum gastrale, ventral view. Figure 44. *Xerosaprinus* (*Xerosaprinus*) *lubricus* (J.L. LeConte, 1851), aedeagus, lateral view.

88. *Apical end of spiculum gastrale, apical 'tails'*: pointing downwards (Fig. 36) (0); pointing upwards (Fig. 41) (1); horizontal (Fig. 42) (2); differently shaped (for fig. see Ôhara, 1994: fig. 126E) (3); CI = 0.50; RI = 0.00.
89. *Apical end of spiculum gastrale, surface between the apical 'tails'*: straight or only slightly emarginate (Fig. 36) (0); deeply emarginate (Fig. 41) (1); with narrow but prominent median notch (for fig. see Lackner, 2010: fig. 673) (2); with tiny median notch (Fig. 42) (3); outwardly arcuate (for fig. see Ôhara, 1994: fig. 126E) (4); CI = 0.67; RI = 0.33.
90. *Apical end of spiculum gastrale*: with prominent lateral projections (for fig. see Lackner, 2010: fig. 504) (0); without such projections (Fig. 36) (1); with

faint lateral projections (Fig. 43) (2); CI = 0.25; RI = 0.00.
91. *Apical end of spiculum gastrale – lateral sides strongly sclerotized and connected by apical bridge*: no (Fig. 36) (0); yes (for fig. see Lackner, 2010: fig. 314) (1); CI = 0.25; RI = 0.40.
92. *Apex of aedeagus with microscopic setae*: no (for fig. see Lackner, 2010: fig. 626) (0); yes (Fig. 44) (1); CI = 0.50; RI = 0.00.
93. *Eighth tergite, apex*: straight or only faintly emarginated (for fig. see Lackner, 2010: fig. 621) (0); distinctly outwardly arcuate (for fig. see Lackner, 2010: fig. 706) (1); deeply inwardly emarginated (Fig. 45) (2); CI = 0.22; RI = 0.00.
94. *Eighth tergite, apex*: medially without deep narrow notch (for fig. see Lackner, 2010: fig. 621) (0); me-
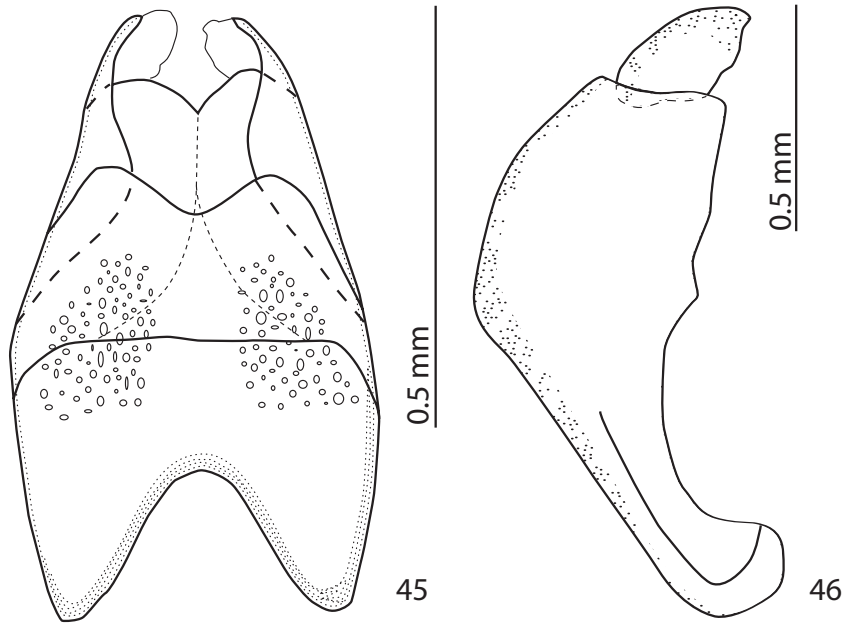
**Figures 45, 46.** Figure 45. *Parahypocaccus weyrichi* Vienna, 1995, eighth sternite and tergite, dorsal view. Figure 46. *Chelyoxenus xerobatis* Hubbard, 1894, ninth and tenth tergites, lateral view.

dially with deep narrow notch (Fig. 40) (1); CI = 1.00; RI = 0.00.

95. *Ninth sternite, sclerites, laterally*: without distinct projection (for fig. see Lackner, 2010: fig. 624) (0); with distinct projection (Fig. 46) (1); CI = 0.13; RI = 0.13.

