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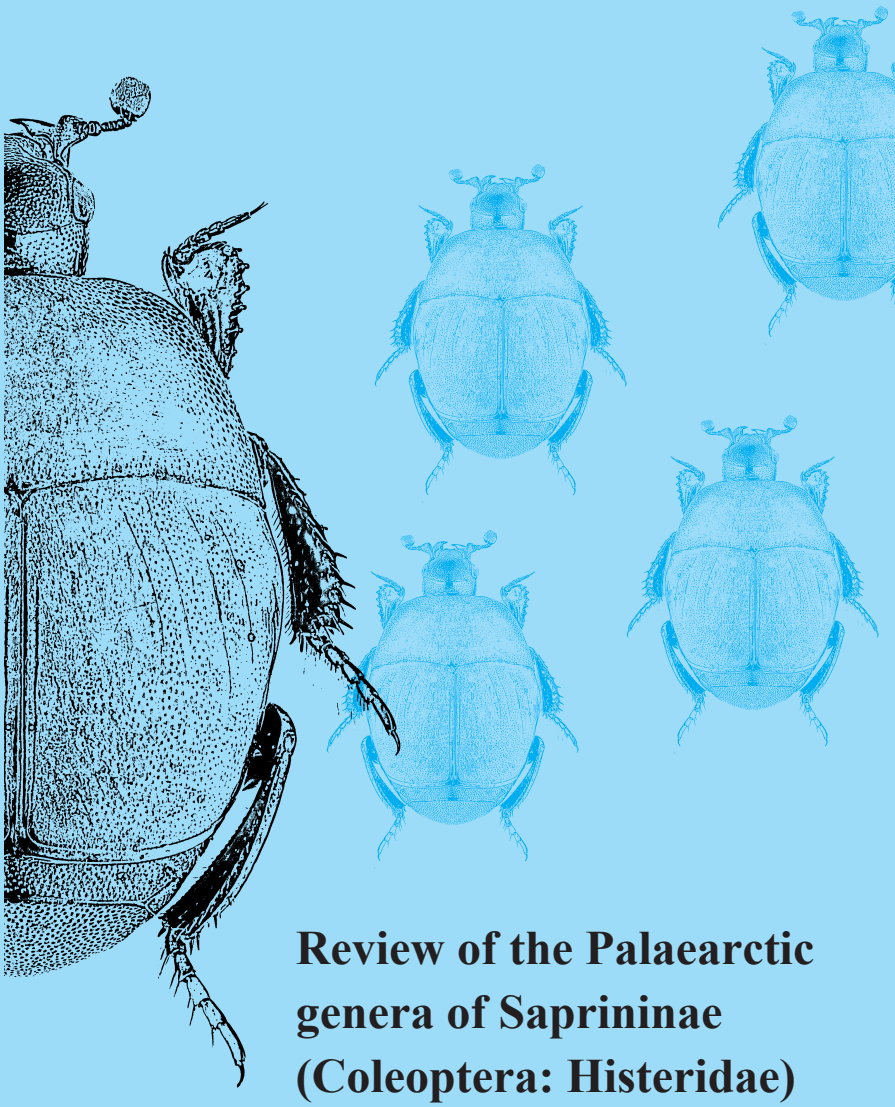

Review of the Palaearctic genera of Saprininae (Coleoptera: Histeridae)

Tomáš Lackner

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Cover: *Saprinus proximus simillimus* Wollaston, 1865 (Coleoptera: Histeridae). Photo: Martin Fikáček.

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volume 50 (supplementum)

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To all fellow histeridologists,
and especially to my wife Pepina
and my daughter Ida

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Review of the Palaearctic genera of Saprininae (Coleoptera: Histeridae)

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Abstract. Genera and subgenera of the subfamily Saprininae from the Palaearctic Region are reviewed. Thirty-three genera and subgenera are recognized as native to the Palaearctic Region. Historical background of the Saprininae subfamily, updated generic checklist of the subfamily and review of the adult external morphology is provided. New terminology regarding mouthparts and legs is introduced. Genera and subgenera of the Palaearctic Saprininae are diagnosed and the type species of each genus and subgenus are redescribed. Male genitalia of the type species of each genus and/or subgenus are illustrated. Genitalia of three type species of Palaearctic genera: *Axelinus ghilarovi* (Kryzhanovskij, 1976), *Paravolvulus ovillum* (Solskij, 1876), and *Ammostyphrus cerberus* Reichardt, 1924 are illustrated for the first time. Mouthparts and antennal club (with emphasis on its sensory structures) of most of the species are illustrated for the first time. *Microsaprinus* Kryzhanovskij, 1976, stat. nov., formerly a subgenus of *Saprinus* Erichson, 1834, is raised to generic rank, and four resulting new combinations are proposed: *M. bonairii* (Fairmaire, 1884) comb. nov., *M. gomyi* (Secq & Secq, 1995) comb. nov., *M. pastoralis* (Jacquelin-Duval, 1852) comb. nov. and *M. therondianus* (Dahlgren, 1973) comb. nov. A key to the genera of Saprininae is provided. Neotypes for *Styphrus corpulentus* Motschulsky, 1845 and *Xenonychus tridens* (Jacquelin-Duval, 1852) are designated. *Reichardtiolus duriculus* (Reitter, 1904) is for the first time recorded from Jordan, *Microsaprinus therondianus* (Dahlgren, 1972) from Iran, and *Euspilotus* (*Neosaprinus*) *perrisi* (Marseul, 1872) from Tajikistan.

Key words. Coleoptera, Histeridae, Saprininae, genus, subgenus, morphology, review, taxonomy, Palaearctic Region

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Contents

Introduction

With more than 620 described species worldwide, the Saprininae represent the second largest subfamily of the family Histeridae, after the Histerinae. The subfamily is fairly species-rich in the Palaearctic Region with more than 270 species estimated to occur in the area. Throughout the Palaearctic Region there are many endemic genera, especially in the desert regions of the Sahara and Central Asia (Mazur 1997, 2004).

Generic classification for many Palaearctic species was first published by Reichardt (1932, 1941). Later, based on Reichardt's unpublished manuscripts, Kryzhanovskij published a detailed study of the fauna of the superfamily Histeroidea of the USSR (Kryzhanovskij & Reichardt 1976). That study treated the majority of the Saprininae taxa from the entire Palaearctic Region, unfortunately omitting some taxa from the Sahara and Arabian Peninsula. These three major publications have been supplemented by numerous papers describing several new genera (Olexa 1980, Penati & Vienna 1996, Tishechkin 2005, Kanaar 2008) and new species (Olexa 1984a,b, 1990, 1992; Dahlgren 1985; Kryzhanovskij 1987; Mazur 1994; Kanaar 1998, 2008; Yélamos 2001; Lackner 2001, 2003, 2009a,b). Regional studies containing elaborate accounts of the subfamily Saprininae at the species level are available, e.g., for Central Europe (Witzgall 1971), Italy (Vienna 1980), Poland (Mazur 1973), Hungary (Mazur & Kaszab 1980), Iberian Peninsula (Yélamos 2002), and France (Secq & Secq 1995, 1997a,b; Secq & Gomy 1999).

The classification of the subfamily is currently based on Reichardt (1932) and Kryzhanovskij & Reichardt (1976); both treatments were based on morphologic similarity and autapomorphies. Newly created genera and subgenera are being established within the existing classification, ignoring the need for a serious phylogenetic analysis of the taxa.

As Opitz (2008: 3) stated: 'One of the most difficult tasks in the preparation of generic revisions is the assessment of species level discontinuities which is usually based on the morphological gaps'. Therefore, this review aims to provide diagnoses for all presently known genera and subgenera found throughout the Palaearctic Region, redescriptions of the type species for each genus and/or subgenus and drawings of the male genitalia for all species examined and of the mouthparts for most species, and to supplement these with SEM micrographs. This work will provide the foundation for a thorough phylogenetic analysis of the world genera and lead towards a sound higher classification of the Saprininae (Lackner in prep.)

Material and methods

Selection of the taxa in the present study was based on the Saprininae catalogued in Mazur (1997) but restricted to the Palaearctic Region (sensu Löbl & Smetana 2004). When constructing the diagnosis of all taxa used in this paper, only the Palaearctic representatives are considered due to lack of material and time constraints.

Two genera, *Neopachylopus* Reichardt, 1926 and *Dahlgrenius* Penati & Vienna, 1996 are excluded from this study. *Neopachylopus* is an arbitrarily constructed genus lacking synapomorphies with two species occurring on the western coast of North America, one in New Zealand, one in Somalia, one in Djibouti and Yemen and one in southern Pakistan (Mazur 1997, Kanaar 1998, Lackner 2001). It is not considered here as a part of the Palaearctic fauna and it will remain untreated until its taxonomic status is clarified. Similarly, *Dahlgrenius* is primarily an Afrotropical taxon with the bulk of species occurring in Subsaharan Africa. Only five species are known to enter the Palaearctic Region (for details see Penati & Vienna 1995, Mazur 1997, Gomy et al. 2004) and this genus will be treated in a subsequent paper.

Other species also require additional comments. *Paravolvulus syphax* (Reitter, 1904) has been repeatedly moved between genera until Kryzhanovskij (1987) placed it into the genus *Paravolvulus* Reichardt, 1932. This placement was followed by Mazur (1997) and is retained also here. However, according to the present study, this species does not belong to *Paravolvulus* and its taxonomic placement will be resolved later. According to Kryzhanovskij's (1959) description, which omits the characters of the prosternum (highly informative for the taxonomy and phylogeny of the Saprininae), *Reichardtiolus pavlovskii* Kryzhanovskij 1959 most likely does not belong to the genus *Reichardtiolus* Kryzhanovskij, 1959. However, its taxonomic status is retained here until the type species is inspected.

The genus *Euspilotus* Lewis, 1907 is primarily distributed in North and South America, with only one species, *E.* (*Neosaprinus*) *perrisi* (Marseul, 1972), in the Palaearctic Region and only *E.* (*Neosaprinus*) *loebli* Mazur, 1974 in the Oriental Region. Therefore, when dealing with the genus *Euspilotus*, only *E.* (*N.*) *perrisi* is redescribed and figured, since the type species of *Neosaprinus* Bickhardt, 1909, *E.* (*N.*) *rubriculus* (Marseul, 1855) (= *Saprinus gnathoncoides* Bickhardt, 1909) is native to South America and does not occur in the Palaearctic Region. Similarly, only characters of *E.* (*N.*) *perrisi* are used when reconstructing the diagnosis of this subgenus.

Finally, the subgenus *Hesperosaprinus* Wenzel, 1962 of the genus *Euspilotus* is distributed exclusively in North and South America and does not occur in the Palaearctic Region. The only exception could be *E.* (*H.*) *russatus* (Marseul, 1855), which was described from Egypt, but its exact origin has been questioned. Mazur (1997: 238) labelled its occurence in Egypt and Turkey by a question mark; the latter record was based on a specimen that he ascribed to this species in the 1970s, albeit with doubt. The whereabouts of this specimen are currently unknown (Mazur, pers. comm. 2009). According to Gerardo Arriagada (pers. comm. 2007), who inspected the type specimen, this species should be transferred to the genus *Xerosaprinus* Wenzel, 1962, which occurs exclusively in North and Central America. The subgenus *Hesperosaprinus* of the genus *Euspilotus* has been therefore excluded from this paper.

In order to make the key to the genera of the Palaearctic Saprininae more useful, the Palaearctic representatives of the genera *Dahlgrenius*, *Neopachylopus* and *Paravolvulus syphax* are included. On the other hand, *Reichardtiolus pavlovskii* has not been included, because no specimen has been available. When constructing the diagnosis of all taxa used in this paper, only the Palaearctic representatives are considered due to lack of material and time constraints.

Material examined. The majority of specimens studied comes from the collections of Aldo Olexa and Oldřich Kapler. These two collections were acquired during 2003 and 2005 and are presently part of author's private collection (TLAN). Since the identification of the species in these two large private collections can be considered highly reliable and these collections contain almost all known species of the Palaearctic Saprininae, borrowing type specimens of all type species was deemed not necessary. Attempts were made to borrow the type specimens of most of the less known and rare species and the type species of genera or subgenera not available in the two collections.

The following acronyms of museums and private collections are used throughout the text:

BMNH The Natural History Museum, London, United Kingdom (R. Booth);
EIHU Laboratory of Systematic Entomology, Hokkaido University, Sapporo, Japan (M. Ôhara);
HNHM Hungarian Museum of Natural History (O. Merkl);
MNHN Muséum National d'Histoire Naturelle, Paris, France (Th. Deuve & A. Taghavian);
TLAN Tomáš Lackner collection, Amsterdam, The Netherlands (partly temporarily housed in Sapporo, Japan);
ZIN Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (B. Kataev);
ZMHB Museum für Naturkunde der Humboldt Universität zu Berlin, Berlin, Germany (M. Uhlig & B. Jaeger);
ZMUM Zoological Museum, Moscow State University, Moscow, Russian Federation (N. Nikitsky).

Abbreviations. Abbreviations of morphological measurements follow Ôhara (1994: 8) and are used throughout the text as follows:

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

Following abbreviations are used in the checklist and throughout the text:

N – north/northern
NE – northeastern
NW – northwestern
W – west/western
C – central
S – south/southern
SE – southeastern
SW – southwestern
E – east/eastern

Separate lines of the same label are marked by forward slash (/); separate labels are indicated by double forward slash (//).

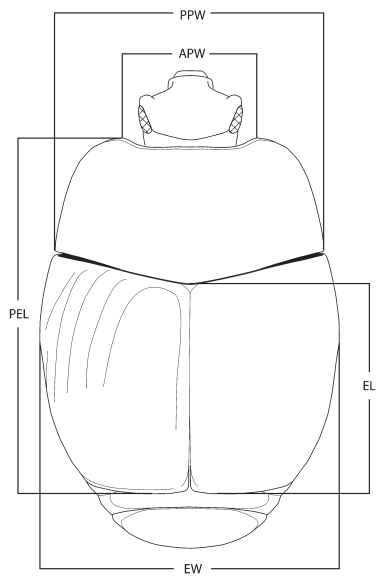


Fig. 1. Saprininae, biometric measurements.

Specimen preparation and examination. All specimens were dry mounted and required relaxation 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 binocular microscope with diffuse light. Observations of the male genitalia, mouthparts and antennae required dissection, using methods described in Ôhara (1994): the head and male genitalia were first macerated in hot 10% KOH solution for up to 45 minutes, cleared in 80% alcohol, macerated in lactic acid with fuchsine and heated at 60ºC for an hour, and subsequently treated with aceto-salycilate heated at 60ºC for 15 minutes and cleared in xylene. They were observed in α-terpineol in a small glass dish. The mentum, labium, labrum and mandibles were carefully removed; the antenna was occasionally removed from the antennal cavity using forceps and severed behind the antennal scape.

Digital photographs of the male terminalia, mouthparts and antenna were taken by a Nikon 4500 Coolpix camera and edited in Adobe Photoshop CS3. Based on the photographs or direct observations, the genitalia, mouthparts and antennal structures were drawn using a light-box HAKUBA KLV-7000. All illustrations (except for the male genitalia) were later scanned and finished using Adobe Illustrator CS3. SEM micrographs were taken with a JSM 6301F camera at the laboratory of Faculty of Agriculture, Hokkaido University, Sapporo, Japan. The genitalia were subsequently mounted in Canada balsam on a small glass slide following the methods described by Maruyama (2004).

All available specimens were measured with an ocular micrometer.

Historical overview of the genera and subgenera of the Saprininae

In the following list a chronology of key papers for all genera and subgenera is presented, rather than treating exclusively the Palaearctic representatives of the subfamily. The most important works dealing with higher classification of the subfamily are mentioned as well. This was necessitated by the fact that many genera present in the Palaearctic Region occur outside this geographical region as well.

1834 Erichson described *Saprinus* and *Pachylopus*.
1845 Motschulsky described *Styphrus*.
1854 Lacordaire created the subtribe *Saprinides,* which included the genera described by Erichson (1834).
1855 Marseul created 'Tribu Sapriniens' and divided *Saprinus* into six groups.
1858 Jacquelin-Duval described *Gnathoncus*.
1862 Marseul added *Gnathoncus* to his classification of 'Tribu Sapriniens', omitted the genus *Styphrus* and described *Myrmetes, Phoxonotus* (originally included in 'Tribu Histériens') and *Tomogenius* (a neglected genus, rediscovered only by Dahlgren in 1976).
1864 Wollaston described *Xenonychus*.
1867 Thomson described *Hypocaccus*.
1891 Lewis described *Saprinodes*.
1894 Hubbard described *Chelyoxenus*.

1907 Lewis described *Euspilotus*.

1909 Bickhardt split the genus *Euspilotus* into the subgenera *Euspilotus* s. str. and *Neosaprinus*.

1910 Bickhardt treated the genera *Pachylopus*, *Hypocaccus* and *Euspilotus* as subgenera of the genus *Saprinus* and listed six genera in the subfamily Saprininae: *Saprinodes*, *Saprinus* (including *Saprinus* s. str., *Euspilotus*, *Hypocaccus* and *Pachylopus*), *Styphrus*, *Chelyoxenus*, *Gnathoncus* and *Myrmetes*.

1912 Bickhardt described *Satrapister*.

1914 Bickhardt described *Hypocacculus*.

1916–1917 Bickhardt recognized the subfamily Saprininae with 12 genera (*Satrapister*, *Euspilotus*, *Saprinus*, *Hypocacculus*, *Hypocaccus*, *Pachylopus*, *Xenonychus*, *Chelyoxenus*, *Saprinodes*, *Gnathoncus*, *Myrmetes*, and a new genus *Platysaprinus*), synonymized the subgenus *Neosaprinus* with the genus *Euspilotus* and *Styphrus* with *Xenonychus* and maintained the genus *Phoxonotus* in the subfamily Dendrophilinae.

1924 Reichardt described *Ammostyphrus*.

1926 Reichardt redefined the genus *Pachylopus* and established three new genera: *Baeckmanniolus*, *Exaesiopus* and *Neopachylopus* with the subgenus *Eopachylopus*.

1929 Bruch described *Paramyrmetes*.

1930 Reichardt described *Philothis* with the subgenus *Farabius*.

1932 Reichardt published a detailed treatment in which he treated about one third of all known species, created three new genera (*Zorius*, *Chalcionellus* and *Pholioxenus*) and divided genus *Hypocacculus* into six subgenera, five of which were new (*Toxometopon*, *Colpellus*, *Nessus*, *Nannolepidius*, *Paravolvulus*). His generic diagnoses were based mainly upon characters of (a) the head and prosternum; (b) dorsal surface sculpture, and (c) presence or absence of vestiture on the ventral surface.

1936 Peyerimhoff presented a critical review of earlier Reichardt's works and proposed a classification of psammophilous Saprininae, especially from North Africa.

1939 Ross described *Eremosaprinus* as a new subgenus of *Saprinus*.

1940 Ross described *Geomysaprinus* and proposed full generic status for *Eremosaprinus* for the first time without any explanation and without listing any of its species.

1941 Reichardt recognized 15 genera of the Saprininae, elevating the subgenus *Eopachylopus* into generic rank, created two new subgenera (*Phaonius* of the genus *Saprinus*, and *Erebidus* of the genus *Gnathoncus*) and illustrated the male 8th abdominal segment for many species for the first time.

1944 Wenzel described *Reichardtia*.

1948 Blackwelder & Blackwelder listed *Eremosaprinus* as a genus referring to Ross (1940) in a footnote 'Considered a distinct genus'; see the genus *Eremosaprinus* for details.

1959 Kryzhanovskij described *Reichardtiolus*.

1962 Wenzel recognized 11 genera and six subgenera of the Saprininae, creating new genera *Aphelosternus* and *Xerosaprinus* (with three new subgenera, *Auchmosaprinus*, *Vastosaprinus* and *Lophobregmus*) and new subgenus *Hesperosaprinus* of the genus *Euspilotus* and new subgenus *Priscosaprinus* of *Geomysaprinus.*

1964–1985 Dahlgren in numerous papers dealt with the taxonomy of the subfamily Saprininae, mostly on the species level, and cleared many synonymies by recognizing the importance of the apical part of 8th abdominal segment of male for distinguishing many cryptic species.

1972 Kryzhanovskij described *Notosaprinus.*

1972 Mazur described the subgenus *Izpaniolus* of *Chalcionellus.*

1974 Mazur described *Myrmeosaprinus*.

1974 Kryzhanovskij described *Saprinillus.*

1976 Kryzhanovskij & Reichardt recognized 19 genera and eight subgenera of the Saprininae in the former USSR: *Gnathoncus*, *Myrmetes*, *Eremosaprinus*, *Euspilotus* (with subgenus *Neosaprinus*), *Saprinus* (with subgenera *Saprinus* s. str., *Hemisaprinus*, *Microsaprinus* and *Phaonius*), *Styphrus*, *Zorius*, *Eopachylopus*, *Chalcionellus*, *Pholioxenus*, *Hypocacculus* (with subgenera *Hypocacculus* s. str., *Nessus* and *Colpellus*), *Axelinus*, *Paravolvulus*, *Hypocaccus* (with the subgenera *Hypocaccus* s. str. and *Baeckmanniolus*), *Exaesiopus*, *Reichardtiolus*, *Xenonychus*, *Ammostyphrus* and *Philothis* (with subgenera *Philothis* s. str. and *Farabius*); the genus *Axelinus* and the subgenera *Hemisaprinus* and *Microsaprinus* of the genus *Saprinus* were described as new and the subgenus *Erebidus* of the genus *Gnathoncus* was synonymized with the genus *Eremosaprinus*. All species known to occur in the territory of USSR were redescribed and some notes on the phylogeny and biogeography of the subfamily were provided.

1980 Olexa described *Chivaenius.*

1987 Kryzhanovskij described *Ctenophilothis* and *Xenophilothis.*

1987 Vienna described *Terametopon.*

1990 Olexa created a new subgenus *Atavinus* of the genus *Philothis.*

1991 Mazur described *Philoxenus* and *Monachister.*

1993 Secq & Yélamos synonymized the subgenus *Izpaniolus* of the genus *Chalcionellus* with *Chalcionellus.*

1994 Vienna described *Paraphilothis.*

1995 Vienna described *Parahypocaccus.*

1996 Penati & Vienna described *Dahlgrenius.*

1996 Kanaar described a new subgenus *Pilisaprinus* of the genus *Saprinus.*

1996 Gomy & Vienna described a new subgenus *Psammoprinus* of the genus *Terametopon.*

1997 Mazur synonymized *Myrmeosaprinus* with *Neosaprinus.*

2005 Tishechkin described *Turanostyphrus.*

2008 Kanaar described *Alienocacculus.*

Updated checklist of the genera and subgenera of the Saprininae

Due to the lack of any sound phylogenetic analysis the genera presented here are listed in alphabetical order. The species diversity and distributional summary is given for each taxon. The data are taken primarily from MAZUR (1997); doubtful species, species *incertae sedis* and *nomina nuda* are not counted within the number of species-group taxa (Sp. / Ssp.) but subspecies are included.

The following table indicates the authorship of each taxon name with the publication year. Further on, names of taxa are given without authorship. Taxa treated in this paper are indicated in bold.

Genus	Subgenus	Sp. / Ssp.	Distribution
1. *Alienocacculus* Kanaar, 2008	–	2	Tunisia, Israel, United Arab Emirates
2. *Ammostyphrus* Reichardt, 1924	–	1	Turkmenistan, Kazakhstan, Uzbekistan
3. *Aphelosternus* Wenzel, 1962	–	1	USA (California)
4. *Axelinus* Kryzhanovskij, 1976	–	1	Uzbekistan, Turkmenistan
5. *Chalcionellus* Reichardt, 1932	–	35	Palaearctic and Afrotropical Regions, Indo-Malayan Subregion; one species introduced to Australia
6. *Chelyoxenus* Hubbard, 1894	–	1	USA (Florida, Georgia)
7. *Chivaenius* Olexa, 1980	–	1	Uzbekistan
8. *Ctenophilothis* Kryzhanovskij, 1987	–	2	Algeria, Egypt
9. *Dahlgrenius* Penati & Vienna, 1996	–	62	Afrotropical Region, Middle Eastern & Mediterranean Subregions, India, Sri Lanka
10. *Eopachylopus* Reichardt, 1926	–	1	Russian Far East, Japan, Hong-Kong
11. *Eremosaprinus* Ross, 1939	–	5	USA (California, Nevada), Mexico (Baja California), Turkmenistan, Uzbekistan, Kazakhstan

Genus	Subgenus	Sp. / Ssp.	Distribution
12. *Euspilotus* Lewis, 1907	total	79	New World, Palaearctic Region, Réunion Isl., Indo-Malayan Subregion
	Euspilotus Lewis, 1907	11	Neotropical Region
	Hesperosaprinus Wenzel, 1962	57	Nearctic and Neotropical Regions
	Neosaprinus Bickhardt, 1909	9	Nearctic and Neotropical Regions, St. Helena Is., Reunion Is.; one species from Palaearctic Region and one species from Malaysia
	Platysaprinus Bickhardt, 1916	2	Argentina, Brazil
13. *Exaesiopus* Reichardt, 1926	–	7	S and C Europe, N Africa, Caucasus, Central Asia, Somalia
14. *Geomysaprinus* Ross, 1940	total	28	Nearctic and Neotropical Regions
	Geomysaprinus Ross, 1940	3	Nearctic Region
	Priscosaprinus Wenzel, 1962	25	Nearctic and Neotropical Regions
15. *Gnathoncus* Jacquelin-Duval, 1858	–	25	Mainly Holarctic Region, one species from Congo, one species from SE Asia and one cosmopolitan species
16. *Hypocaccus* Thomson, 1867	total	72	Primarily Holarctic and Afrotropical Regions, also in Neotropical and Indo-Australian Regions
	Hypocaccus Thomson, 1867	57	Primarily Holarctic and Afrotropical Regions, also in Neotropical and Indo-Australian Regions
	Baeckmanniolus Reichardt, 1926	15	Primarily Holarctic and Afrotropical Regions, also in Neotropical and Indo-Australian Regions

Genus	Subgenus	Sp. / Ssp.	Distribution
17. *Hypocacculus* Bickhardt, 1914	total	80	Primarily Palaearctic and Afrotropical Regions, some species in Indo-Australian Region, one species introduced to Australia
	Hypocacculus Bickhardt, 1914	13	Primarily Palaearctic and Afrotropical Regions, two species in Indo-Australian Region
	Colpellus Reichardt, 1932	8	Palaearctic and Afrotropical Regions, one species in India
	Nannolepidius Reichardt, 1932	1	Republic of South Africa
	Nessus Reichardt, 1932	56	Primarily Palaearctic and Afrotropical Regions, some species in Indo-Australian Region, one species introduced to Australia
	Toxometopon Reichardt, 1932	2	Republic of South Africa, Namibia
18. *Microsaprinus* Kryzhanovskij, 1976 **stat. nov.**	–	4	France, N Africa, Canary Isl., Iran, Kazakhstan, Uzbekistan, Turkmenistan, Mongolia
19. *Monachister* Mazur, 1991	–	1	USA (California)
20. *Myrmetes* Marseul, 1862	–	1	Western Palaearctic Subregion
21. *Neopachylopus* Reichardt, 1926	–	6	W coast of N America (2 species); New Zealand (1 species); Yemen, Djibuti (1 species); Somalia (1 species); Pakistan (1 species)
22. *Notosaprinus* Kryzhanovskij, 1972	–	1	Australia
23. *Pachylopus* Erichson, 1834	–	2	one species in Republic of South Africa and Namibia; one species in Mexico (Baja California and Sonora)

Genus	Subgenus	Sp. / Ssp.	Distribution
24. *Parahypocaccus* Vienna, 1995	–	1	Zimbabwe, Malawi
25. *Paramyrmetes* Bruch, 1929	–	1	Argentina
26. *Paraphilothis* Vienna, 1994	–	1	Namibia
27. *Paravolvulus* Reichardt, 1932	–	11	C Asia, Near East, one species in N Africa and Saudi Arabia
28. *Philothis* Reichardt, 1930	total	15	Algeria, Oman, Iran, Turkmenistan, Uzbekistan, Kazakhstan, Azerbaijan
	Philothis Reichardt, 1930	8	Algeria, Turkmenistan, Uzbekistan, Kazakhstan, Azerbaijan
	Atavinus Olexa, 1990	5	Algeria, Oman, Iran, Turkmenistan, Uzbekistan, Kazakhstan
	Farabius Reichardt, 1930	2	Turkmenistan, Kazakhstan
29. *Philoxenus* Mazur, 1991	–	1	USA (California), Mexico (Sonora)
30. *Pholioxenus* Reichardt, 1932	–	25	Palaearctic and Afrotropical Regions
31. *Phoxonotus* Marseul, 1862	–	5	French Guiana, Peru, Brazil, Surinam
32. *Reichardtia* Wenzel, 1944	–	1	New Zealand
33. *Reichardtiolus* Kryzhanovskij, 1959	–	2	Jordan, Kazakhstan, Uzbekistan, Turkmenistan, Iran, W China
34. *Saprinillus* Kryzhanovskij, 1974	–	2	Kazakhstan, Turkmenistan, Mongolia
35. *Saprinodes* Lewis, 1891	–	2	Australia (Queensland, New South Wales)

Genus	Subgenus	Sp. / Ssp.	Distribution
36. *Saprinus* Erichson, 1834	total	167	Primarily Holarctic and Afrotropical Regions, also in Neotropical and Indo-Australian Regions, several species introduced worldwide
	Saprinus Erichson, 1834	159	Primarily Holarctic and Afrotropical Regions, also in Neotropical and Indo-Australian Regions, several species introduced worldwide
	Hemisaprinus Kryzhanovskij, 1976	3	Cyprus, S Russia, Kazakhstan, Middle East, Siberia, India, Pakistan, China, Myanmar
	Phaonius Reichardt, 1941	4	SW Palaearctic Region, Madagascar, Seychelles, Réunion Island, Mauritius, Somalia, Australia
	Pilisaprinus Kanaar, 1996	1	Congo, Benin, Ivory Coast
37. *Satrapister* Bickhardt, 1912	–	1	? Peru
38. *Styphrus* Motschulsky, 1845	–	3	Algeria, Libya, Chad, Somalia, C Asia, S Russia
39. *Terametopon* Vienna, 1987	total	6	Botswana, Namibia
	Terametopon Vienna, 1987	4	Namibia
	Psammoprinus Gomy & Vienna, 1996	2	Botswana, Namibia
40. *Tomogenius* Marseul, 1862	–	7	Papua New Guinea, SW Australia (Victoria, Tasmania, New South Wales), New Zealand

Genus	Subgenus	Sp. / Ssp.	Distribution
41. *Turanostyphrus* Tishechkin, 2005	–	2	Uzbekistan, Turkmenistan
42. *Xenonychus* Wollaston, 1864	–	2	Mediterranean Subregion, Sahara, Cape Verde Archipelago, Arabian Peninsula, C Asia
43. *Xenophilothis* Kryzhanovskij, 1987	–	1	Algeria, Arabian Peninsula
44. *Xerosaprinus* Wenzel, 1962	total	27	Nearctic and Neotropical Regions
	Xerosaprinus Wenzel, 1962	23	Nearctic and Neotropical Regions
	Auchmosaprinus Wenzel, 1962	1	USA (New Mexico)
	Lophobregmus Wenzel, 1962	1	USA (Nevada, Oregon)
	Vastosaprinus Wenzel, 1962	2	USA (California, Nevada, Arizona, Colorado), Mexico
45. *Zorius* Reichardt, 1932	–	2	Palestine, Israel

Morphology and terminology

This chapter presents a general account of the external morphology of the adult Palaearctic Saprininae. It explains how the structural terms are used throughout the present paper and where necessary, illustrations are provided to clarify the terminology. Besides the essential terminology widely used in morphological accounts on the Histeridae (such as Kryzhanovskij & Reichardt 1976; Ôhara 1994; Hansen 1991, 1997; Kanaar 1997; Caterino & Vogler 2002; Kovarik & Tishechkin 2004; Tishechkin 2007) several new terms are proposed. To indicate a newly proposed term, **bold** font is used. The terms used for surface sculptures were adopted from Harris (1979).

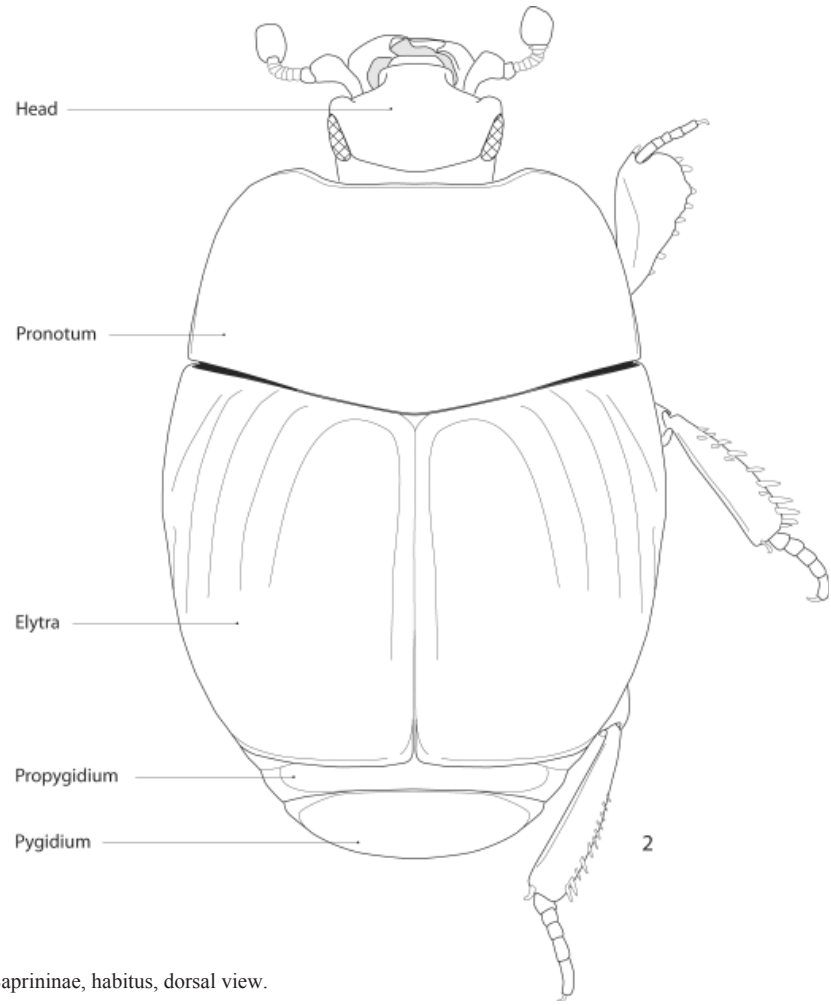


Fig. 2. Saprininae, habitus, dorsal view.

Head

The dorsal part of the head of the Saprininae is often divided into two parts, clypeus and frontal disc, by a single line called the frontal stria (Fig. 3).

Clypeus. The region anterior to the frontal stria is termed clypeus (Wenzel 1944; Bousquet & Laplante 2006: 'epistoma'), region posterior to it is called frontal disc. Limits of the clypeus are less certain in cases where there is no frontal stria present, or where the frontal stria is widely interrupted. In such cases, the term clypeus is used to designate the dorsal region of the head in front of an imaginary line between the bases of antennae. Kovarik & Caterino (2001: 212) refer to the clypeus as follows: 'The indistinguishable clypeus is fused to the frons forming an epistoma…'

The structure of the clypeus presents a remarkable degree of variability regarding the punctation, presence of the lateral and anterior margins and, to a lesser extent, also the shape. Most psammophilous taxa have their clypeus rectangular, flat and impunctate (e.g., *Ctenophilothis chobauti* (Théry, 1900) and *Philothis* (*Philothis*) *arcanus* Reichardt, 1930). In cases when the clypeus is punctate, its punctation varies from puncticulate (e.g., *Pholioxenus phoenix* (Reichardt, 1929) to imbricate-punctate and/or lacunose-rugulose (e.g., *Hypocacculus* (*Nessus*) *rubripes* (Erichson, 1834), *Hypocacculus* (*Colpellus*) *praecox* (Erichson, 1834) and *Saprinillus paromaloides* Kryzhanovskij, 1974). In some taxa the clypeus is medially depressed with its anterior margin usually elevated (e.g., *Zorius funereus* (Schmidt, 1890) and *Exaesiopus grossipes* (Marseul, 1855)); in others, the lateral margins of clypeus are elevated (e.g., *Hypocacculus* (*Nessus*) *rubripes* and *Hypocacculus* (*Colpellus*) *praecox*). Another group of taxa have the lateral margins of the clypeus simply rounded (e.g., *Eremosaprinus vlasovi* (Reichardt, 1941) and *Gnathoncus rotundatus* (Kugelann, 1792).

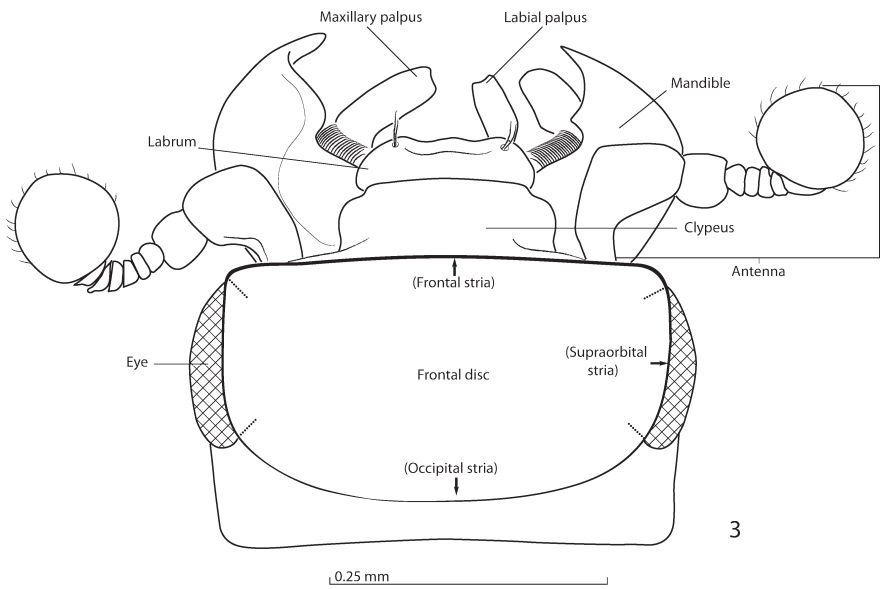


Fig. 3. Saprininae, head, dorsal view, schematic.

The shape of the clypeus also varies. A group of taxa have their clypeal and frontal discs on the same plain and the lateral margins of the clypeus are sharply sloping down (e.g., *Saprinus* (*Hemisaprinus*) *subvirescens* (Ménétriés, 1832), *Euspilotus* (*Neosaprinus*) *perrisi* (Marseul, 1872), *Saprinus* (*Phaonius*) *pharao* Marseul, 1855 and *Saprinus* (*Saprinus*) *semistriatus* (Scriba, 1790)). Few Saprininae taxa have their clypeus constricted between the antennal insertions (e.g., *Chivaenius kryzhanovskii* Olexa, 1980 and *Xenophilothis choumovitchi* (Thérond, 1965)). The clypeus of *Xenophilothis choumovitchi* is peculiarly shaped. It is anteriorly broadened and partly smooth, with posterior half covered by fine granules.

Frontal disc. By the term frontal disc is understood the space delimited anteriorly by the frontal stria, laterally by the supraorbital striae and posteriorly by the occipital stria. In cases when one or all of the striae are vaguely impressed or even absent, the frontal disc is delimited by an imaginary line connecting one anterior end of the eye with the other, running above the eye and linking the posterior ends of eyes (Fig. 3).

The structure of the frontal disc is highly variable and is important in discriminating between the genera or subgenera of the Saprininae. The frontal disc can have variously coarse and dense punctation (e.g., in *Pholioxenus phoenix* and *Myrmetes paykulli* Kanaar, 1979), rugulose-lacunose surface or be covered by coarse rugae (e.g., *Hypocaccus* (*Hypocaccus*) *rugiceps* (Duftschmid, 1805) and *Hypocaccus* (*Baeckmanniolus*) *dimidiatus* (Illiger, 1807)) or smooth surface (e.g., *Philothis* (*Philothis*) *arcanus*, *Ctenophilothis chobauti* and *Styphrus corpulentus* Motschulsky, 1845). Rarely, a single tiny shallow fovea is present in the median part of the posterior half of frontal disc (e.g., in *Turanostyphrus ignoratus* Tishechkin, 2005 and *Zorius funereus*).

Frontal stria. The frontal stria, together with the surface of the frontal disc, has been an important character in distinguishing between taxa of the Saprininae since the earliest classifications (Erichson 1834). In this paper the term frontal stria is used for a simple line or a distinct carina starting anterior to the eye and continuing posteriad of the antennal insertions and delimiting the frontal disc from the clypeus regardless of its curvature (Fig. 3). It is usually a well-developed line (e.g., in *Hypocacculus* (*Colpellus*) *praecox*) but can be also largely interrupted although still present dorsad of the antennal insertions (e.g., in *Saprinillus paromaloides*) or completely absent (e.g., in *Gnathoncus rotundatus*). In species with a coarse punctation of the frontal disc, the frontal stria can be obsolete or obliterated (e.g., in *Axelinus ghilarovi* (Kryzhanovskij, 1976)). In some littoral taxa (e.g., in *Hypocaccus* and *Exaesiopus*) the frontal stria is not a simple line but a strongly carinate structure. For more discussion concerning the variation of frontal stria see Peyerimhoff (1936: 213).

Supraorbital stria. The term supraorbital stria is ambiguously treated in the Histeridae. Wenzel (1962) and Ôhara (1994) refer to the supraorbital stria as to the stria that runs posterior to the eyes, demarcating the frontal disc from the vertex. On the other hand, Kryzhanovskij & Reichardt (1976) and Kanaar (1997) refer to the supraorbital stria as the stria that runs dorsad of the eye. The latter view is adopted here (Fig. 3), since the supraorbital stria is here interpreted rather as a posterolateral extension of the frontal stria than a demarcation line between the frontal disc and the vertex. Its position, running dorsad of the eye corresponds well with the Latin prefix 'supra'. Posteriorly the supraorbital stria is often connected

to a line truly demarcating the frontal disc from the vertex, which is termed here the occipital stria (sensu Kanaar 1997) (Fig. 3).

The supraorbital stria is often present even in cases when the frontal stria is interrupted or absent, although in some taxa it cannot be clearly distinguished (e.g., in *Axelinus ghilarovi*, see above). Several taxa have very acute antero-lateral angles between the frontal and supraorbital stria (e.g., *Alienocacculus neftensis* (Olexa, 1984), *Saprinillus paromaloides*, *Xenophilothis choumovitchi* and *Hypocacculus* (*Colpellus*) *praecox*). Supraorbital stria of these taxa is usually elevated, forming an acute angle, and is carinate. In some psammophilous taxa, on the other hand, the supraorbital stria is absent (e.g., in *Philothis* (*Farabius*) *hexeris* Reichardt, 1929).

Eyes. The compound eyes can vary in size in the Saprininae. They can be convex and well visible from above (e.g., in *Euspilotus* (*Neosaprinus*) *perrisi* and *Saprinus* (*Hemisaprinus*) *subvirescens*), flattened but still visible from above (e.g., in *Turanostyphrus ignoratus* and *Saprinillus paromaloides*), or flattened and invisible from above (e.g. in *Ctenophilothis chobauti* and *Chivaenius kryzhanovskii*) (Fig. 3). So far, no Saprininae without eyes are known.

Antennae. The antennal insertion in the Saprininae is situated on the lateral edge of the frontal disc between the eye and the base of the mandible. The antenna is 11-segmented, clavate and composed of the scape, pedicel and antennal flagellum. The flagellum is composed of the funicle (= six consecutive antennomeres that follow the pedicel) and the antennal club, which consists of the terminal three antennomeres. In the Saprininae, the antennal club bears sensory structures, frequently referred to as the Reichardt's organ (see, e.g., De Marzo & Vienna 1982a) (Fig. 4).

