Elevation of *Pilisaprinus* to full generic status
with notes on the evolution of termitoxeny
in the Saprininae (Coleoptera: Histeridae)

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Abstract. *Pilisaprinus* Kanaar, 1996, a monospecific Afrotropical termitoxenous subgenus of the genus *Saprinus* Erichson, 1834 is recognized as a valid genus based on the results of recent phylogenetic analysis. *Pilisaprinus* is redefined using a combination of plesiomorphic and apomorphic morphological characters, and its type species, *Saprinus (Pilisaprinus) verschureni* Théond, 1959 is re-described, with male genitalia, mouthparts and sensory organs illustrated and complemented with SEM micrographs. Notes on the evolution of termitoxeny in the Saprininae subfamily are provided.

Key words. *Pilisaprinus* stat. nov., Coleoptera, Histeridae, Saprininae, taxonomy, termitoxeny, Afrotropical Region

Introduction

The subgenus *Pilisaprinus* Kanaar, 1996 of the genus *Saprinus* Erichson, 1834 was erected by KANAAR (1996: 230) based on the species *Saprinus verschureni* Théond, 1959, occurring in dead termitaria in the Democratic Republic of Congo (former Zaire), Ivory Coast and Benin (MAZUR 2011). KANAAR (1996) already observed that several morphological characters (unusual pilosity of the antennal scape, setose prosternal process and setose elytral epipleuron) of this taxon do not correspond with the characters typical for the members of the genus *Saprinus* and therefore he established a new subgenus for it. KANAAR (1996) noted that the setose prosternal process of *Pilisaprinus* is a shared character with the subgenus *Phaonius* Reichardt, 1941 of the genus *Saprinus*; however, he also pointed out the differences between the shape of the prosternal process and variation of the configuration of prosternal striae between the two subgenera. The present contribution to the on-going revisionary works of the Saprininae subfamily (see e.g. LACKNER 2009a,b,c; 2010; 2011a,b; 2012; 2013; TISHECHKIN & LACKNER 2012; LACKNER & GOMY 2013) relies on the results of phylogenetic analysis of the Saprininae subfamily (LACKNER, unpublished) as well as on the careful study of the morphological characters of members of
the Saprininae subfamily. Based on these results, the subgenus *Pilisaprinus* is raised to full genus and its type species, *S. (P.) verschureni* is herein re-described and provided with SEM micrographs. Its mouthparts structures, sensory structures of the antenna and male genitalia are likewise illustrated. Notes on the possible multiple origins of termitoxeny within the Saprininae subfamily are given.

### Material and methods

All dry-mounted specimens were relaxed in warm water for several hours or overnight, depending on the 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 ŌHARA (1994): the head and male genitalia were macerated in a hot 10% KOH solution for about 15 minutes, cleared in 80% alcohol, macerated in lactic acid with fuchsin, incubated at 60°C for two hours, and subsequently transferred into a mixture of glacial acetic acid (1 part) and methyl salicylate (1 part) heated at 60°C for 15 minutes and cleared in xylene. Specimens were then observed in α-terpineol in a small glass dish. The mentum, labium, labrum, mandibles and antennae were disarticulated. Digital photographs of the male terminalia, mouthparts and antenna were taken by a Nikon 4500 Coolpix camera and edited in Adobe Photoshop CS4. Based on the photographs or direct observations, the genitalia, mouthparts and antennal structures were drawn using a light-box Hakuba klv-7000. SEM photographs were taken with a JSM 6301F microscope at the laboratory of Faculty of Agriculture, Hokkaido University, Sapporo, Japan. All available specimens were measured with an ocular micrometer. Beetle terminology follows that of ŌHARA (1994) and LACKNER (2010). Separate lines of the same label are marked by slash (/). The following acronyms of museums and private collections are used throughout the text:

- RMCA: Musée Royal de l’Afrique Centrale, Tervuren, Belgium (M. De Meyer);
- RMNH: Nationaal Natuurhistorische Museum (Naturalis), Leiden, The Netherlands (A. van Aartsen);
- TLAN: Tomáš Lackner collection, temporarily housed at Leiden, Netherlands.