*List of characters not included in the analysis*

- *Mentum, particularly its anterior margin* (for more information and figs see Lackner, 2010: 34; figs 109–141) varies greatly within the Saprininae. After much consideration, I decided not to include this character in the analysis, as I was unable to unambiguously score its possible discrete states.
- *The chaetotaxy of the mentum* was likewise considered amongst the characters to be included in the analysis, but many specimens of the ingroup material were available only in limited numbers and the setae of their menta were broken off.
- *Labral shape* likewise strongly varies within the Saprininae (for more information and figs see Lackner, 2010: 27: figs 45–73) and I had difficulties in parsing this considerable variation into discrete character states. Although in general the inquilinous taxa that come out at the bottom of the tree usually have a flattened labrum lacking any protuberances, and most of the taxa belonging to the class of large free-living generalist predators (*Saprinus*, *Notosaprinus* etc.) usually possess a large

convexity interrupting the median concavity, it is the enormous variation in that convexity within the Saprininae that causes problems. By contrast, I can confidently state that most labra of the highly derived, specialized Saprininae have an evenly flattened labral disc, occasionally slightly concave medially, but never with any protuberance. It is possible that the plesiomorphic condition here is a flattened and even labrum, as found also in the outgroup, that has undergone numerous variations exhibiting median protuberances and reverting to the plesiomorphic condition once again. The bottom line here is that there is still significant work to be carried out in examining this character in detail amongst various taxa.

- *Chaetotaxy of the antennal scape* is probably strongly correlated to the way of life. Although in general the inquilinous and free-living generalist forms possess only a few setae on their antennal scape, and psammophilous forms usually have their scape furnished with numerous setae, in my opinion this character is not informative for the phylogeny and I decided not to include it in the analysis.
- *Shape of the terminal maxillary palpomere* is another highly variable character that was dropped from the analysis.
- *Shape of the mesoventrite.* The mesoventrite is transversely oblong almost in all in- and outgroup taxa. However, as mentioned earlier (Lackner, 2010: 47), in the burrowing forms the mesoventrite is actually narrower than long, or at least square-shaped;

**Figure 47.** The strict consensus cladogram representing the relationships amongst the Saprininae, with bootstrap values at nodes resolved during the standard bootstrapping with 1000 replicates shown for presentation purposes. Double-digit numbers above branches show the percentage of bootstrap support (bootstrap values below 50% are not shown); single-digit numbers at nodes show Bremer indices for the nodes.
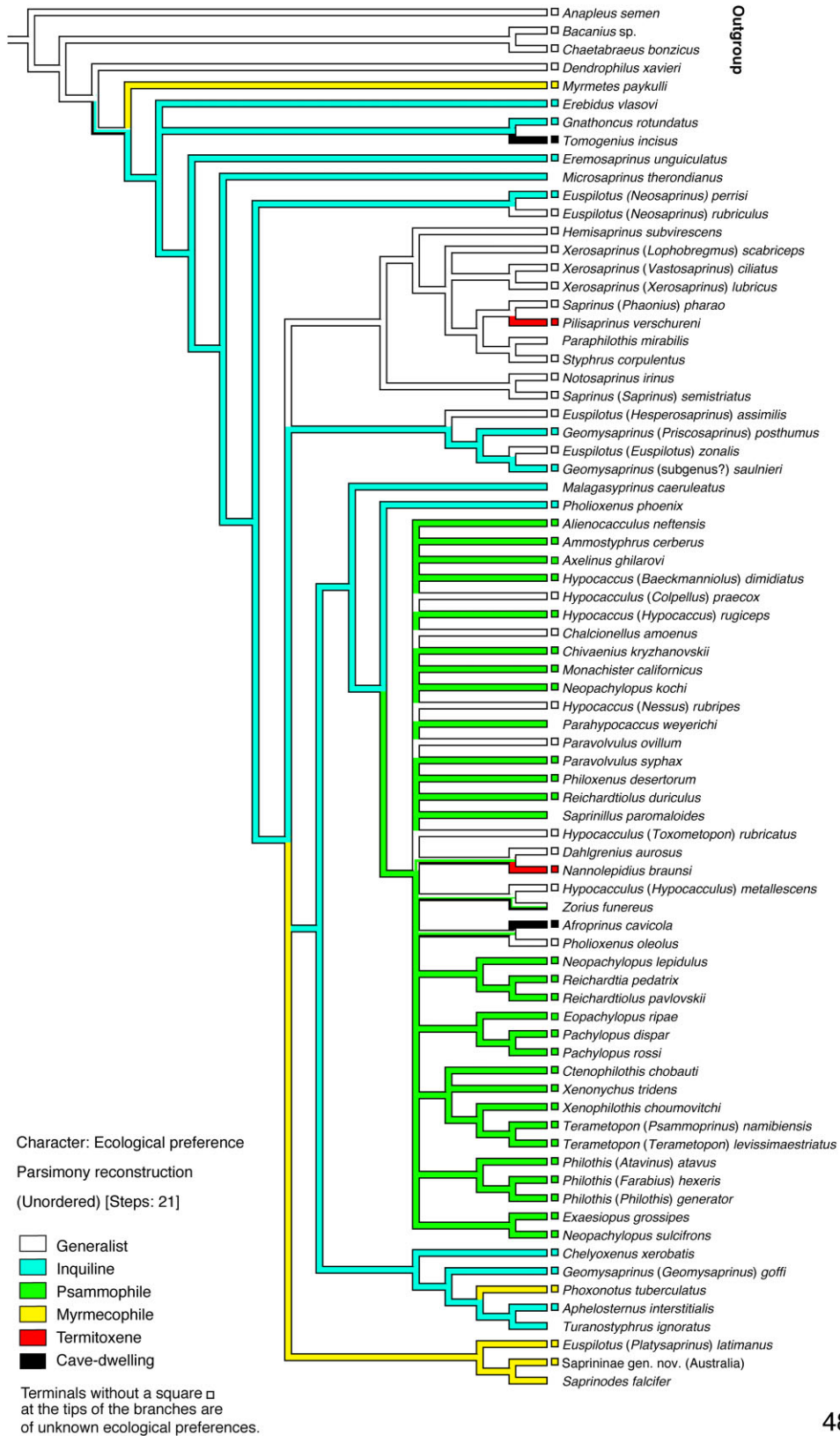
**Figure 48.** Parsimony reconstruction of the ecological preferences amongst the Saprininae mapped on the strict consensus tree.