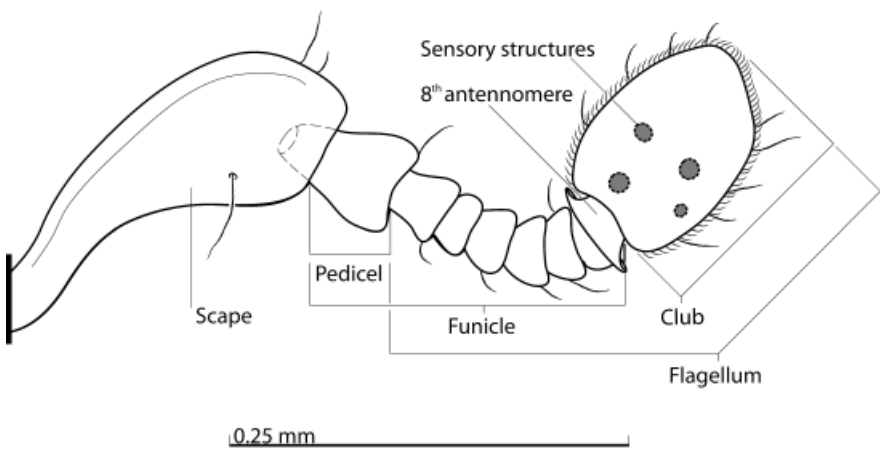
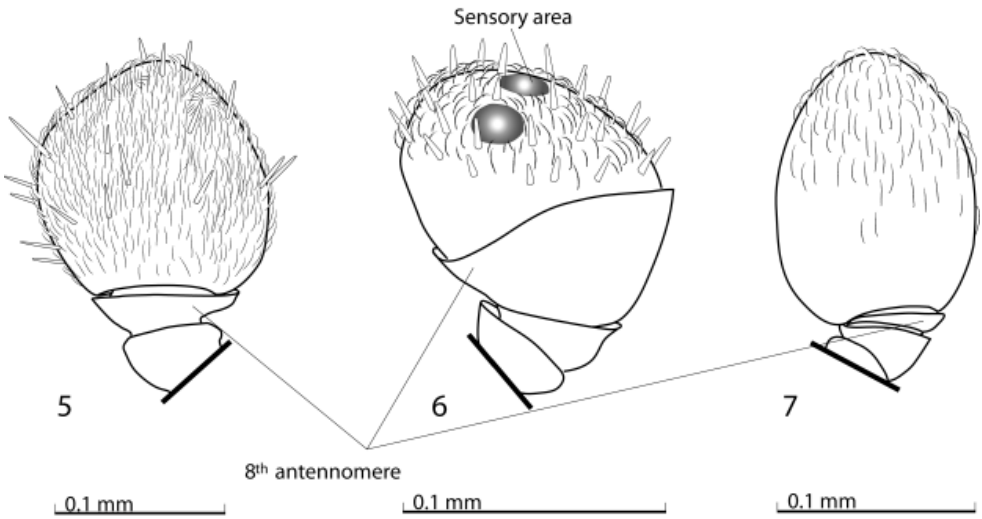


Fig. 4. Saprininae, antenna, dorsal view, schematic.



Figs. 5–7. Saprininae, 8th antennomere: 5 – *Paravolvulus ovillum* (Solskij, 1876); 6 – *Philothis* (*Atavinus*) *atavus* (Reichardt, 1931); 7 – *Turanostyphrus ignoratus* Tishechkin, 2005.

Antennal scape. The scape is often distinctly depressed in the apical part. Its shape varies from fairly elongate and slender (e.g., in *Eremosaprinus vlasovi*), to moderately thickened (most of the taxa), extremely thickened (e.g., in *Alienocacculus neftensis*) or even bulbous (e.g., in *Xenophilothis choumovitchi*).

The dorsal surface of the scape is in most cases imbricate distally around the apical depression and either punctate or smooth proximally. The scape always bears setae, which can vary in density, sclerotization and length. In psammophilous taxa, these setae are usually numerous and long (e.g., *Xenophilothis choumovitchi* and *Ctenophilothis chobauti*). In littoral taxa (e.g., *Eopachylopus ripae*) or inquilinous taxa (e.g., *Eremosaprinus vlasovi* and *Myrmetes paykulli*) the setae are often short, weakly sclerotized and sparse.

Pedicel. The pedicel is usually fairly thickened, cylindrical and in most cases larger than the following six antennomeres. If the 8th antennomere has a saucer-like ring (see below), the pedicel width can be surpassed by the ring's diameter. In some rare cases, the 8th antennomere is broader and bigger than pedicel (e.g., *Ctenophilothis chobauti* and *Philothis* (*Atavinus*) *atavus* Reichardt, 1931). The slender and elongated pedicel of *Eremosaprinus vlasovi* is exceptional.

Eighth antennomere. The apical part of the 8th antennomere is concealed by the antennal club; the basal part can be shaped like a simple ring of various diameter and depth (e.g., in *Euspilotus* (*Neosaprinus*) *perrisi*), or more frequently, when its edges are elevated, it resembles a shallow saucer (e.g., in *Paravolvulus ovillum*; Fig. 5). Sometimes the edges are extraordinarily elevated and the 8th antennomere is shaped as a cupule that surrounds the antennal club up to one-third of its length (e.g., in *Ctenophilothis chobauti*, *Philothis* (*Philothis*) *arcanus*

and *Philothis* (*Farabius*) *hexeris*) or even more (e.g., in *Philothis* (*Atavinus*) *atavus*; Fig. 6). Seldom the 8th antennomere is indicated by a tiny projection (e.g., in *Alienocacculus neftensis*, *Eremosaprinus vlasovi*, *Styphrus corpulentus*, *Xenophilothis choumovitchi* and *Turanostyphrus ignoratus*; Fig. 7).

Antennal club. The club antennomeres are mostly fused without a trace of inter-segmental sutures. In rare cases, the sutures are visible (e.g., in *Saprinus* (*Phaonius*) *pharao*). The club is usually round (most of the taxa) or oval (e.g., in *Eremosaprinus vlasovi*, *Myrmetes paykulli* and *Microsaprinus therondianus* (Dahlgren, 1973)); it can also be depressed dorso-ventrally (e.g., in *Chalcionellus amoenus* (Erichson, 1834)) or slightly pointed apically (e.g., in *Saprinus* (*Hemisaprinus*) *subvirescens*).

The antennal club bears a variety of sensilla. Although Kovarik & Caterino (2005) recognized three types of sensilla (*sensillum chaeticum*, *trichoideum* and *basiconicum*), this classification is not used here since no histological procedures required sensu Schneider (1964), Borden (1968) and Slifer (1970) have been undertaken. Based on the SEM photography, three types of sensilla can be distinguished (Fig. 8), but it is not clear how they correspond with those of Kovarik & Caterino (2005).

> ***Type I.*** Short sensillum with a pointed tip (Fig. 8). Adhesive and, if present, usually fairly abundant. Type I sensilla can cover the antennal club in its entirety (e.g., in *Paravolvulus ovillum*) or originate from its apical five-sixths to two-thirds, thus leaving the basal third to sixth asetose (e.g., in *Pholioxenus phoenix* and *Turanostyphrus ignoratus*). Rarely these sensilla can be absent altogether (e.g., in *Saprinus* (*Phaonius*) *pharao*).

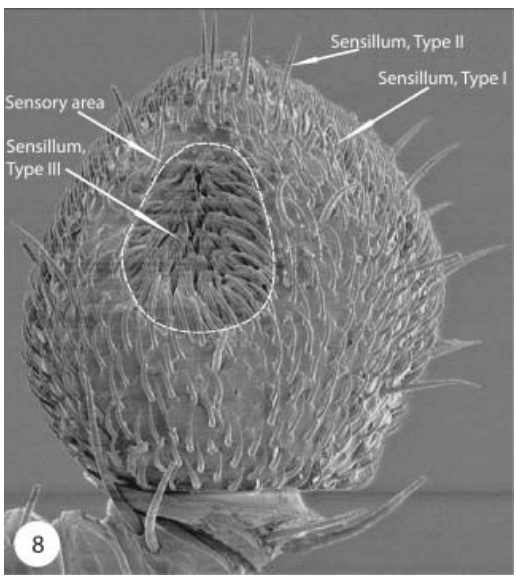


Fig. 8. Antennal club of Saprininae showing three types of sensillum.

Type II. Usually a longer erect sensillum with a pointed tip (Fig. 8). It is always protruding and rather sparse. It can be as long as Type I sensillum (e.g., in *Reichardtiolus duriculus* (Reitter, 1904)) or up to 5 to 6 times longer (e.g., in *Saprinus* (*Hemisaprinus*) *subvirescens*). Sensilla of Type II are in most cases asymmetrically distributed throughout the antennal club and sometimes also grow out from the sensory areas (e.g., in *Styphrus corpulentus*).

Type III. Short sensillum with rounded tip (Fig. 8), most probably '*sensillum basiconicum*' sensu De Marzo & Vienna (1982a) and Kovarik & Caterino (2005). These are very dense and numerous, arranged exclusively in sensory areas and slit-like orifices; see also Sensory structures of the antennal club.

Despite the fact that the most common type of antennal club chaetotaxy has all three of these types of sensilla, many variations exist, especially in psammophilous taxa (e.g., in *Philothis* (*Atavinus*) *atavus*, *Ctenophilothis chobauti* and *Xenonychus tridens* (Jacquelin-Duval, 1852)). Rarely, the antennal club can be entirely glabrous from the ventral side (e.g., in some specimens of *Ctenophilothis chobauti* and in *Xenophilothis choumovitchi*). The antennal club of *Microsaprinus therondianus* bears only several short sensilla situated in the vague sutures between antennomeres IX, X and XI and in the sensory area on the top of antennomere XI.

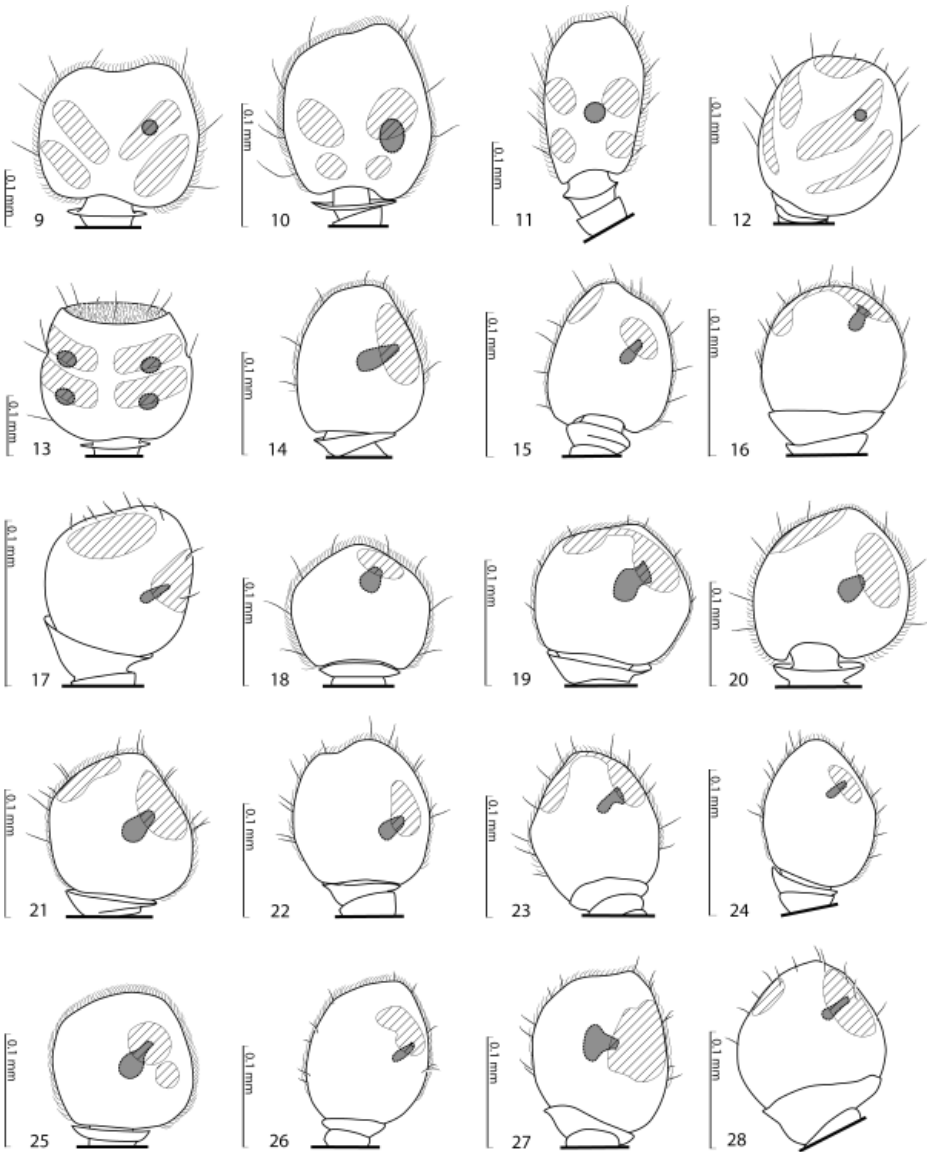
Sensory structures of the antennal club. The presence of a distinctive sensory apparatus on the antennal club of the Saprininae was mentioned for the first time by Reichardt (1941: 201–202, Fig. 100), who observed 'matt, fine-haired depressions' ['... булава крупная, кругловатая, нерасчлененная, с матовыми нежноволосистыми углублениями...'] on the ventral side of the antennal club of *Saprinus gilvicornis* Erichson, 1834. Wenzel (1962: 374) confirmed those observations describing this distinctive sensory apparatus as: 'oval sensory plaques [...] usually rather large and well defined, sometimes invaginated within slit-like pits'; and listed this sensory apparatus among one of the discriminating characters separating *Saprinus* from the other genera.

Based on the study of 51 species belonging to 12 genera, De Marzo & Vienna (1982a) provided the first comprehensive study of the morphology and histology of this structure and deemed it a particular sensory apparatus, which is neither sex nor infra-species specific, and is present on both antennae. They named the apparatus 'Reichardt's organ', that according to them, in general consists of the presence and/or combination of the following sensory structures:

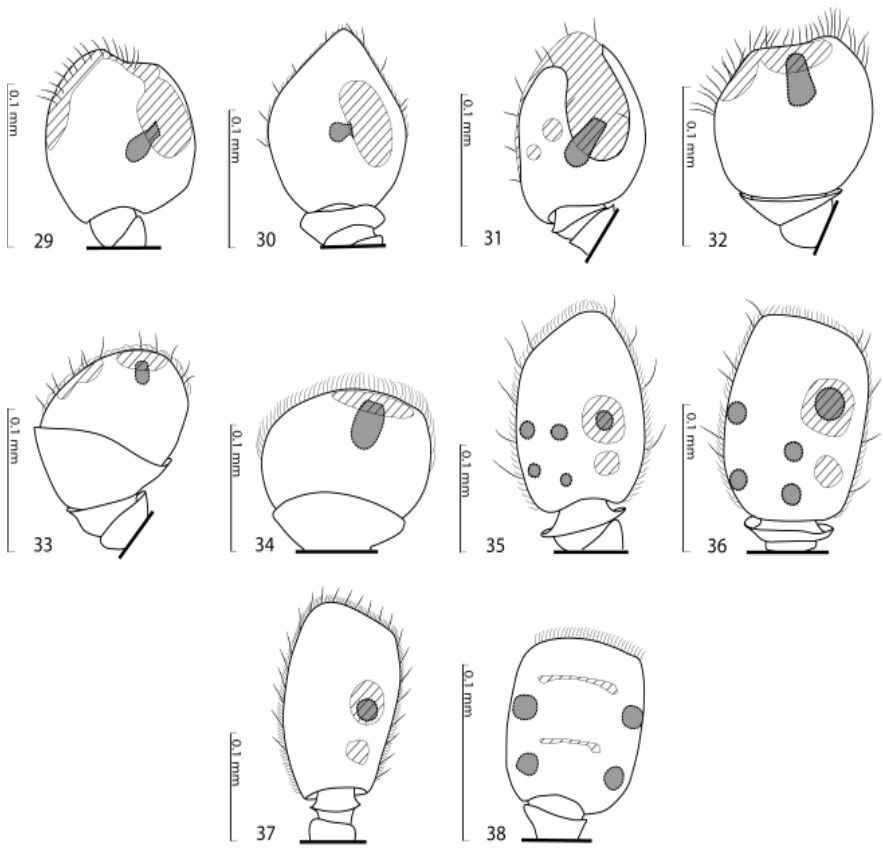
Slit-like pits (De Marzo & Vienna 1982a: 'fossette') – deep oblong-shaped indentations (two or six in number) of the cuticle, apparently corresponding to the sutures between antennomeres IX, X and XI.

Sensory areas (De Marzo & Vienna 1982a: 'aree sensoriali') – variously shaped, mostly oval areas (one to four in number) with dense aggregations of Type III sensilla.

Vesicles (De Marzo & Vienna 1982a: 'vescicole') – one, three or five ball- or stipe-shaped cavities, one of which is the main vesicle (*V*) (Figs. 18, 21 in the above-mentioned study), opening to the surface of the antennal club with a small orifice.



Figs. 9–28. Saprininae, sensory structures of the antennal club (vesicles marked with grey; sensory areas shaded): 9 – *Saprinus* (*Saprinus*) *semistriatus* (Scriba, 1790); 10 – *Saprinus* (*Hemisaprinus*) *subvirescens* (Ménétries, 1832); 11 – *Myrmetes paykulli* Kanaar, 1979; 12 – *Styphrus corpulentus* Motschulsky, 1845; 13 – *Saprinus* (*Phaonius*) *pharao* (Marseul, 1855); 14 – *Ammostyphrus cerberus* Reichardt, 1924; 15 – *Chalcionellus amoenus* (Erichson, 1834); 16 – *Chivaenius kryzhanovskii* Olexa, 1980; 17 – *Ctenophilothis chobauti* (Théry, 1900); 18 – *Eopachylopus ripae* (Lewis, 1885); 19 – *Exaesiopus grossipes grossipes* (Marseul, 1855); 20 – *Hypocaccus* (*Hypocaccus*) *rugiceps* (Duftschmid, 1805); 21 – *Hypocaccus* (*Baeckmanniolus*) *dimidiatus dimidiatus* (Illiger, 1807); 22 – *Hypocacculus* (*Hypocacculus*) *metallescens* (Erichson, 1834); 23 – *Hypocacculus* (*Colpellus*) *praecox* (Erichson, 1834); 24 – *Hypocacculus* (*Nessus*) *rubripes* (Erichson, 1834); 25 – *Paravolvulus lateristrius* (Solskij, 1876); 26 – *Pholioxenus phoenix* (Reichardt, 1930); 27 – *Reichardtiolus duriculus* (Reitter, 1904); 28 – *Xenonychus tridens* (Jacquelin-Duval, 1852).



Figs. 29–38. Saprininae, sensory structures of the antennal club (vesicles marked with grey; sensory areas shaded): 29 – *Xenophilothis choumovitchi* (Thérond, 1965); 30 – *Zorius funereus* (Schmidt, 1890); 31 – *Alienocacculus neftensis* (Olexa, 1984); 32 – *Philothis* (*Philothis*) *arcanus* Reichardt, 1930; 33 – *Philothis* (*Atavinus*) *atavus* (Reichardt, 1931); 34 – *Philothis* (*Farabius*) *hexeris* Reichardt, 1930; 35 – *Euspilotus* (*Neosaprinus*) *perrisi* (Marseul, 1872); 36 – *Gnathoncus rotundatus* (Kugelann, 1792); 37 – *Eremosaprinus vlasovi* (Reichardt, 1941); 38 – *Microsaprinus therondianus* (Dahlgren, 1973).

These three main sensory structures manifest themselves in several morphological variations, which can differ from each other significantly. Nonetheless, De Marzo & Vienna (1982a) considered them homologous in nature because of the constant presence of the main vesicle.

In the present paper the term 'Reichardt's organ' is rejected for three reasons. Firstly, the main vesicle could not be located in all studied taxa. For example, the antennal club of *Saprinus* (*Phaonius*) *pharao* contains four vesicles, each under a corresponding slit-like pit on the ventral surface (Fig. 13). The antennal club of *Microsaprinus therondianus* likewise contains four vesicles (Fig. 38). In both species it has been impossible to determine which vesicle is the main one, since all are approximately equal in size. Secondly, the antennal club of *Gnathoncus rotundatus* bears five vesicles, one large and four smaller ones (Fig. 36).

Table 1. Morphological types of sensory structures of the antennal club observed in the Saprininae.

No.	Form & Characteristics	De Marzo & Vienna (1982a)	this paper
1.	• four rather large sensory areas (ventral side) • one vesicle (internal distal margin of ventral side) [Figs. 9, 10; De Marzo & Vienna (1982a: Figs. 7–12)]	*Saprinus* (*Saprinus*) *acuminatus* *S. aegialius* (=*incognitus*) *S. aeneus* *S. beduinus* *S. bicolor* *S. caerulescens* (=*semipunctatus*) *S. calatravensis* *S. chalcites* *S. cupreus* *S. detersus* *S. furvus* *S. georgicus* *S. immundus* *S. intricatus* *S. ornatus* *S. planiusculus* *S. politus* ***S. semistriatus*** *S. subnitescens* *S. tenuistrius sparsutus* ***Saprinus* (*Hemisaprinus*) *subvirescens*** ***Styphrus corpulentus*** ***Myrmetes paykulli*** (= *piceus*)	***Saprinus* (*Saprinus*) *semistriatus*** ***S.* (*Hemisaprinus*) *subvirescens***
1a.	• four rather small circular sensory areas (ventral side) • one large vesicle (internal distal margin of the ventral side) [Fig. 11]	–	***Myrmetes paykulli*** (= *piceus*)
1b.	• four rather large ventral sensory areas and one large apical sensory area • one vesicle (internal distal margin of the ventral side) [Fig. 12]	–	*Styphrus corpulentus*
2.	• three sensory areas (two on ventral and one on dorsal side) • one vesicle (internal distal margin of the ventral side) two slit-like pits (ventral side) [De Marzo & Vienna (1982a: Figs. 13–15)]	*Saprinus (Saprinus) purpuricollis*	–

Table 1 (continued)

No.	Form & Characteristics	De Marzo & Vienna (1982a)	this paper
3.	• four slit-like pits (ventral side) • two slit-like pits (dorsal side) • one vesicle (internal distal margin of the ventral side [Fig. 8; De Marzo & Vienna (1982a: Figs. 16–21)]	*Saprinus* (*Saprinus*) *algericus* *S. biterrensis* *S. maculatus*	–
4.	• four slit-like pits (ventral side) • two slit-like pits (dorsal side) • four vesicles each under corresponding slit-like pit (ventral side) [Fig. 13]	–	*Saprinus* (*Phaonius*) *pharao*
5.	• one or two large sensory areas occasionally vaguely connected apically (internal distal margin of the ventral side) • one vesicle, mostly stipe-shaped [Figs. 14–30; De Marzo & Vienna (1982a: Figs. 22–30)]	*Chalcionellus aemulus* ***Ch. amoenus*** *Ch. decemstriatus* ***Exaesiopus grossipes*** ***Hypocacculus* (*Hypocacculus*) *metallescens*** *H.* (*Nessus*) *puncticollis* ***H.* (*Nessus*) *rubripes*** *Hypocaccus* (*Hypocaccus*) *brasiliensis* *H. crassipes* *H. metallicus* *H. pelleti* ***H. rugiceps*** *H. rugifrons* ***H.* (*Baeckmanniolus*) *dimidiatus*** *Pachylopus dispar* *Pholioxenus schatzmayri* ***Xenonychus tridens***	*Ammostyphrus cerberus* ***Chalcionellus amoenus*** *Chivaenius kryzhanovskii* *Ctenophilothis chobauti* *Eopachylopus ripae* ***Exaesiopus grossipes*** ***Hypocaccus* (*Hypocaccus*) *rugiceps*** ***H.* (*Baeckmanniolus*) *dimidiatus*** ***Hypocacculus* (*Hypocacculus*) *metallescens*** *H.* (*Colpellus*) *praecox* ***H.* (*Nessus*) *rubripes*** *Paravolvulus lateristrius* *Pholioxenus phoenix* *Reichardtiolus duriculus* ***Xenonychus tridens*** *Xenophilothis choumovitchi* *Zorius funereus*
5a.	• one large apical sensory area • two small round sensory areas on the ventral side • one stipe-shaped vesicle [Fig. 31]	–	*Alienocacculus neftensis*
5b.	• one apical sensory area • one stipe-shaped vesicle situated under apical sensory area [Figs. 32–34]	–	*Philothis* (*Philothis*) *arcanus* *Ph.* (*Atavinus*) *atavus* *Ph.* (*Farabius*) *hexeris*

(The table continues on the next page)

Table 1 (continued)

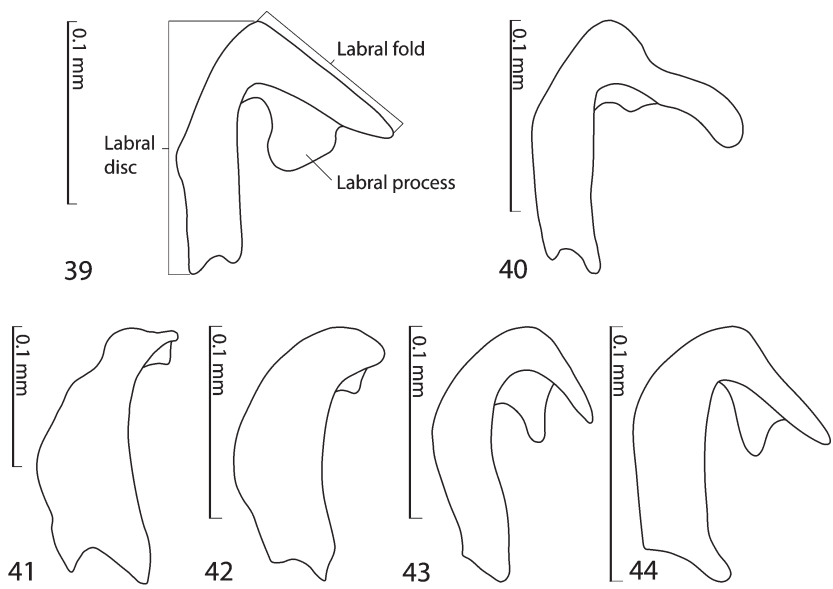
No.	Form & Characteristics	De Marzo & Vienna (1982a)	this paper
6.	• two sensory areas (ventral side) • five vesicles, one of them larger than the other four; four vesicles arranged in two pairs on ventral and dorsal side respectively [Figs. 35–36; De Marzo & Vienna (1982a: Figs. 31–34)]	***Euspilotus* (*Neosaprinus*) *perrisi*** *Gnathoncus buyssoni* *G. nannetensis* ***G. rotundatus* (= *nanus*)** *G. schmidti*	***Euspilotus* (*Neosaprinus*) *perrisi*** ***Gnathoncus rotundatus* (= *nanus*)**
7.	• two differently sized sensory areas (ventral side) • one large round vesicle situated under the distal sensory area [Fig. 37]	–	*Eremosaprinus vlasovi*
8.	• one sensory area (ventral side) • three vesicles [De Marzo & Vienna (1982a: Figs. 35–36)]	*Euspilotus* (*Hesperosaprinus*) *azurescens* (= *nigrita*) *E. flaviclava* (= *auzati*)	–
9.	• two thin slit-like pits situated in vague sutures between antennomeres IX, X and XI (ventral side) • four vesicles situated in two pairs on the ventral side [Fig. 38]	–	*Microsaprinus therondianus*

Although it is tempting to state that the large vesicle is the main one, it is rather difficult to determine the exact origin of the remaining four vesicles. The position of the main vesicle has been observed to vary in this review, although it should always be situated on the ventral side of the club according to De Marzo & Vienna (1982a). In the psammophilous species of the genus *Philothis* it is situated directly under the dorsal surface of the antennal club. Thirdly, the theory that the origin of the sensory apparatus is clearly derived from the sutures between antennomeres IX, X and XI (and its forms are phylogenetically linked and can be arranged in two evolutionary paths), is likewise considered dubious, especially given the lack of a phylogenetical analysis of the genera. The sensory structures of the antennal clubs of, e.g., *Styphrus corpulentus* and *Euspilotus perrisi* are so different that it is difficult to believe that they both originated from the sutures between antennomeres IX, X and XI. In summary, the sensory organ present in and on the antennal club of the Palaearctic Saprininae is a composite structure, most likely not homologous in nature, and its subcomponents have probably arisen several times independently during evolution. Therefore, in this work it is referred to as **sensory structures of the antennal club** and its shape and forms are described in detail within each taxon (see also Figs. 9–38).

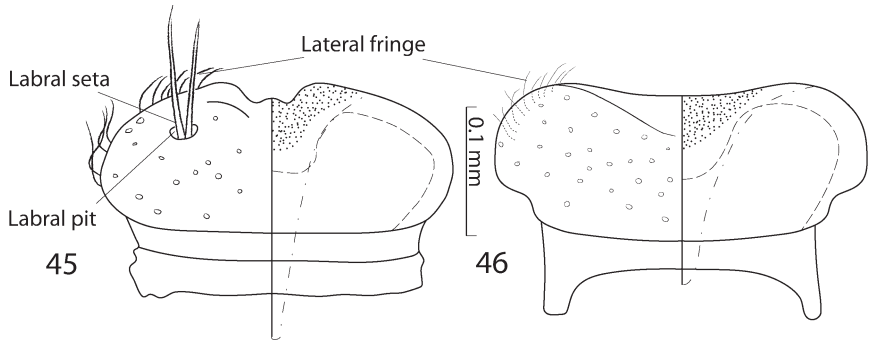
Table 1 sums up the possible morphological variations of these structures as observed by De Marzo & Vienna (1982a) and in this study. Taxa that were included in both studies and showed identical results are given in **bold**. From the 33 genera and subgenera that were subject to this study (each genus except *Paravolvulus* has been represented by its type species), the sensory structures of the following three taxa were not examined due to the lack of specimens: *Axelinus ghilarovi*, *Saprinillus paromaloides* and *Turanostyphrus ignoratus.* The type species of the genus *Paravolvulus*, *Paravolvulus ovillum*, was only available from a limited number of specimens whose dissection has not been permitted. Instead, *Paravolvulus lateristrius* (Solskij, 1876) was used for this study.

Mouthparts. The terminology in this section follows Ślipiński & Mazur (1999), Kovarik & Caterino (2001) and Kovarik & Tishechkin (2004), and some additional terminology is introduced. Currently, no comparative study of the mouthparts of the Saprininae is available.

Labrum. The labrum is dorsally usually punctate, smooth or covered with coarse sculpture, and its surface is often similar to the surface of the clypeus. It is shorter than broad, truncate in front and never margined. The labrum is here subdivided into three areas – **labral disc**, **labral fold** and **labral process** (Fig. 39). The dorsal structure of the labral disc shows a remarkable amount of variation (Figs. 47–73). Usually it is moderately to strongly convex (e.g., in *Hypocacculus* (*Colpellus*) *praecox*), sometimes medially depressed (e.g., in *Eremosaprinus vlasovi*), yet in some cases has a small median convexity which is interrupting



Figs. 39–44. Saprininae, labrum, lateral view: 39 – *Philothis* (*Farabius*) *hexeris* Reichardt, 1930; 40 – *Philothis* (*Atavinus*) *atavus* (Reichardt, 1931); 41 – *Saprinus* (*Phaonius*) *pharao* (Marseul, 1855); 42 – *Eremosaprinus vlasovi* (Reichardt, 1941); 43 – *Ctenophilothis chobauti* (Théry, 1900); 44 – *Philothis* (*Philothis*) *arcanus* Reichardt, 1930.

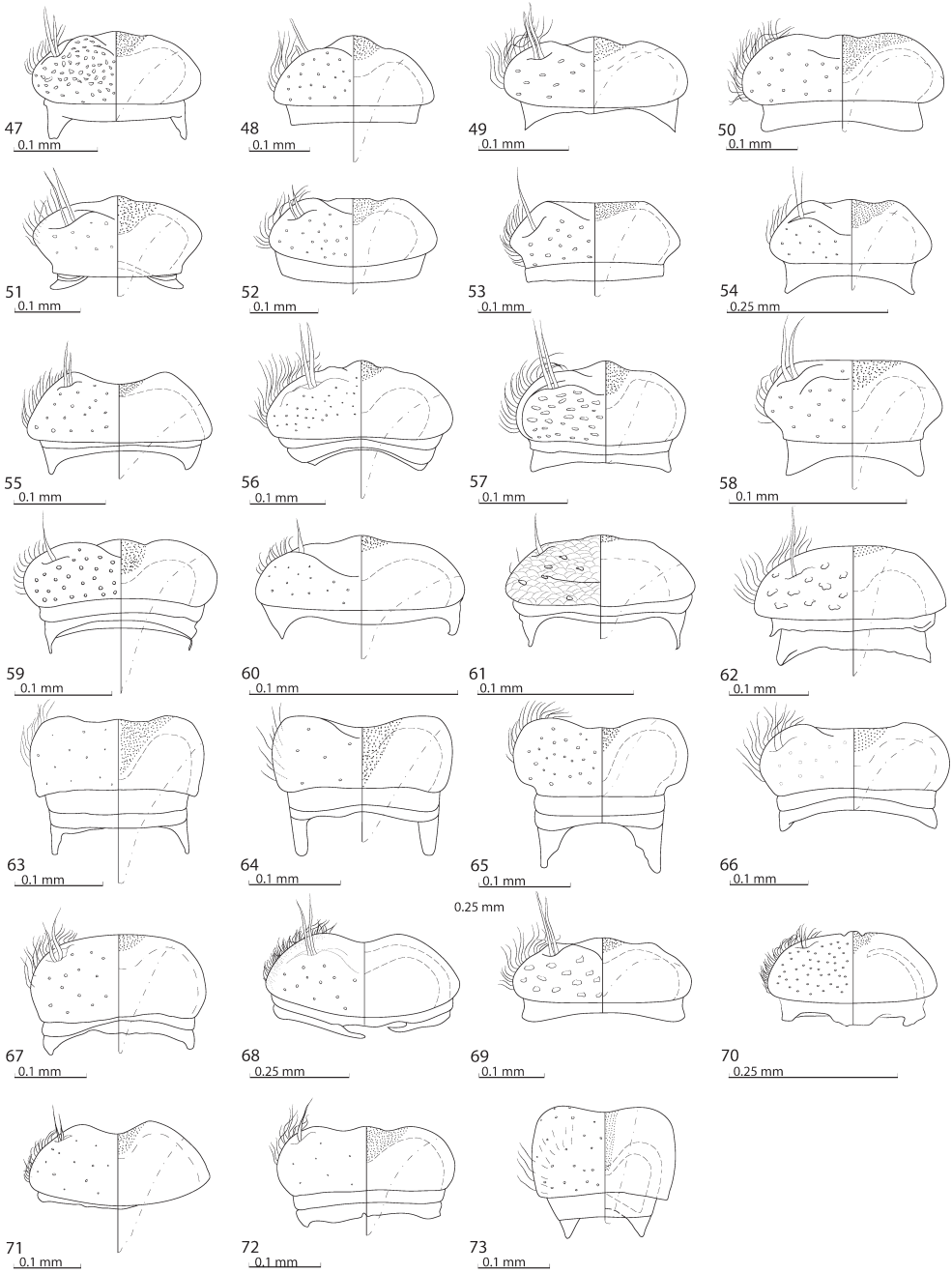


Figs. 45–46. Dorsal structure of labrum showing presence/absence of labral pit and seta (left half showing external and right half showing internal structures): 45 – *Hypocaccus* (*Baeckmanniolus*) *dimidiatus* (Illiger, 1807); 46 – *Ctenophilothis chobauti* (Théry, 1900).

concavity (e.g., in *Chalcionellus amoenus*). The labral structure of *Ctenophilothis chobauti*, *Philothis* (*Atavinus*) *atavus, Philothis* (*Farabius*) *hexeris, Philothis* (*Philothis*) *arcanus* and *Xenophilothis choumovitchi* is readily distinguishable from the other taxa examined in this study. It is substantially flattened with a shallow median depression and lacks labral pits and labral setae arising from them (Fig. 46). In all other taxa examined here, the labral pits and labral setae are truly absent only in *Chivaenius kryzhanovskii.* Other taxa have two labral pits (situated in the antero-lateral area of the labrum) with one or, more often, two stiff labral setae (Fig. 45). In some cases the pits are difficult to see, since they can be vaguely impressed and the setae can be worn off, especially in older specimens. The lateral fringe is present in all studied taxa. The setae that form the lateral fringe vary in length and density; in *Xenophilothis choumovitchi* they do not grow out from the lateral area but from the ventral side of labrum (Fig. 73).

The ventral side of the labral disc in most taxa bears a variously developed, sclerotized structure termed here the **labral process** (Figs. 39–44). This structure is hidden under the epipharynx and its function is unclear. It is significantly less developed in *Gnathoncus*

Figs. 47–73. Saprininae, labral structures, dorsal view (left half showing external and right half showing internal structures): 47 – *Alienocacculus neftensis* (Olexa, 1984); 48 – *Ammostyphrus cerberus* Reichardt, 1924; 49 – *Chalcionellus amoenus* (Erichson, 1834); 50 – *Chivaenius kryzhanovskii* Olexa, 1980; 51 – *Eopachylopus ripae* (Lewis, 1885); 52 – *Eremosaprinus vlasovi* (Reichardt, 1941); 53 – *Euspilotus* (*Neosaprinus*) *perrisi* (Marseul, 1872); 54 – *Exaesiopus grossipes grossipes* (Marseul, 55); 55 – *Gnathoncus rotundatus* (Kugelann, 1792); 56 – *Hypocaccus* (*Hypocaccus*) *rugiceps* (Duftschmid, 1805); 57 – *Hypocacculus* (*Hypocacculus*) *metallescens* (Erichson, 1834); 58 – *Hypocacculus* (*Colpellus*) *praecox* (Erichson, 1834); 59 – *Hypocacculus* (*Nessus*) *rubripes* (Erichson, 1834); 60 – *Microsaprinus therondianus* (Dahlgren, 1973); 61 – *Myrmetes paykulli* Kanaar, 1979; 62 – *Paravolvulus lateristriatus* (Solskij, 1876); 63 – *Philothis* (*Philothis*) *arcanus* Reichardt, 1930; 64 – *Philothis* (*Atavinus*) *atavus* (Reichardt, 1931); 65 – *Philothis* (*Farabius*) *hexeris* Reichardt, 1930; 66 – *Pholioxenus phoenix* (Reichardt, 1930); 67 – *Reichardtiolus duriculus* (Reitter, 1904); 68 – *Saprinus* (*Saprinus*) *semistriatus* (Scriba, 1790); 69 – *Saprinus* (*Hemisaprinus*) *subvirescens* (Ménétries, 1832); 70 – *Saprinus* (*Phaonius*) *pharao* (Marseul, 1855); 71 – *Styphrus corpulentus* Motschulsky, 1845; 72 – *Xenonychus tridens* (Jacquelin-Duval, 1852); 73 – *Xenophilothis choumovitchi* (Thérond, 1965).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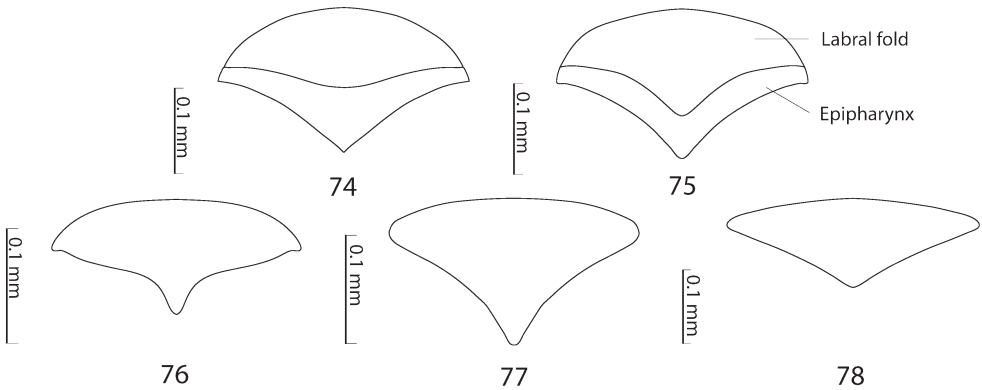
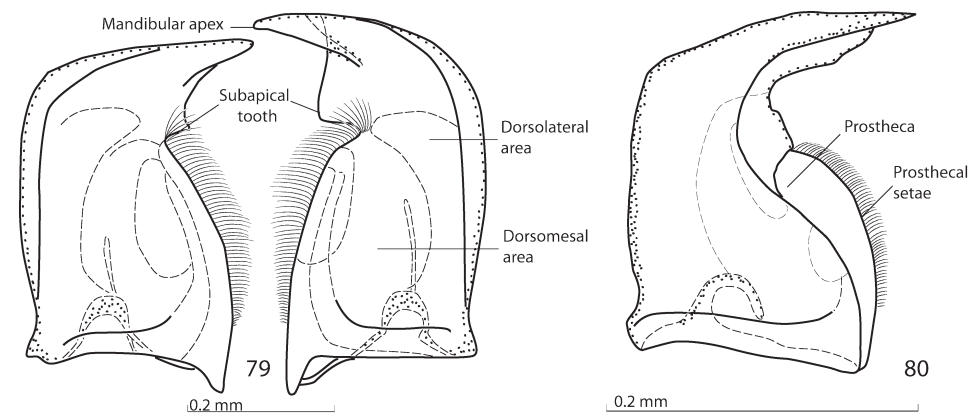


Figs. 74–78. Saprininae, labrum, frontal view: 74 – *Euspilotus* (*Neosaprinus*) *perrisi* (Marseul, 1872); 75 – *Pholioxenus phoenix* (Reichardt, 1930); 76 – *Philothis* (*Atavinus*) *atavus* (Reichardt, 1931); 77 – *Philothis* (*Farabius*) *hexeris* Reichardt, 1930; 78 – *Ctenophilothis chobauti* (Théry, 1900).

rotundatus, *Myrmetes paykulli*, *Euspilotus* (*Neosaprinus*) *perrisi*, *Eremosaprinus vlasovi*, *Saprinus* (*Saprinus*) *semistriatus* and *Saprinus* (*Phaonius*) *pharao*.

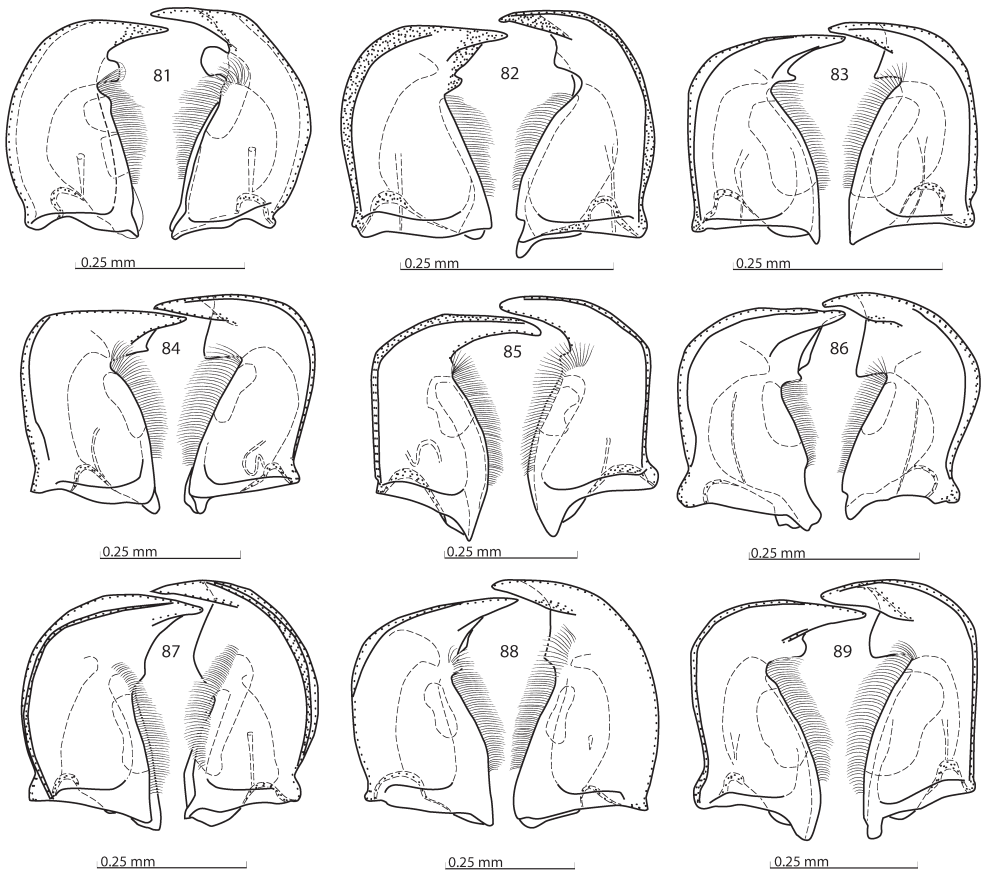
Labral fold (Figs. 39, 75) is the inwardly bent anterior part of the labral disc; it serves probably as an anterior protection to the epipharynx. In most taxa the epipharynx is not protected completely and protrudes laterally (Figs. 74–75). In several taxa the epipharynx is almost completely hidden under the labral fold, thus it is laterally almost not protruding, although transitional forms also occur (Figs. 76–78). This is the situation with, e.g., *Hypocaccus* (*Baeckmanniolus*) *dimidiatus*, *Ctenophilothis chobauti*, *Philothis* (*Farabius*) *hexeris*, *Myrmetes paykulli*, *Xenonychus tridens*, *Xenophilothis choumovitchi*, *Alienocacculus neftensis*, *Philothis* (*Atavinus*) *atavus*, *Chivaenius kryzhanovskii* and *Exaesiopus grossipes*.