Abbreviations of body measurements (from ŌHARA 1994) are as follows:

- PEL: length between anterior angles of pronotum and apices of elytra;
- APW: width between anterior angles of pronotum;
- PPW: width between posterior angles of pronotum;
- EL: length of elytron along sutural line;
- EW: maximal width between outer margins of elytra.

### Taxonomy

*Pilisaprinus* Kanaar, 1996 stat. nov.

*Pilisaprinus* Kanaar, 1996: 130, as a subgenus of *Saprinus*. Type species: *Saprinus verschureni* Théron, 1959, original designation.


**Diagnosis.** Rather large Saprininae taxon (PEL 4.50–4.75 mm) with black, non-metallic dorsum, wholly punctate. Antennal club with slit-like pits and 6 sensory vesicles; frontal and
supraorbital striae absent; pronotal hypomeron, prosternum and elytral epipleuron setose. Inner subhumeral elytral stria fused with humeral elytral stria forming another, complementary dorsal elytral stria. Carinal prosternal striae rudimentary, present only on prosternal apophysis. **Differential diagnosis.** By the peculiar chaetotaxy and sensory structures of the antennal club, setose elytral epipleuron as well as fused inner subhumeral and humeral elytral striae this taxon cannot be confused with any other currently described Afrotropical taxon of Saprininae (see also Lackner 2013 for the Key to the Afrotropical genera of the Saprininae). **Distribution.** Described from Democratic Republic of Congo (former Zaïre), found also in Ivory Coast and Benin. Presumably distributed across the entire tropical Africa.

**Pilisaprinus verschureni** (Théond, 1959) comb. nov. (Figs 1–19)


**Type locality.** Democratic Republic of Congo (former Zaïre).

**Type specimen examined.** *Saprinus verschureni*. **Holotype:** “Congo Belge, P.N.G. / Miss. H. De Saeger / II/gd/4, 29-v-1952 / J. Verschuren. 3545” (printed); “HOLOTYPUS” (orange, red-margined label, printed); “Saprinus / verschureni nov. sp. / J. Théond det., 1958” (printed-written); “TYPE” (purple label, printed) (RMCA). The specimen is of unidentified sex: genitalia lost, sixth abdominal tergite broken in two, left antenna missing, both protibiae missing, right mesotibia broken off glued to the same triangular point with specimen, both mesotarsi missing side-mounted on a triangular point.