however, this character has been observed not to be consistent and is strongly correlated to the sand-dwelling forms. It was therefore regarded as homoplastic and excluded from the analysis.

- *Length of dorsal elytral striae.* The elytral striae vary greatly within the Saprininae (even intraspecifically) and therefore this character was regarded as non-informative for the phylogeny and excluded from the analysis.
- *Configuration of carinal and lateral prosternal striae.* The configuration of the two sets was found to be highly variable and therefore excluded from the analysis as it was not possible to parse this variation into unambiguous character states.

## RESULTS OF THE PHYLOGENETIC ANALYSIS

The heuristic search resulted in 1152 equally parsimonious trees of tree length (TL) = 564, CI = 0.31, RI = 0.61. The strict consensus of the equally parsimonious trees had the following characteristics: TL = 668, CI = 0.26, RI = 0.51, and was selected as the cladogram to be discussed here (Fig. [13]47). The strict consensus tree is mostly resolved, but bootstrapping resulted in low support values for most of the recovered branches. Therefore, most of the focus in the following paragraphs is on the branches that are shown to have the highest support, with some additional focus on several other monophyletic groupings with lower support. The discussion of the evolution and history of the ecological adaptations follows the results of the phylogeny (see below).

The monophyly of the Saprininae is strongly supported, with 96% BS, DI = 4, and two unique synapomorphies: presence of sensory organs inside the antennal club and presence of antennal cavity, as well as several weaker synapomorphies. *Myrmetes* branches off first, sister to the remaining Saprininae, but although always recovered near the root, it has been variously placed in a weakly supported clade together with *Erebidus*, *Gnathoncus*, and *Tomogenius* or as sister to the remaining three in other analyses. Based on the phylogenetic analyses performed, *Gnathoncus* and *Tomogenius* are closely related, forming a well-supported clade (BS = 72%, DI = 1) with three unique synapomorphies: presence of median fovea(e); double marginal epipleural stria; and presence of short, hooked appendix between the fourth dorsal elytral and sutural striae. However, their relationships to their presumably closest relative, *Erebidus*, are unresolved. This basal grade, consisting of *Erebidus*, *Gnathoncus*, and *Tomogenius* is plesiomorphic mainly in the form of the ninth tergite, which is longitudinally undivided in the rest of the Saprininae.

The genus *Euspilotus*, represented in the analyses by five taxa (four are type specimens of their respective subgenera, plus one included in the analyses to test the monophyly of the subgenus *Neosaprinus*), comes out as polyphyletic, consistent with the previous hypotheses of Dégallier (1981) and DeMarzo & Vienna (1982). The genus *Euspilotus* is species-rich, with the bulk of its species found on the South American continent. It is interesting to remark that the two Australian endemics, *Saprinodes* and one undescribed taxon, were recovered by the analyses as sister to South American *Euspilotus* (*Platysaprinus*) *latimanus*; however, support for their relationship is low and this finding is mostly likely the result of the presence of homoplastic characters. The relationship between the two Australian sister taxa is supported by one unique synapomorphy: horizontal apical 'tails' of spiculum gastrale of the male terminalia.

Most of the taxa that represent the (former) subgenera of the genus *Saprinus* are Holarctic: *Hemisaprinus*, *Phaonius*, *Saprinus s.s.*, and *Xerosaprinus* (*Lophobregmus*, *Vastosaprinus*, *Xerosaprinus s.s.*), and, as well as their presumed Palaearctic relative (see e.g. Kryzhanovskij & Reichardt, 1976) *Styphrus*, are grouped in a clade supported by a single unambiguous character of the sensory structures of the antenna (forming regular patches, mostly oval, and four in number). *Notosaprinus*, too, was separated from *Saprinus* only recently (Kryzhanovskij, 1972) and is also amongst the members of this clade, as are Afrotropical *Pilisaprinus* (recently elevated from subgenus to fully fledged genus; Lackner, 2013c) and *Paraphilothis*. *Notosaprinus*'s relationship with the type species of the genus *Saprinus* (*Saprinus semistriatus*) is further confirmed by the DI = 1, which suggests that *Notosaprinus* should be analysed together with the rest of the members of *Saprinus* in the future phylogeny of the genus. The position of *Paraphilothis* between the *Saprinus* and *Xerosaprinus* relatives is rather surprising, given the overall morphological characters of *Paraphilothis*, but the character of the antennal club supports it. *Paraphilothis*, a monotypic genus known only from several specimens from Namibia, shows a rather close relationship with Palaearctic *Styphrus* (DI = 3).