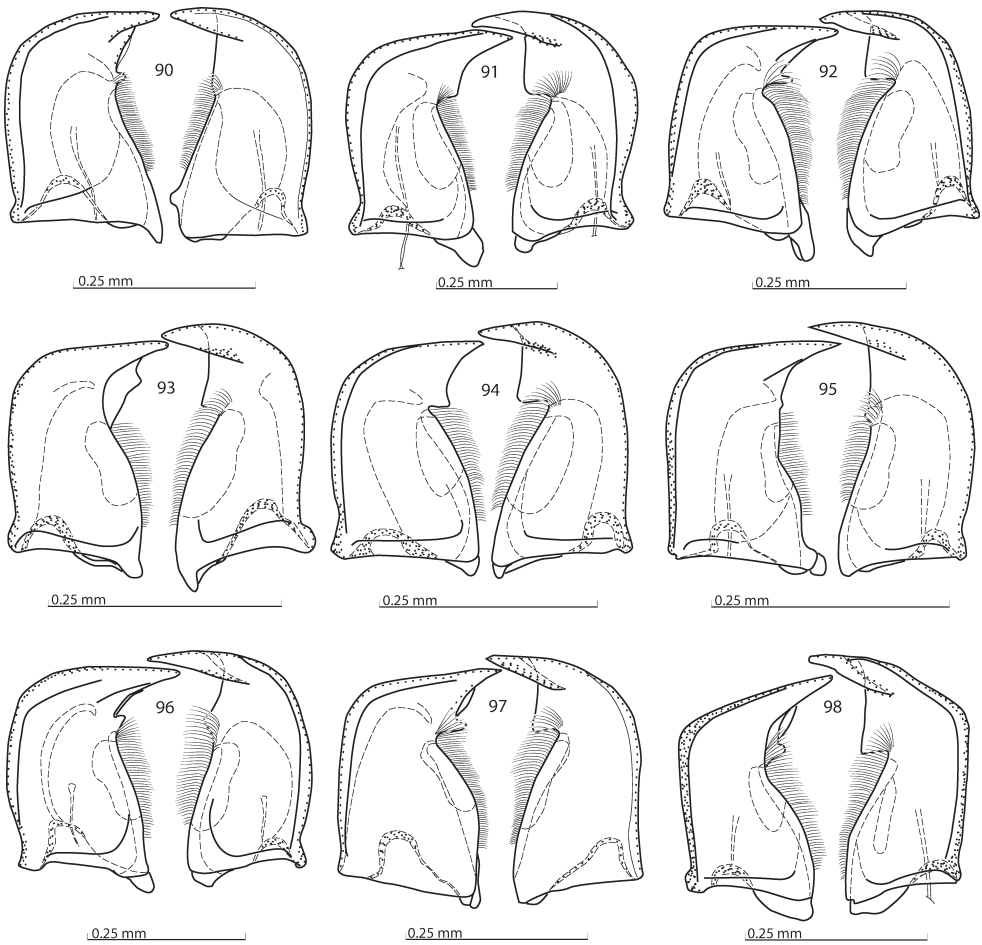
Figs. 79–80. Saprininae, mandibular structures, ventral view: 79 – *Hypocaccus* (*Hypocaccus*) *rugiceps* (Duftschmid, 1805); 80 – *Microsaprinus therondianus* (Dahlgren, 1973).

Mandibles. Kovarik & Tishechkin (2004) divide the dorsal mandibular surface into a dorsolateral area (DL) and a dorsomesal area (DM). The dorsolateral area of the mandibles of the taxa that are the subject of this study are devoid of chemoreceptors (setae), except for *Saprinus* (*Phaonius*) *pharao*, in which a few short scattered setae are present (Fig. 104).

The mandibular apex is usually acute. However, in *Philothis* (*Farabius*) *hexeris* and *Saprinus* (*Saprinus*) *semistriatus* it is rather obtuse. The inner margin of the left mandible (observed from dorsal view) usually bears one variously sized and shaped subapical tooth, situated in its apical third and sometimes overlaid by the prosthecal setae. The inner margin of the left mandible typically bears a massive, protruding, almost perpendicular subapical

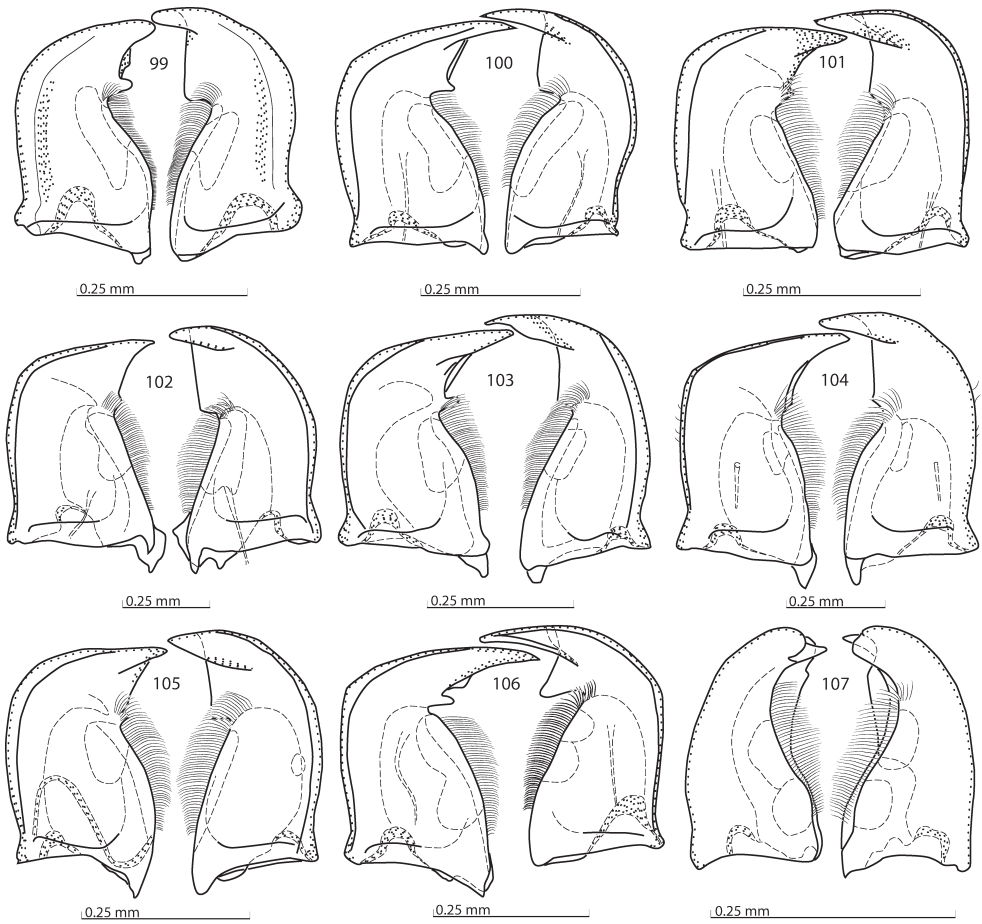


Figs. 81–89. Saprininae, mandibles, ventral view: 81 – *Alienocacculus neftensis* (Olexa, 1984); 82 – *Ammostyphrus cerberus* Reichardt, 1924; 83 – *Chalcionellus amoenus* (Erichson, 1834); 84 – *Chivaenius kryzhanovskii* Olexa, 1980; 85 – *Ctenophilotis chobauti* (Théry, 1900); 86 – *Eopachylopus ripae* (Lewis, 1885); 87 – *Eremosaprinus vlasovi* (Reichardt, 1941); 88 – *Euspilotus* (*Neosaprinus*) *perrisi* (Marseul, 1872); 89 – *Exaesiopus grossipes grossipes* (Marseul, 1855).



Figs. 90–98. Saprininae, mandibles, ventral view: 90 – *Gnathoncus rotundatus* (Kugelann, 1792); 91 – *Hypocaccus* (*Baeckmanniolus*) *dimidiatus dimidiatus* (Illiger, 1807); 92 – *Hypocacculus* (*Hypocacculus*) *metalescens* (Erichson, 1834); 93 – *Hypocacculus* (*Colpellus*) *praecox* (Erichson, 1834); 94 – *Hypocacculus* (*Nessus*) *rubripes* (Erichson, 1834); 95 – *Myrmetes paykulli* Kanaar, 1979; 96 – *Paravolvulus lateristrius* (Solskij, 1876); 97 – *Philothis* (*Philothis*) *arcanus* Reichardt, 1930; 98 – *Philothis* (*Atavinus*) *atavus* (Reichardt, 1931).

tooth (Fig. 79). Several variations to this arrangement exist. The subapical tooth of the left mandible can be extraordinarily small (e.g., in *Gnathoncus rotundatus*, *Myrmetes paykulli* and *Ctenophilothis chobauti*), obtuse (e.g., in *Saprinus* (*Saprinus*) *semistriatus*, *Saprinus* (*Hemisaprinus*) *subvirescens*, *Saprinus* (*Phaonius*) *pharao*, *Euspilotus* (*Neosaprinus*) *perrisi*, *Reichardtiolus duriculus*, *Eremosaprinus vlasovi* and *Paravolvulus lateristrius* (Solskij, 1876)) or rounded (e.g., in *Alienocacculus neftensis*). The variability in the shape of the mandibles



Figs. 99–107. Saprininae, mandibles, ventral view: 99 – *Philothis* (*Farabius*) *hexeris* Reichardt, 1930; 100 – *Pholioxenus phoenix* (Reichardt, 1930); 101 – *Reichardtiolus duriculus* (Reitter, 1904); 102 – *Saprinus* (*Saprinus*) *semistriatus* (Scriba, 1790); 103 – *Saprinus* (*Hemisaprinus*) *subvirescens* (Ménétries, 1832); 104 – *Saprinus* (*Phaonius*) *pharao* (Marseul, 1855); 105 – *Styphrus corpulentus* Motschulsky, 1845; 106 – *Xenonychus tridens* (Jacquelin-Duval, 1852); 107 – *Xenophilothis choumovitchi* (Thérond, 1965).

is shown in Figs. 81–107. The most peculiar mandibular structure is found in *Xenophilothis choumovitchi*, whose mandibular apex is obtuse, concealing a tiny acute tooth that is situated between the dorsal and ventral mandibular face. The subapical tooth on the inner margin of both mandibles is absent in this species (Fig. 107).

The membranous prostheca situated on the inner mandibular margin is narrow as a rule and its setae form a dense brush. In *Microsaprinus therondianus* the prostheca is unusually wide and its setae are short (Fig. 80).

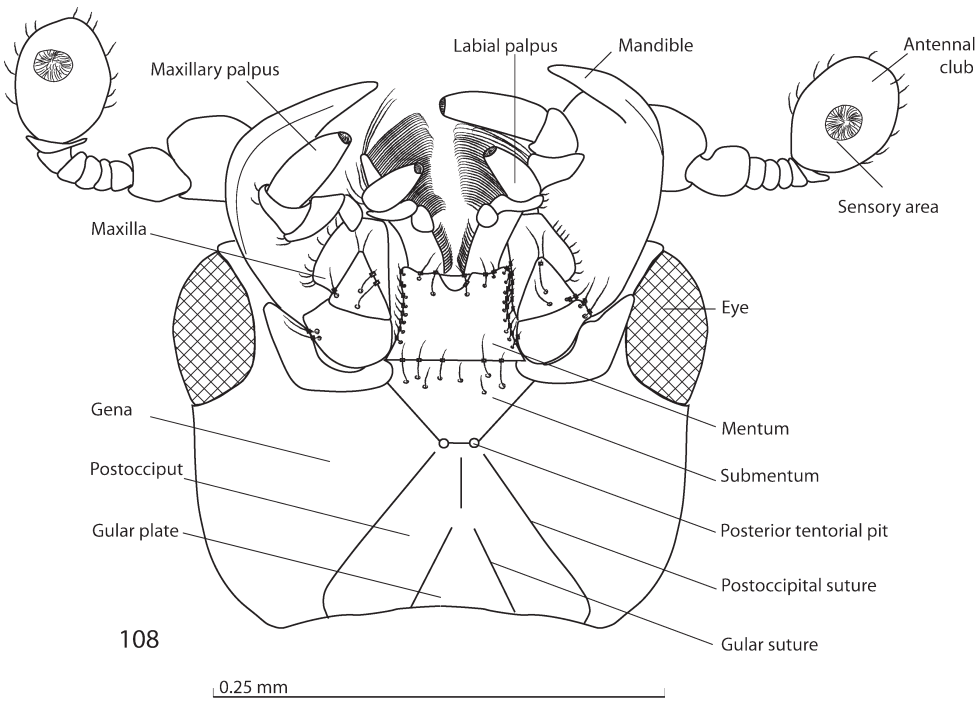
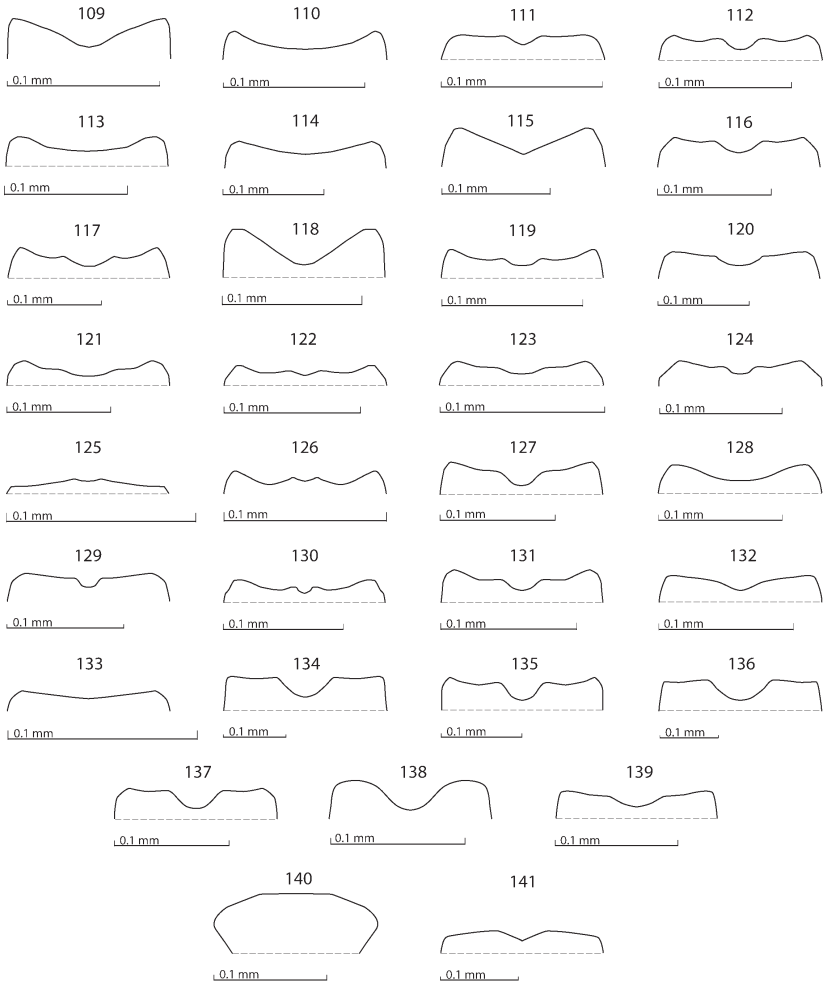


Fig. 108. Saprininae, head, ventral view, schematic.

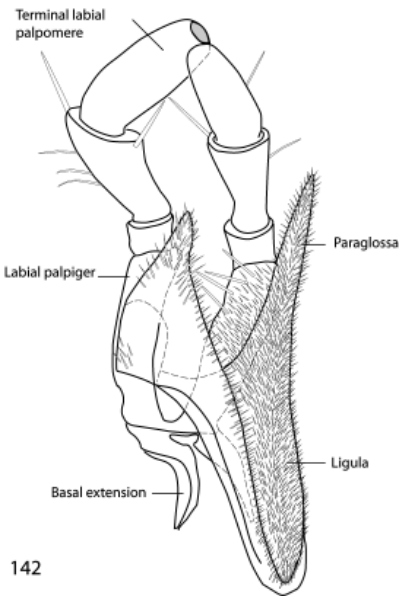
Mentum. The mentum in the Saprininae can be sub-trapezoidal, square-shaped or rectangular. A notable exception to this is *Xenophilothis choumovitchi*, in which the mentum is distinctly broadened anteriorly (Figs. 140, 732). While the posterior margin of the mentum is always straight and its lateral margins are in most cases slightly curved inwardly, it is the anterior margin that shows the highest degree of variation. The anterior margin can be straight or variously concave, at times also with a median notch (Figs. 109–141). The surface of the mentum is usually imbricate and often setose. A single or double row of short ramose setae is almost always present on the lateral margins; the posterior margin is always asetose. The anterior margin rarely bears short ramose setae in *Philothis* (*Atavinus*) *atavus* and *Philothis* (*Philothis*) *arcanus* or long and dense lamelliform setae in *Xenophilothis choumovitchi* (Fig. 143). The disc of the mentum can bear setae of various density and length, often concentrated on its anterior third.

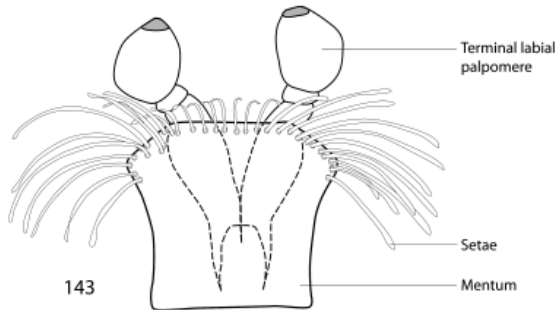
Submentum. The short and transverse submentum (Fig. 108) is fairly generalized in the Saprininae. It has a row of short setae on the front margin. These setae are often broken in older specimens. The setae are more numerous in the psammophilous taxa.

Labium. Not too much attention has been paid to the morphological structure of the labium of the Histeridae in general (but see Kovarik & Tishechkin 2004). In this paper the labial



Figs. 109–141. Sapininae, anterior margin of mentum, ventral view: 109 – *Alienocacculus neftensis* (Olexa, 1984); 110 – *Ammostyphrus cerberus* Reichardt, 1924; 111 – *Axelinus ghilarovi* Kryzhanovskij, 1976; 112 – *Chalcionellus amoenus* (Erichson, 1834); 113 – *Chivaenius kryzhanovskii* Olexa, 1980; 114 – *Ctenophilotis chobauti* (Théry, 1900); 115 – *Eopachylopus ripae* (Lewis, 1885); 116 – *Eremosaprinus vlasovi* (Reichardt, 1941); 117 – *Euspilotus* (*Neosaprinus*) *perrisi* (Marseul, 1872); 118 – *Exaesiopus grossipes grossipes* (Marseul, 1855); 119 – *Gnathoncus rotundatus* (Kugelann, 1792); 120 – *Hypocaccus* (*Hypocaccus*) *rugiceps* (Duftschmid, 1805); 121 – *Hypocaccus* (*Baeckmanniolus*) *dimidiatus dimidiatus* (Illiger, 1807); 122 – *Hypocacculus* (*Hypocacculus*) *metallescens* (Erichson, 1834); 123 – *Hypocacculus* (*Colpellus*) *praecox* (Erichson, 1834); 124 – *Hypocacculus* (*Nessus*) *rubripes* (Erichson, 1834); 125 – *Microsaprinus therondianus* (Dahlgren, 1973); 126 – *Myrmetes paykulli* Kanaar, 1979; 127 – *Paravolvulus ovillum* (Solskij, 1876); 128 – *Philothis* (*Philothis*) *arcanus* Reichardt, 1930; 129 – *Philothis* (*Atavinus*) *atavus* (Reichardt, 1931); 130 – *Philothis* (*Farabius*) *hexeris* Reichardt, 1930; 131 – *Pholioxenus phoenix* (Reichardt, 1930); 132 – *Reichardtiolus duriculus* (Reitter, 1904); 133 – *Saprinillus paromaloides* Kryzhanovskij, 1974; 134 – *Saprinus* (*Saprinus*) *semistriatus* (Scriba, 1790); 135 – *Saprinus* (*Hemisaprinus*) *subvirescens* (Ménétries, 1832); 136 – *Saprinus* (*Phaonius*) *pharao* (Marseul, 1855); 137 – *Styphrus corpulentus* Motschulsky, 1845; 138 – *Turanostyphrus ignoratus* Tishechkin, 2005; 139 – *Xenonychus tridens* (Jacquelin-Duval, 1852); 140 – *Xenophilotis choumovitchi* (Thérond, 1965); 141 – *Zorius funereus* (Schmidt, 1890).





Figs. 142–143. 142 – *Saprinus* (*Saprinus*) *semistriatus* (Scriba, 1790), labium, oblique lateral view (mentum and substructural legs (sensu Kovarik & Tishechkin 2004) removed). 143 – *Xenophilothis choumovitchi* (Thérond, 1965), mentum and labial palpi, ventral view.

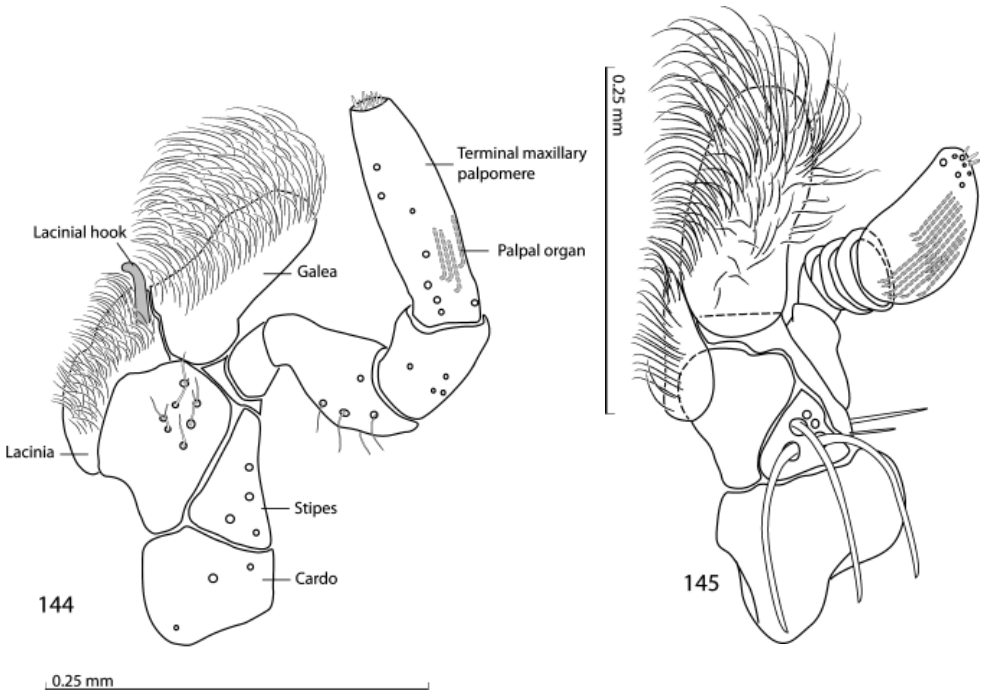
structures of only one taxon (*Saprinus* (*Saprinus*) *semistriatus*) are described and figured (Fig. 142). The labial palpigers, which bear the three-segmented labial palpus, are in this species widely separated distally and proximally connected with a short bridge that may be homologous with the prementum. While the distal part of the paraglossae, which lie lateral to the labial palpus, forms two widely separated and readily recognizable membranous lobes fringed with dense minute setae apically, the paraglossae are proximally indistinguishably fused with the glossae forming a setose ligula.

The terminal labial palpomere is the longest of the three palpomeres and can be thickened to a various degree. It is usually elongate, but in the psammophilous taxa it is often thickened. The palpal organ (sensu Kovarik & Tishechkin 2004) is presumed to be present in all taxa but could not be observed in several species.

Maxilla. Since a detailed description of the maxilla is given in Kovarik & Caterino (2001) and some additional terminology can also be found in Kovarik & Tishechkin (2004), it is not necessary to repeat it here. The maxilla in the Saprininae is fairly generalized and only the following morphological characters are treated in this paper: the chaetotaxy of the stipes, the lacinial hook and the terminal maxillary palpomere with the palpal organ (Fig. 144).

The stipes is always triangular. It usually bears three long sclerotized setae, although rarely four or five setae are present (e.g. *Chivaenius kryzhanovskii* and *Saprinus* (*Phaonius*) *pharao*); the psammophilous species have their stipes furnished with numerous long setae (e.g., in *Philothis* (*Atavinus*) *atavus* or *Ctenophilothis chobauti*).

As early as in Williams (1938: 273, Plate XV, Fig. 23), a finger-like structure has been identified to be present on the apex of the lacinia in several members of the superfamily Staphylinoidea, among them also in *Hister obtusatus* Harris, 1837 (= *Margarinotus* (*Ptomister*)



Figs. 144–145. Left maxilla, ventral view. 144 – *Eremosaprinus vlasovi* (Reichardt, 1941); 145 – *Xenophilotis choumovitchi* (Thérond, 1965).

brunneus (Fabricius, 1775)) and termed as 'digitus' (Williams 1938), 'lacinial hook' (Ślipiński & Mazur 1999) and 'lacinial tooth' (Kovarik & Tishechkin 2004). In the present paper the term 'lacinial hook' is used. According to Kovarik & Caterino (2001), who gave a general description of the North American members of the family Histeridae, the lacinial hook should be present in all members of the family. On the other hand, Ślipiński & Mazur (1999) coded it as absent in 17 of the 50 studied taxa. Contrary to their paper, which claims that it is absent in *Gnathoncus rotundatus*, this study proved it to be clearly present and well defined in this species as well as in the presumably closely related species *Eremosaprinus vlasovi*. In all other studied taxa it is absent.

The terminal maxillary palpomere can be elongate or thickened, and it is always longer than the penultimate palpomere. Its apex is in most cases truncate and has a sensory region apically (sensu McHugh et al. 1997); in the case of *Ctenophilothis chobauti* this sensory region is curiously shaped, cap-like. Very peculiar is the structure of maxillary palpomeres of *Xenophilothis choumovitchi*, in which the terminal palpomere is several times longer than the penultimate (Fig. 145). The palpal organ (sensu Kovarik & Tishechkin 2004) is present in all studied taxa and is markedly developed especially in the psammophilous species.

Thorax

Prothorax. The prothorax is divided into the pronotum and the prosternum forming the dorsal and ventral plates. The lateral inflexed part of the pronotum is the pronotal hypomeron.

Pronotum. The shape of the pronotum in the Saprininae does not differ from the majority of other Histeridae. It is more or less rectangular, widest at base and narrowing apically. The lateral margin always bears a marginal pronotal stria. The stria is continuous along the anterior pronotal margin, where it can be weakened, interrupted or even missing. Occasionally, a lateral pronotal stria is also present (e.g., in *Ammostyphrus cerberus* (Fig. 198) and in several

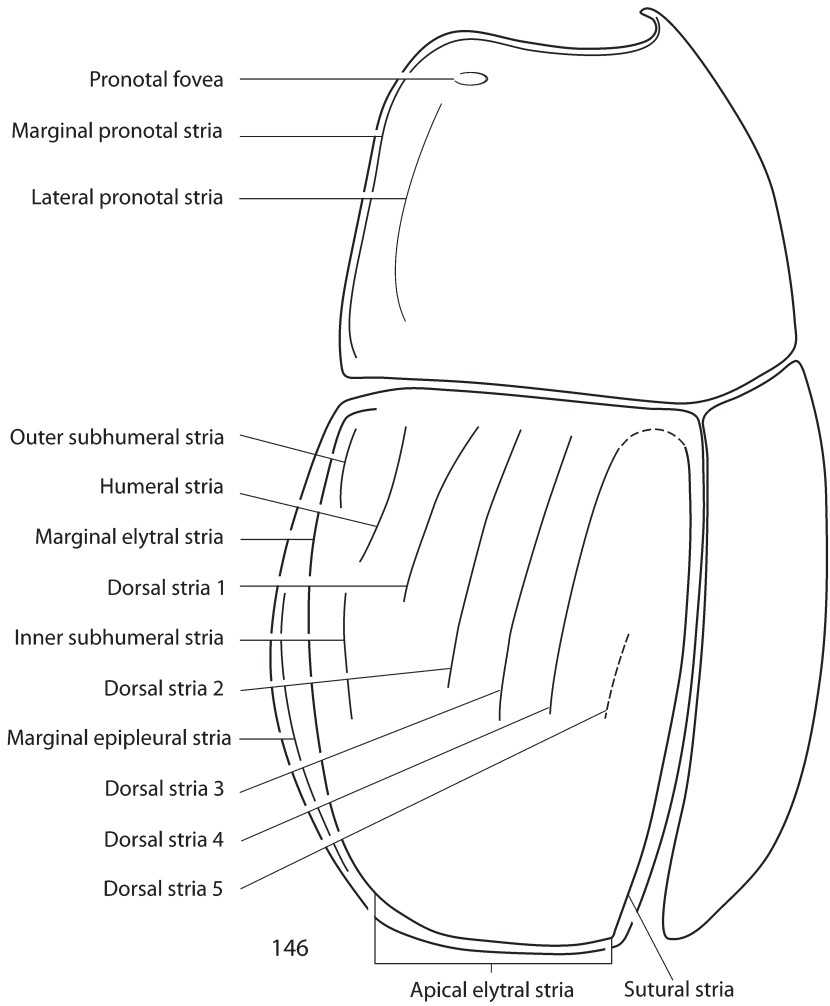


Fig. 146. Saprininae, pronotum and elytra, oblique lateral view.

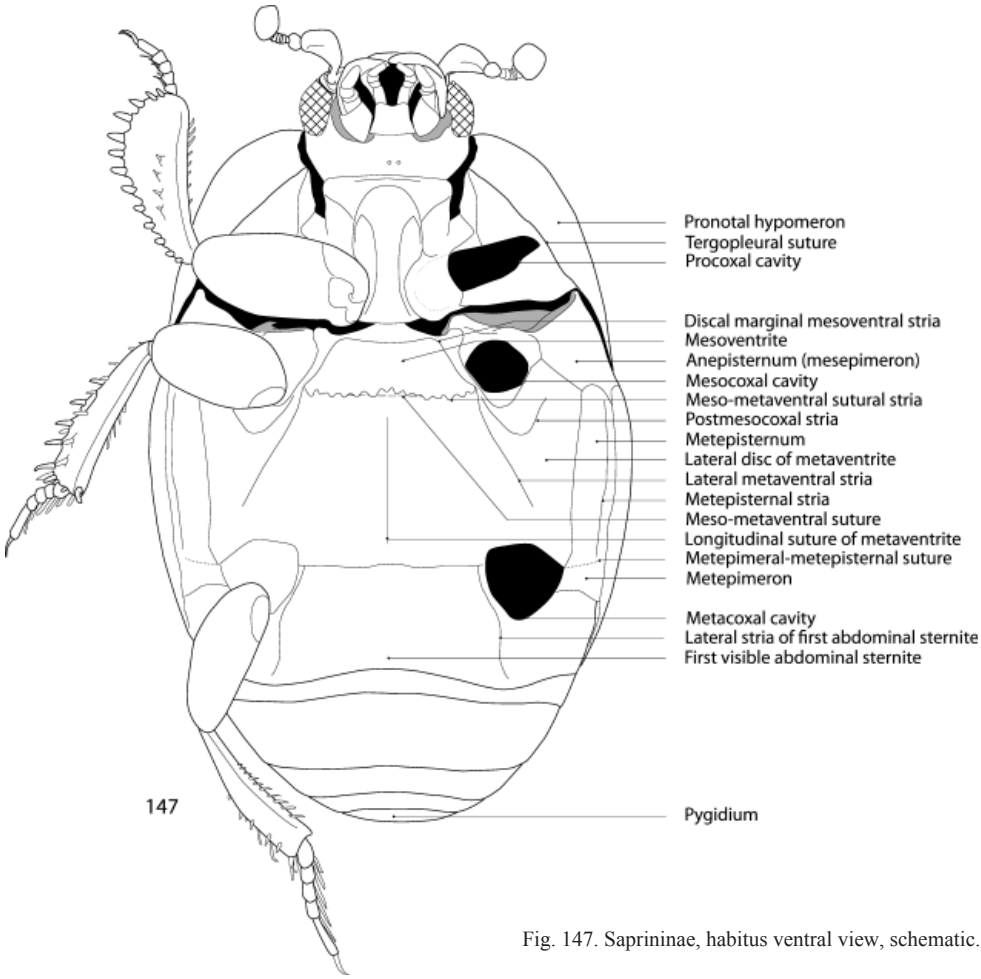


Fig. 147. Saprininae, habitus ventral view, schematic.

species of the genus *Paravolvulus*). In some species of the genus *Philothis*, there are two distinct lateral protuberances and a single deep fovea on each side in the medio-lateral part of the pronotum. At times there is a (vague) pre-scutellar depression just before the scutellum. In most Palaearctic Saprininae the pronotum is punctate. The punctation is very variable regarding its density and coarseness. It can cover the pronotum partially or entirely and some species possess a longitudinal lateral depression in which the punctation is even coarser and denser or forms elongate wrinkles. In general, the punctation is coarser towards the lateral margins and finer towards the middle. A completely smooth pronotum is rare (in some littoral taxa, e.g., in *Eopachylopus ripae* (Lewis, 1885): Fig. 282). Usually there is at least a row of round or ellipsoid punctures along the pronotal base. Many species have circular depressions, called the pronotal foveae, situated behind the eyes (Fig. 146). These foveae can be variously

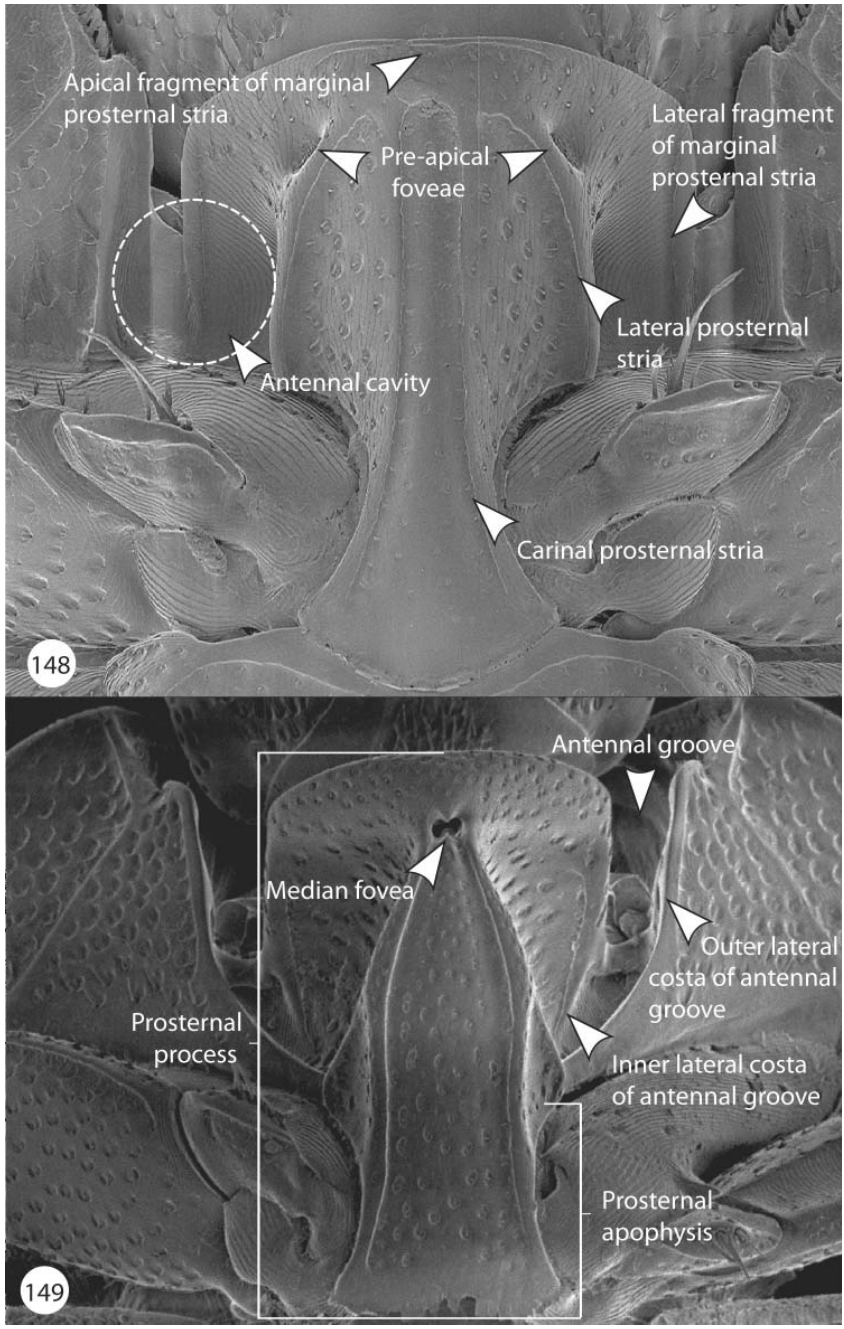
deep and are important for species and genera identification. The median part of the pronotal disc of *Gnathoncus kiritshenkoi* Reichardt, 1930 bears a curious tubercle (Kryzhanovskij & Reichardt 1976: Fig. 158) absent in other members of the genus *Gnathoncus*.

Pronotal hypomeron. The pronotal hypomeron is the lateral inflexed part of the prothorax. It is separated from the dorsal part of the pronotum by a distinct notohypomeral ridge (Ôhara 1994: 24, Fig. 10C; Fig. 147). In the Saprininae, the pronotal hypomeron can be glabrous or bear setae of variable density and length, especially in the psammophilous taxa. It is presumed that these setae prevent minute grains of sand from entering the ventral body cavity. On the contrary, inquilinous or littoral taxa have their pronotal hypomeron usually asetose. A few taxa possess very short setae on the inner part of the hypomeron, near the tergopleural suture.

Prosternum. The prominent prosternal lobe of the prosternum (Ôhara 1994: 'presternum'), present in several groups of the Histeridae and historically considered as an important distinctive feature for the classification of the Histeridae (Wenzel 1944), is not present in the Saprininae. In this subfamily the prosternum is truncate, without any apparent anterior production or transverse suture. The median portion of the composite ventral plate (sensu Ôhara 1994) is elevated and forms the prosternal process, which can be differently shaped and sometimes form a keel. The prosternal process, its shape and anterior margin are among the most important morphological characters for the distinction between the genera and species of the Saprininae. The prosternal process is always constricted by the procoxae. Its posterior portion, located between and posterior to the procoxal cavities, is termed the prosternal apophysis (sensu Bousquet & Laplante 2006). In extreme cases, when the procoxae are greatly enlarged, the prosternal apophysis forms a well-margined triangular disc (e.g., in *Ctenophilothis chobauti*). The basal margin of the prosternal apophysis can be straight, rounded or notched (Figs. 148–149).

The surface of the prosternal process can be glabrous, imbricate-punctate, substrigulate or even setose. The carinal prosternal striae extend along much of the length of the prosternal surface except in *Euspilotus* (*Neosaprinus*) *perrisi* (Fig. 323), in which the carinal striae are divergent on the base of prosternal process and run parallel to the elevated prosternal process. A pair of lateral prosternal striae (this term is disputable as in the majority of species, the lateral stria is distinctly elevated and forms a strongly costate, ridge-like structure; it is probably a carina rather than a stria in strict morphological sense) are located on the lateral side of the prosternal process. The variable configuration including the absence or presence of the carinal and lateral prosternal striae are valuable diagnostic characters. The anterior margin of the composite ventral plate is bordered by a thin marginal prosternal stria, although this is rarely complete (e.g., in *Ctenophilothis chobauti* and *Philothis* (*Farabius*) *hexeris*; Figs. 271 and 564). In most cases the marginal prosternal stria is represented only by lateral fragments and occasionally an apical fragment is also present.

A pair of variously deep and large pits known as pre-apical foveae is present on the apical third or, less frequently, in the middle (e.g., in *Alienocacculus neftensis*) of the prosternal process of numerous taxa of the Saprininae (Fig. 148). The pre-apical foveae are probably unique to the Saprininae and their exact function remains unknown. Sometimes these are actual apertures of the cuticle, but more often they are just shallow circular or elliptical impressi-



Figs. 148–149. Saprininae, prosternum: 148 – *Hypocacculus* sp.; 149 – *Gnathoncus* sp.

ons. Seldom are these foveae connected by a variously deep sulcus (e.g., in *Chalcionellus suspectus*). Occasionally, it is hard to determine whether the pre-apical foveae are present at all, as they can be minute or obsolete (e.g., in several species of the genus *Pholioxenus* and in some specimens of *Chivaenius kryzhanovskii*). Some species of the genus *Gnathoncus* possess a curious single pit, situated on the apex of the prosternal process, which is described here for the first time and termed **median fovea** (Fig. 149). It is not clear whether the median fovea represents a joined pair of pre-apical foveae or whether the pre-apical foveae arose from a division of the median fovea. When the median fovea is present, the convergent carinal prosternal striae terminate in or just before it (Fig. 149). Like in the pre-apical foveae, the exact function of this fovea is not known.

The antennal cavity is an impression on the inner portion of prosternum adjacent to the prosternal process (Fig. 148). It is enclosed by the antennal groove (Ôhara 1994: 'longitudinal deep furrow') that serves for reposing the antennal funicle and a circular or longitudinal impression on the prosternum, which is designed to accommodate the antennal club in repose. The size and depth of the antennal cavity probably correlates with the size of the antennal club. In the psammophilous taxa it is usually weakly developed, but in other cases it is well impressed and margined; in *Saprinillus kryzhanovskyi* Lackner, 2009, the antennal cavity even interrupts the lateral prosternal striae. According to the present study, the antennal cavity is absent only in the genus *Ctenophilothis* (both species of the genus, *C. chobauti* and *C. altus* (Lewis, 1885), have been examined) as well as in *Philothis* (*Farabius*) *hexeris*. Ślipiński & Mazur (1999) listed the genus *Philothis* as devoid of the antennal impression or cavity, but they based their results on *P.* (*Atavinus*) *arabicus* Mazur, 1994, which was unavailable for this study. On the other hand, other species of the subgenera *Atavinus*, *Farabius* and *Philothis* s. str. of the genus *Philothis* available for this study always possess a distinct antennal cavity, even if somewhat shallow and weakly developed.

The lateral costa of the antennal groove is always elevated in the Saprininae and present in three different morphological variations: i) the costa terminates anterior to the procoxa and does not reach the prosternal process; in this case the antennal cavity is partially enclosed also by the procoxa on its basal part (Fig. 148) (most of the studied taxa); ii) the costa reaches the prosternal process, but its basal margin is not distinctly elevated (e.g., in *Hypocaccus* (*Baeckmanniolus*) *dimidiatus*, *Exaesiopus grossipes*, *Hypocaccus* (*Hypocaccus*) *rugiceps* and *Eopachylopus ripae*; Fig. 287); iii) the costa reaches the prosternal process and its basal margin is distinctly elevated. It is presumed that in the latter case the antennal club in repose does not touch the procoxa (e.g., in *Eremosaprinus vlasovi*, *Gnathoncus rotundatus* and *Myrmetes paykulli*; Fig. 149).

Mesothorax. The terms mesoventrite and metaventrite are used here in place of the misapplied terms mesosternum and metasternum, following Lawrence (1999) and Beutel & Haas (2000). In the Saprininae diagnostics, only the mesoventrite has been used so far. Lateral to the mesoventrite are the mesocoxae, anepisternum and mesepimeron. Kovarik & Caterino (2001: 209) discuss the fusion of the anepisterna and epimeral plates and the occasional absence of the pleural suture in the Saprininae. The scutellum is small and triangular in the Saprininae and almost always well visible. This paper focuses on the mesoventrite, its striation and structure (Fig. 147).