**Redescription.** Body moderately convex, PEL: 4.50–4.75 mm; APW: 1.85–2.00 mm; PPW: 3.75–4.00 mm; EL: 2.75–3.00 mm; EW: 4.00–4.25 mm, dorsally with various kinds of punctuation, cuticle black, not metallic; legs, mouthparts and antennae rufopiceous. Antennal scape (Fig. 4) slightly dilated and thickened, densely punctate, with numerous long amber setae; antennal club (Figs 3, 12) ventrally with two slit-like pits almost encircling it entirely, dorsally with two complementary slit-like pits; lower half (approximately) glabrous or fringed only with few microscopic setae, upper half (approximately) with dense short setae; sensory structures of antennal club (Fig. 12) in form of six vesicles, four of them situated in pairs under ventral slit-like pits and another two of them situated under each other under dorsal surface medially. Mandibles (Figs 4, 10) stout, moderately punctate, with evenly rounded outer margin strongly curved inwardly; acutely pointed; sub-apical tooth on inner margin of left mandible moderately large, almost perpendicular; labrum (Fig. 11) slightly convex, slightly depressed medially, finely punctate; labral pits rather deep and large with two short amber setae arising from each; terminal labial palpomere elongate, its width about one-fourth its length; mentum (Fig. 5) square-shaped, anterior angles slightly produced, anterior margin with a shallow notch; disc of mentum covered with numerous short setae that are almost absent along posterior margin; cardo of maxilla laterally with numerous short setae; stipes triangular, with four short setae; terminal maxillary palpomere elongate, its width about one-fifth its
Figs 1–9. External morphology of *Pilisaprinus verschureni* (Thérond, 1959). 1 – habitus, dorsal view; 2 – same, ventral view; 3 – antennal club, latero-ventral view; 4 – head, dorsal view; 5 – mentum, ventral view; 6 – prosternum; 7 – propygidium and pygidium; 8 – lateral disc of metaventrite + metepisternum; 9 – protibia, dorsal view.
length, about three times as long as penultimate; labial palpomeres with dense brush of long setae. Clypeus and frons (Fig. 4) rectangular, broad, with moderate punctures and fine transverse wrinkles; frontal and supraorbital striae absent; eyes slightly flattened, well visible from above. Pronotal sides (Fig. 1) strongly narrowing anteriorly; anterior emargination for head deep; apical angles acute and conspicuous, marginal pronotal stria slightly carinate, complete, slightly weakened behind head; disc entirely covered with coarse round punctuation, punctures separated by about their diameter, laterally coarser than medially; pronotal depressions rather deep and large; scutellum very small; pronotal hypomeron with dense long amber setae (Fig. 2). Elytral epipleuron (Fig. 8) with long amber setae; marginal epipleural stria thin, complete, continued as complete apical stria; marginal elytral stria well impressed, complete, slightly carinate, apically attaining marginal epipleural stria. Humeral elytral stria deeply impressed.
on basal third, joined with inner subhumeral stria forming a supplementary dorsal elytral stria parallel to first dorsal elytral, reaching about half of elytral length apically; elytral disc with four deeply impressed dorsal elytral striae 1–4, in shallow punctures, all about the same length, reaching about half of elytral length apically, fourth dorsal elytral stria basally connected with sutural elytral stria; sutural elytral stria well impressed, reaching about two-thirds of elytral length apically, otherwise obliterated. Elytral disc entirely with fine small dense punctuation (with the exception of fourth elytral interval and elytral flanks) intermingled with dense and coarse punctures separated by about half their diameters.

Propygidium (Fig. 7) partly covered by elytra; with dense and coarse punctures becoming sparser and finer medially; pygidium (Fig. 7) long, convex, with very coarse and dense pun-
ctuation, punctures separated by less than half of their diameter. Anterior margin of median portion of prosternum (Fig. 6) rounded; marginal prosternal stria very thin; prosternal foveae absent; prosternal process compressed, dorso-laterally with irregular coarse to fine punctures with long amber setae; carinal prosternal striae present as tiny fragments on prosternal apophysis, otherwise absent (in some specimens reaching approximately half the length of the prosternum apically, weakened and very approximate); lateral prosternal striae (Fig. 6) well impressed, carinate, somewhat divergent anteriorly, united in front by anterior stria.

Anterior margin of mesoventrite medially emarginate; discal marginal mesoventral stria well impressed, carinate; disc of mesoventrite with dense shallow punctures separated by about their own to twice their diameters; meso-metaventral suture weakly impressed, curved outwardly.

Intercoxal disc of metaventrite with long median excavation (male), with punctation similar to that of mesoventrite, punctures becoming sparser and finer medially; lateral metaventral stria well impressed, carinate, straight, curved outwardly, connected to metaventral-metepisternal suture; lateral disc of metaventrite (Fig. 8) excavated, with large deep setiferous punctures; metepisternum on basal two-thirds with even coarser and denser punctuation with long amber setae, punctuation on apical third becoming much sparser and finer, metepisternum (Fig. 8) laterally with an additional straight, well-impressed metepisternal stria.