A clade comprising of *Chelyoxenus*, *Geomysaprinus* (*Geomysaprinus*) *goffi*, *Phoxonotus*, *Aphelosternus*, and *Turanostyphrus* is supported only by several homoplastic characters. This may also be influenced by the fact that two of the above-mentioned taxa (*Phoxonotus* and *Turanostyphrus*) are only very poorly known and many important character states could not be assessed. A male of *Phoxonotus tuberculatus* is not known despite several examined specimens (T. Lackner, unpubl. data) and the spiculum gastrale of *Turanostyphrus ignoratus*, which is known from the holotype only, was lost during manipulation of the genitalia (see also

Lackner, 2010). However, it is worth remarking that the position of the other two members of the genus *Geomysaprinus* [*Geomysaprinus saulnieri* and *Geomysaprinus* (*Priscosaprinus*) *posthumus*)] are situated rather distantly from the type species of the genus, rendering it polyphyletic. *Geomysaprinus* should receive further attention in the future.

The grade comprising *Malagasyprinus*, *Pholioxenus phoenix*, and a large clade with mostly psammophilous taxa is characterized by the presence of a stipe-or pear shaped single vesicle inside the antennal club (see more on the shape of vesicles below, in the section 'Morphological implications'). With several exceptions, the relationships amongst the members of the large clade are unresolved. Most of the taxa included in this clade are typically present in arid or semi-arid biotopes, inhabiting sandy beaches and also inland sands, and include some of the most 'derived' members of the subfamily. Their inter-relationships are obscured in part by the rampant ecomorphological parallelisms that apparently occurred when occupying this niche. Several small clades, nested within this large polytomy, are, however worth discussing. First, a clade comprising three *Philothis* subgenera (*Atavinus* (*Farabius* + *Philothis s.s.*)) with BS = 68%, DI = 2 and two unambiguous characters supporting their monophyly: position of the single vesicle inside the antennal club (situated under apical surface of the club) as well as metatibial denticles (which form rows markedly shifted from each other, outer row only observable from ventral view, see also Olexa, 1990 or Lackner, 2010 for more discussion). Second, a clade consisting of *Neopachylopus lepidulus* (*Reichardtia* + *Reichardtiolus pavlovskii*) with DI = 2, confirming the polyphyly of the genus *Neopachylopus* as well as *Reichardtiolus*. I recently revised the genus *Reichardtiolus* (see Lackner, 2014), but because of the low resolution of the present cladogram opted to keep the species *Reichardtiolus pavlovskii* inside the genus despite its distant position on the cladogram from the type of the genus, *Reichardtiolus duriculus*; this conservative inaction was mainly because of the absence of a male of *R. pavlovskii*. Regarding the genus *Neopachylopus*, the type species of the genus, the North American *Neopachylopus sulcifrons* was not recovered as sister to its putative relative, *Neopachylopus lepidulus*, a New Zealand endemic. The genus *Neopachylopus* contains likewise several Afrotropical and South Asian species and its revision is required. Third, a clade comprising *Xenophilothis* (*Terametopon* + *Psammoprinus*). The relationship of *Xenophilothis* to the latter two (both members of the same genus *Terametopon*, represented by their respective subgenera) has DI = 1, and is supported by the single unique synapomorphy of extremely acute anterior pronotal angles with a corresponding very narrow

space for the head, which is accordingly very small. Recently, another undescribed taxon exhibiting these features has been discovered in South Yemen (Lackner & Ratto, in press). However, not all taxa included in this large clade are necessarily psammophilous (see the discussion on the Ecological implications below).

## DISCUSSION

Based on a data matrix of 95 adult characters, some of which are new, I conclude that Saprininae are monophyletic. In spite of the large data set, phylogenetic relationships amongst the genera of Saprininae remain uncertain as a result of rampant homoplasy within the adult data set. Although all efforts have been made to discover the largest number of characters that would bear meaningful phylogenetic signal, only a handful of characters proved to exhibit these qualities (see the morphological discussion below). Based on the results of my own studies (see e.g. Lackner, 2010), several large taxa of the Saprininae (e.g. *Saprinus*, *Euspilotus*, and *Hypocaccus*) have been demonstrated to be nonmonophyletic and their revisions are badly needed.