***Mesoventrite*.** The mesoventrite is distinctly broader than long in most taxa, or at least half as long as broad (in some littoral taxa, e.g., in *Exaesiopus grossipes* and *Eopachylopus ripae*). It is usually margined by the discal marginal mesoventral stria (Kanaar (1997): 'discal marginal mesosternal stria', Ôhara (1994): 'marginal mesosternal stria'), which can be variously deeply impressed; anteriorly it is often vague, interrupted or weakened. In some taxa, e.g., in *Ctenophilothis chobauti*, this stria can be anteriorly almost completely absent (Fig. 272). Usually, it is anteriorly shallowly emarginate; seldom it is straight (e.g., in *Philothis* (*Farabius*) *hexeris*; Fig. 566) or curved outwardly (e.g., in *Xenophilothis choumovitchi*; Fig. 737).
The meso-metaventral sutural stria (Kanaar (1997): 'meso-metasternal sutural stria') is present in the postero-median area of the mesoventrite and usually overlies the meso-metaventral suture. Typically, the meso-metaventral sutural stria is undulate or crenulate; in some cases it can be deeply impressed and carinate (e.g., in *Ctenophilothis chobauti*; Fig. 272), or sinuate (e.g., in *Pholioxenus phoenix*; Fig. 583). This stria is completely absent in several taxa, e.g. in *Myrmetes paykulli*. The surface of the mesoventrite can vary from completely glabrous and finely punctulate (e.g., in *Myrmetes paykulli* and *Exaesiopus grossipes*; Fig. 347) to coarsely and densely punctate. In few psammophilous taxa these punctures bear very short setae (e.g., in *Reichardtiolus duriculus* and *Xenophilothis choumovitchi*; Fig. 737).

Metathorax. In the Saprininae systematics, usually only the metaventrite and the plate lateral to it, the so-called 'lateral disc of metaventrite' are used. In the present paper attention was paid also to the plates that border the lateral disc of the metaventrite – the metepisternum and metepimeron (Fig. 147).

The metaventrite is separated from the lateral disc by the lateral metaventral stria (Kanaar 1997: 'inner lateral metasternal stria'). If this stria is complete and ends close to the metacoxa, boundaries between these two plates are well defined; however, this stria is often shortened (e.g., in several species of *Philothis* (*Philothis*); Fig. 532) or curved outwardly (e.g., in *Ammostyphrus cerberus*; Fig. 200) and the distinction between the metaventrite and its lateral disc is then somewhat more difficult to determine. This stria is almost never interrupted and is usually well impressed.

The lateral disc of the metaventrite is anteriorly bordered by the post-mesocoxal stria that is present in most Saprininae. When present, it runs mesal to the mesocoxa and then curves either anterolaterad towards the mesepimeron or leads towards the mesepimeral-metepisternal suture. The plate situated next to the lateral disc of the metaventrite is the metepisternum (Ôhara 1994: 30, Fig. 16A: 'anepisternum 3'). It is situated anterior to the metepimeron (Ôhara 1994: 30, Fig. 16A: 'epimeron 2') and posterior to the mesepimeron (Ôhara 1994: 30, Fig. 16A: 'epimeron 3') (Fig. 147).

***Hind wings*.** The hind (metathoracic) wings of the Histeridae have not been studied extensively. Most information and terminology can be obtained from Ôhara (1994: 35–44). Due to the structural complexity of the hind wings, the present paper only summarizes Ôhara's findings that deal with the hind wings in the Saprininae. Ôhara (1994), in accordance with Crowson (1955), considers the position of a loop between the veins media and cubitus (M-Cu) in the middle area of the wing in the Saprininae as well as in several other genera of the Histeridae

as a primitive state. A characteristic and unique anal vein situated close to the post-cubitus vein (PCu) with a curve at its middle is shared between the Saprininae and the genus *Dendrophilus* Leach, 1817, making the hind wings of these taxa very similar.

Metaventrite. The metaventrite is usually shaped as an isosceles trapezoid, bordered anteriorly by the meso-metaventral suture, laterally by the lateral metaventral stria and posteriorly by the first visible abdominal sternite. The metaventrite is strongly vaulted in most psammophilous taxa (e.g., in *Philothis* (*Philothis*) *arcanus*) and in such cases the lateral disc of the metaventrite is concave. The surface of the metaventrite is usually punctate or imbricate-punctate in the Saprininae; the punctures are more prominent and coarser along the lateral and posterior margins and a completely impunctate metaventrite is rare. In all studied taxa, there is a longitudinal suture of the metaventrite (as an imaginary line of symmetry), although it is not always clearly visible. Males of several taxa possess also a distinct longitudinal depression on the metaventrite. It is believed that this depression helps males to gain purchase of the females during copulation. In *Gnathoncus rotundatus* there is a well-defined, oval glabrous area margined with microscopic setae along the longitudinal suture (Fig. 367).

The posterior margin of the metaventrite of several species of *Saprinus* (e.g., *S.* (*Saprinus*) *calatravensis* Fuente, 1899) and *Hypocacculus* (e.g., *H.* (*Hypocacculus*) *balux* Reichardt, 1932) bears one or two small tubercles, which can be situated in front of the posterior margin of the metaventrite or placed directly on it.

The lateral disc of the metaventrite is usually covered with variously coarse and dense punctures, and sometimes is imbricate-punctate. The punctures are shallow and often bear recumbent, short to long (especially in the psammophilous taxa), yellow or amber-coloured setae. In most cases, the punctures become coarser and denser anteriorly and towards the metaventral-metepisternal suture.

Metepisternum. The metepisternum is basally fused to the metepimeron and together they somewhat resemble a test-tube, with a rounded anterior and divergent posterior margin. Actual fusion of the metepisternum and the metepimeron can be marked with a distinct depression, and thin remnants of the suture between the metepisternum and the metepimeron are observable in some taxa. Parallel to the outer lateral margin of the fused metepisternum and metepimeron there is a variously deep and long stria, which can be abbreviated basally or apically or intermittent (often in the place of the actual fusion of the metepisternum and the metepimeron). The stria is frequently well developed and present only on the fused metepimeron. It is disputable whether it is homologous with Kanaar's (1997) 'metepisternal stria', but the term is kept here for the sake of consistency (Fig. 147).

The surface of the metepisternum is in most cases covered by a coarse and dense punctation, usually coarser than that of the lateral disc of the metaventrite. However, the punctation is often unrecognizable beneath the long and dense recumbent setae in pubescent taxa. The punctation and setae are in many cases weakened or obliterated in the area of the actual fusion between the metepisternum and the metepimeron or around it, especially on the metepimeron.

Elytra. The elytra are elongate-oval or rounded-oval in the Saprininae (Fig. 146). The striation and dorsal surface of the elytra is highly variable and plays a major role in species recognition rather than in recognition of genera. In the following text the dorsal elytral surface and the

inflexed lateral part, the elytral epipleuron, are treated separately. The gently elevated and angulate elytral humerus is also useful in the species or generic recognition of the Saprininae, and in such case it is mentioned with the particular taxon. The two terminal abdominal tergites, the propygidium and the pygidium, are mostly exposed by the elytra; seldom only the pygidium is exposed.

Elytral epipleuron. The elytral epipleuron can be medially depressed or even. Usually there are two striae on the epipleuron, the marginal epipleural and the marginal elytral stria, which can also define the junction of the elytral epipleuron and the elytral disc. The surface between the two striae sometimes bears scattered punctation and in rare cases (e.g., in the genus *Gnathoncus*) an additional epipleural stria is present between these two. The marginal elytral stria mostly continues as an apical elytral stria, although occasionally it is the marginal epipleural stria that is prolonged onto the elytral apex (e.g., in *Saprinus* (*Phaonius*) *pharao*). Psammophilous taxa often have their elytral epipleuron fringed with setae (e.g., *Xenophilothis choumovitchi* and *Alienocacculus neftensis*). These setae can, in extreme cases, be visible from the dorsal view and reach as far as the lateral edge of the elytron.

Elytral disc. The elytral striae vary in number and length and the recognition of striae is often difficult. Counting from the outer lateral edge there are: the outer subhumeral, inner subhumeral and humeral striae, followed by up to five dorsal striae and the sutural stria (Fig. 146).

Kryzhanovskij & Reichardt (1976: 108) believe that 'the short and weak stria, located laterally to elytral humerus near marginal elytral stria should not be qualified as the outer subhumeral stria'. In more recent papers, Yélamos (2003) or Bousquet & Laplante (2006), as well as in the present paper, the opposite opinion is held true, even if this stria is not important for the Saprininae diagnostics, as already pointed out by Kryzhanovskij & Reichardt (1976). When present, the outer subhumeral stria is typically situated in the anterolateral corner of the elytron, laterad to the elytral humerus. It is frequently connected to the marginal elytral stria at the base of the elytron; in most cases it is a short thin stria, sometimes represented by only a tiny fragment.

The stria that comes first mesad to the elytral humerus is the thin humeral elytral stria. Its course is at times unclear; it can appear irregular or it can be doubled or even tripled. The surface around it can be crossed by a number of fine oblique rugae. The humeral elytral stria often reaches the basal elytral margin and usually occupies the basal elytral fourth or third. Exceptionally it intercepts the first dorsal stria.

The course of the inner subhumeral stria is also often unclear and many times this stria is limited to a short median fragment. Its extent and position can vary between the taxa as follows: i) situated below the elytral humerus between an imaginary continuation of the outer subhumeral stria and the humeral elytral stria; or ii) joining the humeral stria (the joined humeral and inner subhumeral striae should not be misinterpreted as a true dorsal elytral stria); iii) situated between the first dorsal elytral and humeral striae; iv) exceptionally almost complete, carinate and long, originating close to the base of elytron (e.g., in *Xenophilothis choumovitchi* and *Myrmetes paykulli*; Fig. 730).

The dorsal elytral striae are numbered from the most lateral stria towards the elytral suture as the first, second, third, fourth and fifth dorsal stria. In most cases, four or fewer dorsal elytral striae are present. They run from the elytral base towards the elytral apex but do not

attain the basal edge. Rarely they are entire (e.g., in *Xenonychus tridens*; Fig. 711); in most cases they stop short of the elytral apex, and in many cases they are erased on their posterior part or intermittent. Sometimes they are marked as rows of deeply impressed punctures, especially on their posterior halves. The fourth dorsal elytral stria is often basally connected to the sutural elytral stria under a rounded arch, or at least bent towards it. Most species of the genus *Gnathoncus* possess a characteristic, short and hooked appendix between the fourth dorsal elytral and the sutural striae; the appendix is probably not homologous with the fifth dorsal stria. The fifth dorsal elytral stria is very rarely present in the Palaearctic Saprininae; in *Philothis* (*Atavinus*) *atavus* it is present as a true dorsal stria, whereas in two taxa, *Xenophilothis choumovitchi* and *Eremosaprinus vlasovi*, it is present only as a short apical fragment. Even if the dorsal elytral striae are absent, at least the sutural elytral stria is always present. The sutural stria is absent in *Myrmetes paykulli*, the sole exception among the Palaearctic Saprininae, but this species has four distinct dorsal elytral striae.

The sutural elytral stria, which runs along the elytral suture, can be variously shortened or complete and joining the apical elytral stria. In some species of the genus *Pholioxenus*, the sutural elytral stria can have the form of large round protruding punctures, especially on its apical half. In several species of the genus *Philothis*, the sutural elytral stria can be slightly distanced from the elytral suture on basal half, with the interspace between it and the elytral suture on basal third forming a longitudinal bulge. When the sutural elytral stria is continuous along the elytral base, it is termed here as the **basal elytral stria**. This stria sometimes surrounds a vague low bulge and in rare cases connects to the marginal elytral stria on one end and to the sutural elytral stria on other. If, moreover, the apical elytral stria connects both to the marginal elytral and to the sutural elytral stria, one continuous stria encircles the entire elytron (e.g., in *Philothis* (*Farabius*) *hexeris*). Occasionally there is a dotted line or an additional thin stria between the sutural elytral stria and the elytral suture (e.g., in *Saprinus* (*Saprinus*) *beduinus* Marseul, 1862). The apical elytral stria (Kovarik & Caterino 2001: 'marginal elytral stria') runs along the elytral apex. It is usually thin and often shortened, not reaching the sutural elytral stria. Costae are never present on the elytra of the Palaearctic Saprininae and bulges are rare (e.g., present in several species of the genus *Philothis*).

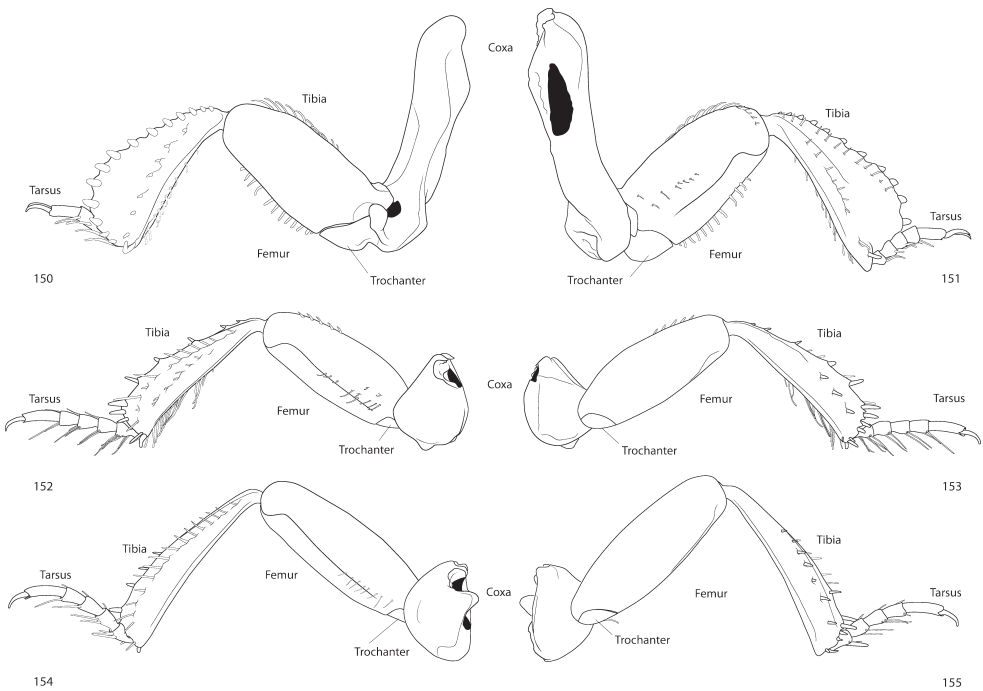
The interspaces between the dorsal elytral striae are called elytral intervals and they are numbered as follows: surface between stria 1 and 2 = interval 1; between 2 and 3 = interval 2; between 3 and 4 = interval 3; between 4 and 5 (rare) = interval 4.

The surface of the elytra is covered with variously coarse and dense punctation in the majority of species; smooth elytra are rare. Occasionally the punctures form elongate wrinkles, especially on the apical third of the elytron (e.g., in several species of the genus *Gnathoncus*); in some taxa the punctation is denser apically. Punctation of the elytral disc is important in species and sometimes also in genus recognition. In most cases the punctation of the elytra does not reach the lateral edge and often stops short of the elytral apex, leaving thus an impunctate band. This band should not be confused with a narrow space between the apical stria (if present) and the elytral apex, which is always smooth. Very coarse and dense elytral punctation sometimes gives rise to the so-called 'mirrors'. These are shining impunctate areas, usually situated between the elytral intervals, most commonly between the fourth dorsal and the sutural striae. Elytral striae are occasionally unrecognizable underneath the punctation.

Legs. The legs are composed of the trochantins (generally hidden in most Histeridae; the mesotrochantin is visible in the Saprininae, see also Ślipiński & Mazur (1999) and Caterino & Vogler (2002)), coxae, trochanters, femora, tibiae, tarsi and pretarsi (including claws; Figs. 151–155). They are generally long and slender in the inquilinous forms (e.g., in *Eremosaprinus vlasovi*) and thick and expanded in the psammophilous or littoral forms (see below).

Wenzel (unpublished) stated that: 'There is probably a mechanical advantage to burrowing forms of having the coxae closer together and femora dilated since it is a common feature of these insects, especially the ones that burrow in damp sand. In this case the mesosternum is actually narrower than long, or at least square-shaped rather than transversely oblong as it is true with most other Saprininae. The metasternum is narrowed, too. With the highly specialized forms the femora tend to become swollen, this is apparently a reflection of skeleto-muscular adaptation for digging. The shorter femora and tibiae can operate more effectively in a restricted space as when burrowing, but must be swollen to accommodate the larger number of shorter muscle bundles needed to offset the loss in length. More numerous shorter bundles also provide greater muscular pulling power.'

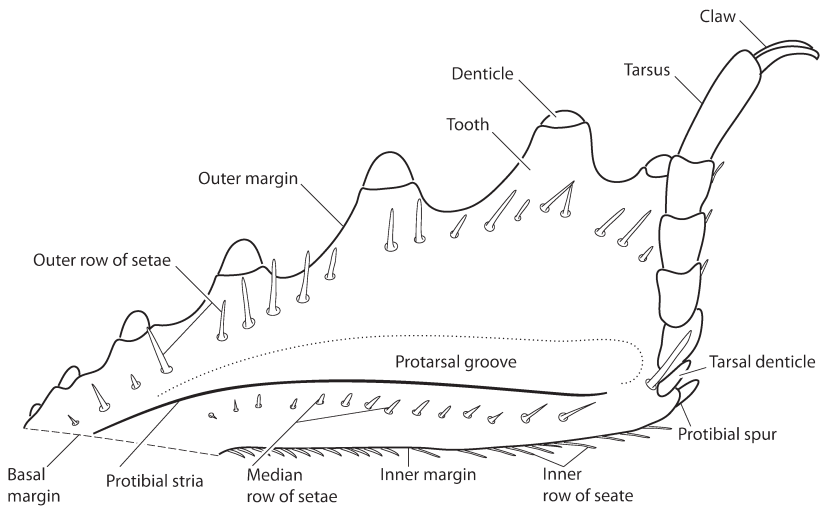
According to Bousquet & Laplante (2006: 9), 'the legs offer a few good taxonomic characters.' The present study of the Saprininae is concerned only with the structure and modifications of the tibiae and tarsi, including claws; their examination not only permits the introduction



Figs. 150–155. Saprininae, legs, schematic: 150 – protibia, ventral view; 151 – ditto, dorsal view; 152 – mesotibia, ventral view; 153 – ditto, dorsal view; 154 – metatibia, ventral view; 155 – ditto, dorsal view.

of new terminology but also offers interesting taxonomical characters. The new terminology related to the anterior and posterior surfaces of tibiae is illustrated in Figs. 156–159.

Protibia. The outer margin of the protibia can be variously shaped and it was perhaps its modifications that led authors to use a variety of different, sometimes confusing terms to describe them ('spines', 'denticles', 'teeth', 'thorns', etc.). In the present paper, the variously expanded or protruding outgrowths of the actual outer margin are named 'teeth'. These are in most cases topped with modified sclerotized setae, termed here as denticles. Typically, the outer margin of the protibia bears 3–8 moderately large teeth gradually growing in size apically, with the three closest to the apex being the largest. Numerous modifications of this



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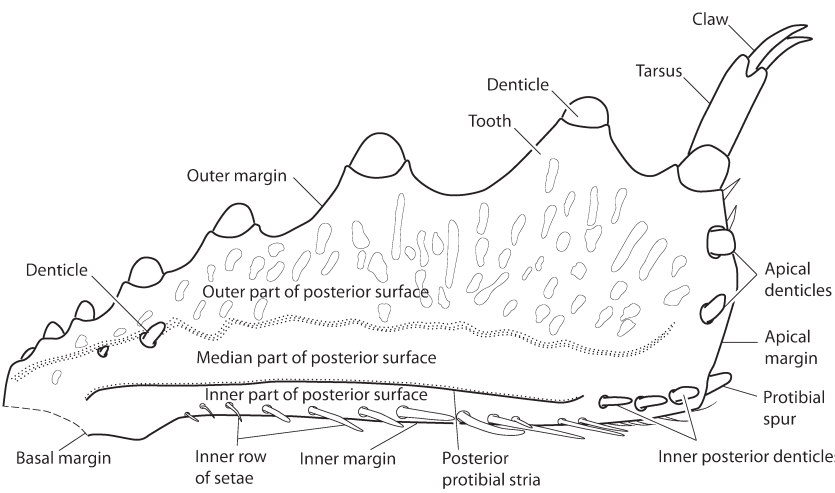

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Figs. 156–157. Saprininae, protibia, schematic: 156 – dorsal view; 157 – ventral view.

pattern exist, ranging from extremely reduced or even absent teeth and straight outer margin (or even explanate outer margin and the denticles present on the posterior surface) to the outer margin being formed by two massive triangular teeth topped by a tiny denticle (in such case the apical margin of the protibia is formed by the apical margin of the apical tooth). The denticles, usually two or three, continue also along the apical margin of the posterior protibial surface, but they are growing directly from the apical margin, never forming teeth. Denticles, if present apically are usually very short and rounded; in psammophilous taxa they are often absent. Occasionally, these denticles are as long as those of the outer margin (e.g., in *Eremosaprinus vlasovi* and *Turanostyphrus ignoratus*).

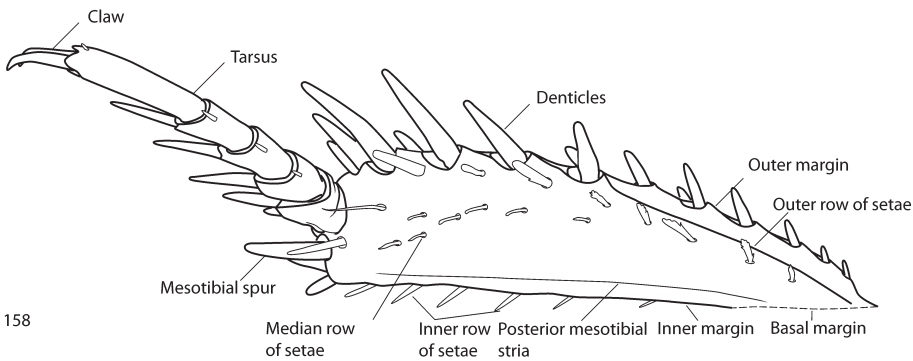
The anterior surface of the protibia typically bears a variously deep protarsal groove where the tarsus (if present) is laid in repose. Two rows of setae are usually likewise present on the anterior surface of the protibia: the outer row of setae borders the outer margin of the protibia, while the median row of setae runs next to the **protibial stria**, typically situated in the median area of protibia. The size and density of the setae on the anterior surface is far from uniform. The most peculiar modifications occur in the psammophilous taxa, where the outer row of setae can be present only basally (the setae are considerably long, thick and sparse), setae of the median row (Fig. 567) are sparse, strongly sclerotized and thick, and the protibial stria is shortened apically to completely absent. The protibial stria can be absent even if both rows of setae are fully developed. Exceptionally, both of these rows of setae and the protibial stria are absent.

The protibia usually bears a well-developed, five-segmented protarsus. The longest protarsi are found among the inquilinous taxa, while the protarsi of the psammophilous forms can be rudimentary (e.g., in *Philothis* (*Farabius*) *hexeris* and *Philothis* (*Philothis*) *arcanus*) or even completely absent (e.g., in *Philothis* (*Atavinus*) *atavus* and *Ctenophilothis chobauti*). Males in the Saprininae differ from the females by the presence of one or two wide, flat and translucent setae on the underside of each protarsomere 1–4 (Bousquet & Laplante 2006: 79). The basal protarsomere is in most cases surrounded by one or more weakly to strongly modified setae, termed here as the **tarsal denticles**. A single protibial spur usually grows out from the inner corner of the apical margin of the protibia and is better observable from the ventral view. In some taxa it is larger than usual, strongly bent and grows out from near the base of the protarsus (e.g., in *Alienocacculus neftensis*; Fig. 188). The spur is in some cases rather difficult to distinguish; for example, it is strongly atrophied in most psammophilous taxa.

The posterior surface of the protibia can be divided into three more or less clearly definable parts: the outer, median and inner part. The outer part is often areolate-rugose and occasionally bears several short denticles. It is usually clearly separated from the glabrous median part by a demarcation line or a definite stria, which can also bear short sclerotized setae or even short denticles. Sometimes this demarcation is far from clear and occasionally none of the three parts can be distinguished. The median part is in most cases separated from the inner margin by a well-impressed **posterior protibial stria**. This stria often bears short sclerotized setae along its length, which apically turn into short and stout **inner posterior denticles**. The posterior protibial stria of *Saprinus* (*Phaonius*) *pharao* (Fig. 662) bears a dense row of long and thick, well-sclerotized setae. In the psammophilous taxa this stria can be apically shortened, unclear or even absent.

The inner margin of the protibia in most taxa bears one or two rows of short dense setae. These setae can be rudimentary (as in *Eopachylopus ripae*) or very long, strongly sclerotized and lamellate in most of the specialized psammophilous forms.

Mesotibia. The outer margin of the mesotibia typically bears two rows of denticles, mostly growing out directly from the mesotibia and rarely from low teeth. In several cases only one row of denticles is present (e.g., in *Myrmetes paykulli* and *Gnathoncus rotundatus*; Figs. 160–161), but occasionally there are three (*Hypocaccus* (*Baeckmanniolus*) *dimidiatus*) or even four rows (e.g., in *Eopachylopus ripae*; Fig. 284). The rows of denticles often diverge on the apical third, creating a glabrous free space between the denticles; in some cases they are densely abutting each other. The denticles increase in length and density towards the apex of the mesotibia. Their shape and thickness varies between the taxa, but several trends can be observed: taxa that live as inquilines of mammals, birds and ants have the denticles rather thin and short (e.g., *Eremosaprinus vlasovi*, *Myrmetes paykulli*, *Pholioxenus phoenix*); specialized psammophilous and littoral taxa have their denticles stout and often long. The denticles of the outer margin often continue also along the apical margin of the mesotibia and occasionally they double near the tarsal insertion.



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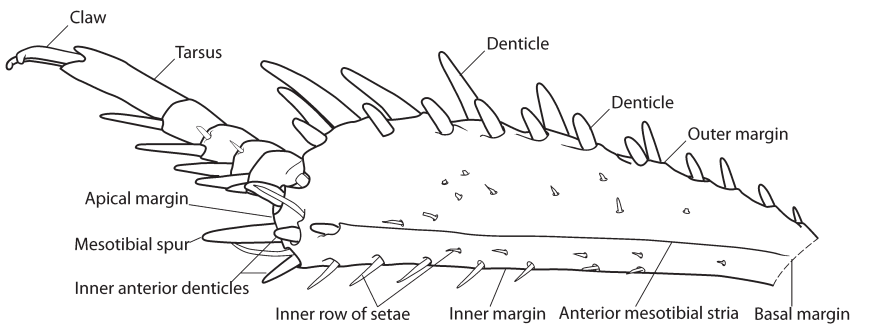

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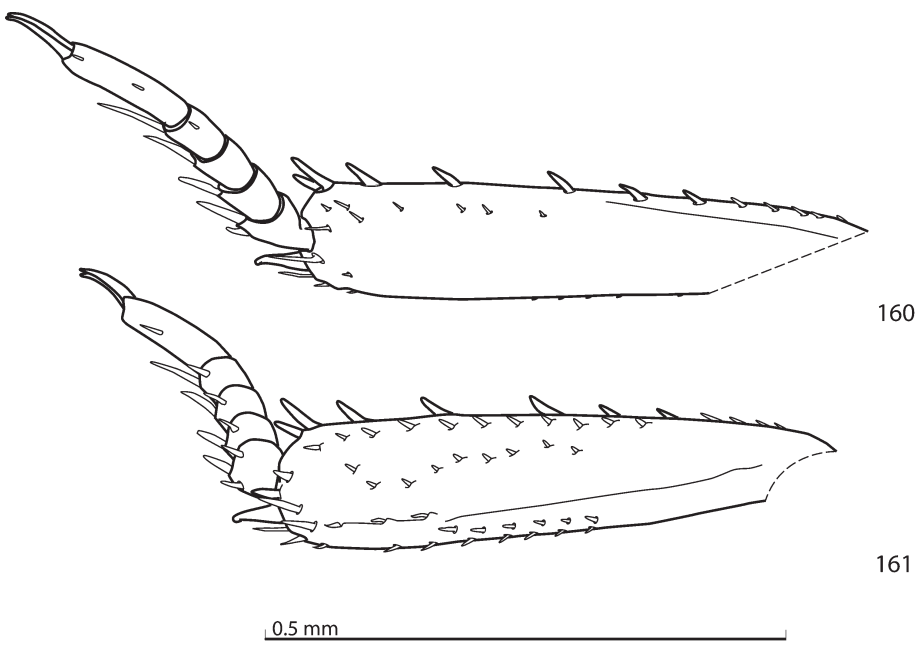
Figs. 158–159. Saprininae, mesotibia, schematic: 158 – dorsal view; 159 – ventral view.

The posterior surface of the mesotibia usually bears two rows of setae. The outer row is in most cases well developed and consists of dense and strongly sclerotized long setae; on the other hand, the median row consists of relatively short setae, often scattered in an irregular row. Psammophilous taxa have the outer row in a lower position (approximately in the middle of the posterior surface of the mesotibia), with long setae often reaching the apices of denticles of the outer margin. The median row of setae is in these cases approximate to the outer row. The setae of the median row are in all cases finer and shorter than those of the outer row. Occasionally (especially in several psammophilous taxa) only one row of setae is present, situated approximately in the middle of the posterior surface of the mesotibia. In such cases it is impossible to determine which of the two rows it is. A well-defined cariniform stria, termed here **posterior mesotibial stria**, is found near the inner margin of mesotibia, in most cases running parallel to it; in the psammophilous taxa this stria can be shortened apically.

The apical margin of the mesotibia bears a five-segmented tarsus, attached medially. Each tarsomere usually bears three setae: one microscopic dorsal seta (about as long as 1/8 of the tarsomere), one microscopic ventral seta and a much longer, easily visible, strongly sclerotized ventral seta. Some species of the genus *Saprinus* can be sexually dimorphic, with males having their mesotarsomeres with brush-like sclerotized setae, while the females have their setae shorter and less dense. Several highly specialized psammophilous taxa (e.g., *Ctenophilothis chobauti*, *Philothis* (*Philothis*) *arcanus*, *Philothis* (*Farabius*) *hexeris* and *Xenonychus tridens*) possess two strongly sclerotized lamelliform setae, one posterior and one anterior, on each



Figs. 160–161. *Myrmetes paykulli* Kanaar, 1979, mesotibia: 160 – dorsal view; 161 – ventral view.

mesotarsomere. The tarsomeres of the above mentioned specialized psammophilous taxa (with the exception of *Xenonychus tridens*) are markedly narrower apically. In these taxa, the first tarsomere is usually the thickest and the fifth tarsomere is the longest and thinnest one. The mesotarsal claws are usually short and curved, but in the highly specialized psammophilous forms become finer and may be several times as long as the fifth tarsomere. In such cases the claws may be half as long or as long as the fifth tarsomere. The apical margin of the mesotibia also usually bears a single long mesotibial spur, visible from the dorsal view. This spur is often surrounded by several shorter stout denticles anteriorly. The anterior surface of mesotibia is often clothed with scattered microscopic punctures; the interspaces are often finely wrinkled. The psammophilous taxa have the anterior surface of mesotibia impunctate as a rule. Several taxa that live as inquilines of birds, mammals and ants (e.g., *Gnathoncus rotundatus* and *Myrmetes paykulli*; Fig. 161) possess two rows of short dense sclerotized setae on the anterior surface of the mesotibia. A single cariniform stria, termed here **anterior mesotibial stria**, runs along the inner margin ventrally, it is usually complete and parallel to inner mesotibial margin; in the psammophilous forms this cariniform stria can be shortened apically. The inner margin of the mesotibia usually bears one and rarely two rows of variously dense setae, which can be particularly long in the psammophilous species.

Metatibia. The metatibia is in general more slender and longer than the mesotibia and the denticles on its outer margin are shorter and sparser. However, this is not true in some psammophilous or littoral taxa, in which the metatibia can be moderately to strongly thickened (e.g., in *Exaesiopus grossipes*, *Ammostyphrus cerberus* and *Reichardtiolus duriculus*; Fig. 349). In most cases the outer margin of the metatibia bears two rows of sparse short denticles, but in several taxa it bears more than two rows of denticles (e.g., *Hypocaccus* (*Baeckmanniolus*) *dimidiatus* has three rows and *Eopachylopus ripae* has four). On the other hand, only one row of denticles may be present as in *Gnathoncus rotundatus*, *Xenophilothis choumovitchi* and *Myrmetes paykulli* (the outer margin of metatibia of the latter species bears only one well-defined short denticle in the apical fifth and a row of microscopic setae that can not be considered as denticles in strict morphological sense). The denticles typically grow out directly from the outer margin of the metatibia, but in some cases the denticles of apical half grow out from low or intermediate teeth (e.g., in *Gnathoncus rotundatus* and *Xenophilothis choumovitchi*). The rows of denticles of the outer margin are usually tightly spaced; occasionally they become sparser on the apical third, creating a glabrous free space between the denticles. At times this divergence is so prominent that the entire appearance of metatibia is radically modified. While one doubled row of morphologically different denticles remains positioned on the outer margin, another one is markedly shifted from it and is observable only from the ventral view. This modification of the metatibia is found mainly among the species of the genus *Philothis*; *Ammostyphrus cerberus* could be considered as a transitional form between the modified and typical metatibia. As already pointed out by Olexa (1990: 149, Figs. 24–26), the metatibia is strongly dilated in these cases.

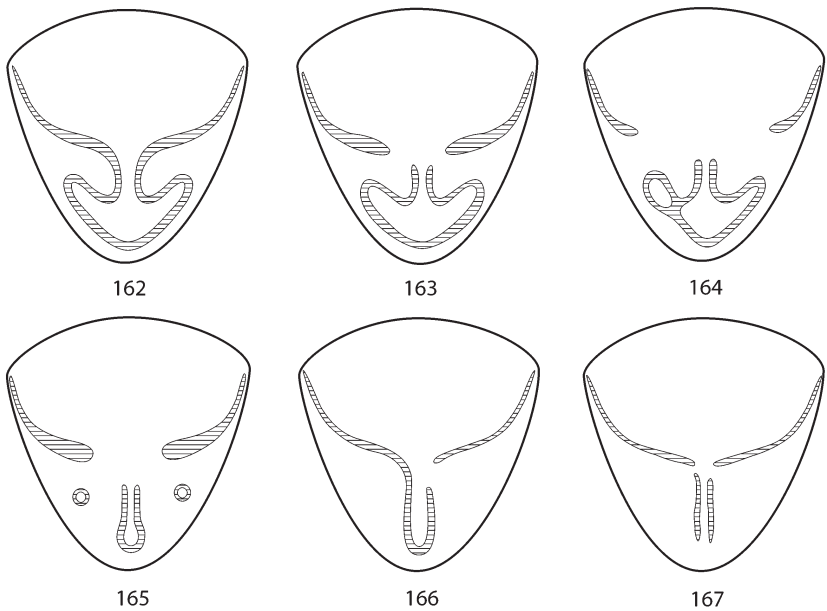
The posterior surface of the metatibia is similar to that of the mesotibia, with most exceptions found among the psammophilous taxa, where the posterior surface of metatibia is densely covered with a brush of long sclerotized setae. The apical margin, ventral surface, inner margin and the tarsus of the metatibia are also very similar to the mesotibia, with only minute

differences. A very peculiar shape of the metatibia is found in *Turanostyphrus ignoratus*. The metatibia of this species is strongly flattened dorso-ventrally, its outer margin is explanate and completely devoid of denticles. In this case both rows of the denticles are situated on the anterior surface of the metatibia (Figs. 703–704).

Abdomen

The abdomen of the Saprininae is short and broad with seven tergites and five visible ventrites. The first five tergites are invisible when the elytra are closed; the 6th and 7th tergite (i.e., the propygidium and pygidium; Fig. 2) are usually exposed. Eighth, 9th and 10th segments are modified into copulatory structures and telescoped into the 7th segment; in this paper they are treated under the genitalia section.

The propygidium is usually transverse and trapezoidal. In most cases it is covered with punctation and the punctures usually become coarser and denser along the posterior margin. In many taxa, the propygidium is partly covered by the elytra; in other (e.g., in the genus *Philothis*) it is significantly prolonged, almost half as long as broad and completely exposed. The pygidium is always exposed; it is rounded laterally, narrowing apically and almost always punctate, rarely imbricate-punctate. Punctation of the pygidium is in some cases useful for species diagnostics, e.g. among the species of the genus *Gnathoncus*. In rare cases, the punctation of the pygidium is erased laterally and present only medially, or vice-versa; at times



Figs. 162–167. *Euspilotus* (*Neosaprinus*) *perrisi* (Marseul, 1872), variability of female pygidial sulci. Figs. 162–165 after Olexa (1975).

lateral depressions are also present. *Euspilotus* (*Neosaprinus*) *perrisi* is the sole Palaearctic species whose females possess curious longitudinal sulci on the pygidium. Olexa (1975) observed a considerable variability of these sulci; females of this species without sulci are unknown (Figs. 162–167).

The first visible abdominal sternite (Fig. 147) is considerably longer and larger than the remaining four. It is usually square-shaped or rectangular, often with depressions. The surface is punctate, at least on the basal and apical margins, and rarely completely smooth (e.g., in *Eopachylopus ripae*). The lateral stria of the first abdominal sternite is present in most cases and usually almost reaches the posterior margin of the sternite. Most Palaearctic Saprininae possess a thin row of tiny punctures along the posterior margin of all visible abdominal sternites. Moreover, the lateral sides of all abdominal sternites are often fringed with setae of various length and density in psammophilous taxa.

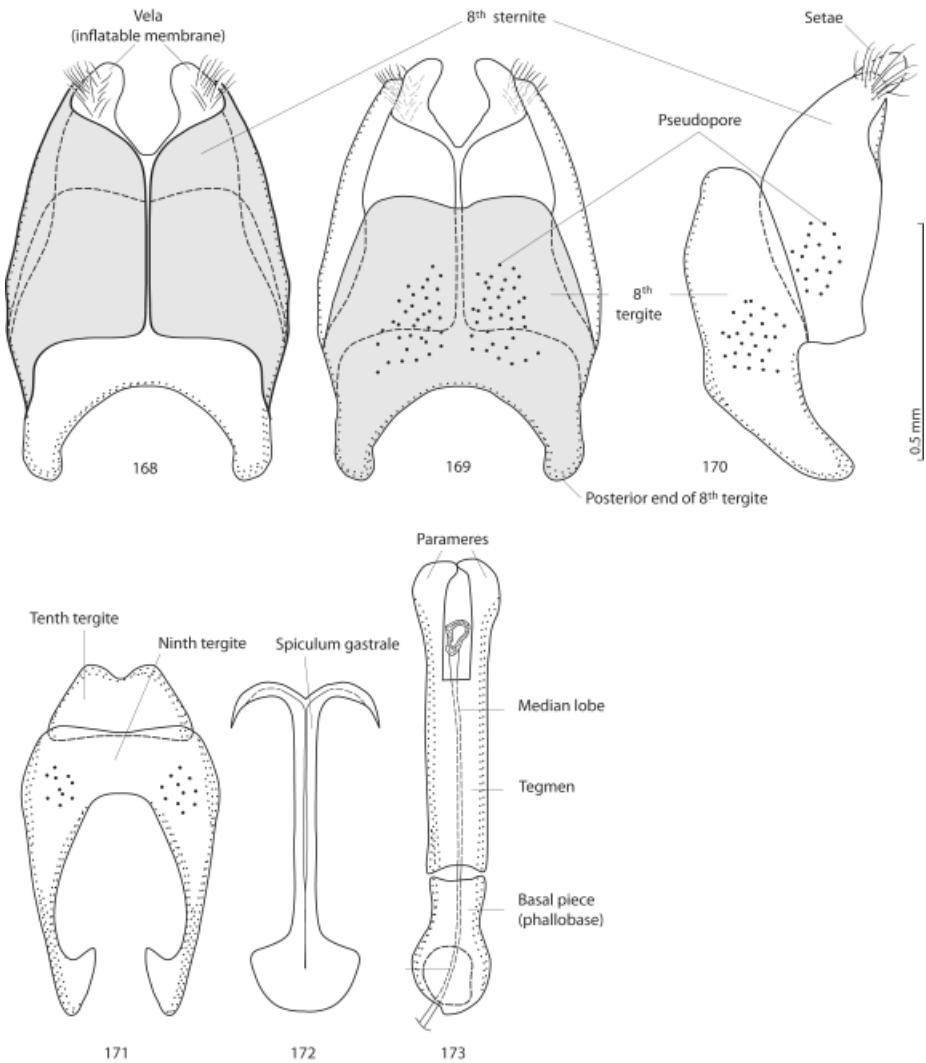
Genitalia

Male genitalia. The terminology used in this section primarily follows Reichardt (1941), Ôhara (1994), Caterino & Vogler (2002) and Tishechkin (2007). This study fully agrees with the opinion of Tishechkin (2007: 20), who states that 'the recent, rather radical revision (Kovarik et al. 1999, Kovarik & Caterino 2001, Kovarik & Tishechkin 2004) of the widely accepted consensus of genital sclerite nomenclature, going back to Reichardt (1941) seems to be incompletely developed yet'. Therefore, the more conventional genitalic terminology has been adopted in this paper.

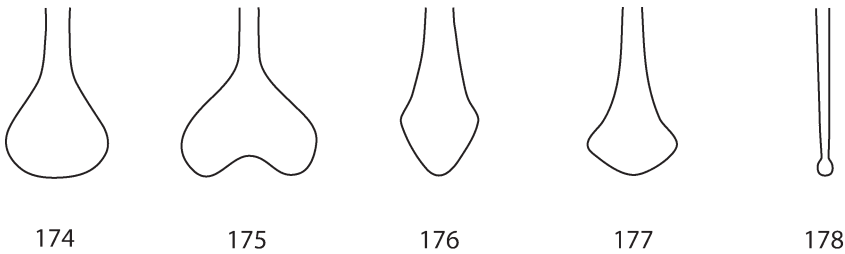
Genital segments. The genital segments of the male consist of the eighth sternite, eighth tergite, ninth sternite (spiculum gastrale), ninth tergite and tenth tergite (Figs. 168–172). The eighth tergite is anteriorly straight or slightly emarginate medially, occasionally strong-ly so. Posteriorly it is emarginate, sometimes with tailed posterior ends; pseudopores are occasionally present on its ventral and/or dorsal surfaces (Figs. 169–170). The eighth sternite is more modified than the eight tergite. It is usually rectangular to sub-rectangular and in numerous cases slightly to strongly narrowing towards the apex; it is mostly longitudinally divided, although it can also be fused at various lengths. Occasionally, the eighth sternite is fused medially along its entire length, but in the case of *Microsaprinus therondianus* it is widely separated (Figs. 479–480). The apical part of the eighth sternite often bears inflatable membranes or paired vela with variously long apical and sometimes also lateral setae. These inflatable membranes or vela have been suggested to support the males to gain purchase during copulation (Kovarik et al. 1999). The eighth sternite and the eighth tergite are often fused laterally. In the Saprininae, the apical part of the eighth sternite shows a great variation and this character is very important for the identification of taxa on the species level as well as for the higher phylogeny (Lackner, in prep.).

The ninth tergite is proximally emarginate and tailed; its anterolateral corners are slightly projected. It is usually longitudinally fused, but in three of the studied taxa, *Gnathoncus rotundatus*, *Eremosaprinus vlasovi* and *Myrmetes paykulli*, it is divided (Figs. 314, 374 and 501). The tenth tergite (Ôhara 1994: '10th tergum') is never longitudinally bisected in the Saprininae (Fig. 171) and in rare cases it apically bears two minute setae (in *Eremosaprinus vlasovi* and *Myrmetes paykulli*; Figs. 314–315, 504–505).

The ninth sternite is called the spiculum gastrale (Fig. 172). It is usually long and slender and dilated on both ends, rarely it is dilated only on the apical end. In *Saprinus* (*Phaonius*) *pharao* it is considerably dilated apically (Fig. 673). The basal end of the spiculum gastrale can be variously shaped, the most usual shapes being spoon-like or cordate (emarginate medially), although other, less frequent shapes can occur (Figs. 174–178).



Figs. 168–173. Saprininae, male terminalia, schematic: 168 – 8th sternite, ventral view; 169 – 8th sternite and tergite, dorsal view; 170 – ditto, lateral view; 171 – ninth tergites and tenth tergite, dorsal view; 172 – spiculum gastrale (10th sternite), ventral view; 173 – aedeagus, dorsal view.



Figs. 174–178. Variability of the caudal end of spiculum gastrale: 174 – *Philothis* (*Farabius*) *hexeris* Reichardt, 1930; 175 – *Hypocacculus* (*Nessus*) *rubripes* (Erichson, 1834); 176 – *Microsaprinus therondianus* (Dahlgren, 1973); 177 – *Saprinus* (*Saprinus*) *semistriatus* (Scriba, 1790); 178 – *Euspilotus* (*Neosaprinus*) *perrisi* (Marseul, 1972).