Intercoxal disc of first abdominal sternite almost completely striate laterally, with punctation similar to that of metaventrite; lateral disc of all visible abdominal sternites setose laterally.

Protibia (Fig. 9) dilated, outer margin with two low triangular distal teeth topped by tiny denticle, followed by two tiny denticles rather distant from the two distal teeth and another two microscopic denticles visible only from ventral view; setae of outer row regular, diminishing in size apically; protarsal groove deep; anterior protibial stria present on basal two-thirds, otherwise obliterated; setae of median row similar in length to those of outer row, present only along the shortened anterior protibial stria; tarsal denticles absent; protibial spur well developed, bent, inserted near protarsal insertion; apical margin of protibia posteriorly with about nine minuscule denticles abutting each other; outer part of posterior surface obscurely variolate-punctate, delimitation of outer and median parts of posterior surface non-existent; posterior protibial stria absent; inner row of setae double, setae dense, increasing in length apically.

Mesotibia slender, outer margin with several closely-set thin denticles near mesotarsal insertion; setae of outer row shifted to approximately middle of posterior mesotibial surface, very regular and dense; setae of median row situated right below the setae of outer row, much shorter; posterior mesotibial stria present only on basal third, otherwise (or apically) obliterated; anterior surface of mesotibia with dense row of thin closely-set denticles near outer margin, rest of surface of anterior mesotibial stria imbricate-punctate; anterior mesotibial stria almost complete; inner anterior denticles absent; mesotibial spur short, thick; apical margin of mesotibia anteriorly with two widely-spaced short denticles; inner margin of mesotibia with sparse row of long thin setae; claws of apical tarsomere bent, shorter than half its length; each mesotarsomere with a single long seta ventrally; dorsally without setae; metatibia more slender and longer than mesotibia, in all aspects similar to it.
Male genitalia. Eighth sternite (Figs 13–14) separated longitudinally; vela absent; apex of eighth sternite laterally with dense brush of short setae (Figs 13–15); eighth tergite and eighth sternite fused laterally (Fig. 15). Ninth tergite (Figs 16–17) longitudinally fused medially; spiculum gastrale (Fig. 16) gradually dilated from middle in most of apical half, basal end only slightly triangularly dilated. Aedeagus (Figs 18–19) slender, almost parallel-sided; basal piece of aedeagus short, ratio of its length : length of parameres 1 : 5; parameres of aedeagus fused almost along their basal three-fourths; aedeagus only slightly curved ventrad, apex of aedeagus flattened dorso-ventrally (Fig. 19).

**Sexual dimorphism.** Females are devoid of longitudinal metaventral depression.

**Discussion**

Before the author began his work on the higher phylogeny and systematics of the sub-family Saprininae, the genus Saprinus (see e.g. MAZUR 1997) contained four subgenera (in addition to Saprinus s. str.): Microsaprinus Kryzhanovskij, 1976 (given full generic status by LACKNER 2010); Hemisaprinus Kryzhanovskij, 1976; Pilisaprinus Kanaar, 1997 and Phaonius Reichardt, 1941. Based on the results of unpublished phylogenetic analyses of the Saprininae (LACKNER, unpublished data), Pilisaprinus, Phaonius and Hemisaprinus are only distantly related to the genus Saprinus and should be all excluded from it (Fig. 20). In this paper, I focus only on the systematic position of the monotypic Pilisaprinus, and leave the taxonomic ranks of Phaonius or Hemisaprinus alone for two main reasons: 1) Phaonius and Hemisaprinus both contain several species each and only the type species of each has been examined in the aforementioned analysis; 2) the phylogenetic study of Saprinus s.l. is planned for the future and should include all possible species.