Some of the character states (e.g. vestiture of the body) are probably homoplasies and reversals, and the ancestral state is not obvious. One of the major problems in reconstructing the phylogeny of Saprininae is the fact that the eighth sternites and spiculum gastrales of the males are sometimes so different amongst genera that it is a major challenge to establish homologies amongst various structures. It is perfectly possible to call the spectrum of shapes and details of the male terminalia (especially the spiculum gastrale and eighth sternite and tergite) very diverse, which reflects intergeneric variation in male copulatory organs. Another important character, the sensory organs of the antennal club, shows a large degree of variation, especially amongst the members of the genera *Euspilotus* and *Saprinus*. The phylogenetic analysis of the Saprininae presented here must be treated as preliminary as the support values for most of the recovered branches were too low for the tree topology to be fully conclusive. Disentangling the intergeneric relationships of the remaining taxa included in the large polytomous grade will require molecular methods, as these taxa show a large number of evolutionarily convergent characters associated with adaptation to psammophily.

Saprininae have undergone a remarkable ecological evolution (see below), colonizing some noteworthy ecological niches (ant-nests, dead termitaria, rodent burrows) and adapting to the most seemingly uninviting of environments (e.g. the Old World's deserts). They have conquered the burrows of mammals, nests of birds, ants, termites, and in one case have even

become specialized for living inside tortoise burrows (*Chelyoxenus xerobatis*). Their life histories are so varied that several lineages were able to diversify into a remarkable array of terrestrial niches.

### ECOLOGY OF THE SAPRININAE

As I did not focus on the early branching of the Histeridae, these results shed little light on the ecology of the ancestor of the Saprininae. In order to propose ancestral ecological preferences of the Saprininae, a reliable hypothesis resolving the relationships amongst the subfamilies should be proposed first. Regarding the higher phylogeny of the family, however, Caterino & Vogler (2002) published their results based on combined larval and adult morphologies with molecular data (*18S rDNA*). According to their study, the basal forms of the Histeridae (two of them used here as outgroups) are ovoid-shaped and generalists and include the genera *Onthophilus* Leach, 1817, *Anapleus* Horn, 1873, and *Dendrophilus* Leach, 1817.

In the present paper, the evolution of the ecological preferences was optimized under the maximum parsimony (MP) criterion on the strict consensus tree in Figure 47. Altogether, 21 steps were needed to explain the evolution of the ecological preferences of the Saprininae (Fig. 48). The basal taxa of the Saprininae are the (partly) inquilinous *Gnathoncus*, cave-dwelling *Tomogenius*, myrmecophilous *Myrmetes*, and strictly inquilinous *Erebidus*. Based on the optimization, a nidicolous lifestyle (or myrmecophily) is most likely to be the plesiomorphic lifestyle of the Saprininae subfamily.

Concerning the nidicolous lifestyle, it is present at the deepest nodes of the cladogram and has seen several transformations into other lifestyles, e.g. in a clade of generalist predators. Nidicolous Saprininae diversified most successfully in the arid regions of Middle Asia and North America, spawning several lineages. It is interesting to observe that the sister taxon to the clade *Aphelosternus interstitialis* + *Turanostyphrus ignoratus* is the attaphilous *Phoxonotus tuberculatus* from South America; here thus, the inquilinous lifestyle underwent a transition to myrmecophily. The putative inquiliny of *Turanostyphrus* is also worth remarking upon; one of the two described species was indeed found inside a burrow of a Middle Asian rodent. Inquiliny is hence the possible lifestyle of this enigmatic taxon. Another putative inquiline is the Palaearctic genus *Microsaprinus*, some of whose specimens were indeed found in the burrows of small rodents (Lackner, 2010). Regarding the transformations to a nidicolous lifestyle, according to the reconstructed ancestral states of the ecological preferences on the cladogram it happened six times: (1) early on, on the branch below *Tomogenius*, which is sister to *Gnathoncus*; (2) on the

branch below *Euspilotus* (*Neosaprinus*) *rubriculus*, which is sister to the nidicolous *Euspilotus* (*Neosaprinus*) *perrisi*; (3) on the branch below a large clade containing mostly species-rich genera of mostly Holarctic generalist predators (but with apparent evolution of termitoxeny in *Pilisaprinus*, see below); (4) on the branch below *Euspilotus* (*Hesperosaprinus*) *assimilis* (and most species of the subgenus *Hesperosaprinus*); (5) on the branch below *Euspilotus* (*Euspilotus*) *zonalis* (and most species of the subgenus *Euspilotus*); and (6) on the branch below *Phoxonotus* (mentioned above).

Regarding myrmecophily, it has evolved three times independently during the history of the group: (1) on the branch below *Myrmetes*, a monotypic genus, the most basal taxon of the ingroup, which lives inside the nests of *Formica* spp. in Europe and Siberia; (2) on the branch below *Phoxonotus*, which is an attaphilous genus from South America; and (3) on the branch below a clade containing *Platysaprinus* (a subgenus of *Euspilotus* with both species associated with nests of *Acromyrmex* spp.) + the undescribed genus from Australia found in a nest of *Iridiomyrmex purpureus* + the Australian endemic genus *Saprinodes* (of unknown biology, predicted as myrmecophile under the MP optimization).