***Aedeagus*.** The male aedeagus consists of the basal piece (= phallobase), a pair of always-fused parameres forming the tegmen, and the median lobe (Fig. 173). In the Saprininae the basal piece is always well developed as a variously long ring surrounding the basal part of the median lobe; its posterior margin is connected with the basal margin of the parameres. Most Saprininae have a weakly sclerotized and flat median lobe (Ôhara 1994: 49). The median lobe is tube-shaped and often becomes damaged during the chemical or mechanical treatment of the male genitalia. The parameres are usually fused at least on the basal half, forming a tube-like structure with a dorsal opening, but in *Microsaprinus therondianus* (Fig. 484) they are widely separated and only fused on their basal sixth. The shape and curvature of the aedeagus is very important in species identification.

Female genitalia. The female genitalia have not been studied. The reader is referred to the works of De Marzo & Vienna (1982b) and Ôhara (1994), respectively, for the overview of the variation of coxites, styli and especially the spermatheca.

Systematic part

Saprininae Blanchard, 1845

Saprininae Blanchard, 1845 (as Saprinites Blanchard, 1845)
Saprininae: Fowler (1912)
Myrmetini Portevin, 1929. Synonymized by Mazur (1984).
Saprinini: Yélamos & Ferrer (1988)

Diagnosis. Small to moderately sized beetles (PEL: 1.4–10.0 mm). Body oval, roundly oval, rarely elongate oval, usually convex to very convex, at times slightly flattened dorsally, or strongly vaulted ventrally. Cuticle often metallic, sometimes without metallic luster, usually brown, brown-red, black, at times light brown. Elytra occasionally with red, orange or yellow patches, maculae or transverse bands.

Head prognathous, much shorter than pronotum and well retractable. Frontal stria usually well developed, in some cases interrupted (at times prolonged onto clypeus) or entirely absent; supraorbital stria usually present, sometimes elevated above eyes, occasionally absent; occipital stria usually present. Antennal insertion located on lateral edge of frontal disc between eye and base of mandible. Antennal scape and flagellum differ in chaetotaxy, but generally similar within the subfamily. The most variation is found in the eighth antennomere, which can be saucer-like or cupuliform in some sand-dwelling forms. Antennal club with specialized sensory organ in form of vesicles, sensory areas, slit-like pits or their combination.

Labrum in most cases with two labral pits, each with one (rarely) or two setae, occasionally these pits and setae absent. Mandibles usually punctate, short and stout, sub-apical tooth usually well developed; prostheca very narrow. Mentum with setae, in most cases sub-trapezoid or rectangular, usually with small notch in middle of anterior margin. Terminal labial and maxillary palpomeres in most species with palpal organ. Lacinia of maxilla in most taxa without lacinial hook.

Dorsal surface. Pronotum and elytra usually variously punctate, only rarely smooth; 'mirrors' may be present on pronotum and elytra if punctation is extremely coarse and dense (degree of coarseness and density of punctation is expressed by a comparison of puncture diameter with interspaces between punctures; interspaces between punctures sometimes imbricate or substrigulate). Pronotum always, at least in anterior corners, with marginal pronotal stria that can be interrupted anteriorly; lateral pronotal stria rarely also present. Pronotum often with pronotal foveae, rarely with bulges; pre-scutellar depression often present; pronotal hypomeron often setose. Elytral epipleuron usually with punctures, marginal epipleural stria almost always present, sutural elytral stria in most cases present, usually complete.

Elytra usually punctate; inner subhumeral stria almost universally present, outer subhumeral stria often absent, if present then usually very short; humeral stria almost always present, in many cases vague, surface around it often with fine oblique rugae; elytra with four (rarely five) dorsal striae, almost never reaching elytral apex. Dorsal striae can be reduced down to two, often intermittent. Sutural elytral stria almost universally present and usually basally connected with fourth dorsal elytral stria. Propygidium in most cases punctate, short, transverse, often partly covered by elytra. Pygidium well developed, usually punctate, rarely with sulci.

Ventral surface. Anterior lobe of prosternum absent; antennal cavities open, not covered by prosternal 'alae', lying next and usually encroaching upon prosternal process, sometimes outer lateral costa of antennal groove distinctly reaching prosternal process. Prosternum usually with two pairs of striae, carinal and lateral, their configuration and/or presence being important in genera determination. Pre-apical foveae of prosternum present in many genera, sometimes united by a transverse sulcus; prosternal process rarely with median fovea.

Mesoventrite usually wider than long, in littoral taxa as long as wide, usually with marginal stria, often covered with punctation. Metaventrite in males often with a longitudinal depression, often punctate, at least laterally, basal area of metaventrite occasionally with two bulges. Pronotal hypomeron, pleura and sterna often with variously long vestiture.

Legs. Protibia usually dilated, outer margin with denticles or teeth topped with denticle; anterior margin dorsally in most cases with a distinct apical protibial spur that can be variously long. Posterior surface of protibia smooth or with wrinkles, denticles, punctures or combination of these. Protarsomeres 1–4 of males with one or two leaf-like translucent modified setae.

Mesotibia and metatibia in most cases slender, sometimes expanded, outer margin with denticles, or seldom with teeth topped with denticle; some psammophilous taxa with separately extended ventro-lateral part. Hind legs of some littoral species strongly thickened. Meso- and metatarsi with variously bent and long claws; empodium absent.

Genitalia. Male genitalia with shape and chaetotaxy of the eighth tergite and sternite are greatly variable within subfamily, providing important characters for species identification; the ninth tergite is occasionally divided longitudinally; spiculum gastrale (the ninth sternite) in most cases dilated on both ends; aedeagus usually with fused parameres along the entire length, only sporadically parameres separated from base. Aedeagus tube-like, median lobe little sclerotized; basal piece present, uniform, usually short. Female genitalia as described in Ôhara (1994) and de Marzo & Vienna (1982b).

Biology and distribution. Subfamily Saprininae contains about 620 described species worldwide (Mazur 1997), occurring in all geographic regions, except for the Antarctic and Arctic. The Palaearctic Region harbors approximately 270 described species (Mazur 1997). The most genus- and species-level diversity, including many endemic genera and species, seems to be found in the desert regions of Central Asia (especially in Turkmenistan and Uzbekistan and to a lesser extent also in Kazakhstan) and Sahara (to a lesser extent also in the Arabian Peninsula). Each continent has its own unique lineages. For example, the genus *Euspilotus* is particularly species-rich in South America but almost absent from the Palaearctic Region, while the genus *Hypocacculus* is almost entirely absent from the Nearctic or Neotropical Regions and very species-rich in the Palaearctic or Afrotropical Regions.

The Saprininae are most abundant in arid places, where they are often found on carrion or in dung. Only rarely they inhabit more mesic habitats such as forests. They are most commonly found at lower altitudes up to 1500 m, but some are known to reach high mountains (more than 3500 m) as well. For example, *Saprinus* (*Saprinus*) *stussineri* Reitter, 1909 is often found at elevations above 1500 m; *Saprinus* (*Saprinus*) *pamiricus* Reichardt, 1930 lives at altitudes above 2800 m (Kryzhanovskiy & Reichardt 1976), and several species of *Paravolvulus* were found at almost 2000 m in the vicinity of Kabul in Afghanistan (Kryzhanovskij 1987).

The Saprininae are typically predators of soft-bodied larvae and eggs of flies or other arthropods. However, according to Reichardt (1941), some species of the genus *Saprinus* capture adult flies on dung. Carlton et al. (1996) reported similar behavior of the South American *Euspilotus* (*Euspilotus*) *bisignatus* (Erichson, 1834), which eats heads of living flies after having captured them. Some species of *Saprinus* are attracted to fetid fragrances emitted by the blooming flowers (for details see Thérond 1931, Reichardt 1941, Vienna 1980 and Kovarik & Caterino 2005). The species *Chalcionellus hauseri* (Schmidt, 1894) and *Paravolvulus syphax* (Reitter, 1904) develop in the drying stalks of *Cystanche* plants (Reichardt 1941, Kryzhanovskij & Reichardt 1976, Kryzhanovskij 1987, Kovarik & Caterino 2005). Several species of *Saprinus* prey upon fly larvae that develop in rotting fungi, e.g., *S.* (*Saprinus*) *lautus* Erichson, 1839 (Lackner, pers. observ.).

Specialized littoral species occupy riparian habitats and are found on beaches almost throughout the world. They prey upon insect larvae that develop in the coastal wrack. Here belongs the majority of species in the genus *Hypocaccus*, all species of the subgenus *Baeckmanniolus* and *Eopachylopus ripae.* Several species of the genus *Hypocaccus,* e.g., *H.* (*Hypocaccus*) *speculum* (Schmidt, 1884), *H.* (*Hypocaccus*) *specularis* (Marseul, 1855), *H.* (*Hypocaccus*) *axeli* (Kryzhanovskij, 1976) and *H.* (*Hypocaccus*) *pelleti* (Marseul, 1862), are typical inhabitants of shoals of rivers, occasionally occurring at higher altitudes; they presumably prey on fly larvae developing in organic debris (Ôhara 1994, Kryzhanovskij & Reichardt 1976). However, other species of *Hypocaccus* and other genera, e.g., *H.* (*Hypocaccus*) *rugiceps* or *Exaesiopus grossipes*, can be found on the seashores as well as deep inland on landlocked sandy dunes (Lackner, pers. observ.).

The Saprininae also include many specialized psammophilous species, occasionally living deep in the sand (most of the psammophilous Histeridae belong to the Saprininae). These usually show various degrees of adaptation to the sandy conditions, often having dense vestiture on the ventral surface of the body, shovel-like protibiae and thickened and dilated meso-and metatibiae. The typical representatives of this group include all taxa in the genera *Philothis*, *Ctenophilothis* and *Xenophilothis* (for details on their morphology and biology see Olexa 1990) and the genera *Ammostyphrus*, *Reichardtiolus*, *Axelinus*, *Alienocacculus*, *Chivaenius* and *Turanostyphrus* (Kryzhanovskij & Reichardt 1976; Olexa 1980, 1984; Tishechkin 2005).

The Saprininae are also regular inhabitants of mammal and birds nests (for more details see Kovarik & Caterino 2005). A very thorough survey of species of the genus *Gnathoncus* and *Saprinus* (as well as other histerids) frequenting bird nests can be found in Hicks (1959: 52–64). Examples are found within the genera *Gnathoncus*, *Eremosaprinus* and *Pholioxenus* (Reichardt 1941, Kryzhanovskij & Reichardt 1976, Olexa 1984). Several species of the genera *Gnathoncus* or *Saprinus* are found in the nests of birds and occasionally on carrion, e.g., *Gnathoncus nannetensis* (Marseul, 1862) and *Saprinus* (*Saprinus*) *aeneus* (Fabricius, 1775) (Kryzhanovskij & Reichardt 1976; Lackner, pers. observ.). This behavior can indicate that the ancestral taxon was predominantly free-living and subsequently entered the nests of mammals or birds. *Saprinus* (*Saprinus*) *rugifer* (Paykull, 1809) has been reported to frequent the nests of Sand Martin (*Riparia riparia* Linnaeus, 1758), which presumably represent its true habitat, but is also occasionally found on dead birds or even in mole burrows (*Talpa europea*

Linnaeus, 1758) (Kryzhanovskij & Reichardt 1976). The sole Palaearctic representative of the genus *Euspilotus*, *E.* (*Neosaprinus*) *perrisi*, lives in the nests of the European Bee-Eater (*Merops apiaster* Linnaeus, 1758) (Olexa, pers. comm. 1995; Kryzhanovskij & Reichardt 1976). This species is also seldom collected on carrion (Kanaar, pers. comm. 2008). Almost all species of the genus *Pholioxenus*, some species of the genus *Gnathoncus* as well as *Eremosaprinus vlasovi* live in the burrows of ground squirrels, e.g., *Spermophilopsis* (Sciuridae). *Myrmetes paykulli* is the sole Palaearctic species known to frequent nests of *Formica* ants, especially those of *Formica rufa* Linnaeus, 1761 and less frequently those of *F. sanguinea* Latreille, 1798. This species is most likely not strictly myrmecophilous, since it has also been found on a dead frog (Kryzhanovskij & Reichardt 1976).

Although most of the known taxa are apparently diurnal, the Saprininae found in the desert regions are sometimes attracted to light, e.g., *Saprinus* (*Saprinus*) *lucemseductus* Kanaar, 2008 recently described from the United Arab Emirates and *Alienocacculus vanharteni* Kanaar, 2008 (Kanaar 2008; Pavlíček, pers. comm. 2007).

This permits the conclusion that the Saprininae are very active and appear to be highly adapted to unwelcoming dry habitats. They have also invaded nests of various birds as well as mammal burrows and are even present in ant colonies. This remarkable ecological plasticity is not seen in any other subfamily of the Histeridae.

Key to the genera of the Palaearctic Saprininae

Although this work omits several taxa that are either not considered as a part of the Palaearctic fauna or their taxonomic placement is questionable (see Material and methods for details), the key presented here contains most of them. It is hoped that this will add more value to the work presented and permit the reader to identify every taxon that is presently thought to occur in the Palaearctic Region. The subgenera are, with a few exceptions, excluded from this key; keys to the subgenera are given with the corresponding genus.

1 (10) Frontal and supraorbital striae completely absent (Fig. 363).
2 (9) Prosternum without pre-apical foveae (Fig. 305).
3 (8) Elytral epipleuron asetose (Fig. 368).
4 (7) Lateral prosternal striae usually strongly reduced, but present; carinal prosternal striae usually sharply convergent on anterior half (Fig. 366).
5 (6) Elytra with prominent punctation; outer margin of protibia with teeth topped with denticles; protibial groove present; each elytron between fourth dorsal elytral stria and sutural stria with a characteristic, short and hooked appendix, sutural stria often significantly shortened apically but always present. ..... ***Gnathoncus*** Jacquelin-Duval, 1858
6 (5) Elytra without prominent punctation, mat; outer margin of protibia without teeth, topped only with short denticles; protarsal groove absent; sutural elytral stria absent, each elytron between fourth dorsal elytral stria and sutural stria without short and hooked appendix. ..... ***Myrmetes*** Marseul, 1862

7 (4) Lateral prosternal striae absent; carinal prosternal striae 'open' anteriorly (Fig. 305); meso- and metatarsi long, together with tarsal claws as long as meso- and metatibiae, respectively; outer margin of protibia explanate, concealing about 15 short denticles. ..... ***Eremosaprinus*** Ross, 1939

8 (3) Elytral epipleuron setose (Fig. 700); carinal prosternal striae slightly divergent, vaguely united anteriorly; protibia widened, outer margin explanate, completely concealing numerous denticles; metatibia flattened, outer margin explanate, denticles almost entirely concealed. ..... ***Turanostyphrus*** Tishechkin, 2005

9 (2) Pre-apical foveae of prosternum present, vague, anteriorly connected by groove; prosternal process between carinal prosternal striae distinctly convex (Fig. 323); carinal prosternal striae widely divergent anteriorly; pygidium of female with sulci. .... ***Euspilotus***, subgenus ***Neosaprinus*** Bickhardt, 1909

10 (1) At least supraorbital stria always present, usually frontal stria also present, often well developed or carinate, sometimes widely interrupted medially and in some cases prolonged onto clypeus.

11 (12) Labrum conspicuously large, larger than clypeus, flattened and expanded anteriorly (Fig. 733); mentum also distinctly broadening anteriorly (Fig. 732); anterior margin of mentum with long dense lamelliform setae; protibia with four teeth topped with short denticle; 1st and 3rd teeth about the same size, 2nd tooth conspicuously larger. ..... ***Xenophilothis*** Kryzhanovskij, 1987

12 (11) Labrum not larger than clypeus; often semicircular or elongate oval, dorsally usually convex, sometimes depressed medially; mentum sub-trapezoid, trapezoid or square-shaped (Fig. 683), never distinctly broadening anteriorly; protibial teeth or denticles usually diminishing in size in proximal direction.

13 (60) Labrum with punctures or coarse structures, convex or medially depressed, in most cases with labral pits fringed with one or, more often, two setae; protarsi well developed; underside of body moderately convex.

14 (29) Pre-apical foveae absent (Fig. 203).

15 (16) Lateral pronotal stria present (Fig. 198); protibia with two large triangular teeth topped with large triangular denticle, followed by one short and one almost invisible denticle; carinal prosternal striae absent; prosternal process setose (Fig. 203); underside of body with short setae. ..... ***Ammostyphrus*** Reichardt, 1924

16 (15) Lateral pronotal stria absent (Fig. 282).

17 (18) Pronotum except for a row of punctures along hind margin and elytra almost impunctate; cuticle never metallic; elytra often with red macula; prosternal process compressed, knife-like (Fig. 287); carinal prosternal striae present only on prosternal apophysis; ventral surface of protibia with numerous denticles (Fig. 290); outer margin of metatibia with at least four rows of denticles. .... ***Eopachylopus*** Reichardt, 1926

18 (17) Pronotum almost always punctate, at least laterally or in antero-lateral angles; hind tibia on outer margin with no more than two rows of denticles; elytra punctate at least on its apical third; prosternal process never knife-like, surface between carinal prosternal striae usually flat or slightly convex, only rarely somewhat concave.

19 (28) Anterior margin of clypeus not elevated; frontal stria usually interrupted, rarely complete; eyes in most species convex, well visible from above.
20 (21) Body very small for the subfamily (1.40–1.95 mm long), not metallic; protibia without teeth, outer margin with short denticles; 8th sternite of males sickle-shaped (Fig. 482). ..... ***Microsaprinus*** Kryzhanovskij, 1976
21 (20) Body usually larger than 2.00 mm, often metallic; outer margin of protibia usually with teeth topped with denticles; 8th sternite of males never sickle-shaped.
22 (27) Prosternal process setose (Fig. 685); underside of body setose.
23 (24) Both sets of prosternal striae rudimentary, carinal prosternal striae present only on prosternal apophysis, frontal stria complete. ..... ***Neopachylopus pakistanicus*** Lackner, 2001
24 (23) Prosternal striae not rudimentary, both sets well developed, frontal stria often interrupted medially.
25 (26) Prosternal process somewhat concave, lateral prosternal striae widely 'open' anteriorly (Fig. 685); frontal disc smooth; tarsal claws long, slightly bent; underside of body with setae. ..... ***Styphrus*** Motschulsky, 1845
26 (25) Prosternal process flattened; lateral prosternal striae strongly convergent anteriorly, merging in front of merged carinal prosternal striae; frontal disc densely punctate; tarsal claws shortened, bent. ..... ***Paravolvulus syphax*** (Reitter, 1904)
27 (22) Prosternal process in most cases asetose; underside of body normally without setae[1]. ..... ***Saprinus*** Erichson, 1834
28 (19) Anterior margin of clypeus elevated (Fig. 750); frontal stria complete, slightly carinate anteriorly; eyes flattened, but visible from above. ..... ***Zorius*** Reichardt, 1932
29 (14) Pre-apical foveae present (Fig. 719)[2].
30 (33) Prosternal process compressed, knife-like (Fig. 253).
31 (32) Carinal prosternal striae absent (Fig. 253); cuticle entirely castaneous brown. ..... ***Chivaenius*** Olexa, 1980
32 (31) Carinal prosternal striae present, approximate; pronotum black, elytra rufous. ..... ***Neopachylopus secqi*** Kanaar, 1998
33 (30) Prosternal process differently shaped, not knife-like.
34 (35) Frontal disc smooth; elytral epipleuron setose; dorsal elytral striae almost reaching elytral apex; outer margin of protibia with three large teeth, topped with short denticle, followed by five short denticles (Fig. 720). ..... ***Xenonychus*** Wollaston, 1864
35 (34) Frontal disc never completely smooth; elytral epipleuron almost always glabrous (setose only in *Alienocacculus* Kanaar, 2008); dorsal elytral striae usually terminating before apical fifth, often shorter.

[1] Some desert or semi-desert species of *Saprinus* may possess setae on underside of their bodies.
[2] Several species of the genus *Pholioxenus*, or even some specimens of the species *Chivaenius kryzhanovskii* may have minuscule, or even absent pre-apical foveae, but in those cases the frontal stria is always well impressed and complete. Species *Hypocacculus* (*Colpellus*) *solieri* (Marseul, 1862) does not posses pre-apical foveae, but likewise the frontal stria of this species is complete.

36 (41) Frontal disc with several, usually one or two, deep or carinate rugae (Fig. 342), sometimes with numerous deep rugae, but in that case elytra usually with very coarse and dense punctures; frontal stria always strongly carinate (Fig. 342), usually straight.

37 (38) Underside of body with short setae; protibia usually with two to four teeth, topped with short denticle (Fig. 348); rugae on frontal disc prominent (Fig. 342). ..... ***Exaesiopus*** Reichardt, 1932

38 (37) Underside of body without setae, at most with extremely short setae on lateral disc of metaventrite or metepisternum.

39 (40) Pronotum almost smooth, at most with fine punctation in antero-lateral corners. .... ***Hypocaccus***, subgenus ***Baeckmanniolus*** Reichardt, 1932

40 (39) Pronotum always with punctation, at least laterally. ..... ***Hypocaccus***, subgenus ***Hypocaccus*** C. Thomson, 1867

41 (36) Frontal disc with variously coarse or dense punctation, but never smooth and never with several deep rugae.

42 (43) Protibia without typical articulated teeth, outer margin (Fig. 618) with numerous (10–12) short denticles; clypeus rugulose-lacunose (Fig. 615); major part of frontal disc densely punctate but not rugulose-lacunose; body cylindrical or sub-cylindrical, small (PEL = 1.50–1.85 mm); metatibia very slender. ..... ***Saprinillus*** Kryzhanovskij, 1974

43 (42) Protibia with typical articulated teeth topped with denticle; body oval or roundly oval, never cylindrical, usually larger (PEL usually larger than 1.70 mm).

44 (47) Antennal scape strongly thickened (Fig. 184).

45 (46) Antennal scape resembling a trapezoid, furnished with long strongly sclerotized setae; elytral epipleuron setose (Fig. 185). ..... ***Alienocacculus*** Kanaar, 2008

46 (45) Antennal scape strongly thickened, resembling a triangle with broadly rounded apex, with variously long setae; elytral epipleuron asetose. ..... ***Dahlgrenius*** Penati & Vienna, 1996

47 (44) Antennal scape not particularly thickened.

48 (51) Frontal disc rugulose-lacunose and densely punctate; frontal stria usually interrupted, rarely complete.

49 (50) Frontal stria shortly interrupted (Fig. 596); metatibia thickened and dilated; protibia with two large teeth, topped with triangular denticle, followed by single low tooth topped with short denticle (Fig. 603). ..... ***Reichardtiolus*** Kryzhanovskij, 1959

50 (49) Frontal stria widely interrupted medially; metatibia not particularly thickened or dilated; protibia with three large teeth topped with short denticle, followed by two very low teeth topped with minuscule denticle (Fig. 217). ..... ***Axelinus*** Kryzhanovskij, 1976

51 (48) Frontal disc with variously coarse or dense punctation but never rugulose-lacunose; frontal stria usually complete.

52 (53) Frontal stria largely interrupted and prolonged onto clypeus; carinal prosternal striae divergent anteriorly, open; lateral prosternal striae straight, terminating in deep preapical foveae (Fig. 648). ..... ***Saprinus***, subgenus ***Hemisaprinus*** Kryzhanovskij, 1976

53 (52) Frontal stria in most cases complete, only occasionally interrupted, at times prolonged onto clypeus; clypeus sometimes depressed; carinal prosternal striae almost always convergent apically, often united in front.

54 (55) Pronotum often with pronotal foveae, if devoid of them then frontal stria prolonged onto clypeus and body metallic; clypeus and anterior part of frontal disc sometimes depressed. ..... ***Chalcionellus*** Reichardt, 1932

55 (54) Pronotum without pronotal foveae, frontal stria usually complete.

56 (57) Pronotum only slightly convex, with both lateral margins visible along their entire length in dorsal view; pre-apical foveae usually very small, sometimes absent; protibia dilated, outer margin with 4–6 short broad teeth, topped with slender short denticle (Fig. 585); metatarsus rather long; cuticle often imbricate; eyes markedly convex. ..... ***Pholioxenus*** Reichardt, 1932

57 (56) Pronotum rather convex, with lateral margins not simultaneously visible along their entire length in dorsal view; pre-apical foveae usually larger and well developed; metatarsi moderately long; cuticle usually not imbricate, eyes usually flattened, as a rule not very convex.

58 (59) Frontal stria usually complete, medially uninterrupted; pronotum never with lateral pronotal stria; cuticle often metallic; elytra never with red maculae; protibia moderately dilated, outer margin with 6–15 low teeth, topped with short denticle getting progressively smaller in proximal direction. ..... ***Hypocacculus*** Bickhardt, 1914

59 (58) Frontal stria usually interrupted medially; pronotum often with lateral pronotal stria; cuticle usually not metallic; elytra often reddish or with red macula; frontal disc often with rather coarse and dense punctation. ..... ***Paravolvulus*** Reichardt, 1932

60 (13) Labrum always smooth, substantially flattened with shallow median depression, labral pits absent; underside of body strongly convex, with long setae; eyes flattened, invisible from above (Fig. 269); protarsi either rudimentary, reduced or absent (Fig. 551).

61 (62) Outer margin of protibia with numerous long movable denticles (Fig. 274); metatibia dilated as a whole; elytral epipleuron setose. ..... ***Ctenophilothis*** Kryzhanovskij, 1987

62 (61) Outer margin of protibia with two large distal teeth, topped with minuscule denticle (Fig. 551); elytral epipleuron glabrous; outer margin of metatibia with two strongly divergent rows of denticles, one of the rows markedly shifted away from outer margin and observable only from ventral view. ..... ***Philothis*** Reichardt, 1930

Alienocacculus Kanaar, 2008

Alienocacculus Kanaar, 2008: 187. Type species: *Hypocacculus* (*Nessus*) *neftensis* Olexa, 1984, original designation.

Diagnosis. Antennal scape strongly dilated and thickened, resembling a trapezoid, furnished with long strongly sclerotized setae; both mandibles with large sub-apical tooth; penultimate labial palpomere with single long seta; frontal stria interrupted medially; frontal disc rugulose-lacunose; head rather small; eyes flattened but visible from above; pronotal foveae absent; pronotal hypomeron and elytral epipleuron setose; pre-apical foveae large, deep, situated antero-laterally from lateral prosternal striae; lateral parts of pleura and sterna setose; protibial spur large, stout.

Differential diagnosis. *Alienocacculus* resembles most closely the subgenus *Nessus* of the genus *Hypocacculus* (the type species of *Alienocacculus* has originally been described as *Nessus*), but differs chiefly by the setose elytral epipleuron, the size and unusual position of the pre-apical foveae and the interrupted frontal stria. A setose elytral epipleuron is found in several other Palaearctic genera of the subfamily: *Xenophilothis*, *Turanostyphrus*, *Xenonychus* and *Ctenophilothis*. From these genera, *Alienocacculus* chiefly differs by the following characters: from *Xenophilothis* by the differently shaped protibia, differently shaped and asetose prosternal process and the presence of pre-apical foveae (absent in *Xenophilothis*); from *Turanostyphrus* by the differently shaped tibiae and prosternal process and the presence of pre-apical foveae (absent in *Turanostyphrus*); from *Xenonychus* by the different elytral striation, structure of the frontal disc (almost completely smooth in *Xenonychus*, rugulose-lacunose in *Alienocacculus*) and the medially interrupted frontal stria (complete in *Xenonychus*); and from *Ctenophilothis* by the differently shaped protibia, less convex ventral surface of the body, the presence of the antennal groove (absent in *Ctenophilothis*), different elytral striation, rugulose-lacunose frontal disc (smooth in *Ctenophilothis*) and the large and globular sub-apical tooth on the left mandible (minute in *Ctenophilothis*).

Biology. Although the biology of this taxon is poorly documented, one species, *A. neftensis* (Olexa, 1984) was collected in sand dunes near the Tunisian city of Nefta and *A. vanharteni* was collected at light in a desert area (Kanaar 2008; Pavlíček, pers. comm. 2007). The morphological characteristics of this genus (underside of body with dense vestiture, small head and flattened eyes) and the collecting sites suggest that it belongs to the group of specialized psammophilous Saprininae mentioned by Olexa (1984) and Kanaar (2008).

Distribution. This recently erected genus occurs in desert regions and is known from the Nefta oasis in Tunisia and from the Negev Desert in southern Israel and the environs of Dubai in the United Arab Emirates.

Species examined. *Alienocacculus neftensis* (Olexa, 1984) and *A. vanharteni* Kanaar, 2008.

Discussion. This genus is characerized by several putative synapomorphies: strongly dilated antennal scape resembling a trapezoid, large sub-apical tooth of mandibles and penultimate labial palpomere with single long seta. Other characters including rugulose frons, setose elytral epipleuron and small flattened eyes are most likely homoplasies and do not constitute characters useful for a phylogenetic delineation of this taxon. The monophyly of this taxon should be tested in the future, especially with respect to the presumably related taxa like *Hypocacculus* (*Nessus*) and *Dahlgrenius*.

Alienocacculus neftensis (Olexa, 1984)

(Figs. 31, 47, 81, 109, 179–197)

Hypocacculus (*Nessus*) *neftensis* Olexa, 1984: 377, Figs. 1–7.
Hypocacculus (*Nessus*) *neftensis*: Mazur (1984): 90; Mazur (1997): 254.
Alienocacculus neftensis: Kanaar (2008): 187.

Type locality. Tunisia, Nefta.
Type material examined. Paratype: ♂, 'Tunisia / Nefta / 9.–10.vi.1982 / A. Olexa lgt. [printed] // PARATYPUS / *H. neftensis* sp.n. / A.Olexa det. [red label, printed-written] // 06–031 [light-blue label, written] // D07–017 [pink label, written] // D08–011 [yellow label, written]' (TLAN). Three paratypes (2 ♂♂ 1 ♀), same data and collector (TLAN).

Redescription. Body length: PEL: 2.25 mm; APW: 0.75–0.875 mm; PPW: 1.625–1.75 mm; EL: 1.375 mm; EW: 1.875 mm.

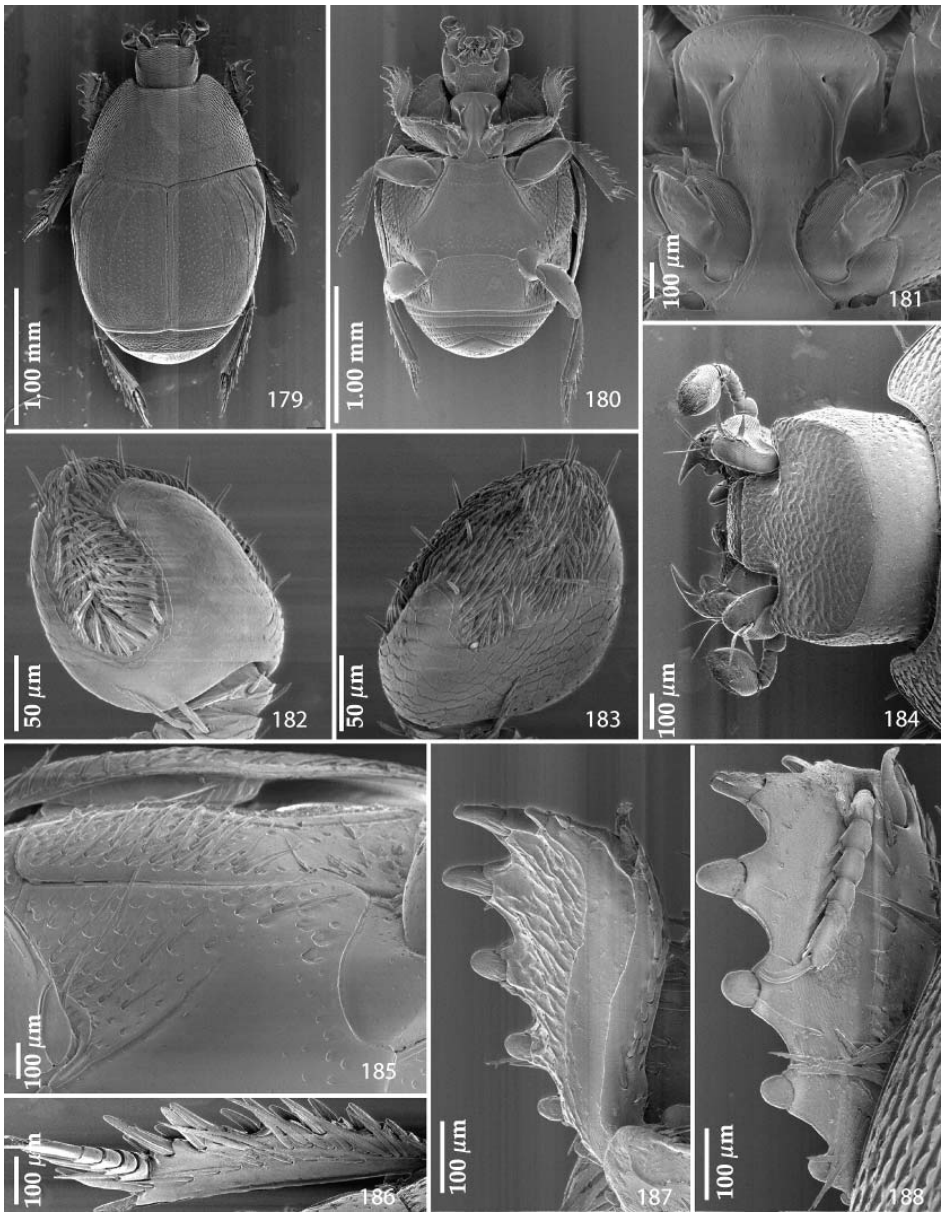
Body (Figs. 179–180) elongate oval, convex, elytral humeri slightly prominent; cuticle castaneous brown, with distinct metallic luster, legs, antennae and mouthparts light-brown, antennal club yellow. Antennal scape (Fig. 184) thickened and dilated, resembling a trapezoid with several long setae; club (Figs. 182–183) rounded, without visible articulation, apical surface with sensory area covered with very short sensilla, intermingled with sporadic longer erect sensilla; surface apart from the sensory area imbricate, glabrous; sensory structures of antennal club including one large apical sensory area, two small round sensory areas on ventral side and one stipe-shaped vesicle (Fig. 31).

Mouthparts. Mandibles (Fig. 81) thin, rounded, coarsely and densely punctate, apically pointed, sub-apical tooth of both mandibles large; labrum (Fig. 47) flattened, rugulose-lacunose; labral pits well developed, with two labral setae; terminal labial palpomere thickened, its width about half its length; penultimate labial palpomere with single long seta; cardo of maxilla with several short setae, stipes triangular, with three long setae; terminal maxillary palpomere thickened, its width about half its length, about twice as long as penultimate; mentum sub-trapezoid, anterior margin (Fig. 109) with deep emargination, disc in apical third with several long setae, medially glabrous; lateral margins with one row of sparse microscopic setae.

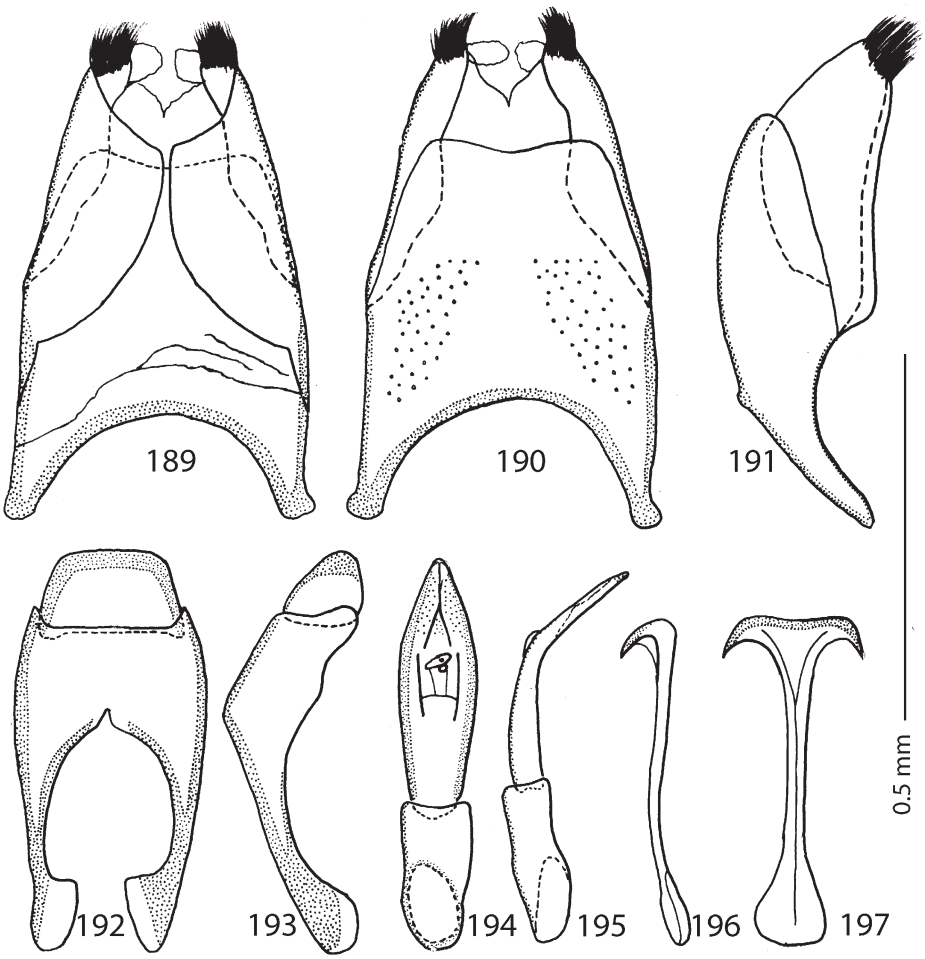
Clypeus (Fig. 184) rectangular, lateral margins depressed, rugulose-lacunose; structure of frontal disc (Fig. 184) similar to clypeus; frontal stria largely interrupted medially; supraorbital stria fine, arcuate, elevated above eyes, posteriorly connected with complete occipital stria; eyes flattened, almost invisible from above.

Pronotum (Fig. 179) distinctly convergent apically; pronotal foveae absent; anterior angles acute; anterior incision for head deep; marginal pronotal stria complete, slightly carinate; disc laterally with dense and coarse punctures forming elongate rugae, medially punctation becomes finer and sparser; pronotal hypomeron with long amber setae.

Elytral epipleuron with scattered punctures with amber setae (Fig. 185); marginal epipleural stria well impressed, complete; marginal elytral stria complete, carinate, continued as complete apical elytral stria; elytra with well impressed dorsal striae 1–4, all subequal in length, reaching about three-fourths of elytral length apically, all striae vaguely connected basally; fourth dorsal elytral stria basally connected to sutural elytral stria; sutural elytral



Figs. 179–188. *Alienocacculus neftensis* (Olexa, 1984), SEM micrographs: 179 – habitus, dorsal view; 180 – ditto, ventral view; 181 – prosternum; 182 – antennal club, ventral view; 183 – ditto, dorsal view; 184 – head, dorsal view; 185 – lateral disc of metaventrite, metepisternum and fused metepimeron; 186 – mesotibia, dorsal view; 187 – protibia, ventral view; 188 – ditto, dorsal view.



Figs. 189–197. *Alienocacculus neftensis* (Olexa, 1984), male terminalia: 189 – 8th sternite and tergite 8, ventral view; 190 – ditto, dorsal view; 191 – ditto, lateral view; 192 – 9th tergites and 10th tergite, dorsal view; 193 – ditto, lateral view; 194 – aedeagus, dorsal view; 195 – ditto, lateral view; 196 – spiculum gastrale, lateral view; 197 – ditto, ventral view.

stria weakly impressed, connected to apical elytral stria. Humeral elytral stria well impressed on basal third; inner subhumeral stria present medially, rather short; outer subhumeral stria present as short basal fragment; elytral surface with scattered deep punctation, punctures separated by 2–4 times their diameter; apically forming a band of much denser punctures; lateral margins and elytral humeri with much sparser and finer punctation; extreme apex of elytra impunctate.

Propygidium almost completely exposed, with dense and coarse punctures, becoming confluent along apical margin; pygidium long, convex, with sparser and finer regular punctation.

Anterior margin of median portion of prosternum (Fig. 181) rounded; marginal prosternal stria complete; pre-apical foveae well impressed, deep, situated outside lateral prosternal striae next to their lateral bend; prosternal process dorsally rounded, slightly concave, dorso-laterally substrigulate-punctate; carinal prosternal striae present only on prosternal apophysis, thence obliterated; lateral prosternal striae well impressed, parallel on their basal half, suddenly strongly convergent anteriorly, finer, united in front.

Anterior margin of mesoventrite shallowly emarginate medially; discal marginal mesoventral stria complete, slightly carinate; disc of mesoventrite with scattered fine punctures; meso-metaventral sutural stria well impressed, straight, crenulate.

Intercoxal disc of metaventrite convex, with fine scattered punctures; band of much coarser punctures present along base; lateral metaventral stria well impressed, slightly carinate, extending obliquely and shortened apically; longitudinal suture of metaventrite fine, distinct; lateral disc of metaventrite (Fig. 185) concave, with deep sparse setiferous punctures; metepisternum on apical half with even coarser punctation with dense setae, apical third and fused metepimeron mostly glabrous, with very sparse punctures, several of them with setae. Intercoxal disc of the first visible abdominal sternite with complete striae laterally; disc basally with scattered round punctures, separated by 2–4 times their diameter, becoming finer and sparser apically.

Protibia (Figs. 187–188) dilated, outer margin with six low teeth topped by short denticle, diminishing in size in proximal direction; protibial groove deep; tarsus short but not rudimentary; protibial spur stout, bent, articulated near tarsal insertion; apical margin posteriorly with two minute denticles; outer part of posterior surface of protibia (Fig. 187) areolate-rugose with intermingled microscopic punctures, clearly separated from glabrous median part of posterior surface by complete stria, median part separated from inner part by complete posterior protibial stria; inner margin with one row of moderately dense strongly sclerotized setae.

Mesotibia (Fig. 186) not particularly dilated, outer margin with two sparse rows of short denticles growing abreast each other, posterior surface with two rows of setae: outer row consisting of long dense setae and median row consisting of much shorter and sparser setae; posterior mesotibial stria reaching about two-thirds of mesotibial length apically; anterior surface almost glabrous, with scattered microscopic punctation; apical margin of mesotibia with prominent long mesotibial spur surrounded by numerous shorter inner anterior denticles; claws of apical tarsomere bent, about half its length; metatibia more slender than mesotibia but otherwise similar; denticles on outer margin sparser.

Male genitalia. Eighth sternite (Figs. 189–190) longitudinally separated medially, apically with inflatable membrane (velum) with dense brush of moderately long setae. Eighth tergite and eighth sternite not fused laterally (Fig. 191). Morphology of ninth tergite (Figs. 192–193) typical for the subfamily; spiculum gastrale (ninth sternite) expanded on both ends (Figs. 196–197). Basal piece of aedeagus (Figs. 194–195) well- developed, ratio of its length to length of parameres approximately 1 : 1.5; parameres fused almost along basal half; aedeagus strongly curved ventrad (Fig. 195).

Ammostyphrus Reichardt, 1924

Ammostyphrus Reichardt, 1924: 164. Type species: *Ammostyphrus cerberus* Reichardt, 1924, original designation).

Ammostyphrus: Reichardt (1941): 336; Kryzhanovskij & Reichardt (1976): 112, 240; Mazur (1984): 103; Mazur (1997): 266; Mazur (2004): 90.

Diagnosis. Body ovoid, strongly convex; frontal stria carinate; pronotum strongly narrowing anteriorly, apical margin about twice as broad as pronotal base; pronotal foveae absent; pronotal disc smooth, only in antero-lateral angles several shallow punctures present; lateral pronotal stria present; prosternal process narrow, setose; carinal prosternal striae absent; pre-apical foveae absent; lateral prosternal striae present, convergent anteriorly; lateral metaventral stria curved outwardly, almost reaching metepisternum; pronotal hypomeron setose; lateral part of all visible abdominal sternites setose. Outer margin of protibia with two large triangular teeth topped with large triangular denticle, followed by one low tooth topped with short denticle and another minuscule denticle; protarsi shortened; metatibia slightly dilated and thickened; both meso- and metatibiae with long yellow setae on dorsal surface; tarsal claws bent, shortened.

Differential diagnosis. *Ammostyphrus* is easily distinguished from all other Palaearctic Saprininae by the absence of the lateral prosternal striae and the presence of the lateral pronotal stria.

Biology. *Ammostyphrus* is a psammophilous taxon, often collected with other psammophilous Saprininae.

Distribution. This is a rare monotypic genus, spread in the desert province of Turan in Central Asia. It was collected in sandy regions of southern Kazakhstan, Turkmenistan and Uzbekistan.

Species examined. *Ammostyphrus cerberus* Reichardt, 1924.

Discussion. This genus is characterized by a least one autapomorphy (lateral metaventral stria curved outwards, almost reaching metepisternum) and several synapomorphies, e.g., the presence of the lateral pronotal stria and the absence of carinal prosternal striae. It is probably a monophyletic taxon with several features that show its adaptation to the sandy environment, including the vestiture of the ventral part of the body, a typically shaped outer margin of the protibia and thickened metatibia.