Based on the phylogenetic analyses performed, Pilisaprinus and Phaonius form a clade with Lophobregmus Wenzel, 1962, Vastosaprinus Wenzel, 1962, Xerosaprinus Wenzel, 1962, Paraphilothis Vienna, 1994, and Staphyrus Motschulsky, 1845, defined by three synapomorphies: (1) presence of oval, slit-like sensory areas situated on the ventral side of the club (most likely corresponding to original divisions between antennal segments IX–X–XI) which are covered by thick sensilla (unique synapomorphy), (2) a complementary apical sensory ‘cap’ situated on the apex of the antennal club (unique synapomorphy), and (3) setose pronotal hypomeron. Pilisaprinus and Phaonius were revealed as sister taxa. However, the two genera differ in the number of the antennal vesicles (6 in Pilisaprinus and 4 in Phaonius), configuration of two sets of prosternal striae (carinal prosternal striae rudimentary and present only on prosternal apophysis in Pilisaprinus, well developed and complete in Phaonius) and differently arranged lateral prosternal striae (compare Fig. 6 with that of LACKNER 2010: Fig. 666). Furthermore, Pilisaprinus has a setose elytral epipleuron (Phaonius does not), the prosternal process is compressed but not convex in Pilisaprinus (convex between procoxae in Phaonius; see above-mentioned figures for direct comparison), and the spiculum gastrale between the two genera are likewise very different (compare Fig. 16 with that of LACKNER 2010: Fig. 673).

The monotypic Pilisaprinus is characterized by a mix of plesiomorphic and apomorphic characters. The high number of sensory vesicles inside the antennal club is plesiomorphic, as
indicated by my recent analysis (supporting the contention by DeMarzo & Vienna (1982)). The same state is present in other putatively basal taxa, e.g. *Gnathoncus* Jacquelin du Val, 1858 and *Euspilotus* Lewis, 1907. On the other hand, the setose elytral epipleuron, setose prosternal process of antennal scape, and prementum furnished with numerous long setae are reconstructed as apomorphic characters.

Termitoxeny (friendly residence in the termite-inhabited part of the termitary; sensu Wheeler 1936: 179) is not uncommon in the Histeridae, with entire genera, especially of the tribe Exosternini (e.g. *Paratropus* Gerstaecker, 1867), being confined to the environment of dead termitaria (see e.g. Kanaar 1997 for details). In the Saprininae subfamily, however, this specialization has been observed only twice: in the monospecific subgenus *Nannolepidius* Reichardt, 1932 of the genus *Hypocacculus* Bickhardt, 1914, and in *Pilisaprinus*. *Hypocacculus* (*Nannolepidius*) *braunsi* Bickhardt, 1921 has been collected in dead termitaria of various *Hodoterms* species (*H. havilandi* Sharp, 1895, *H. viator* Latreille, 1804, etc.) (Bickhardt 1921). On the other hand, *Pilisaprinus* has been collected in dead termitaria of *Macrotermes bellicosus* (Smeathman, 1781) (Kanaar 1990). Emerging ideas of phylogenetic relationships in the subfamily indicate that the association with termites has evolved twice independently among the members of the Saprininae.

Fig. 20. Excerpt from the unpublished phylogenetic analysis of the Saprininae (Lackner, unpubl. data) showing the position of *Pilisaprinus verschurenii*, *Saprinus* (*Phaonius*) *pharao* Marseul, 1855 and *Saprinus* (s.str.) *semistriatus* (Scriba, 1790). Synapomorphies relevant for the phylogenetic placement of *Pilisaprinus* are numbered: 1 – apical third of 8th sternite of male terminalia with dense setae; 2 – majority of antennal club glabrous apart from large oval or slit-like sensory areas situated on ventral side of club which are densely covered with sensilla (see also Fig. 3); 3 – sensory areas of the antennal club complemented with an apical sensory cap (see also Fig. 3); 4 – pronotal hypomeron setose; 5 – prosternal foveae absent; 6 – metepisternum setose; 7 – antennal annuli present; 8 – sensory structures of the antennal club in a form of slit-like pits not surrounded by sensilla; 9 – inner subhumeral stria absent.
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