Preference for a lifestyle inside caves has apparently evolved twice independently during the evolution of the group: on the branch below the Australasian genus *Tomogenius* (including *Tomogenius incisus* and additional cavernicolous species) and secondly on the branch below the recently erected genus *Afroprinus* from Kenya, which has also colonized this habitat.

The tree topology suggests that the subfamily experienced a major ecological split early in its history. This implies that the comparatively species-poor *Gnathoncus*, *Erebidus*, and *Eremosaprinus* (mostly inquilines) were not as successful in their specialized habits as the lineages containing the species-rich free-living generalist predators *Euspilotus*, *Saprinus*, *Hemisaprinus*, and *Xerosaprinus*. These form a large clade represented in the analysis only by their type species, but in fact these are the most species-rich genera of the subfamily, containing a multitude of free-living generalist predators inhabiting the open landscapes of North America, the Palaearctic Region, and Australia, as well as some mesic areas of South East Asia. The members of this clade are species-poor only in South America, where they are present only as a handful of species, possibly outcompeted by the more successful *Euspilotus*. It is interesting to note that an apparent member of this clade, the monotypic African genus *Pilisaprinus*, colonized the niche of dead termitaria (see more on termitoxeny below). The biology of another African monotypic genus *Paraphilothis* was not known hitherto, but the reconstructed ecological preference on the cladogram places it amongst the

free-living generalist predators as well. Generalist predators appear also in other clades of the tree: (1) on the branch below *Euspilotus* (*Hesperosaprinus*) *assimilis* (and most of the *Hesperosaprinus* members), which is sister to a small clade of inquilinous *Geomysaprinus* (*Priscosaprinus*) *posthumus* + (generalist *Euspilotus* (*Euspilotus*) *zonalis*; and most members of the nominotypical subgenus *Euspilotus*)) + inquilinous *Geomysaprinus* (subgenus?) *saulnieri*))); and (2) several times within the large clade containing mostly psammophilous taxa (see below).

Termitoxeny arose twice independently in the history of the subfamily: once on the branch below *Pilisaprinus* and secondly on the branch below *Nannolepidius*. These two taxa are each adapted to different genera of termites, and whereas *Pilisaprinus* is found in dead termitaria, *Nannolepidius* apparently colonizes active ones (see also Lackner, 2013c for details).

Judging from the data at hand, it can be hypothesized that later in the history of the group an ancestor favouring psammophily appeared and became very successful, spawning many lineages that diversified mainly in the arid or semi-desert and desert regions of the Old World (at least two of them species-rich: *Hypocaccus* and *Dahlgrenius*). It is hypothesized here that psammophily arose only once, but has been secondarily lost several times within the corresponding psammophilous clade. Relatively few lineages favouring other lifestyles (termitoxeny, cavernicolous, and generalist predatory lifestyles) are also present; those of the latter lifestyle are: (1) *Hypocacculus* (*Colpellus*) *praecox* (and most of the members of the subgenus *Colpellus*); (2) with *Chalcionellus amoenus* (and most of the *Chalcionellus* members); (3) with *Hypocaccus* (*Nessus*) *rubripes* (and the bulk of *Nessus* species); (4) with *Paravolvulus ovillum* (which has been coded here as a free-living generalist predator; however, the exact biology of the *Paravolvulus* members is not sufficiently known); (5) with *Hypocacculus* (*Toxometopon*) *rubricatus* [as well as its second species *Hypocacculus* (*Toxometopon*) *pseudorubricatus*]; (6) with *Dahlgrenius aurosus* (and most of the *Dahlgrenius* members); (7) with *Hypocacculus* (*Hypocacculus*) *metallescens* (and most of the members of the nominotypical subgenus *Hypocacculus*); and (8) with *Pholioxenus oleolus* (and probably most of the African members of *Pholioxenus*).

Unfortunately, several taxa inside the large clade containing mostly psammophiles are of unknown biology, e.g. *Saprinillus* or *Zorius*. Based on the attempted reconstruction of the ancestral states they are predicted to be either possible inquilines (*Malagasyprinus*) or psammophiles (*Parahypocaccus*, *Saprinillus*), although there is some ambiguity as to the lifestyle of the rare and localized *Zorius*.

## MORPHOLOGICAL IMPLICATIONS

As seen from the list of characters (see above), the data include both rather stable and extremely homoplastic characters, and the analyses put equal weights on both reliable and unreliable characters. In the following section, I deal with the characters and their states that I consider most useful for understanding the Saprininae phylogeny, as well as several other characters that I consider worthwhile to discuss.