Ammostyphrus cerberus Reichardt, 1924

(Figs. 14, 48, 82, 110, 198–214)

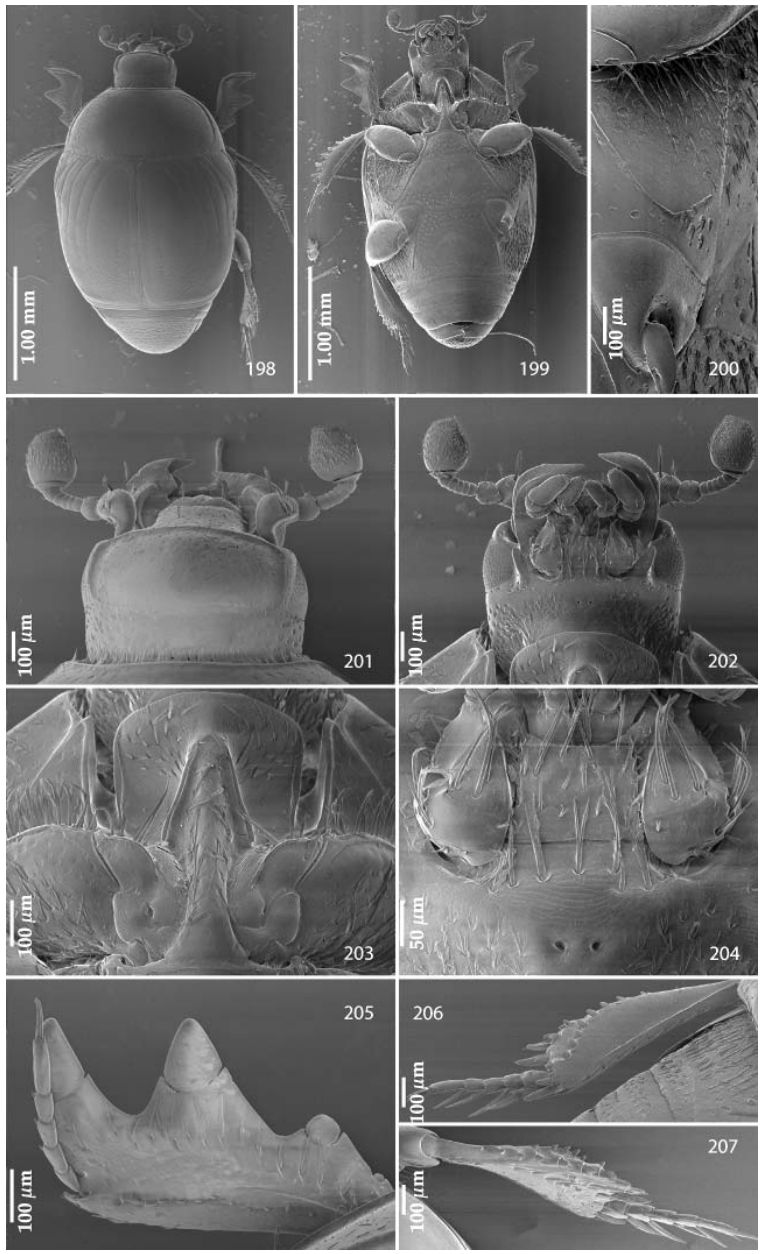
Ammostyphrus cerberus Reichardt, 1924: 165.

Ammostyphrus cerberus: Reichardt (1941): 337, Fig. 174; Kryzhanovskij & Reichardt (1976): 241, Fig. 469; Mazur (1984): 103; Mazur (1997): 266; Mazur (2004): 90.

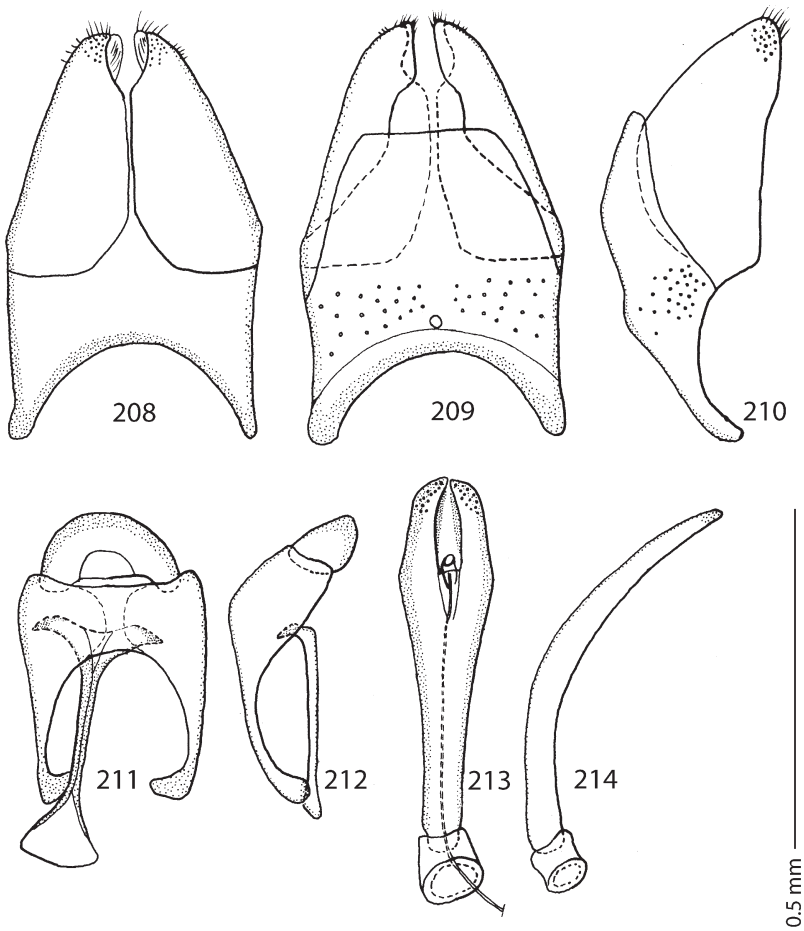
Type locality. Kazakhstan, Perovskiy uezd, Chirkeili.

Type material examined. Holotype: spec., 'Perovskij u. / Peschannaya Pustina / Chirkeili / 23.iv.[19]09 [printed] // Type / *Ammostyphrus* / *cerberus* m. / A. Reichardt det. [printed-written] // Holotypus [red label, printed]' (ZIN).

Additional material examined. UZBEKISTAN: 1 ♂, 1 spec., Buchara, Kyzylkum, 27.iv.1978, A. Olexa lgt.; 1 spec., ditto, but 30.vi.1976; 2 spec., Karakum, Chiva [= Khiva] / 1.–5.v.1979, A. Olexa lgt.; 1 ♂, Buchara, Shafrikan, 29.iv.1979, A. Olexa lgt. (TLAN).



Figs. 198–207. *Ammostyphrus cerberus* Reichardt, 1924, SEM: 198 – habitus, dorsal view; 199 – ditto, ventral view; 200 – lateral disc of metaventrite, metepisternum and fused metepimeron; 201 – head, dorsal view; 202 – ditto, ventral view; 203 – prosternum; 204 – mentum and cardines and stipites of maxilla, ventral view; 205 – protibia, dorsal view; 206 – metatibia, ventral view; 207 – ditto, dorsal view.



Figs. 208–214. *Ammostyphrus cerberus* Reichardt, 1924, male terminalia: 208 – 8th sternite and tergite, ventral view; 209 – ditto, dorsal view; 210 – ditto, lateral view; 211 – 9th tergite, 10th tergite (dorsal view) and spiculum gastrale (ventral view); 212 – 9th tergite, 10th tergite and spiculum gastrale, lateral view; 213 – aedeagus, dorsal view; 214 – ditto, lateral view.

Redescription. Body length: PEL: 2.0–2.25 mm; APW: 0.625–0.75 mm; PPW: 1.5–1.625 mm; EL: 1.45–1.625 mm; EW: 1.375–1.875 mm.

Body (Figs. 198–199) ovoid, strongly convex, cuticle dark brown with a stark bronze metallic luster; legs, antennae and mouthparts reddish-brown.

Antennal scape (Fig. 201) slightly thickened, with several short setae; club rather large, oval, without visible articulation, with thick short sensilla becoming slightly sparser basally, basal fourth of surface glabrous; sensory structures of antennal club (Fig. 14) in form of stipe-shaped vesicle situated under a large circular sensory area on internal distal margin of the ventral side of antennal club.

Mouthparts. Mandibles (Fig. 82) stout, outer margin straight, strongly curved inwardly; acutely pointed, sub-apical tooth on left mandible moderately large, obtuse; labrum (Fig. 48) sparsely punctate; labral pits present, with two setae; anterior margin medially with prominent convexity interrupting concavity; terminal labial palpomere thickened, its width about half its length; mentum (Fig. 204) sub-trapezoid, anterior margin (Fig. 110) shallowly emarginate, disc of mentum setose; cardo of maxilla with several moderately long setae; stipes triangular, with three moderately long setae; terminal maxillary palpomere thickened, its width about half its length; about three times as long as penultimate.

Clypeus (Fig. 201) flat, rounded laterally, rectangular, almost smooth, only with scattered microscopic punctation; frontal stria (Fig. 201) well impressed, carinate, somewhat curved outwardly, continued as well impressed and carinate supraorbital stria; frontal disc slightly convex; frontal disc almost smooth, with scattered fine punctures; eyes flattened, visible from above.

Pronotal sides (Fig. 198) strongly convergent forwardly; apical angles blunt; marginal pronotal stria complete, well impressed and carinate; lateral pronotal stria carinate, posteriorly and anteriorly shortened, somewhat distant from lateral pronotal margin, on both ends curved inwardly; pronotal disc convex, almost smooth, only antero-lateral angles inside of the lateral pronotal stria with inconspicuous scattered shallow punctures; base of pronotal disc with a row of round punctures; pronotal hypomeron with short amber setae; scutellum small, but visible.

Elytral humeri gently prominent; epipleura almost smooth, only with scattered microscopic punctation; marginal epipleural stria complete; marginal elytral stria strongly impressed, carinate, continued as complete apical elytral stria. Humeral elytral stria distinctly impressed on basal third, occasionally doubled; inner subhumeral stria present medially, shortened; elytra with four dorsal striae 1–4, in fine punctures, increasing in length from first to fourth, fourth stria surpasses elytral half apically, basally connected with sutural elytral stria; sutural stria well impressed, apically connected with apical elytral stria. Elytral disc almost smooth, punctation confined to apical third, along sutural stria reaching about one-third of elytral length anteriorly, punctures separated by about their own to twice their diameter.

Propygidium partially covered by elytra, with dense shallow punctures; pygidium convex, about as long as broad, with coarser and denser elongate punctures than those of propygidium, forming longitudinal rugae.

Anterior margin of median portion of prosternum (Fig. 203) rounded; pre-apical foveae absent; marginal prosternal stria absent anteriorly; prosternal process slightly compressed, setose, rounded dorsally; carinal prosternal striae absent (in some specimens vaguely present between procoxae, as in *Chivaenius*); lateral prosternal striae well impressed, carinate, convergent anteriorly, vaguely united in front.

Anterior margin of mesoventrite almost straight, somewhat curved outwardly; discal marginal mesoventral stria laterally well impressed, carinate, somewhat weakened medially; disc of mesoventrite convex, with dense deep punctures separated about their own to twice their diameter, posteriorly growing in size; meso-metaventral sutural stria formed by a row of large punctures; intercoxal disc of metaventrite flat, almost smooth, only with microscopic punctation, along posterior margin with three rows of deep punctures; lateral metaventral

stria (Fig. 200) well impressed, carinate, curved outwardly, almost attaining meso-metepisternal suture. Lateral disc of metaventrite (Fig. 200) slightly concave, with scattered shallow punctures, fringed with short setae; metepisternum on apical two-thirds with sparse shallow punctures fringed with short setae, basal third + fused metepimeron almost glabrous, only with several shallow punctures.

Intercoxal disc of first abdominal sternite almost completely striate laterally; anterior half of disc with coarse punctures separated by about their own diameter, posteriorly punctures replaced by very fine scattered microscopic punctation; along posterior margin row of larger punctures present; lateral disc of all visible abdominal sternites laterally setose.

Protibia (Fig. 205) on outer margin with two large triangular teeth topped with large triangular denticle, followed by one low tooth topped with minuscule denticle, followed by another microscopic denticle; protarsal groove shallow; tarsi shortened, but not rudimentary; anterior protibial stria shortened apically; protibial spur short, growing out from apical protibial margin; outer part of posterior surface of protibia smooth; median part of posterior surface with irregular setae; posterior protibial stria vaguely impressed; inner margin of protibia with dense row of setae.

Mesotibia not particularly dilated, outer margin with two rows of stout short denticles growing in size in proximal direction; posterior surface with sparse brush of two – outer and median – rows of setae; posterior mesotibial stria reaching half length of mesotibia apically, next evanescent; anterior surface of mesotibia almost smooth, with microscopic wrinkles; anterior mesotibial stria shortened apically; apical margin of mesotibia anteriorly with numerous inner anterior denticles; mesotibial spur short, stout; claws of apical tarsomere longer than half its length.

Metatibia (Figs. 206–207) slightly dilated and thickened, outer margin with two rows of short denticles, one row situated above the other, second row somewhat shifted from outer margin, observable only from ventral view; posterior surface of metatibia with rows of setae similar to those of mesotibia; anterior surface and apical margin of metatibia (Fig. 207) similar to that of mesotibia; claws of apical tarsomere gently bent, longer that half its length.

Male genitalia. Eighth sternite (Figs. 208–209) longitudinally separated medially, apically with inconspicuous velum and sparse short setae; eighth tergite and eighth sternite not fused laterally (Fig. 210), spiculum gastrale (Figs. 211–212) expanded on both ends. Basal piece of aedeagus (Figs. 213–214) very short, ratio of its length : length of parameres approximately 1 : 7; parameres (Figs. 213–214) fused almost along basal three-fourths; apex with pseudopores; aedeagus strongly curved ventrad (Fig. 214).

Axelinus Kryzhanovskij, 1976

Axelinus: Kryzhanovskij (1974): 106 (*nomen nudum*).

Axelinus Kryzhanovskij, 1976 in Kryzhanovskij & Reichardt (1976): 112, 215. Type species: *Axelinus ghilarovi* Kryzhanovskij, 1976 in Kryzhanovskij & Reichardt (1976), original designation.

Axelinus: Mazur (1984): 83; Mazur (1997): 249; Mazur (2004): 90.

Diagnosis. Body moderately convex; frontal stria largely interrupted; frontal disc as well as clypeus rugulose-lacunose; eyes inconspicuous from above. Dorsal surface almost entirely punctate; pronotal foveae absent; pronotal hypomeron with short setae; pre-apical foveae

small; prosternal process narrow, carinal prosternal striae convergent, united in front. Outer margin of protibia with three large teeth topped with short denticle, followed by two minute round denticles; meso- and metatibia somewhat thickened and dilated.

Differential diagnosis. Superficially *Axelinus* is most similar to the genus *Hypocacculus* differing from it chiefly by the shape of protibia as well as rugulose-lacunose frontal and clypeal disc and the largely interrupted frontal stria. From *Reichardtiolus* it also differs by more widely interrupted frontal stria (only shortly interrupted in *Reichardtiolus*) and less thickened and dilated meso- and metatibiae. Shape of the protibia is also different between the two taxa (see Key to genera).

Biology. Biology of *Axelinus* is virtually unknown; the type series was discovered during digging in sandy habitats of Central Asia (Kryzhanovskij & Reichardt 1976: 217).

Distribution. Turkmenistan and Uzbekistan.

Species examined. *Axelinus ghilarovi* Kryzhanovskij, 1976.

Discussion. *Axelinus* is characterized by only a few weak synapomorphies (e.g. shape of protibia and somewhat thickened meso- and metatibiae) that are most likely homoplasies. Its taxonomic validity should be tested in the future with special regard to the presumably related taxa, especially the species-rich genus *Hypocacculus* that is possibly polyphyletic, with respect to other, smaller genera like *Axelinus*.

Axelinus ghilarovi Kryzhanovskij, 1976

(Figs. 111, 215–231)

Axelinus ghilarovi Kryzhanovskij, 1976 in Kryzhanovskij & Reichardt (1976): 216, Figs. 424–427.
Axelinus ghilarovi: Mazur (1984): 83; Mazur (1997): 249; Mazur (2004): 90.

Type locality. Uzbekistan, Karatak.

Type material examined. Paratype: spec., 'Shafirkan, Buchar. / obl. Uzb. 31.iii / 1961 B. Mamaev [written] // XX.VII-8 [written] // Paratypus 1971 / *Axelinus* / *ghilarovi* g. et sp. n. // Kryzhanovskii det [red label, printed-written]' (ZIN).

Additional material examined. UZBEKISTAN: 2 spec., 1 ♂, 1 ♀, Buchara, Kyzylkum, 27.iv.1980, A. Olexa lgt. (TLAN).

Redescription. Body length: PEL: 1.375–1.875 mm; APW: 0.625–0.75 mm; PPW: 1.0–1.375 mm; EL: 0.875–1.125 mm; EW: 1.125–1.5 mm.

Body (Fig. 215) shortly oval, convex, without metallic luster; cuticle brown to dark brown, legs, antennae and mouthparts rufous. Antennal scape (Fig. 218) slightly thickened, with several short setae; club (Fig. 216) without visible articulation, entirely covered with short sensilla intermingled with sparse longer sensilla; sensory structures of antennal club not examined.

Mouthparts. Mandibles stout; mentum rectangular, posterior corners produced, with tiny notch in middle of anterior margin (Fig. 111); anterior margin in anterolateral corners with four moderately long setae, lateral margins with single row of much shorter ramose setae; disc of mentum glabrous. Cardo of maxilla with several short ramose setae on lateral margin; stipes triangular, with four much longer setae; terminal maxillary and labial palpomeres somewhat thickened, their width less than half their respective lengths; other parts of mouth not examined.

Clypeus and frontal disc rugulose-lacunose (Fig. 218); frontal stria widely interrupted anteriorly continued as complete elevated supraorbital stria posteriorly connected with complete occipital stria; eyes flattened, almost invisible from above.

Pronotum (Fig. 215) gently convergent apically; apical angles not produced; anterior emargination for head shallow; marginal pronotal stria complete; disc entirely with punctation, punctures becoming coarser and denser laterally; pronotal hypomeron with short sparse amber setae.

Elytral epipleura with a row of deep punctures; marginal epipleural stria weakly impressed, shortened apically and basally; marginal elytral stria complete, deeply impressed and in punctures, continued as complete apical elytral stria. Elytra with four dorsal elytral striae 1–4, well impressed, in round punctures; all striae about the same length, reaching about three-fourths of elytral length apically; humeral elytral stria well impressed on basal third; inner subhumeral stria short, present as medial fragment; fourth dorsal elytral stria basally connected with complete sutural elytral stria, that is linked with apical elytral stria; between sutural elytral stria and elytral suture a row of tiny punctures present. Entire elytral disc with round, scattered punctation, punctures separated by about 2–4 times their diameter, punctation not becoming denser apically.

Propygidium short, partly covered by elytra, with two rows of coarse and dense punctures; pygidium with dense regular punctures becoming finer apically; interspaces with microsculpture.

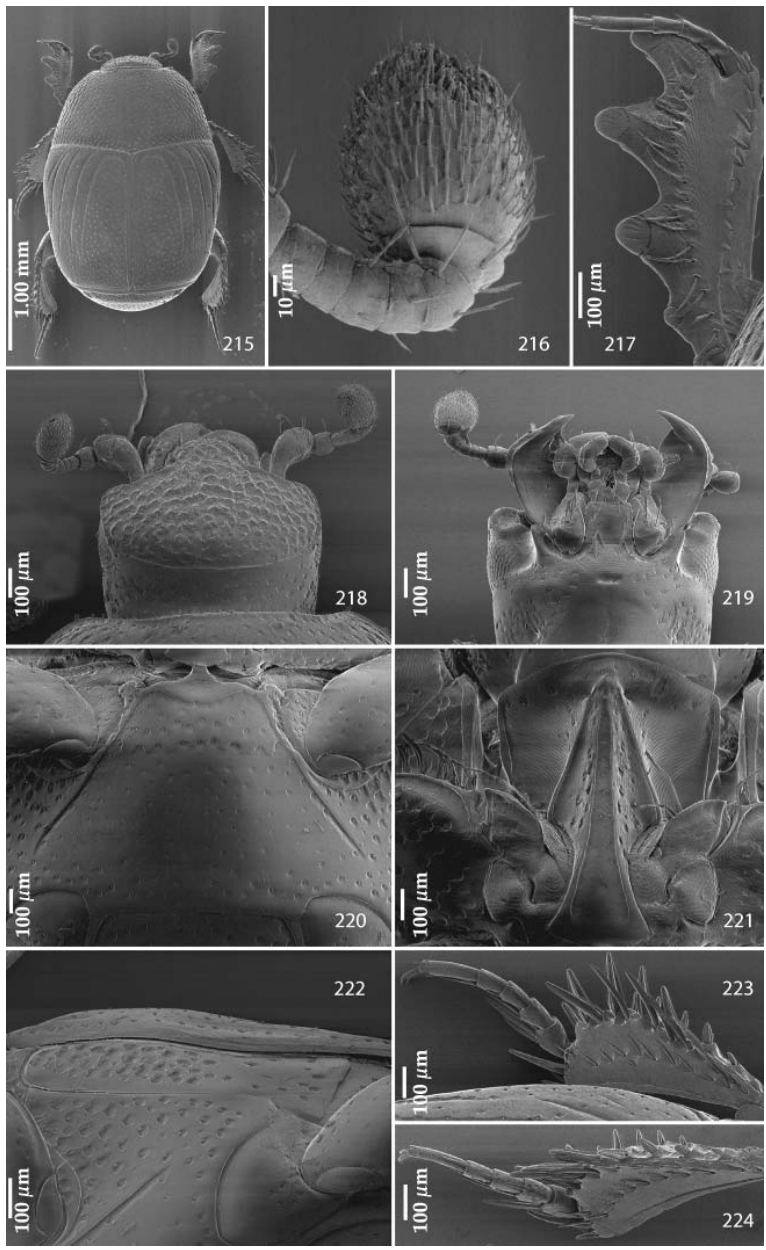
Anterior margin of median portion of prosternum (Fig. 221) rounded; marginal prosternal stria present laterally and as apical fragment; pre-apical foveae small; prosternal process narrow, interspace between carinal prosternal striae with scattered microscopic punctation; surface between carinal and lateral prosternal striae with several large coarse punctures, interspaces substrigulate; remaining surface of prosternal process strigulate, impunctate; carinal prosternal striae convergent anteriorly, united in front of carinate lateral prosternal striae.

Anterior margin of mesoventrite (Fig. 220) deeply emarginate medially; discal marginal mesoventral stria complete; disc with scattered punctures, separated by 1–3 times their diameter; meso-metaventral sutural stria undulate, somewhat distanced from meso-metaventral suture.

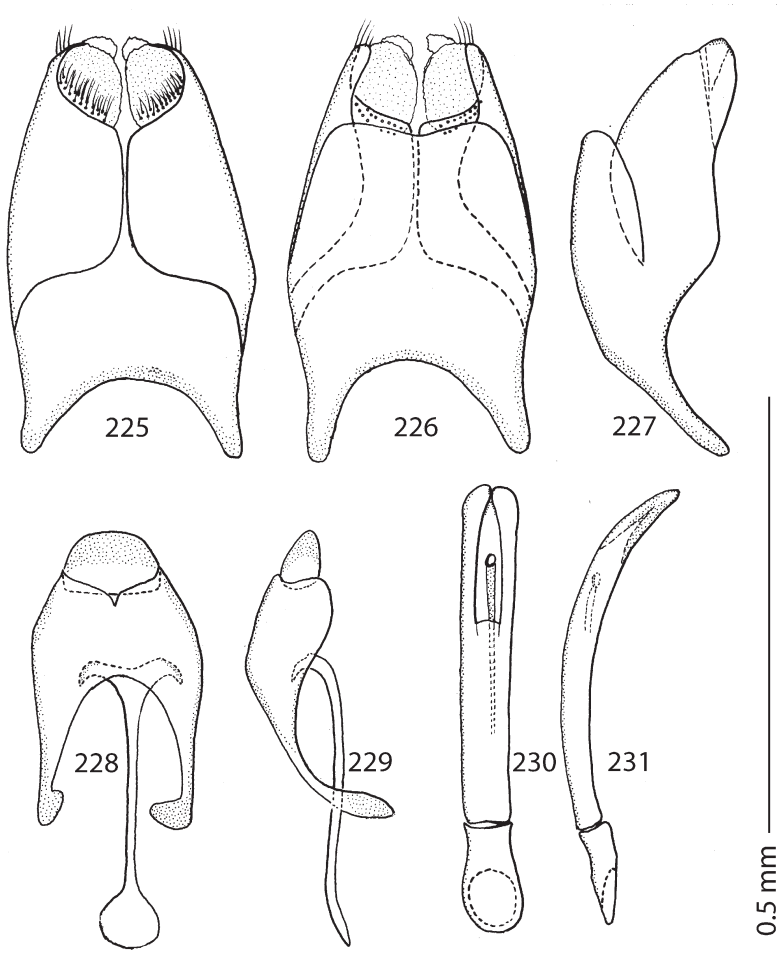
Intercoxal disc of metaventrite (Fig. 220) with scattered punctures, separated by several times their own diameter; lateral metaventral stria well impressed, shortened; lateral disc of metaventrite (Fig. 222) with shallow setiferous punctures; metepisternum with denser punctures, separated by about their own diameter, punctures with microscopic setae, base of metepisternum + fused metepimeron (Fig. 222) almost smooth, with several scattered punctures.

Intercoxal disc of first abdominal sternite completely striate laterally, disc with regular round punctures separated by their own to twice their diameter.

Protibia (Fig. 217) dilated, outer margin with three large teeth, topped by round denticle, followed by two minute round denticles; protarsal groove deep; outer row of setae moderately dense and long; median row of setae sparser, setae shorter; anterior protibial stria shortened apically; protibial spur tiny, growing out from apical margin of protibia; outer part of posterior surface with shallow wrinkles intermingled with sparse umbilicate punctures; median part



Figs. 215–224. *Axelinus ghilarovi* Kryzhanovskij, 1976, SEM micrographs: 215 – habitus, dorsal view; 216 – antennal club, ventral view; 217 – protibia, dorsal view; 218 – head, dorsal view; 219 – ditto, ventral view; 220 – mesoventrite and metaventrite; 221 – prosternum; 222 – lateral disc of metaventrite and metepisternum and fused metepimeron; 223 – mesotibia, dorsal view; 224 – metatibia, dorsal view.



Figs. 225–231. *Axelinus ghilarovi* Kryzhanovskij, 1976, male terminalia: 225 – 8th sternite and tergite, ventral view; 226 – ditto, dorsal view; 227 – ditto, lateral view; 228 – 9th tergite, 10th tergite (dorsal view) and spiculum gastrale (ventral view); 229 – 9th tergite, 10th tergite and spiculum gastrale, lateral view; 230 – aedeagus, dorsal view; 231 – ditto, lateral view

of posterior surface glabrous, separated from outer part by vaguely costiform stria; posterior protibial stria weakly impressed; inner margin of protibia with sparse short ramose setae; single inner posterior denticle present.

Mesotibia (Fig. 223) slightly dilated and thickened, outer margin with two rows of dense denticles growing in size apically; outer row of setae sparse, setae long and strongly sclerotized; setae of median row much shorter and weaker; posterior mesotibial stria almost complete; ventral surface almost smooth, with microscopic wrinkles; anterior mesotibial stria somewhat shortened apically; inner row of setae short; mesotibial spur long; apical margin

of mesotibia anteriorly with three inner anterior denticles; claws of apical tarsomere bent, longer that half its length; metatibia (Fig. 224) somewhat thicker than mesotibia, otherwise in all aspects similar to it.

Male genitalia. Eighth sternite (Figs. 225–226) longitudinally separated medially, apically with large inflatable membrane (velum) with single row of short dense setae; apex laterally with few longer sparser setae; eighth tergite and eighth sternite fused laterally (Fig. 227). Morphology of 9th tergite (Figs. 228–229) typical for the subfamily; spiculum gastrale (Fig. 228) expanded on both ends. Basal piece of aedeagus (Figs. 230–231) short, ratio of its length : length of parameres 1 : 4; parameres fused along their basal two-thirds; aedeagus gently curved ventrad (Fig. 231).

Chalcionellus Reichardt, 1932

Chalcionellus Reichardt, 1932: 15, 16. Type species: *Saprinus amoenus* Erichson, 1834, original designation.

Chalcionellus: Reichardt (1941): 155, 262; Dahlgren (1969a): 59–63, 66–68; Dahlgren (1969b): 230–231; Witzgall (1971): 172; Mazur (1973): 27, 36; Kryzhanovskij & Reichardt (1976): 111, 187; Mazur & Kaszab (1980): 7, 48; Vienna (1980): 116, 163; Mazur (1981a): 71, 94; Mazur (1984): 78; Mazur (1997): 245; Secq & Gomy (1999): 67; Yélamos (2002): 245, 296; Mazur (2004): 90.

Izpaniolus Mazur, 1972: 363. Type species *Saprinus condolens* Marseul, 1864, original designation. Synonymized by Secq & Yélamos (1993): 338.

Diagnosis. Body variously colored, often metallic; frontal stria thin, often curved outwardly, never carinate, usually interrupted (in which case first curved inwardly, thence curved outwardly and prolonged onto clypeus); clypeus in several taxa (e.g. *Chalcionellus decemstriatus*) depressed medially, laterally carinate; frontal disc punctate; eyes always convex. Pronotal foveae generally present, often a band of coarse punctation originates around them running parallel to pronotal margin; marginal pronotal stria always present and well visible, usually complete or slightly distanced on apical tenth from pronotal margin; lateral pronotal stria occasionally present (e.g. *Chalcionellus tyrius* (Marseul, 1857). If pronotal foveae are absent, clypeus usually distinctly carinate (except in some specimens of *Chalcionellus amoenus* (Erichson, 1834) and *C. ibericus* Dahlgren, 1969); pronotal hypomeron glabrous, apart from *Chalcionellus hauseri* (Schmidt, 1890) where the pronotal hypomeron is setose. Pre-apical foveae always present; both sets of prosternal striae present, seldom marginal prosternal stria connecting pre-apical foveae; outer margin of protibia with 5–8 moderately large teeth topped with denticle.

Differential diagnosis. *Chalcionellus* is most similar to the genera *Hypocacculus*, *Zorius*, *Hypocaccus*, or *Pholioxenus*, but differing from them: from *Hypocacculus* by the often present pronotal foveae (if these are absent, then clypeus is margined laterally) and more convex eyes; from *Pholioxenus* it likewise differs chiefly by the presence of pronotal foveae (if these are absent, then clypeus is margined laterally, whereas in *Pholioxenus* it is never margined laterally) as well as absence of microsculpture in-between elytral punctation (often present with *Pholioxenus*), larger pre-apical foveae (usually tiny, occasionally even absent in *Pholioxenus*); from *Zorius* it similarly differs by the presence of pronotal foveae (if these are absent, then the clypeus is margined laterally, whereas in *Zorius* it is never margined laterally) as well as by the present pre-apical foveae (always absent in *Zorius*) and from *Hypocaccus* it again differs by the presence of pronotal foveae, often present microsculpture on the elytra

(normally absent in *Hypocaccus*, present in several species of subgenus *Baeckmanniolus*) and the absence of chevrons or rugae on the frontal disc.

Biology. Species of this genus are mostly found on carrion and in dung, with the exception of *Chalcionellus hauseri* (Schmidt, 1894), which lives within the desiccating stalks of *Cistanche flava* Fedtschenko & Fedtschenko, 1913, as well as in the sand surrounding its roots (Reichardt 1941, Kryzhanovskij & Reichardt 1976, Kovarik & Caterino 2005). Here, these beetles prey upon the fly larvae of the genus *Eumerus* Meigen, 1822 (Syrphidae) (Kryzhanovskij & Reichardt 1976).

Distribution. *Chalcionellus* currently comprises 33 described species worldwide; one species, *Chalcionellus mersinae* (Marseul, 1857), is regarded as *incertae sedis*. This genus is distributed mostly in the Palaearctic and Afrotropical Regions, with several representatives in the Indo-Malayan Region, too. *Chalcionellus aeneovirens* (Schmidt, 1890) has been introduced into Australia. *Chalcionellus* is absent in North and South America and except for the above-mentioned species it is normally absent in Australopacific Region, too (Mazur 1997).

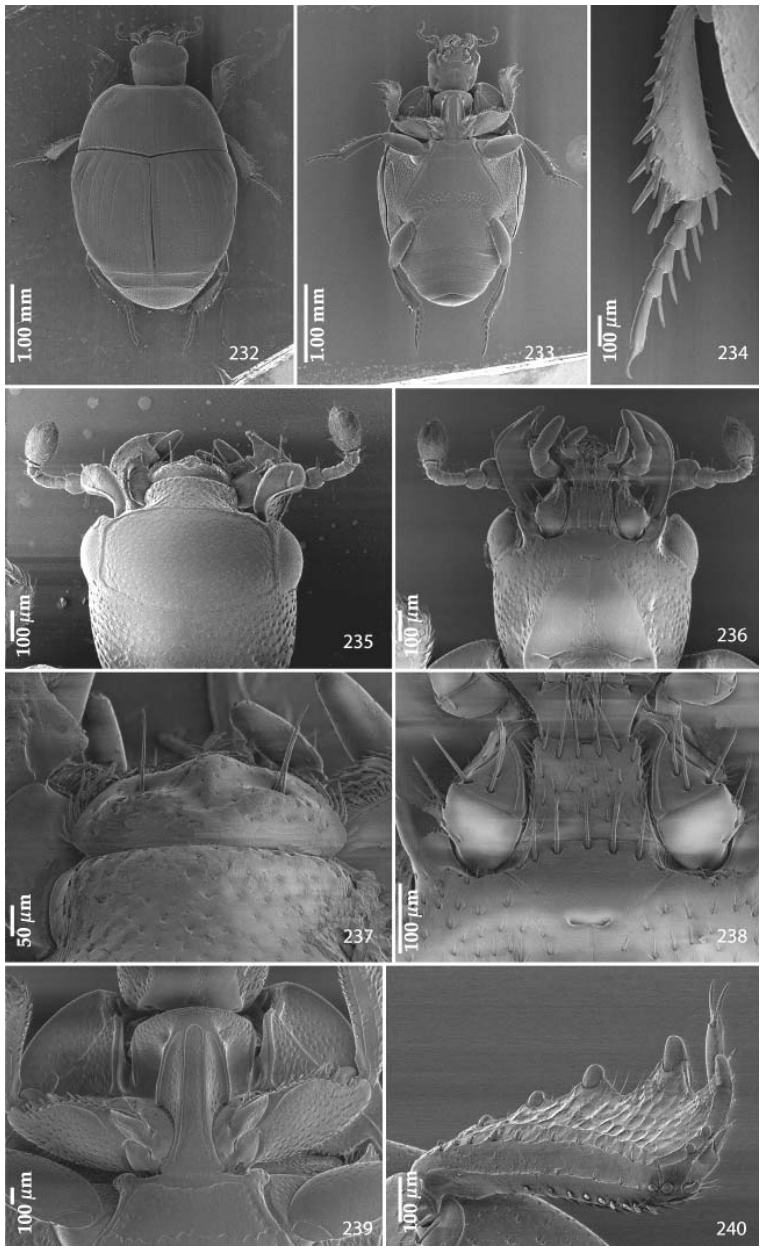
Species examined. *Chalcionellus aemulus* (Illiger, 1807), *C. amoenus* (Erichson, 1834), *C. blanchii blanchii* (Marseul, 1855), *C. blanchii tauricus* (Marseul, 1862), *C. decemstriatus decemstriatus* (Rossi, 1792), *C. decemstriatus tingitanus* Reichardt, 1932, *C. geminus* Dahlgren, 1969, *C. hauseri* (Schmidt, 1894), *C. ibericus* Dahlgren, 1969a, *C. libanicola* (Marseul, 1870), *C. olexai* Lackner, 2002, *C. orcinus* Reichardt, 1932, *C. palaestinensis* (Schmidt, 1890), *C. persicus* Lackner, 2002, *C. sibiricus* Dahlgren, 1969a, *C. suspectus* (Schmidt, 1890), *C. tunisius* (Marseul, 1876), *C. turcicus* (Marseul, 1857), *C. tyrius* (Marseul, 1857), *Chalcionellus* sp. (Iraq).

Discussion. Phylogenetic validity of this taxon is highly questionable, in authors' opinion. It is probably a non-natural taxon, most likely paraphyletic, with respect to *Hypocacculus* and it is characterised by only few weak synapomorphies, especially the presence of pronotal foveae. However, even these are not present in all taxa and several of its species have been shifted between *Hypocacculus* and *Chalcionellus.* Therefore its validity should be tested in the future using modern phylogenetic methods. A species revision, an exciting and noble task in itself, would also be highly desirable in the case of *Chalcionellus*.

Chalcionellus amoenus (Erichson, 1834)

(Figs. 15, 49, 83, 112, 232–247)

Hister aereus: Dejean (1821): 48 (*nomen nudum*). Synonymized by Gemminger & Harold (1868): 782.
Hister mediocris: Dejean (1821): 48 (*nomen nudum*). Synonymized by Dejean (1837): 142.
Saprinus amoenus Erichson, 1834: 190.
Saprinus amoenus: Marseul (1855): 681, t. XIX, Fig. 124.
Saprinus sabuleti Rosenhauer, 1847: 24. Synonymized by Schmidt (1884): 237.
Saprinus conjugens var. *micans* Hochhut, 1872: 228. Synonymized by Schmidt (1890): 17.
Saprinus (*Hypocaccus*) *amoenus*: Schmidt (1885a): 311; Ganglbauer (1899): 388; Jakobson (1911): 650.
Hypocacculus amoenus: Bickhardt (1916): 96.
Chalcionellus amoenus: Reichardt (1932): 22, 79, t. III, Fig. 6; Reichardt (1941): 264, 270; Horion (1949): 340; Dahlgren (1969): 63, 67, Figs. 1H, 3B; Kryzhanovskij & Reichardt (1976): 189, 192, Figs. 383–385; Vienna (1980): 166; Mazur & Kaszab (1980): 49, Fig. 25F; Mazur (1984): 79; Mazur (1997): 246; Secq & Gomy (1999): 68, Figs. 1, 6, 10; Yélamos (2002): 296, 302, Figs. 147C, 148B, 149C, 151C; Mazur (2004): 90.
Chalcionellus amoenus var. *chalybaeus* Reichardt, 1932: 22.



Figs. 232–240. *Chalcionellus amoenus* (Erichson, 1834), SEM micrographs: 232 – habitus, dorsal view; 233 – ditto, ventral view; 234 – mesotibia, dorsal view; 235 – head, dorsal view; 236 – ditto, ventral view; 237 – clypeus and labrum, dorsal view; 238 – mentum and cardines and stipites of maxilla, ventral view; 239 – prosternum and mesoventrite; 240 – protibia, ventral view.

Type locality. Portugal.
Material examined: KAZAKHSTAN: Kujuk, Kara Tau, Jambol, 5.v.1981, 1 ♂, A. Olexa lgt.; Assa env., Jambol, 10.v.1981, 2 spec., A. Olexa lgt.; Alma Arasan, Alma Ata, 10.vii.1976, 1 ♂, A. Olexa lgt. **UZBEKISTAN:** Aman Kutan (Samarqand), 16.v.1974, 1 ♂, A. Olexa lgt. (TLAN).

Redescription. Body length: PEL: 2.375–2.50 mm; APW: 0.825–0.875 mm; PPW: 1.625–1.875 mm; EL: 1.50–1.625 mm; EW: 2.00–2.125 mm.

Body (Figs. 232–247) roundly oval, moderately convex; cuticle shining, dark brown to black, with slight greenish or bluish metallic luster; elytral humeri slightly prominent, legs, antennae and mouthparts reddish-brown.

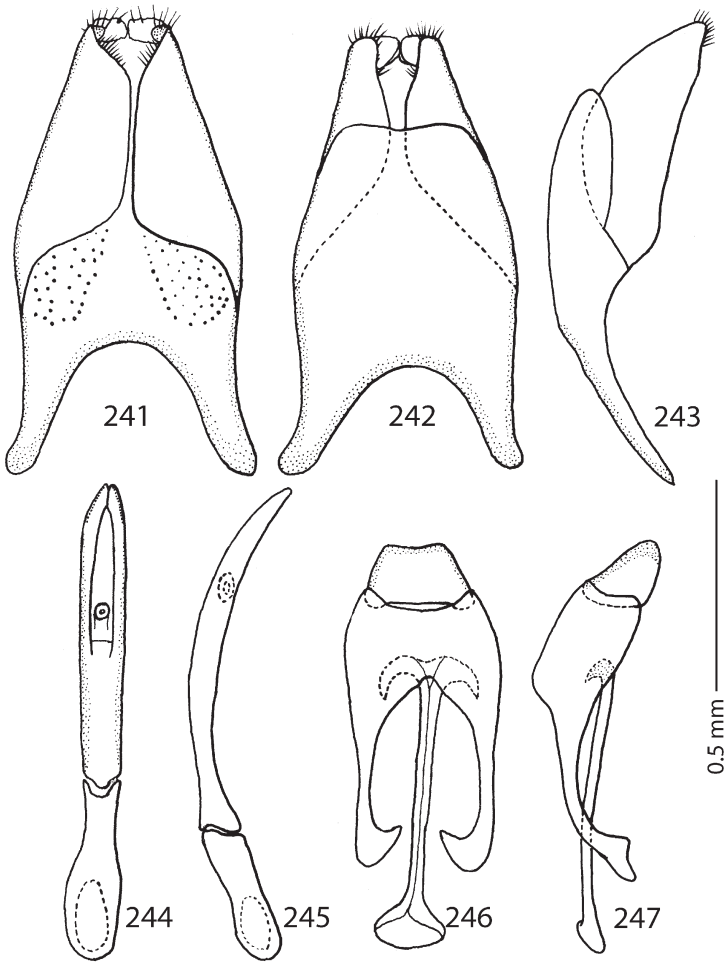
Antennal scape (Fig. 235) moderately dilated, with two short setae; club without visible articulation, entire surface with short dense sensilla, intermingled with sparse longer sensilla; sensory structures of antennal club (Fig. 15) in form of stipe-shaped vesicle situated under a large circular sensory area on internal distal margin of the ventral side of antennal club supplemented by another sensory area under apical surface of club.

Mouthparts. Mandibles (Fig. 83) with rounded outer margin curved inwardly, sub-apical tooth on left mandible large, perpendicular, mandibular apex acutely pointed; labrum (Figs. 49, 237) punctated, anterior margin with median concavity interrupting convexity; disc of labrum with two well impressed labral pits fringed with two setae; terminal labial palpomere elongated, its width about one-third its length; mentum (Fig. 238) sub-trapezoid; anterior margin medially with a small acute notch (Fig. 112); anterior margin with four long setae; disc of mentum entirely with dense, much shorter setae. Cardo of maxilla (Fig. 238) on outer margin with few short setae; stipes (Fig. 238) triangular, with three somewhat longer setae; terminal maxillary palpomere elongated, its width about one-fourth its length, about twice as long as penultimate.

Clypeus (Fig. 237) flat, rounded laterally, coarsely punctate; frontal stria complete, almost straight, somewhat weakened anteriorly, continued as carinate supraorbital stria; frontal disc with fine even punctation, punctures separated by their own to twice their diameter; eyes convex, well visible from above.

Pronotal sides (Fig. 232) moderately convergent anteriorly; apical angles blunt; pronotal foveae large, deeply impressed; disc laterally with a band of coarse punctation running parallel to lateral margin; between it and pronotal margin punctation weakens and becomes very fine; median part of pronotum with scattered microscopic punctures; pronotal base with a row of coarse round punctures; marginal pronotal stria well impressed, carinate, stopping just short of posterior angles; pronotal hypomeron with microscopic setae, almost glabrous.

Elytral epipleuron almost smooth, with microscopic punctation; marginal epipleural stria well impressed, complete; marginal elytral stria well impressed, in deep round punctures; apically shortly prolonged onto elytron, thence obliterated. Humeral elytral stria well impressed on basal third; inner subhumeral stria present as a short medial fragment in a form of row of punctures; elytra with four dorsal striae 1–4; first the shortest, not reaching elytral half apically; second, third and fourth about the same length, reaching about two-thirds of elytral length apically; fourth the longest, basally well connected with the sutural elytral stria; sutural stria well impressed and complete, in deep punctures. Punctation of elytral disc confined to



Figs. 241–247. *Chalcionellus amoenus* (Erichson, 1834), male terminalia: 241 – 8th sternite and tergite, ventral view; 242 – ditto, dorsal view; 243 – ditto, lateral view; 244 – aedeagus, dorsal view; 245 – ditto, lateral view; 246 – 9th tergite, 10th tergite (dorsal view) and spiculum gastrale (ventral view); 247 – 9th tergite, 10th tergite and spiculum gastrale, lateral view.

posterior third, punctures separated by about their own to twice their own diameter; intermingled with very fine scattered punctation.

Propygidium and pygidium with round punctures, separated by about their own to twice their diameter; punctation of propygidium somewhat denser and coarser than that of pygidium.

Anterior margin of median portion of prosternum (Fig. 239) evenly rounded; marginal prosternal stria shortly present anteriorly; pre-apical foveae well impressed, rather deep

(according to KRYZHANOVSKIJ & REICHARDT (1976) some specimens of this species may lack pronotal foveae altogether); prosternal process flattened; dorso-laterally with sparse, moderately-sized punctures; carinal prosternal striae well impressed, almost parallel, united anteriorly; lateral prosternal striae carinate, convergent anteriorly, attaining united carinal striae. Anterior margin of mesoventrite (Fig. 239) moderately emarginate medially, discal marginal mesoventral stria well impressed, slightly carinate; disc of mesoventrite with fine scattered punctation, along lateral margins a row of coarser punctures present; meso-metaventral sutural stria weakly impressed, undulate; intercoxal disc of metaventrite with fine scattered punctures; along apical margin band of coarse punctures present; lateral metaventral stria well impressed, in deep punctures, extending obliquely, stopping short of hind coxa. Lateral disc of metaventrite with shallow, round setiferous punctures, separated by about half to their own diameter, becoming finer apically; metepisternum with similar punctation, punctures without setae, metepisternal stria absent.

Intercoxal disc of first abdominal sternite completely striate laterally; disc antero-laterally with round coarse punctures; medially punctation much finer and sparser; along apical margin a row of fine punctures present.

Protibia (Fig. 240) slightly dilated, outer margin with three moderately large triangular teeth topped with tiny denticle, followed by one low tooth topped by minute denticle and three minuscule denticles, becoming progressively smaller in proximal direction; protarsal groove shallow; outer row of setae sparse, setae short; median row of setae somewhat denser, but setae even shorter; anterior protibial stria shortened apically; near tarsal insertion two tiny tarsal denticles present; protibial spur very short, growing out from apical margin of protibia; outer part of posterior surface of protibia (Fig. 240) obscurely variolate, a row of 7–8 minute denticles separating it from glabrous median part of posterior surface; posterior protibial stria complete, with very sparse minute sclerotized setae, terminating in two tiny inner posterior denticles; inner margin of setae double, setae short and dense.

Mesotibia (Fig. 234) slightly thickened, outer margin with two rows of moderately sized denticles; outer row of setae sparse, setae about as long as denticles, growing in size apically; median row of setae double, setae much finer and shorter; posterior mesotibial stria shortened, present only basally; anterior surface of mesotibia with scattered minute punctures; anterior mesotibial stria almost complete, terminating in two tiny denticles; mesotibial spur moderately large; apical margin of mesotibia with several inner anterior denticles; claws of apical tarsomere slightly bent, about half its length. Metatibia slenderer than mesotibia, outer margin with much sparser and shorter denticles, otherwise in all aspects similar to mesotibia.

Male genitalia. Eighth sternite (Figs. 241–242) longitudinally separated medially, apically with small inflatable membrane (velum) with single row of short dense setae; apex with few longer sparser setae; eighth tergite and eighth sternite not fused laterally (Fig. 243). Morphology of 9th tergite (Figs. 246–247) typical for the subfamily; spiculum gastrale expanded on both ends. Basal piece of aedeagus (Figs. 244–245) rather long, ratio of its length : length of parameres 1 : 2.5; parameres fused along their basal half; aedeagus gently curved ventrad (Fig. 245).

Chivaenius Olexa, 1980

Chivaenius Olexa, 1980: 252. Type species: *Chivaenius kryzhanovskii* Olexa, 1980, original designation.
Chivaenius: Mazur (1984): 91; Mazur (1997): 256; Mazur (2004): 91.

Diagnosis. Terminal labial and maxillary palpomeres thickened, truncate, sensory region of maxillary and labial palpi wide; labral pits absent; head comparatively small; frontal disc with vague shallow punctures and vaguely marked longitudinal rugae; frontal stria straight, carinate, continued as carinate supraorbital stria; eyes inconspicuous from above. Pronotal disc laterally shallowly areolate-rugulose, hypomeron glabrous; marginal pronotal stria carinate, visible along its entire length from dorsal view. Pre-apical foveae very small (in some specimens even absent); carinal prosternal striae absent (at most vaguely marked on prosternal apophysis); lateral prosternal striae strongly convergent anteriorly; prosternal process compressed, almost knife-like; lateral parts of pleura and sterna setose. Protibia strongly dilated, outer margin with three low teeth topped with large triangular denticle, followed by four minuscule denticles; meso- and metatibiae slender, not dilated or thickened.
Differential diagnosis. *Chivaenius* is somewhat superficially similar to the species of the genera *Hypocaccus* and *Hypocacculus* differing from them by the shape of protibia, compressed, almost knife-like prosternal process, absent lateral prosternal striae and tiny (occasionally even absent) pre-apical foveae. Species of the genus *Hypocaccus* are also devoid of ventral vestiture, whereas this taxon is densely setose on pleura and sterna. By the shape of protibia and setose pleura and sterna this genus is, on the other hand, similar to species of the genus *Exaesiopus* differing by the absence of prominent rugae on frontal disc, absent lateral prosternal striae as well as tiny (and at times even absent) pre-apical foveae (large and well developed in *Exaesiopus*). The lateral prosternal striae are (except for this taxon) absent in several Palaearctic genera of Saprininae: *Eremosaprinus*, *Philothis*, *Ctenophilothis* and *Ammostyphrus*. *Chivaenius* differs from *Ammostyphrus* by the shape of protibia as well as absent lateral pronotal stria (present in *Ammostyphrus*); from *Philothis* and *Ctenophilothis* it differs also by the shape of protibia and the shape of prosternal process, as well as the shape of meso- and metatibiae; from *Eremosaprinus* by the present ventral body vestiture and present frontal and supraorbital striae (both absent in *Eremosaprinus*).
Biology. Monotypic genus with *Chivaenius kryzhanovskii* as its only representative collected in the sand dunes. The beetles were found under *Tamarix*, together with other psammophilous species of Saprininae and Tenebrionidae (Olexa 1980).
Distribution. *Chivaenius kryzhanovskii* has been found near the city of Khiva, western Uzbekistan.
Species examined. *Chivaenius kryzhanovskii* Olexa, 1980.
Discussion. *Chivaenius* is most likely a well-defined monophyletic genus characterised by a few putative synapomorphies, the 'strongest' of which is probably the absence of labral pits and setae. Very small (and in some specimens even absent) pre-apical foveae as well as absent carinal prosternal striae can likewise be accounted among synapomorphies of this taxon; most of these are also present with the presumably most derived psammophilous Saprininae like *Philothis*.

Chivaenius kryzhanovskii Olexa, 1980

(Figs. 16, 50, 84, 113, 248–265)

Chivaenius kryzhanovskii Olexa, 1980: 254, Figs. 1–9.
Chivaenius kryzhanovskii: Mazur (1984): 91; Mazur (1997): 256; Mazur (2004): 91.

Type locality. Uzbekistan, Khiva.
Type material. Paratypes: ♂, 'Chiva [= Khiva] / Karakum / Uzbek. 3.v. / A. Olexa 1978 (printed) // *Tamarix* [printed] // PARATYPUS [red label, written] // *Chivaenius* / *kryzhanovski* / A. Olexa det. [red label, printed-written] // D07-018 [pink label, written]'; ♂, ditto, but with blue [instead of pink] label '06-024'; 3 spec., ditto, but without additional pink or blue labels (TLAN).
Additional material examined. UZBEKISTAN: 6 spec., ditto as paratypes, but 1.–5.v.1979 (TLAN).

Redescription. Body length: PEL: 2.25–3.00 mm; APW: 0.775–1.00 mm; PPW: 1.75–2.375 mm; EL: 1.50–2.00 mm; EW: 1.95–2.575 mm.

Body (Figs. 248–249) rectangular oval, strongly convex; cuticle castaneous brown with a feeble metallic luster; legs, antenna and mouthparts reddish-brown.

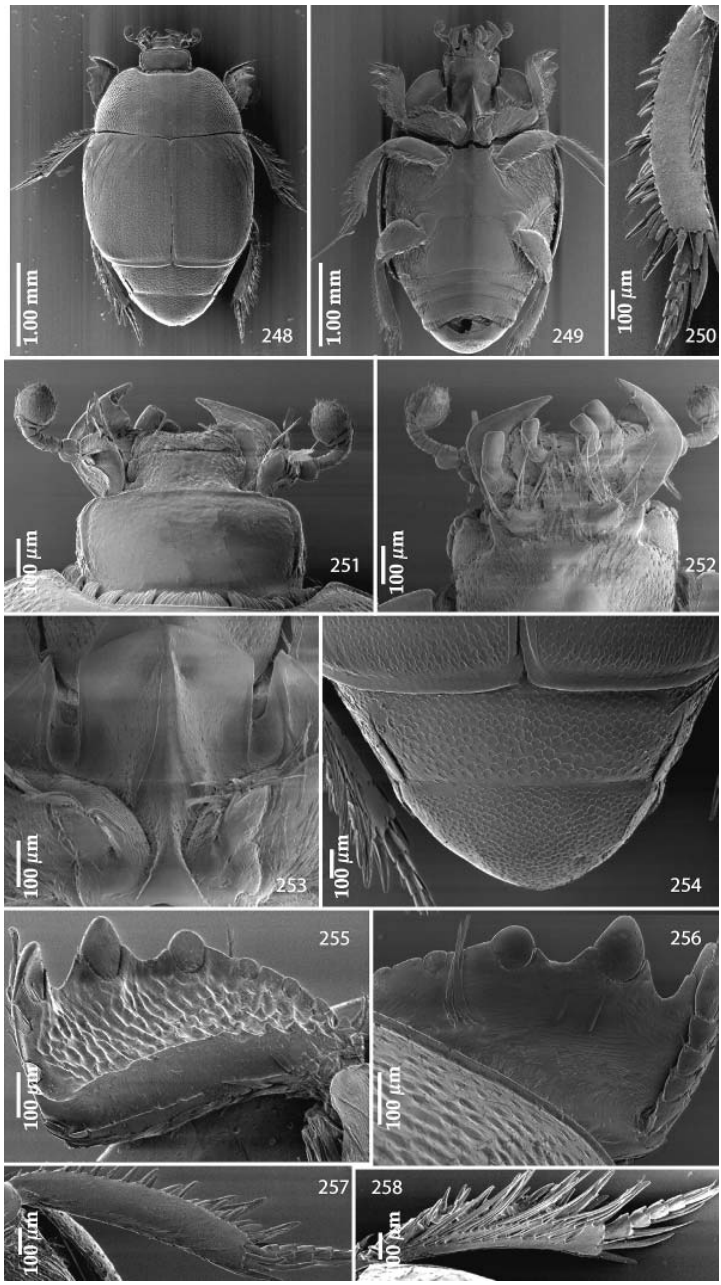
Antennal scape (Fig. 251) gently thickened; with several well sclerotized moderately long setae; club rather small, round, without visible articulation, with short dense sensilla intermingled with much sparser and longer erect sensilla; basal sixth of club glabrous; eighth antennomere saucer-like; sensory structures of antennal club (Fig. 16) in form of stipe-shaped vesicle situated under a large circular sensory area under apical surface of antennal club supplemented by another large sensory area under apical surface of club.

Mouthparts. Mandibles (Fig. 84) with carinate outer margin strongly curved inwardly; mandibular apex acutely pointed; sub-apical tooth on left mandible large, almost perpendicular; labrum (Fig. 50) sparsely punctate; labral pits absent; anterior margin slightly emarginate medially; terminal labial palpomere thickened, its width about half its length, apically truncate, sensory region wide; mentum square shaped, anterior margin (Fig. 113) shallowly emarginate medially, with numerous long setae, lateral margins with one row of sparse shorter setae; cardo of maxilla with two long setae on lateral margin; stipes triangular, with four strongly sclerotized long setae; terminal maxillary palpomere thickened, its width about half its length, apically truncate, sensory region wide.

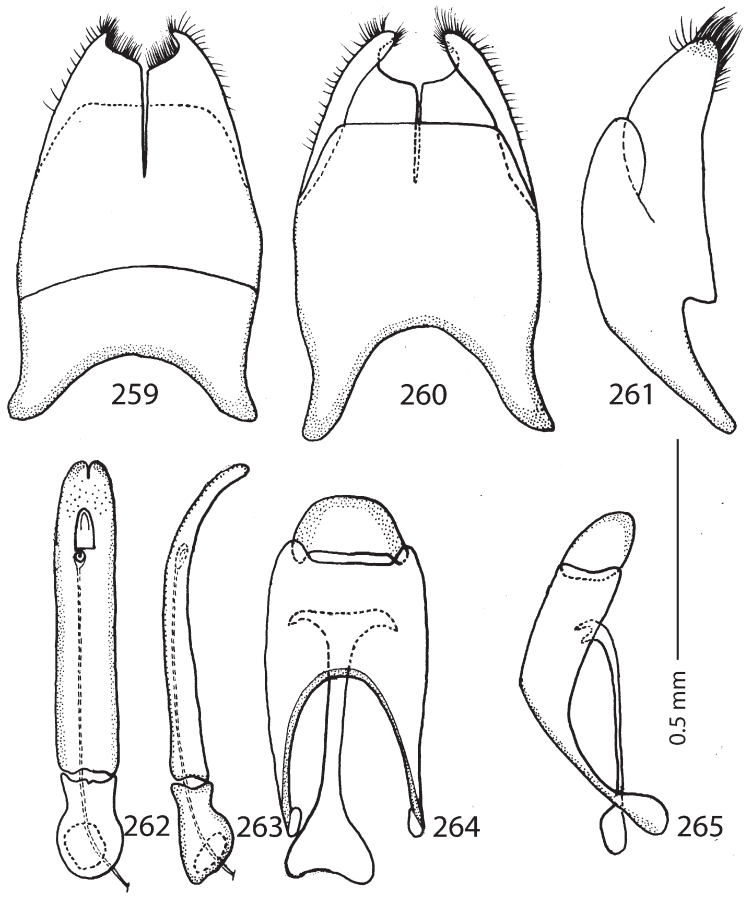
Clypeus (Fig. 251) rounded laterally, anterior margin slightly elevated, somewhat depressed medially, with granulate punctures; frontal stria well impressed, carinate, straight, continued as carinate supraorbital stria, posteriorly connected as complete occipital stria; frontal disc flat, about twice as broad as long; disc with vague shallow punctures and vaguely marked longitudinal rugae; eyes flattened, inconspicuous from above.

Pronotal sides (Fig. 248) almost straight on posterior tenth, thence moderately convergent forwardly; apical angles rather blunt, median incision for head relatively deep, almost straight in middle; marginal pronotal stria well impressed, carinate on outer margin, weakened behind head, along entire length visible from dorsal view; disc rather flattened, laterally shallowly areolate-rugulose, interspaces with microsculpture, punctation medially weakened, antescutellar area almost smooth, with only few scattered punctures; base of pronotal disc with a row of ovoid deep dense punctures; pronotal hypomeron glabrous.

Elytral epipleura smooth; marginal epipleural stria complete, well impressed and carinate; marginal elytral stria well impressed, apically shortly continued along elytral apex, next evanescent. Humeral elytral stria vaguely impressed on basal third; inner subhumeral



Figs. 248–258. *Chivaenius kryzhanovskii* Olexa, 1980, SEM micrographs: 248 – habitus, dorsal view; 249 – ditto, ventral view; 250 – metatibia, ventral view; 251 – head, dorsal view; 252 – ditto, ventral view; 253 – prosternum; 254 – propygidium and pygidium; 255 – protibia, ventral view; 256 – ditto, dorsal view; 257 – mesotibia, ventral view; 258 – ditto, dorsal view.



Figs. 259–265. *Chivaenius kryzhanovskii* Olexa, 1980, male terminalia: 259 – 8th sternite and tergite, ventral view; 260 – ditto, dorsal view; 261 – ditto, lateral view; 262 – aedeagus, dorsal view; 263 – ditto, lateral view; 264 – 9th tergite, 10th tergite (dorsal view) and spiculum gastrale (ventral view); 265 – 9th tergite, 10th tergite and spiculum gastrale, lateral view.

stria present medially as a short fragment; elytra with four dorsal elytral striae 1–4, first the longest, reaching about half of elytral length apically; slightly curved inwardly; second and third dorsal elytral striae rather thin, about the same length, not reaching elytral half apically, fourth elytral stria the shortest, reaching about one-fifth of elytral length apically, basally connected with sutural elytral stria; sutural stria vaguely impressed, on apical half obliterated beneath punctation. Elytral disc (apart from impunctate flanks and elytral intervals), entirely with dense and coarse punctures separated by half to their own diameter, punctures confluent along on elytral apex.

Propygidium (Fig. 254) completely exposed, about twice as broad as long, with large dense shallow punctures, along posterior margin punctures become sparser and confluent,

interspaces with microsculpture; pygidium (Fig. 254) convex, with smaller but even denser punctation; pygidial flanks smooth.

Anterior margin of median portion of prosternum (Fig. 253) obtuse-angulate; marginal prosternal stria absent; pre-apical foveae small (can be completely absent in some specimens); prosternal process compressed, almost knife-like, dorsally concave; laterally finely strigulate; carinal prosternal striae absent (in some specimens vaguely present on prosternal apophysis); lateral prosternal striae well impressed, strongly convergent anteriorly, united in front near pre-apical foveae.

Anterior margin of mesoventrite almost straight, discal marginal mesoventral stria anteriorly weakly impressed; disc with sparse punctures separated by about 2–4 times their diameter; meso-metaventral sutural stria vaguely impressed in a row of large irregular punctures; intercoxal disc of metaventrite medially concave in male, longitudinal suture of metaventrite well impressed, disc microscopically punctate, posterior margin with few scattered punctures; lateral metaventral stria well impressed, carinate, curved outwardly, shortened; lateral disc of metaventrite concave, with scattered shallow punctures fringed with long setae, interspaces with microsculpture; metepisternum + fused metepimeron with long amber setae, punctation unrecognizable.

Intercoxal disc of first abdominal sternite almost completely striate laterally; disc almost smooth, posterior margin with a double row of small shallow punctures; all visible abdominal sternites setose laterally.

Protibia (Figs. 255–256) strongly dilated, outer margin with three low teeth topped with large triangular denticles, followed by three to four minuscule denticles; outer row of setae completely absent on apical two-thirds; protarsal groove deep; protibial spur minuscule, almost unrecognizable; tarsus shortened, but not rudimentary; outer part of posterior surface (Fig. 255) areolate-rugulose, clearly separated from smooth median part of posterior surface; posterior protibial stria intermittent but complete, terminating in two short inner posterior denticles; inner row of setae dense, setae short, ramose; apical margin of protibia ventrally with two short broad denticles.

Mesotibia (Figs. 257–258) slender, outer margin with two rows of dense short denticles abutting each other; outer row of setae long, setae dense, well sclerotized; inner row of setae much shorter and sparser; posterior mesotibial stria intermittent, shortened apically; anterior surface (Fig. 257) smooth; anterior mesotibial stria unrecognizable; inner margin with a single row of moderately dense short setae; mesotibial spur long, prominent, surrounded by numerous denticles on apical margin; each tarsomere ventrally with one long denticle and an additional minuscule sclerotized seta; claws of apical tarsomere thin, slightly bent, longer than half its length; metatibia (Fig. 250) slender, slightly curved, in all aspects similar to mesotibia, but denticles on outer margin and setae of outer- and median rows somewhat sparser.

Male genitalia. Eighth sternite (Figs. 259–260) on apical half longitudinally fused medially; apex laterally with dense brush of longer setae; eighth tergite and eighth sternite fused laterally (Fig. 261). Morphology of 9th tergite (Figs. 264–265) typical for the subfamily; spiculum gastrale (Fig. 264) expanded on both ends. Basal piece of aedeagus (Figs. 262–263) short, ratio of its length : length of parameres 1 : 3; parameres fused almost along their entire length; aedeagus apically gently curved ventrad (Fig. 263).

Ctenophilothis Kryzhanovskij, 1987

Ctenophilothis Kryzhanovskij, 1987: 25. Type species: *Xenonychus chobauti* Théry, 1900, original designation.
Ctenophilothis: Olexa (1990): 143; Mazur (1997): 268; Mazur (2004): 91.

Diagnosis. Frontal stria completely absent, supraorbital stria present, frontal disc at times with weak median furrow; 8th antennomere cupuliform, broader than pedicel, in several cases surrounding antennal club up to one-third of its length; club ventrally glabrous, dorsally with small patches of sparse sensilla; labrum without labral pits or setae, smooth; sub-apical tooth on left mandible extraordinarily small; sensory region of maxillary palpus curiously shaped, cap-like; lateral sides of pronotum fringed with very short setae; pronotal foveae absent; pronotal hypomeron with long amber setae. Elytral epipleuron setose; elytra obscurely variolate; elytral flanks smooth; elytral disc with two dorsal elytral striae 1–2, occasionally third stria also vaguely marked on apical third; inner subhumeral stria almost complete; propygidium and pygidium also obscurely variolate; pygidial flanks smooth. Prosternal apophysis forms a well-margined triangular disc; lateral prosternal striae absent; prosternal process densely setose, gradually sloping down anteriorly; antennal cavities absent; pre-apical foveae absent; discal marginal mesoventral stria anteriorly absent; meso-metaventral sutural stria somewhat elevated, carinate; mesoventral disc almost as long as broad; lateral metaventral stria shortened apically, curved outwardly; post-mesocoxal stria absent. Protibia curved, outer margin with numerous long movable denticles and two low teeth topped with stout denticle; apical margin ventrally with several short stout denticles; posterior surface smooth; protarsus absent; inner row of setae dense, setae lamelliform; meso- and metatibiae dilated; meso- and metatarsi telescope-like, their diameter markedly diminishing apically; each tarsomere with two strongly sclerotized lamelliform setae, one dorsally, one ventrally; claws of meso- and metatarsi thin, long and straight.
Differential diagnosis. *Ctenophilothis* is most similar to the species of the genus *Philothis*, but differing from them chiefly by the shape of protibia that is adorned with numerous long denticles in *Ctenophilothis*, whereas the species of the genus *Philothis* have their outer margin of protibia with two large triangular teeth topped with tiny denticle.
Biology. *Ctenophilothis* is a psammophilous genus with two described species. Its biology is poorly understood, *Ctenophilothis chobauti* has been collected in Algerian Sahara together with several other species of the genus *Philothis*; biology of *Ctenophilothis altus* is virtually unknown.
Distribution. Sahara: Algeria, Egypt.
Species examined. *Ctenophilothis altus* (Lewis, 1885), *C. chobauti* (Théry, 1900).
Discussion. *Ctenophilothis* is most likely a monophyletic taxon, well characterised by several putative synapomorphies, among which can be listed the smooth, flattened labrum devoid of labral pits and setae, extraordinarily small sub-apical tooth of the left mandible, reduced dorsal elytral striae and the peculiarly shaped protibia with numerous long movable denticles on its upper margin. Most of these are present also with the presumably related taxon *Philothis* that lives basically in the same conditions as *Ctenophilothis*. On the other hand, setose ventral part of the body as well as strongly vaulted body and flattened eyes are probably morphological adaptations to the living conditions seen in other psammophilous genera.

Ctenophilothis chobauti (Théry, 1900)

(Figs. 17, 43, 46, 78, 85, 114, 266–281)

Xenonychus chobauti Théry, 1900: 32.
Styphrus chobauti: Bickhardt (1910): 107.
Philothis chobauti: Peyerimhoff (1936): 220, Figs. 2, 225; Mazur (1984): 109.
Ctenophilothis chobauti: Kryzhanovskij (1987): 25, Fig. 1; Olexa (1990): 146, 153, Figs. 6, 9, 10, 22, 27, 52, 53; Mazur (1997): 268; Mazur (2004): 91.

Type locality. Algeria, Touggourt.
Material examined. ALGERIA: Sahara, Béni Abbès, 20.x.1980, 2 ♂♂ 1 ♀, A. Olexa lgt.; Iglu, 12.iv.1988, 1 ♂ 1 ♀, A. Olexa lgt.; Béni Abbès, 11.iv.1988, 1 spec., A. Olexa lgt. (TLAN).
Note. The type specimen(s) of this species were not found in the collection of Théry, housed at MNHN. According to Mrs. Azadeh Taghavian (MNHN), it is possible that a part of Théry's collection is housed elsewehere. Therefore, a neotype for this species is not designated herein, since it is possible that the type specimen(s) may be found in the future.

Redescription. Body length: PEL: 2.00–2.375 mm; APW: 0.825–0.875 mm; PPW: 1.575–1.95 mm; EL: 1.375–1.625 mm; EW: 1.825–2.125 mm.

Body (Figs. 266–267) roundly oval, moderately convex from above, underside very convex, cuticle castaneous, feebly shining; legs and mouthparts reddish-brown, antennal flagellum yellow.

Antennal scape (Fig. 268) thickened, with numerous long setae; 8th antennomere (Fig. 268) cupuliform, in some specimens surrounding antennal club up to one-third its length; club (Fig. 268) moderately sized, sub-conical, without visible articulation, with sparse short sensilla; ventral surface glabrous; sensory structures of antennal club (Fig. 17) in form of stipe-shaped vesicle situated under a large circular sensory area on internal distal margin of the ventral side of antennal club, supplemented by another large sensory area opposite to first one.

Mouthparts. Mandibles (Fig. 85) smooth, thin, evenly curved, mandibular apex acutely pointed, sub-apical tooth on left mandible extremely small, almost absent; labrum (Fig. 46) deeply incised under clypeus, with shallow median depression, smooth; epipharynx completely hidden under labral fold (Figs. 43, 78); labral pits and setae arising from them absent; terminal labial palpomere thickened, its width about half its length; mentum sub-trapezoid, with a shallow median emargination (Fig. 114); anterior and lateral margins with two rows of long setae; several setae present also on disc of mentum; cardo of maxilla on lateral margin with few long setae; stipes triangular, with four-five well sclerotized long setae; terminal maxillary palpomere thickened, its width longer than half its length, about three times as long as penultimate; sensory region of maxillary palpus curiously shaped, cap-like.

Clypeus (Fig. 269) rectangular, rounded laterally, smooth; frontal stria absent; supraorbital stria fine, slightly carinate; postorbital stria interrupted medially; frontal disc broad, rounded, smooth (in some specimens with very fine frontal furrow); eyes flattened, invisible from above.

Pronotal sides (Fig. 266) slightly narrowing anteriorly, anterior angles obtuse; marginal stria laterally carinate, on posterior tenth somewhat distanced from lateral margin, broadly interrupted behind head; surface along lateral margins fringed with short setae; disc moderately convex, with undulate or angular transverse wrinkles, area along anterior margin behind

head smooth; pronotal hypomeron with long amber setae; scutellum almost invisible in some specimens.

Elytral humeri not prominent, epipleura setose (Fig. 273); marginal epipleural stria complete, thin; marginal elytral stria well impressed, carinate, abbreviated on elytral apex; humeral elytral stria vaguely impressed, at times indistinguishable; inner subhumeral almost complete, parallel to first dorsal elytral; outer subhumeral stria vaguely impressed on basal fifth; first and second dorsal striae well impressed; first reaching elytral apex, apically bent inwardly, at times somewhat continued along apical margin; second dorsal elytral stria abbreviated on basal fourth, apically bent inwardly, almost complete; basal elytral stria present, vaguely connected with first dorsal elytral and sutural striae; sutural elytral stria well impressed, apically connected with apical elytral stria, on basal half somewhat distanced from elytral suture; elytral disc obscurely variolate, area between sutural stria and elytral suture, and area between elytral base and basal elytral stria smooth; elytral flanks smooth; wrinkles along elytral apex confluent.

Propygidium completely exposed, almost twice as long as broad, obscurely variolate; pygidium very convex, about as long as broad, obscurely variolate medially, laterally and apically smooth.

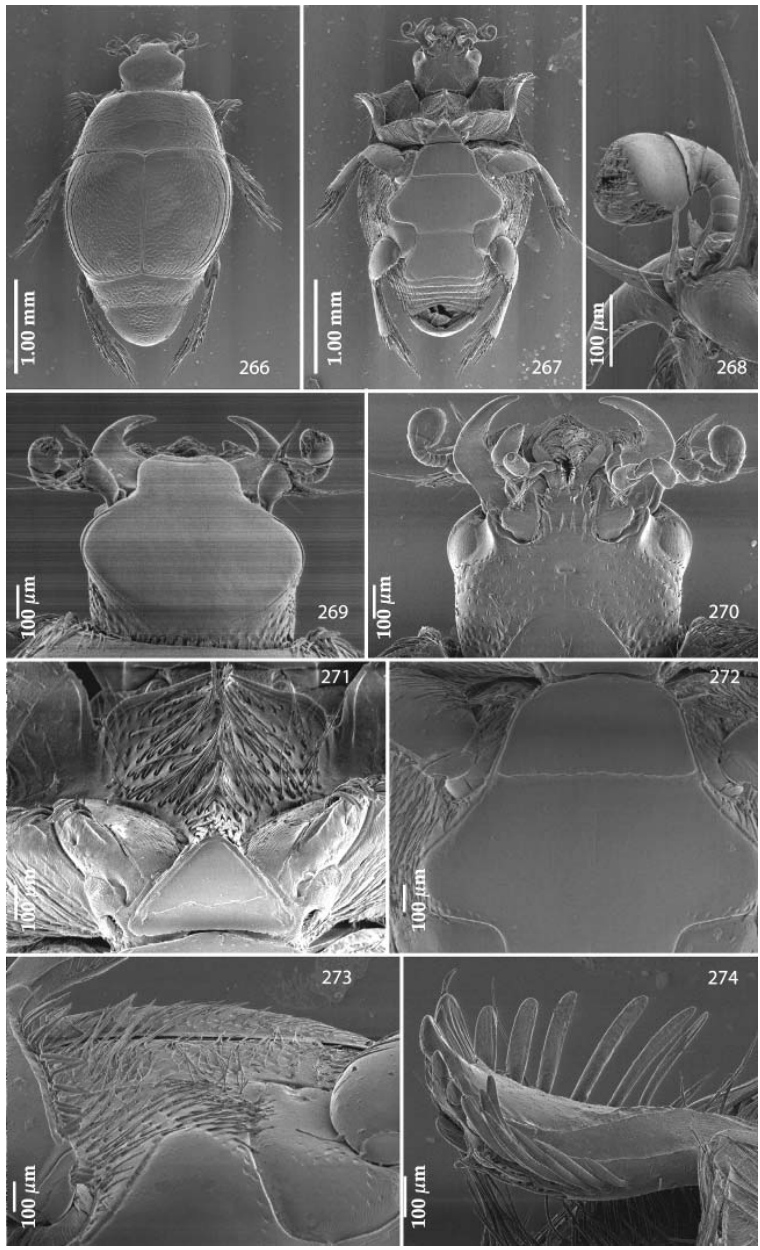
Anterior margin of prosternum (Fig. 271) obtuse-angulate; marginal prosternal stria well impressed and complete; prosternal process densely setose, abruptly and strongly sloping down anteriorly behind striate triangular prosternal apophysis; lateral prosternal striae absent.

Anterior margin of mesoventrite (Fig. 272) somewhat curved outwardly; discal marginal mesoventral stria absent anteriorly, laterally carinate; mesoventral disc smooth; meso-metaventral suture well impressed, straight; meso-metaventral sutural stria somewhat distanced from suture, undulate and carinate; intercoxal disc of metaventrite (Fig. 272) smooth; lateral metaventral stria curved outwardly, shortened; post-mesocoxal stria absent; lateral disc of metaventrite (Fig. 273) concave, with shallow punctures separated several times their diameter, punctures with long amber setae; metepisternum + fused metepimeron (Fig. 273) densely setose, punctation almost unrecognizable beneath setae.

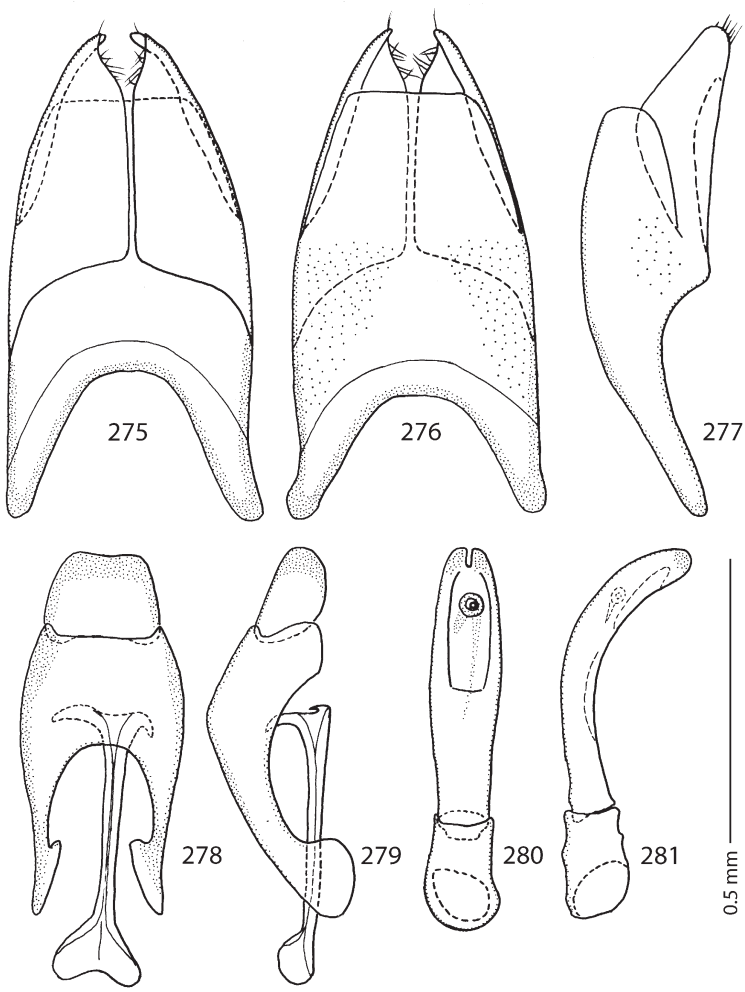
Intercoxal disc of the first abdominal sternite laterally with a thin incomplete stria; disc smooth, in postero-lateral corners with several short setae; dorsal and lateral discs of all visible abdominal sternites setose. All femora on outer and inner margins with long amber setae, profemur with setae on entire surface.

Protibia curved ventrad (Fig. 274), dilated and somewhat thickened, outer margin with sparse row of long movable denticles, apically with two low teeth topped with stout denticle; outer row of setae very dense, setae very long; anterior protibial stria indistinguishable; protarsus absent; posterior surface of protibia (Fig. 274) smooth; outer part of posterior surface separated from median part by thin stria; median part separated from inner part of posterior surface by complete posterior protibial stria; apical margin ventrally with several stout denticles; inner margin with dense row of long lamelliform setae; protibial spur minute.

Mesotibia slightly dilated and thickened, outer margin with two dense rows of long denticles abutting each other, denticles grow in size apically; outer row of setae dense, setae strongly sclerotized, long; median row of setae sparse, setae several times shorter; posterior mesotibial stria present only on basal third, next obliterated; anterior surface of mesotibia



Figs. 266–274. *Ctenophilothis chobauti* (Théry, 1900), SEM micrographs: 266 – habitus, dorsal view; 267 – ditto, ventral view; 268 – right antenna, dorsal view; 269 – head, dorsal view; 270 – ditto, ventral view; 271 – prosternum; 272 – mesoventrite and metaventrite; 273 – lateral disc of metaventrite, metepisternum and fused metepimeron; 274 – protibia, ventral view.



Figs. 275–281. *Ctenophilothis chobauti* (Théry, 1900), male terminalia: 275 – 8th sternite and tergite, ventral view; 276 – ditto, dorsal view; 277 – ditto, lateral view; 278 – 9th tergite, 10th tergite (dorsal view) and spiculum gastrale (ventral view); 279 – 9th tergite, 10th tergite and spiculum gastrale, lateral view; 280 – aedeagus, dorsal view; 281 – ditto, lateral view.

smooth; anterior mesotibial stria shortened apically; apical margin with dense row of thick denticles growing in size towards tarsal insertion; mesotibial spur the longest; tarsus thickened, short, telescope-like, diameter of each tarsomere diminishing apically; each tarsomere with two strongly sclerotized lamelliform setae, one dorsally, one ventrally; claws of meso- and metatarsi thin, long and straight, several times the length of last tarsomere; metatibia generally very similar to mesotibia, but even more dilated.

Male genitalia. Eighth sternite (Figs. 275–276) longitudinally separated medially, apically with row of sparse short setae; eighth tergite and eighth sternite fused laterally (Fig. 276). Morphology of 9th tergite (Figs. 278–279) typical for the subfamily; spiculum gastrale (Fig. 278) expanded on both ends. Basal piece of aedeagus (Figs. 280–281) short, ratio of its length : length of parameres 1 : 3.25; parameres fused along their basal half; aedeagus apically curved ventrad (Fig. 281).

Eopachylopus Reichardt, 1926

Eopachylopus Reichardt, 1926: 14 (as a subgenus of *Neopachylopus* Reichardt, 1926). Type species: *Pachylopus ripae* Lewis, 1885, original designation.

Eopachylopus: Reichardt (1941): 157, 327; Kryzhanovskij & Reichardt (1976): 111, 241; Mazur (1984): 108; Ôhara (1994): 214, 262; Mazur (1997): 266; Mazur (2004): 91.

Diagnosis. Cuticle not metallic, usually black with red elytral maculae; frontal stria carinate; supraorbital, postorbital striae complete; frontal disc smooth; pronotal disc almost smooth, marginal pronotal stria complete, pronotal foveae absent, pronotal hypomeron glabrous; elytral disc smooth, marginal elytral stria complete, apical elytral stria complete, dorsal elytral striae abbreviated, sutural stria well-impressed, basally abbreviated. Propygidium with sparse round punctures and microsculpture; pygidium almost smooth. Prosternal process strongly compressed, knife-like, pre-apical foveae absent; carinal striae present only on prosternal apophysis; lateral prosternal striae very shortened, convergent anteriorly, apically connected attaining about middle of prosternal process; discs of meso- and metaventrite smooth; lateral disc of metaventrite and metepisternum with dense setiferous punctures. Posterior surface of protibia with several rows of denticles; mesotibia and metatibia slightly thickened and dilated apically; anteriorly with at least four dense rows of denticles; claws of apical tarsomere long, thin; metafemora thickened.

Differential diagnosis. By the compressed prosternal process *Eopachylopus* is somewhat similar to the genus *Chivaenius* differing from it by numerous characters: absent pronotal as well as elytral punctation (present in *Chivaenius*), the shape of tibiae, much shorter ventral vestiture (considerably longer in *Chivaenius*) as well as the frequent presence of red elytral maculae (absent in *Chivaenius*).

Biology. *Eopachylopus* is a littoral taxon, occurring under wrack where it probably preys on wrack-associated dipteran larvae (Ôhara, pers. comm. 2006).

Distribution. This is a monotypic genus with *Eopachylopus ripae*, as its only representative. This species is distributed in Japan and in Russian Far East. Recently recorded also from Hong Kong (de Rougemont 2000); the identity of these specimens needs to be confirmed by further studies.

Species examined. *Eopachylopus ripae* (Lewis, 1885).

Discussion. This taxon is defined by several putative synapomorphies, e.g. very shortened lateral prosternal striae or absent pre-apical foveae and knife-like prosternal process. However, its phylogenetic validity should be tested in the future, focusing especially on its relationship with Nearctic as well as Middle-Eastern representatives of the genus *Neopachylopus*. *Eopachylopus* was originally described as a subgenus of *Neopachylopus*.

Eopachylopus ripae (Lewis, 1885)

(Figs. 18, 51, 86, 115, 282–298)

Pachylopus ripae Lewis, 1885: 469.
Saprinus ripae: Bickhardt (1910): 107.
Neopachylopus (*Eopachylopus*) *ripae*: Reichardt (1926): 14.
Eopachylopus ripae: Reichardt (1941): 328; Kryzhanovskij & Reichardt (1976): 241, Figs. 114, 470; Mazur (1984): 108; Ôhara (1994): 264, Figs. 160–162; Mazur (1997): 266; Mazur (2004): 91.
Eopachylopus ripae ab. *therskii* Reichardt, 1941: 407.
Neopachylopus ripae f. *rufofasciatus* Osawa, 1952: 4.

Type localities. Japan, Hakodate and Enoshima.
Type material. *Pachylopus ripae.* Syntype: 1 spec., 'Hakodate / G. Lewis 1880 [written] // *Pachylopus* / *ripae* / Type, Lewis [written] // G. Lewis Coll. / B.M. 1926-369. [printed]' (BMNH).
Additional material examined. JAPAN: Chiba: Ôami, 19.vi.1984, 1 ♂, M. Ôhara lgt.; 3 spec., ditto, 2 spec., ditto, but 1.v.1990. **Fukushima:** Iwaki city, Fujima Coast, 25.vi.1988, 1 spec., K. Tazoe lgt. **Aichi:** Toyohashi city, Hosoya, 21.v.1990, 2 spec., M. Hasegawa lgt.; 1 spec., ditto, but 24.vi.1990. **Kanagawa:** Kamakura, Shichiri-ga-hama, 24.viii.1989, 1 spec., K. Kawada lgt. **Kagoshima:** Tanega-shima, Hamada, Osumi-shotô, 31.vii.1984, 1 ♀ 1 spec., Y. Harada lgt. **Hokkaido:** Minehama, Syari T., 4.viii.1999, 1 spec., N. Ishihama & T. Yoshida lgt., carrion of a seal; Muroran, 25.vi.1960, 2 spec., T. Yamashita lgt. **Ishikawa:** Kanazawa-city, Kanaiwa, 27.vii.1991, 2 spec., K. Nakata lgt.; Uchinada-Sakyu, 31.viii.1968, 7 spec., Ebihara lgt. **Miya:** Mikawa, 1.–2.ix.1947, 1 spec., S. Osawa lgt. **Wakayama:** S-Kii, Nachi, 26.iv.1947, 29 spec., S. Osawa lgt.; 14 spec., ditto, but 29.iv.1947; 2 spec., ditto, but 19.vii.1946 (all spec. EIHU).

Redescription. Body length: PEL: 2.00–2.90 mm; APW: 0.75–1.10 mm; PPW: 1.50–2.00 mm; EL: 1.20–1.80 mm; EW: 1.65–2.50 mm.

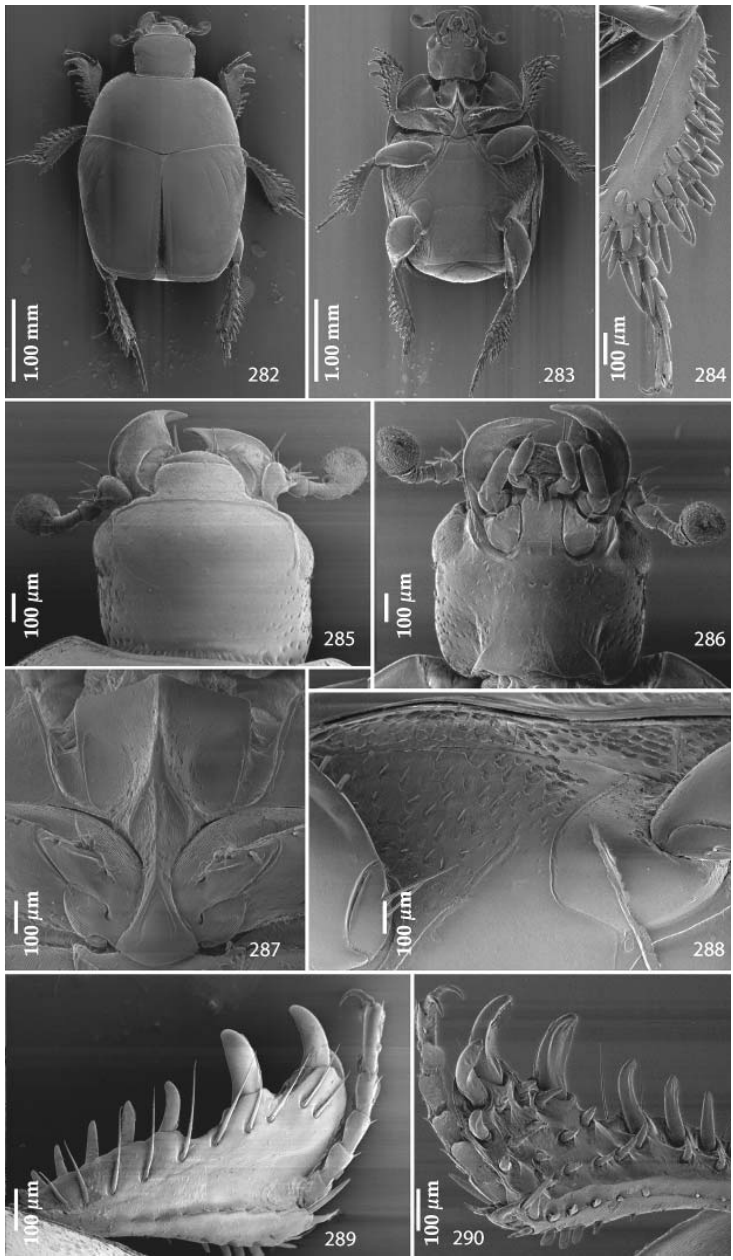
Body (Figs. 282–283) rectangular oval, dorsal surface convex, ventral surface flattened, cuticle shining, entirely black, often with large red macula on each elytron, legs, mouthparts and antenna reddish-brown, antennal club black.