### Head capsule

Sensory structures of the antennal club

The presence of this character amongst the Saprininae has been known since Reichardt (1941) first drew the antennal club of *Saprinus gilvicornis* Erichson, 1834 (see Lackner, 2010, for details). Indeed, this character is one of the autapomorphies of the subfamily and has already received attention in the past (studies of DeMarzo & Vienna 1982 and Lackner, 2010). The present study confirms its presence in all studied taxa; however, in several cases it is rather difficult to observe (e.g. *Phoxonotus tuberculatus*) and its structure remains to be examined in the taxa not available for examination (e.g. *Paramyrmetes foveipennis*). The sensory structures of the antennal club (also called 'Reichardt's organ' in the past, see Lackner, 2010, for discussion) can manifest themselves in many forms regarding their shapes, position and number. Generally speaking though, several observations can be made: (1) taxa near the root of the tree have the largest number of vesicles inside the antennal club (but see the cases of *Myrmetes paykulli*, *Tomogenius incisus*, and *Pilisaprinus verschureni*) and the number of vesicles inside the club decreases further away from the root; (2) free-living generalists (especially members of *Saprinus*, *Styphrus*, and *Xerosaprinus*) tend to have most of their club glabrous apart from large oval or slit-like sensory areas situated on the ventral side of the club, which are densely covered with sensilla (but again, see the clubs of *Pilisaprinus* or *Paraphilothis*; and, furthermore, I am unaware of the antennal structures of most of the free-living South American *Euspilotus*, which are probably also generalists); (3) psammophilous taxa and their close relatives possess a single vesicle inside their club; this vesicle can, however, be situated on different places within the club and can be variously large or modified.

DeMarzo & Vienna (1982) made some assumptions on the phylogeny of the Saprininae based on their studies of the sensory structures of the antennal club without having performed a phylogenetic analysis that included the 'Reichardt's organ' character. I repeat these assumptions here and address them with my own results based on the present cladogram. Assumptions of DeMarzo & Vienna (1982): (1) the apparatus (sensory structures) is present in all examined taxa and is unique

to Saprininae – already addressed above, and I agree with it; (2) all different forms share the constant presence of the main vesicle 'v' – based on my studies I cannot confirm this assumption. In several cases it is impossible to find or determine the main vesicle 'v'; see also my earlier discussion on the topic (Lackner, 2010: 26); (3) the origin of the apparatus from the 'primitive' fusion of the antennal annuli IX–X–XI is evident – this assumption is very hard to interpret as the taxa that are nearest to the root of the tree (e.g. *Myrmetes* and *Tomogenius*) do not show explicit signs of the fusion between the antennal annuli. However, taxa in other lineages like *Pilisaprinus* or *Phaonius* show clear and unambiguous slit-like pits on the ventral and dorsal sides of their clubs, which are possibly evolutionary reversals. Thus, the origin of the apparatus from the fusion of the antennal annuli is not evident judged from the analyses performed; (4) the six main forms of DeMarzo & Vienna (1982) appear to be phylogenetically linked together and can be arranged into two evolutionary paths, which have a common origin – the results of their study indicate that there are more than 'six main forms' of the sensory structures and although my observations offer some pointers towards the evolution of these structures within the Saprininae (e.g. number of vesicles decrease towards the outer branches of the tree), it is not easy to phylogenetically link all the diverse morphologies of the sensory structures of the antennal club and justify strong conclusions regarding the evolutionary paths. Although the study of DeMarzo & Vienna (1982) represented an important step towards a natural classification of the Saprininae based on the structure of the 'Reichardt's organ', it can no longer be maintained or easily 'patched'. This is mostly because of their limited taxon selection compared with the extensive study of the antennal clubs of the Saprininae performed in the past 8 years.

Frontal surface
The plesiomorphic condition presumed here is a simply punctate frontal disk, present in the members of the outgroup as well as most of the ingroup taxa situated near the root of the tree. This character gains various modifications further down the cladogram, and can manifest itself in various forms; e.g. rugae, chevrons, and frons can even be completely smooth. However, the primitive condition of simply punctate frons is also present amongst some of the most 'derived' Saprininae and thus there were probably multiple reversals to this primitive form. The presence of the frontal (+ supraorbital *sensu* Lackner, 2010) stria(e) is another character that appears to carry some phylogenetic value. The primitive condition that is found amongst the members of the outgroup is the complete absence of such stria(e); this condition is likewise shared with the Saprininae taxa found nearest to the root of the tree

and is perhaps a serial homology with the simply punctate frons. In the more 'advanced' Saprininae, the frontal stria appears and can be variously interrupted, prolonged onto the clypeus, or even keel-like; however, one can also observe its complete absence amongst the more deeply nested taxa (e.g. *Pilisaprinus*). This suggests that the character of frontal stria is most likely homoplastic.

Mouthparts
The presence of a lacinial 'hook' amongst the members of the more 'primitive' Saprininae has already been discussed (Lackner, 2010). It is only present in *Gnathoncus*, *Tomogenius*, and *Erebidus*, which were recovered near the root of the tree in most analyses.

The presence and number of labral pits and setae arising from them have also already been mentioned (see Lackner, 2010: 28). The plesiomorphic condition presumed here is a labrum adorned with two labral pits with two setae arising from each. This condition is present amongst almost all studied taxa, with some exceptions: pits and setae are absent amongst the members of most 'derived' psammophilous lineages of Saprininae (*Terametopon*, *Psammoprinus*, *Xenophilothis*, *Ctenophilothis*, *Philothis*, *Farabius*, *Atavinus Philoxenus*, and *Chivaenius*) and the smooth asetose labrum is likewise present in an Australian endemic of unknown biology, *Saprinodes*, which is situated near the root of the tree, suggesting two independent losses during the evolution of the subfamily. Several taxa possess only a single seta in their labral pit, probably representing the intermediate condition between the two character states.

*Thorax*
Antennal cavity
The presence of the antennal cavity amongst the Saprininae is one of the two autapomorphies defining the subfamily. It is present in most of the studied taxa; however, it is very hard to observe in *Phoxonotus* (where it is weakly developed) and is probably secondarily lost in two advanced psammophilous forms (*Ctenophilothis* and *Farabius*).

Median and pre-apical (prosternal) fovea(e) of prosternum
Although it is tempting to homologize the median fovea(e) of *Tomogenius* and *Gnathoncus* with the prosternal (= pre-apical *sensu* Lackner, 2010) foveae found in the rest of the Saprininae, I decided to separate the two pending histological studies of this enigmatic structure. The prosternal foveae are most likely homologous within the Saprininae and I presume that they carry some secretory function [as probably do the median fovea(e)]. It should be noted that such foveae

are most likely absent from other subfamilies and are a likely candidate for another putative autapomorphy of the subfamily. Perhaps because of their frequent absence amongst the Saprininae members ('primitive' and 'derived' alike), this character as it is presently known does not provide substantial phylogenetic signal about the evolution of the subfamily. Additional studies of these foveae are necessary and would be a desired extension of the knowledge of the phylogeny and evolution of the group.

*Male terminalia*

Ninth tergite of the male terminalia

The longitudinally divided ninth tergite of the male terminalia is a synapomorphy defining the clade *Gnathoncus* + *Tomogenius*. This condition is, however, present also in *Myrmetes* and *Erebidus*, which likewise share with *Gnathoncus* + *Tomogenius* prosternal similarities and a lack of frontal and supraorbital striae. Because of the insufficiently supported topology at the bottom of the tree (especially regarding the position of *Myrmetes* in relation to the other three), I refrain from further discussion regarding the relationships of the four taxa in question. By all means, a divided ninth tergite is an important morphological character defining the 'basal' Saprininae.

Other genitalic characters

Despite the level of effort put in, the search for meaningful genitalic characters in males did not yield the desired results. Male genitalia of the Saprininae are 'hyperdiverse', and the search for unambiguous characters with discrete states is far from over. This is perhaps because of the fact that only a fraction of the enormous diversity of taxa has been examined in the present work and there remains much more work to be carried out.

## CONCLUSIONS

This work builds on a previous work of mine (Lackner, 2010) focused exclusively on the Palaearctic fauna of the Saprininae, to examine all world genera and subgenera, and is the first analysis ever to do so. I have presented a strong morphological character set, and an almost complete taxon set upon which to begin exploration of the worldwide generic relationships in this prominent subfamily. The phylogeny presented here provides a framework for forming hypotheses about the evolution of lifestyle in these beetles. I have contributed the first broad morphology-based phylogenetic analysis of the subfamily Saprininae and paved the way for future advances in the systematics of a poorly known group of histerid beetles. In line with the discussion above, I present a general summary regarding the phylogeny of the Saprininae subfamily.

1. Saprininae are a monophyletic subfamily and two unambiguous character states support their monophyly (see above for details).
2. The taxa that are closest to the root of the cladogram are mostly nidicolous (burrow or nest dwelling) or myrmecophilous (occupying active ant nests); the nidicolous lifestyle, which is inferred to be the plesiomorphic lifestyle of the Saprininae, has undergone several transformations to other lifestyles during the evolution of Saprininae (Fig. 48).
3. Association with social insects (myrmecophily and termitoxeny) arose three times (myrmecophily) and two times (termitoxeny; see also Lackner, 2013c for details) independently during the evolution of Saprininae (Fig. 48).
4. Adaptation to life in caves has arisen twice independently during Saprininae evolution.
5. Psammophily has arisen only once during Saprininae evolution; and has been secondarily lost several times (Fig. 48).
6. Most of the branches are weakly supported and most of the 'strong' characters are found on the terminal branches and not on the internal nodes where the most substantial problems lie.
7. Taxa grouped in the large group supported by a single unique synapomorphy of a single vesicle inside the antennal club show the weakest support and their relationships are in most cases completely unresolved.
8. The female genitalia, as well as larval stages of the members of the Saprininae subfamily that were not examined in the present study, should be incorporated in future studies; the inclusion of these as well as of molecular characters could be pivotal for obtaining a robust phylogeny of the Saprininae subfamily.
9. Based on the low resolution of the cladogram I do not suggest here a new classification of the subfamily.

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