Antennal scape (Fig. 285) with few short setae; club round, without visible articulation, entire surface with thick short sensilla, intermingled with sparse longer erect sensilla; sensory structures of antennal club (Fig. 18) in form of stipe-shaped vesicle situated under a large circular sensory area on internal distal margin of the ventral side of antennal club.

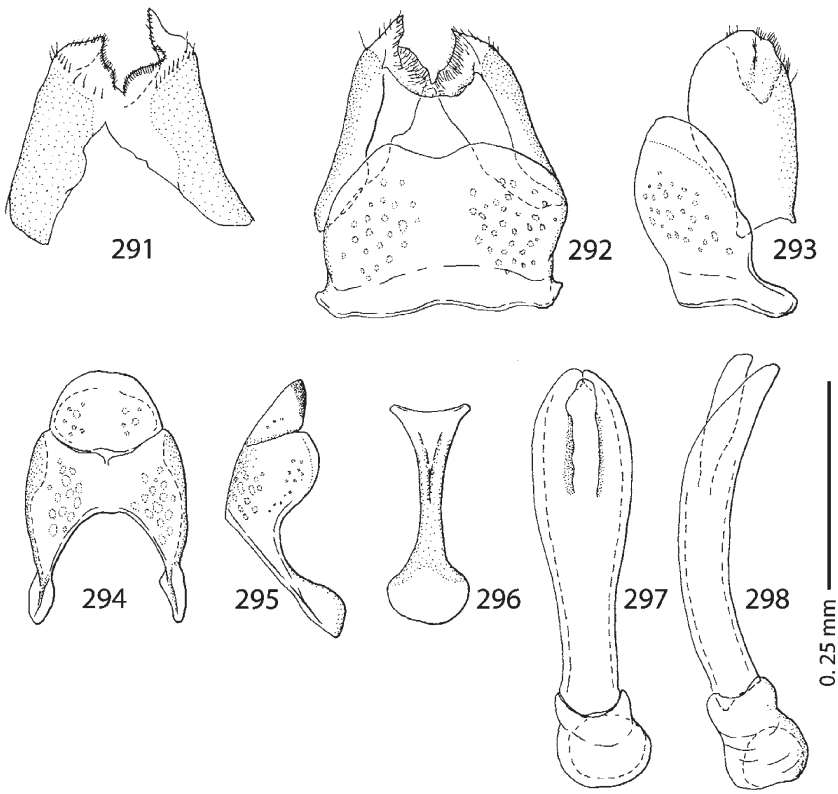
Mouthparts. Mandibles (Fig. 86) with carinate outer margin, strongly curved inwardly, mandibular apex acutely pointed; sub-apical tooth on left mandible large, almost perpendicular; labral disc (Fig. 51) very sparsely punctate, almost smooth, convex medially; labral pits shallow, each with two well-sclerotized long setae; terminal labial palpomere elongated, its width about one-third its length; mentum rectangular, anterior angles produced, anterior margin (Fig. 115) deeply emarginate; with two short setae, lateral margins and disc of mentum glabrous; cardo of maxilla on lateral margin with few minute setae; stipes triangular, with three longer setae; terminal maxillary palpomere elongated, its width about one-third its length, about three times as long as penultimate.

Clypeus (Fig. 285) without elevated anterior margin, flattened, sub-quadrate, smooth, lateral margins rounded; frontal stria well impressed, carinate, almost straight, supraorbital and postorbital striae well impressed; frontal disc entirely smooth; eyes convex, visible from above.

Pronotal sides (Fig. 282) moderately narrowing anteriorly, apical angles obtuse, anterior incision for head shallow, almost straight in middle; marginal pronotal stria complete; pro-



Figs. 282–290. *Eopachylopus ripae* (Lewis, 1885), SEM micrographs: 282 – habitus, dorsal view; 283 – ditto, ventral view; 284 – metatibia, ventral view; 285 – head, dorsal view; 286 – ditto, ventral view; 287 – prosternum; 288 – lateral disc of metaventrite, metepisternum and fused metepimeron; 289 – protibia, dorsal view; 290 – ditto, ventral view.



Figs. 291–298. *Eopachylopus ripae* (Lewis, 1885), male terminalia (after ÔHARA 1994): 291 – 8th sternite and tergite; 292 – ditto, dorsal view; 293 – ditto, lateral view; 294 – 9th tergite and 10th tergite, dorsal view; 295 – ditto, lateral view; 296 – spiculum gastrale, ventral view; 297 – aedeagus, dorsal view; 298 – ditto, lateral view.

notal disc entirely smooth, only with a row of fine scattered punctures along pronotal base in antescutellar area; pronotal hypomeron glabrous; scutellum conspicuous.

Elytral epipleuron smooth on basal half, apical half with shallow depressions; marginal epipleural stria complete; marginal elytral stria bisinuate, well impressed, carinate, continued as weakened but complete apical elytral stria. Humeral elytral stria weakly impressed on basal third; outer and inner subhumeral striae absent; first dorsal elytral stria rudimentary, second and third dorsal elytral striae well impressed, thin, not reaching elytral half apically, fourth dorsal elytral stria absent (at times confined to basal region, represented by a short arch); sutural elytral stria well-impressed, abbreviated on basal third, apically connected with apical elytral stria; entire elytral disc smooth.

Propygidium with sparse round punctures, interspaces finely imbricate; punctation of pygidium even sparser and finer than that of propygidium, becoming smooth apically.

Anterior margin of median portion of prosternum (Fig. 287) obtuse-angulate, marginal prosternal stria absent; pre-apical foveae absent; prosternal process strongly compressed, knife-like, dorso-laterally finely substrigulate; carinal prosternal striae extremely short, present only on prosternal apophysis; lateral prosternal striae well impressed, strongly convergent anteriorly, apically united, attaining middle of prosternal process; outer-lateral costa reaches prosternal process, its basal margin not distinctly elevated.

Anterior margin of mesoventrite deeply emarginate medially; discal marginal mesoventral stria deeply impressed, complete; mesoventral disc smooth, about as long as broad; meso-metaventral sutural stria almost straight; intercoxal disc of metaventrite flat, smooth; lateral metaventral stria well impressed, carinate, curved outwardly, not reaching hind coxa; lateral disc of metaventrite (Fig. 288) slightly concave, with round punctures separated by about their own diameter fringed with short yellow setae; interspaces finely imbricate; metepisternum + fused metepimeron (Fig. 288) with even coarser and denser punctation, on metepisternum punctures fringed with very short yellow setae, on fused metepimeron punctures asetose.

Intercoxal disc of first abdominal sternite with medio-basal depression, completely striate laterally; almost entirely smooth, in postero-lateral corners with scattered fine punctures.

Protibia (Figs. 289–290) on outer margin with three apical low teeth topped with long denticles, followed by seven prominent slender denticles, diminishing in size in proximal direction; protarsal groove deep; setae of outer row sparse, long; anterior protibial stria costiform, complete; setae of median row minuscule; protibial spur growing out from apical margin, well developed, bent; near tarsal insertion single long tarsal denticle present; posterior surface (Fig. 290) with numerous denticles, interspaces between them smooth; border between outer and median part of posterior surface unclear; posterior protibial stria fine, with sparse microscopic setae; setae of inner margin short, strongly sclerotized, confined to apical fourth.

Mesotibia somewhat dilated and apically slightly thickened, outer margin with at least three dense rows of short denticles, continued on anterior surface (Fig. 284); posterior mesotibial stria almost complete; setae of outer row strongly sclerotized, almost as long as denticles itself; setae of median row double, much shorter, finer and sparser; mesotibial spur prominent, long on apical margin surrounded by numerous short dense denticles; anterior mesotibial stria shortened apically; each tarsomere ventrally with two strongly sclerotized long setae; claws of apical tarsomere bent, longer than half its length; metatibia slightly dilated and thickened, in all aspects similar to mesotibia, but rows of denticles on anterior surface even denser; meso- and metafemora thickened.

Male genitalia. Eighth sternite (Figs. 291–292) longitudinally fused medially, apically with row of sparse short setae and broad velum with numerous tiny setae; eighth tergite and eighth sternite not fused laterally (Fig. 293). Morphology of 9th tergite (Figs. 294–295) typical for the subfamily; spiculum gastrale expanded on caudal end, but only slightly so on the apical end. Basal piece of aedeagus (Figs. 297–298) short, ratio of its length : length of parameres 1 : 4; parameres fused along their basal two-thirds; aedeagus gently curved ventrad (Fig. 298).

Eremosaprinus Ross, 1939

Eremosaprinus Ross, 1939: 39 (as a subgenus of *Saprinus*). Type species: *Saprinus unguiculatus* Ross, 1939, original designation.

Eremosaprinus: Ross (1940): 1; Blackwelder & Blackwelder (1948): 11; Wenzel (1962): 374, 380; Kryzhanovskij & Reichardt (1976): 111, 122; Mazur (1984): 106; Mazur (1997): 216; Mazur (2001): 19; Mazur (2004): 91.

Erebidus Reichardt, 1941: 161, 170 (as a subgenus of *Gnathoncus*). Type species: *Gnathoncus vlasovi* Reichardt, 1941, by monotypy. Synonymized by Kryzhanovskij & Reichardt (1976): 122.

Diagnosis. Body flattened from above; cuticle never metallic; frontal, supraorbital striae absent; antennal scape and pedicel slender, elongated; antennal club elongated; lacinial hook present. Pronotal foveae, pre-apical foveae and lateral prosternal striae absent, carinal prosternal striae present; prosternal process flat and broad; outerlateral costa reaches prosternal process, basal margin distinctly elevated; meso-metaventral sutural stria sinuate, distanced from meso-metaventral suture. Venter of body asetose. Protibia on explanate posterior surface with row of about 15 denticles; meso- and metatibiae long, slender; ninth tergite divided longitudinally.

The diagnosis of the genus *Eremosaprinus* is here based not on the genus' type species, but on its single Palaearctic representative instead. This is mainly due to the fact that this work deals primarily with the Saprinine of the Palaearctic region.

Differential diagnosis. This taxon is most similar to the species of the genus *Gnathoncus* differing from it by absent lateral prosternal striae and shape of protibia. From the species of the genus *Saprinus* it differs likewise by the absent lateral prosternal striae, shape of the protibia as well as by the absence of supraorbital stria (present in *Saprinus*).

Biology. *Eremosaprinus* is an inquilinous genus, collected in sandy regions as well as on the clay soils. Beetles are found exclusively in rodent nests, found in the burrows of *Spermophilopsis leptodactylus* (Lichtenstein, 1823), *Meriones erythrourus* (Gray, 1842) and *Rhombomys opimus* (Lichtenstein, 1823) in Central Asia and kangaroo rats (*Dipodomys* sp.) for the North American species, and are morphologically well adapted to the inquilinous way of life (Reichardt 1941, Kryzhanovskij & Reichardt 1976).

Distribution. This genus contains four North American and one Palaearctic species. Palaearctic species *Eremosaprinus vlasovi* occurs in the Central Asian province of Turan (recorded from Turkmenistan, Kazakhstan and Uzbekistan).

Species examined. *Eremosaprinus vlasovi* (Reichardt, 1941).

Notes on taxonomic status. The genus *Eremosaprinus* was originally described as a subgenus of the genus *Saprinus*, but later the same author used it in full generic status without any explanation or listing any of its species (Ross 1940). Blackwelder & Blackwelder (1948) listed it as a valid genus with all its species referring to Ross (1940) in a footnote 'Considered a distinct genus'. Mazur (1997) overlooked the Catalogue of Blackwelder & Blackwelder (1948) and proposed a new combination for all species of *Eremosaprinus*.

Discussion. The preliminary phylogenetic analysis of the genera of the Palaearctic Saprininae (Lackner, in prep.) suggests that taxa *Eremosaprinus* and *Gnathoncus* together with *Myrmetes* compose the most basal clade of the Palaearctic Saprininae, supported by several putative synapomorphies among which are the completely absent frontal and supraorbital striae and ninth tergite of the male genitalia divided into two parts. *Eremosaprinus* shares

similar sensory structures of antennal club with *Gnathoncus*, but is devoid of lateral prosternal striae, which is probably an apomorphic character. Presence of lacinial hook is another 'strong' character supporting its relationship with *Gnathoncus. Eremosaprinus vlasovi* was originally described in a newly created subgenus *Erebidus* of the genus *Gnathoncus* and only later (Kryzhanovskij in KRYZHANOVSKIJ & REICHARDT 1976: 122) transferred it into hitherto North American genus *Eremosaprinus*. It is believed (Tishechkin, pers. comm. 2009) that the North American representatives of this genus are quite different from their Central Asian congener and perhaps they constitute two different genera. It is hoped here that further study of this genus will clarify their exact taxonomic position.

Eremosaprinus vlasovi (Reichardt, 1941)

(Figs. 37, 42, 52, 87, 116, 144, 299–317)

Gnathoncus (*Erebidus*) *vlasovi* Reichardt, 1941: 161, 170, 173, Figs. 74, 83.

Eremosaprinus vlasovi: Kryzhanovskij in KRYZHANOVSKIJ & REICHARDT (1976): 123, Figs. 165–169; MAZUR (1984): 107; MAZUR (1997): 216; MAZUR (2004): 91.

Type locality. Turkmenistan, Ashgabat.

Type material. PARATYPES: 1 spec., 'Okr. [= surroundings of] Ashgabata [= Ashgabat] / Vlasov 26.iv.[19]31 [printed-written] // V glubine nory [= in the depth of a burrow of] / *Rhombomys* / *opimus* (written) // *Gn*. (*Erebidus*) / *vlasovi*, sp. n. Paratyp / Reichardt det. (printed-written) // Paratypus [red label, printed]' (ZIN); 1 spec., 'Okr. [= surroundings of] Ashgabata [= Ashgabat] / Vlasov 8.iii.[19]31 [printed-written] // pri roskopke nory [= digging up the burrow; written] // *Gn*. (*Erebidus*) / *vlasovi*, sp. n. Paratyp / Reichardt det. [printed-written] // Paratypus [red label, printed]' (ZIN).

Additional material examined. UZBEKISTAN: Kyzyl Kum, Buchara, 28.–30.iv.1975, 1 ♂, A. Olexa lgt. **TURKMENISTAN:** Ashgabat, Annau, 23.iv.1979, 1 ♂, A. Olexa lgt.; C Karakul Desert, Yerbent, 39°19'N 58°36'E, ex gerbil burrow, 10.–30.xi.1987, 1 spec., H. Atamuradov lgt.; W Kopet-Dagh Mts., km 64, rd. Kizil-Arvat-Kara-Kala, 1.–18.xi.1984, 1 spec., ex *Meriones erythrourus* burrow, 1 spec., H. Atamuradov lgt. (TLAN).

Redescription. Body length: PEL: 2.375–2.70 mm; APW: 0.925–1.00 mm; PPW: 1.825–2.00 mm; EL: 1.375–1.775 mm; EW: 2.00–2.25 mm.

Body (Figs. 299–300) roundly oval, moderately convex, somewhat flattened from above, cuticle brown without metallic luster; legs, mouthparts and antennae rufous.

Antennal scape (Fig. 302) thin, elongate, with two thin short setae; pedicel rectangular, elongate; club (Fig. 301) elongated, without visible articulation, entirely with dense short sensilla, intermingled with much sparser somewhat longer sensilla; sensory structures of antennal club (Fig. 37) in form of two differently sized sensory areas on ventral side of club and one large round vesicle situated under distal sensory area.

Mouthparts. Mandibles (Fig. 87) regularly rounded, mandibular apex acute; sub-apical tooth on left mandible obtuse; labrum (Fig. 52) depressed medially, sparsely punctate, with labral pits fringed with two setae; labral fold (Fig. 42) weakly developed; mentum sub-trapezoid, anterior margin (Fig. 116) with a tiny median notch, disc of mentum (Fig. 304) substrigulate, with sparse minute setae; terminal labial palpomere elongate, its width about one-fourth its length; maxilla (Fig. 144) with lacinial hook; cardo of maxilla with few short setae; stipes triangular, with three short setae; terminal maxillary palpomere elongate, its width about one-fourth its length.

Clypeus (Fig. 302) large, rectangular, somewhat convex, rounded laterally, with shallow punctures separated by about their own to twice their diameter; frontal and supraorbital striae absent; postorbital stria complete; frontal disc densely punctate, punctures shallow, separated by about their own diameter; eyes moderately convex, visible from above.

Pronotal sides (Fig. 299) on basal two-thirds moderately narrowing anteriorly, on apical third strongly narrowing anteriorly; apical angles blunt; marginal pronotal stria complete, somewhat weakened behind head; disc entirely punctate, punctation becomes coarser and denser laterally; pronotal base with ante-scutellar depression; scutellum very small, almost invisible.

Elytral epipleuron with deep scattered punctures of various sizes; marginal epipleural stria weakly impressed but complete; marginal elytral stria well impressed, carinate, shortly continued along elytral apex as shortened apical elytral stria. Outer and inner subhumeral striae absent; humeral stria vaguely impressed on basal fourth; elytral disc with five dorsal elytral striae 1–5 (fifth dorsal elytral stria present only as short apical fragment), not in punctures, rather thin, reaching about two-thirds of elytral length apically, occasionally fourth dorsal elytral stria slightly shortened basally, not connected with sutural elytral stria; sutural elytral stria shortened on basal fourth, apically stopping just short of elytral apex. Elytral disc with regular dense punctation, becoming sparser anteriorly, on elytral flanks and especially around scutellum, punctures separated by about 1.0–1.5 times their diameter, interspaces finely imbricate. Propygidium transverse, short; pygidium (Fig. 306) about as long as broad; punctation of propygidium and pygidium fine, punctures round, small, separated by about their own to twice their diameter, interspaces with microsculpture.

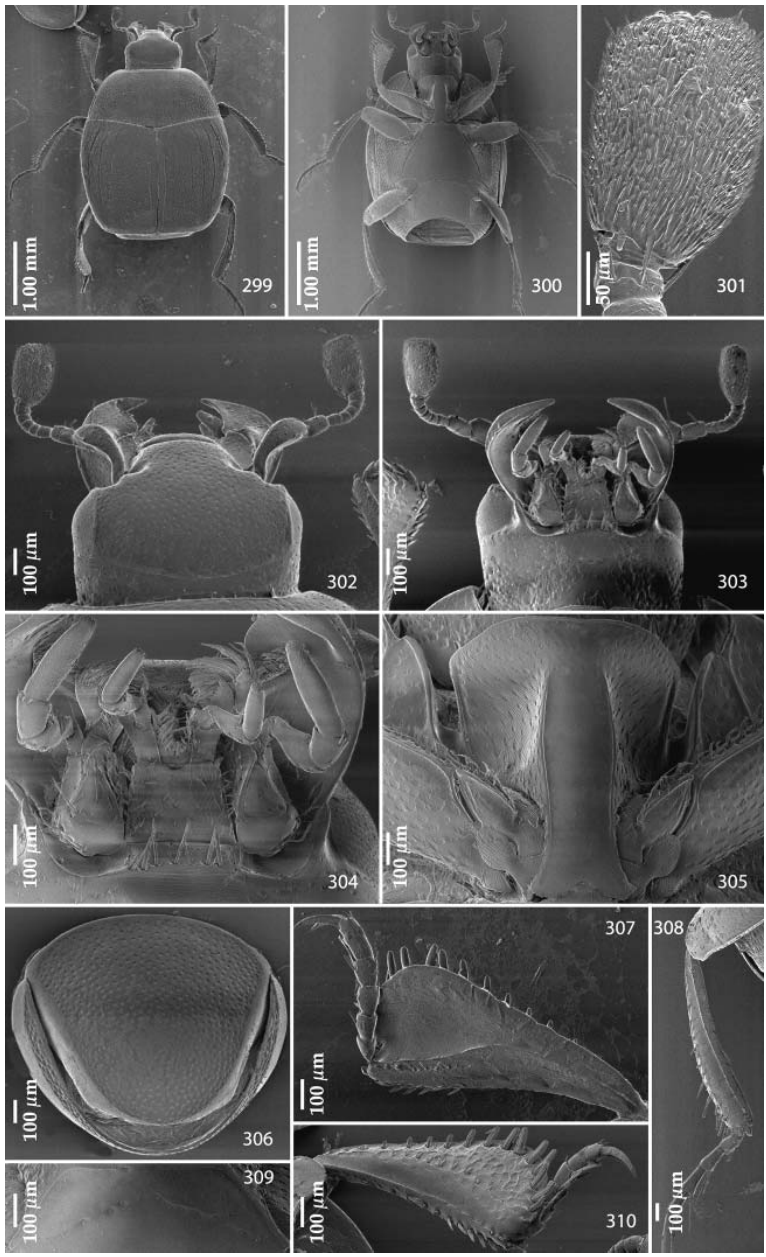
Anterior margin of median portion of prosternum (Fig. 305) straight; marginal prosternal stria anteriorly almost invisible, extremely thin; prosternal process laterally coriarious-punctate, dorsally smooth, flat, broad; carinal prosternal striae slightly sinuous, slightly carinate 'open' anteriorly; lateral prosternal striae absent; outer-lateral costa reaches prosternal process, its basal margin distinctly elevated.

Anterior margin of mesoventrite (Fig. 309) almost straight; discal marginal mesoventral stria well impressed, somewhat weakened anteriorly; meso-metaventral sutural stria (Fig. 309) sinuate, distanced from meso-metaventral suture; meso-metaventral suture vague, almost invisible; disc of mesoventrite flat, surface between discal marginal mesoventral stria and sinuate meso-metaventral stria with shallow scattered punctation, surface between meso-metaventral sutural stria and meso-metaventral suture itself smooth.

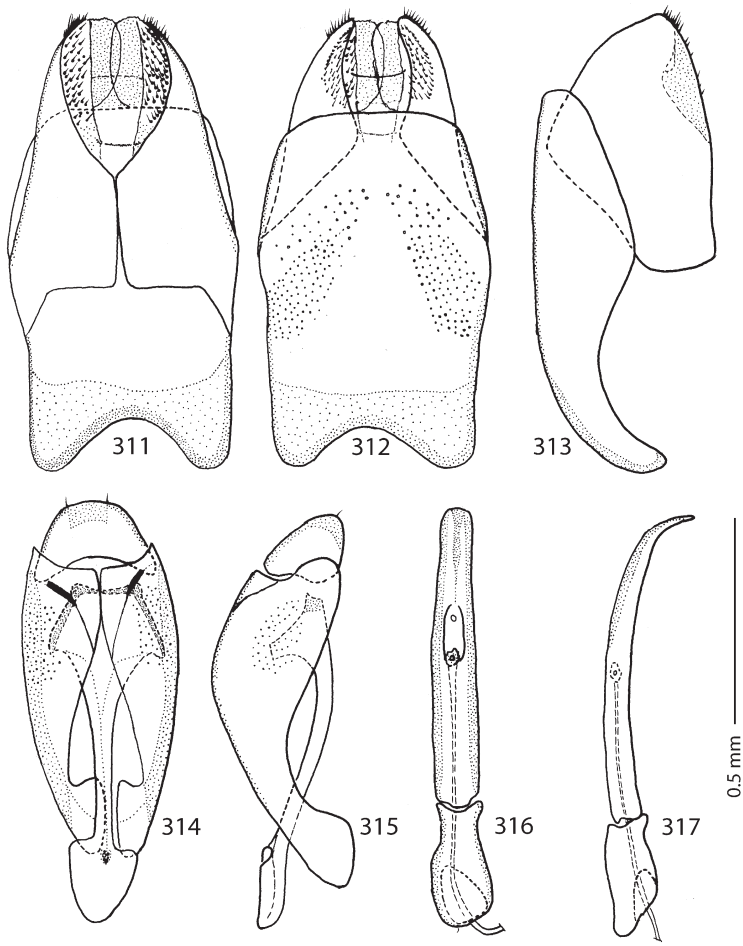
Metaventrite somewhat convex, with scattered punctures of various sizes, becoming larger and denser in the area behind hind coxa and apical margin; lateral metaventral stria well impressed, carinate, almost straight, reaching hind coxa; lateral disc of metaventrite almost flat, with round deep large punctures; metepisternum + fused metepimeron with dense deep punctures.

Intercoxal disc of first abdominal sternite completely striate laterally; surface with sparse scattered round punctation, punctures separated by about 1.5–2.0 times their diameter.

Protibia (Figs. 307–310) flattened and slightly dilated, anterior surface with complete anterior protibial stria; outer row of setae inconspicuous; setae of median row minute, sparse; outer margin explanate, with 14 small denticles growing out from posterior surface (Fig.



Figs. 299–310. *Eremosaprinus vlasovi* (Reichardt, 1941), SEM micrographs: 299 – habitus, dorsal view; 300 – ditto, ventral view; 301 – antennal club, dorsal view; 302 – head, dorsal view; 303 – ditto, ventral view; 304 – mouthparts, ventral view; 305 – prosternum; 306 – pygidium; 307 – protibia, dorsal view; 308 – metatibia, ventral view; 309 – mesoventrite; 310 – protibia, ventral view.



Figs. 311–317. *Eremosaprinus vlasovi* (Reichardt, 1941), male terminalia: 311 – 8th sternite and tergite, ventral view; 312 – ditto, dorsal view; 313 – ditto, lateral view; 314 – 9th tergite, 10th tergite (dorsal view) and spiculum gastrale (ventral view); 315 – 9th tergite, 10th tergite and spiculum gastrale, lateral view; 316 – aedeagus, dorsal view; 317 – ditto, lateral view.

310); protarsal groove deep; protibial spur tiny, growing out from apical margin of protibia; outer part of posterior surface (Fig. 310) obscurely variolate, separated from median part of posterior surface by a vague line with one row of about eight minute denticles; median part of posterior surface finely substrigulate to smooth; posterior protibial stria complete, terminating in two tiny inner ventral denticles; setae of inner row well sclerotized, short.

Mesotibia slender, long, outer margin with two rows of short thin sparse denticles, outer and median rows of setae inconspicuous; posterior mesotibial stria complete; anterior surface

coriarious-punctate; mesotibial spur short; apical margin of mesotibia anteriorly with two short inner ventral denticles; anterior mesotibial stria almost complete, terminating in two minute sclerotized setae; setae of inner row very sparse; tarsus (including claws) about as long as tibia itself; claws of apical tarsomere bent, longer than half its length; metatibia in all aspects similar to mesotibia, but outer margin (Fig. 308) with even sparser denticles.

Male genitalia. Eighth sternite (Figs. 311–312) longitudinally separated medially, on apical half widely separated, vela on distal margin with several rows of minute dense setae; apex laterally with sparse minute setae; eighth tergite and eighth sternite not fused laterally (Fig. 313). Ninth tergite (Figs. 314–315) divided longitudinally; tenth tergite (Figs 314–315) apically with two minute setae; spiculum gastrale (Fig. 314) widely expanded on apical end. Aedeagus (Figs. 316–317) slender; basal piece of aedeagus short, ratio of its length : length of parameres 1 : 3.75; parameres fused almost along their entire length with a small circular slit for ejaculatory duct of median lobe; aedeagus apically slightly curved ventrad (Fig. 317).

Euspilotus Lewis, 1907

Euspilotus Lewis, 1907: 320. Type species: *Euspilotus zonalis* Lewis, 1907, by original designation.

Euspilotus: Bickhardt (1916): 81, 83; Wenzel (1962): 375; Kryzhanovskij & Reichardt (1976): 111, 124; Vienna (1980): 126; Mazur & Kaszab (1980): 6, 47; Mazur (1984): 64; Downie & Arnett (1996): 607, 608; Mazur (1997): 232; Bousquet & Laplante (1999): 142, 158; Mazur (2001): 20, 31; Kovarik & Caterino (2001): 221, 223; Yélamos (2002): 245, 293; Mazur (2004): 91; Bousquet & Laplante (2006): 80, 121.

Distribution. This species-rich genus is distributed across North, Central and South America where it, with 76 described species, dominates the Saprininae subfamily. Two additional species of the subgenus *Neosaprinus* Bickhardt, 1909 have been described from the Palaearctic and Oriental Regions, respectively (see below for details) (Mazur 1997).

Subgenus *Neosaprinus* Bickhardt, 1909

Neosaprinus Bickhardt, 1909: 243. Type species: *Saprinus gnathoncoides* Bickhardt, 1909 (= *Saprinus rubriculus* Marseul, 1855), by monotypy.

Neosaprinus: Wenzel (1962): 380; Kryzhanovskij & Reichardt (1976): 111, 124; Vienna (1980): 115, 127; Mazur & Kaszab (1980): 6, 47; Mazur (1984): 71; Mazur (1997): 238; Mazur (2001): 20, 31; Yélamos (2002): 245, 293; Mazur (2004): 91.

Myrmeosaprinus Mazur, 1974b: 55. Type species: *Myrmeosaprinus brasiliensis* Mazur, 1974b, by original designation. Synonymized by Mazur (1997): 238.

Diagnosis. Frontal, supraorbital striae absent; pronotal foveae absent; eyes convex from above; sensory structures of antennal club in form of two sensory areas on ventral side and five vesicles; one of them is larger than other four vesicles arranged in two pairs on ventral and dorsal side respectively; pronotal hypomeron glabrous; prosternum with vague pre-apical foveae joined by vague sulcus; prosternal process between widely divergent carinal prosternal striae distinctly convex; lateral prosternal striae straight, parallel; pygidium of female with sulci; outer margin of protibia with low teeth topped with short thin denticles.

The diagnosis of this genus was based not on the genus' type species, but on its single Palearctic representative instead. This is maily due to the fact that this work deals primarily with the Palearctic region (for more details see Introduction).

Differential diagnosis. The single Palaearctic species of the subgenus *Neosaprinus*, *E.* (*N.*) *perrisi*, is superficially similar to the species of the genus *Saprinus* but differing from them by the presence of pre-apical foveae, pygidial sulci of the female and absent supraorbital stria. The species could also be confused with the species of the subgenus *Hemisaprinus* of the genus *Saprinus*, that likewise possess pre-apical foveae, but supraorbital stria in the species of this subgenus is present, whereas it is absent in *Euspilotus* (*Neosaprinus*), and the prosternal process is distinctly convex (flattened in *Hemisaprinus*). Absence of the frontal and supraorbital striae could further confuse this taxon with genera *Gnathoncus*, *Myrmetes*, *Eremosaprinus* and *Turanostyphrus*, but all these taxa lack also pre-apical foveae, whereas *Euspilotus* (*Neosaprinus*) possesses them.

Biology. *Euspilotus* (*Neosaprinus*) *perrisi* inhabits the nests of European Bee-Eater (*Merops apiaster* Linnaeus, 1758). In the nests of this bird it can occasionally be collected in larger numbers, but is generally rare in collections. Apart from its normal occurrence in the nests of the above-mentioned birds it has also been collected on carrion (Kanaar, pers. comm. 2008) and it has likewise been collected in a gerbils (*Spermophilus* sp.) burrow (Kryzhanovskij & Reichardt 1976).

Distribution. This subgenus contains 8 described species, distributed mostly in North and South America (Mazur 1997). However, one species – *Euspilotus* (*Neosaprinus*) *loebli* Mazur, 1974a – occurs also in Malaysia and this subgenus has even a single Palaearctic representative: *Euspilotus* (*Neosaprinus*) *perrisi*. The latter is distributed chiefly in southern Europe (reaching its northern distributional boundary in Slovakia), Turkey, Caucasus, and South Russia as far east as Central Asia.

Species examined. *Euspilotus* (*Neosaprinus*) *perrisi* (Marseul, 1872).

Discussion. The only Palaearctic representative of the subgenus *Neosaprinus*, *E.* (*N.*) *perrisi*, shares several putative synapomorphies with the genera *Gnathoncus*, *Myrmetes* and *Eremosaprinus*, notably the total absence of frontal and supraorbital striae as well as similar sensory structures of antenna (especially similar to *Gnathoncus* and *Eremosaprinus*). Furthermore, this taxon is not very 'far' on the cladogram of the preliminary phylogenetic analysis from these three taxa (Lackner, in prep.). Perhaps *Gnathoncus*, *Myrmetes*, *Eremosaprinus* and *E.* (*N.*) *perrisi* are the most derived taxa of the old Gondwanan clades that currently survive only in the Neotropics. Presence of *E.* (*N.*) *perrisi* in the Palaearctic Region can be possibly atributed to the wide extinction of the representatives of this subgenus in the Old World. On the other hand, *Euspilotus* is very numerous in the Nearctic and Neotropical Regions. The presence of peculiar pygidial sulci in the females of this taxon is probably a character developed in the geographical isolation of South American continent from the rest of the continents and it is likewise regarded here as a plesiomorphic character.

Euspilotus (*Neosaprinus*) *perrisi* (Marseul, 1872)

(Figs. 35, 53, 74, 88, 117, 162–167, 178, 318–338)

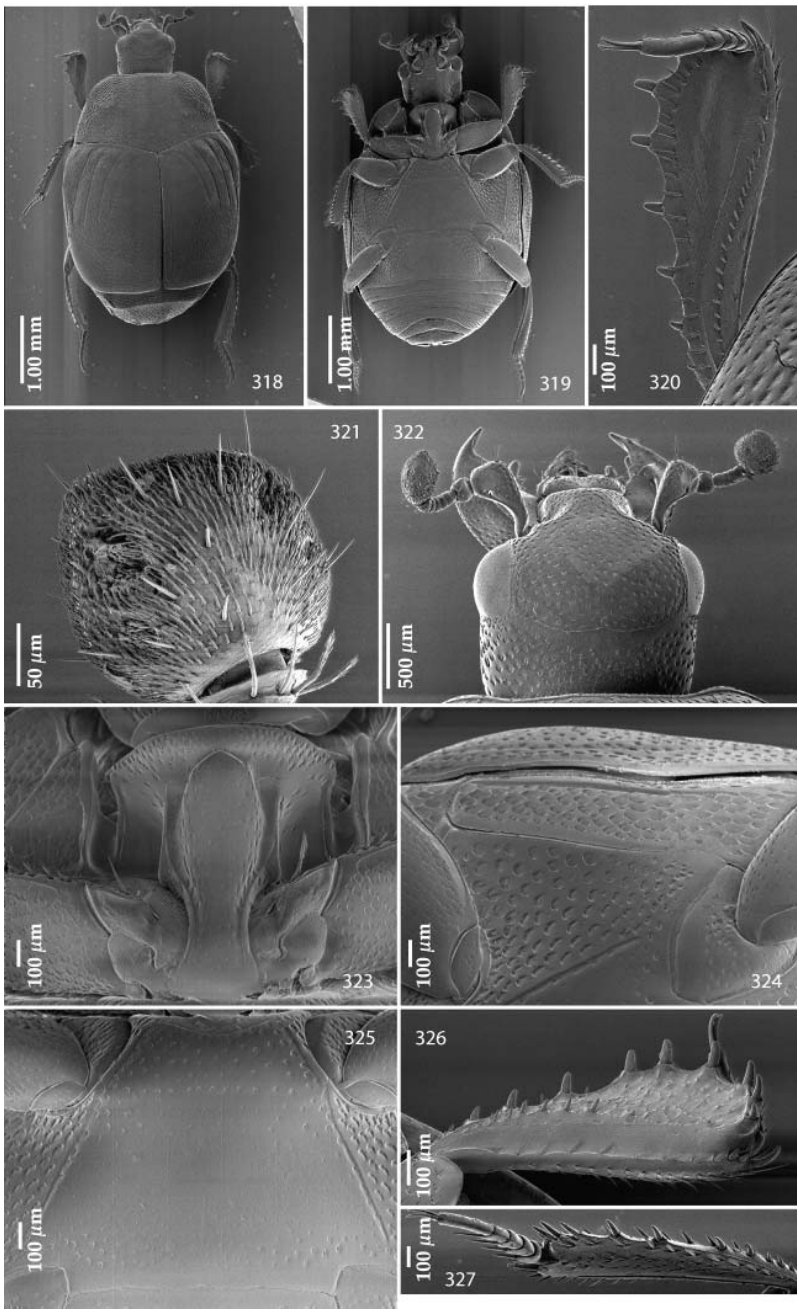
Saprinus perrisi Marseul, 1872: 415.

Saprinus perrisi: Schmidt (1885a): 308.

Saprinus pseudognathoncus Reitter, 1904: 34. Synonymized by Dahlgren (1968): 86.

Saprinus pseudognathoncus: Reichardt (1941): 184, 240, Fig. 82P; Iablokoff-Khnzorian (1964): 109.

Euspilotus (*Neosaprinus*) *perrisi*: Dahlgren (1968): 86, Figs. 24, 4B,C; Kryzhanovskij & Reichardt (1976): 124, Figs. 170–173; Vienna (1980): 128, Figs. 48, 49; Mazur & Kaszab (1980): 48, Figs. 25A–D; Mazur (1984): 71; Mazur (1997): 238; Yélamos (2002): 293, Figs. 145, 146 A–E; Mazur (2004): 91.



Figs. 318–327. *Euspilotus* (*Neosaprinus*) *perrisi* (Marseul, 1872), SEM micrographs: 318 – habitus, dorsal view; 319 – ditto, ventral view; 320 – protibia, dorsal view; 321 – antennal club, ventral view; 322 – head, dorsal view; 323 – prosternum; 324 – lateral disc of metaventrite, metepisternum and fused metepimeron; 325 – mesoventrite + metaventrite; 326 – protibia, ventral view; 327 – metatibia, dorsal view.

Note. Sensory structures of the antennal club and spermatheca were studied by De Marzo & Vienna (1982a,b). Larva was described by Kalashian (1996).

Type locality. France, Corsica.

Type material examined. *Saprinus perrisi*. Syntype: ♀, '*Saprinus* / *perrisi* m / Corse [illegible] / Aug. [?] [18]73 [round label, written] // Pokoy [illegible] [round, written label glued onto a mounting card] // Museum Paris / Coll. De Marseul / 28490 [written] // TYPE [red-printed label]' (MNHN).

Saprinus pseudognathoncus. Holotype: ♂, male genitalia extracted and glued to the same mounting card as the specimen: 'Caucas. / Occid. / Novoross. / 15.vi.[18]99. / Starck [printed-written] // pseudognathon- / cus m. 1904. Typ [written] // coll. Reitter [printed] // Sapr. perrisi / Mars. / G Dahlgren det. [printed-written] // Monotypus 1904 / Saprinus / pseudognathoncus / Reitter [red-framed printed-written]' (HNHM).

Additional material examined. BULGARIA: Harmanli, 27.vi.1975, 4 ♀♀ 4 ♂♂, A. Olexa lgt.; Arkutino, vii.1972, 1 ♂ 1 ♀, A. Olexa lgt. **KAZAKHSTAN:** Ak-Say (Alma-Ata), 1.vi.1974, 1 ♂, A. Olexa lgt. **TAJIKISTAN:** Babatag, Bulbulchashma, 23.v.1974, 3 ♀♀, A. Olexa lgt. **UZBEKISTAN:** Kara Tepe (Samarkand), 28.vi.1976, 1 ♀ 3 ♂♂, A. Olexa lgt. (TLAN).

Redescription. Body length: PEL: 2.75–3.45 mm; APW: 0.875–1.125 mm; PPW: 2.05–2.375 mm; EL: 1.75–2.15 mm; EW: 2.50–3.0 mm.

Body (Figs. 318–319) roundly oval, moderately convex, body color dark brown to black, cuticle not metallic, elytral apex slightly rufous; legs, antenna and mouthparts rufous.

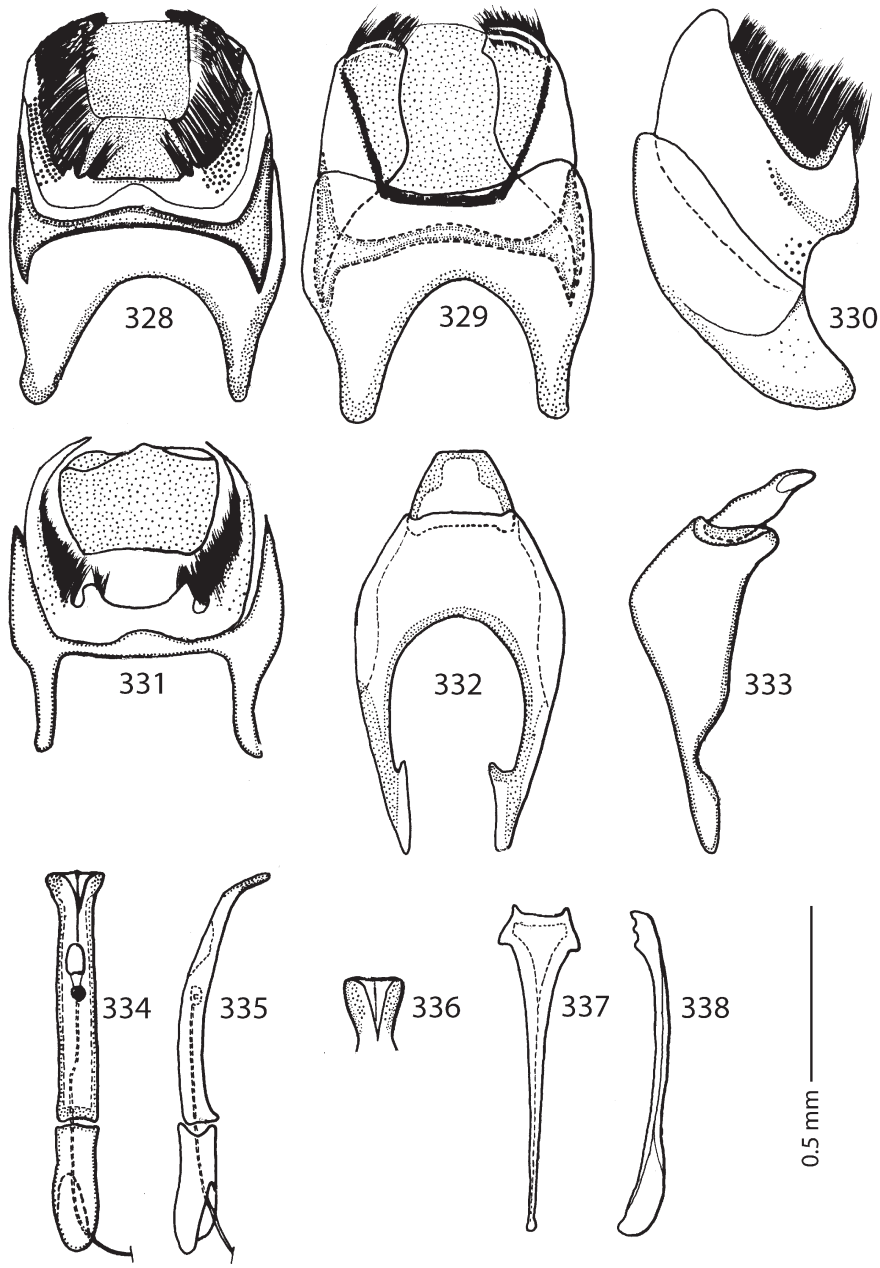
Antennal scape (Fig. 322) darker than antennal flagellum, with sparse punctures with few short setae; club round, without visible articulation, with thick short yellow sensilla intermingled with sparser longer sensilla; sensory structures of antennal club (Fig. 35) in form of two sensory areas on ventral side and five vesicles; one of them is larger than other four; vesicles arranged in two pairs on ventral and dorsal side respectively.

Mouthparts. Mandibles (Fig. 88) densely punctate, lateral margins rounded, mandibular apex acute; subapical tooth on left mandible obtuse; labrum (Fig. 53) sparsely punctate, shallowly depressed medially; labral fold (Fig. 74) weakly developed; two labral pits present, with one seta arising from each; terminal labial palpomere elongated, its width about one-third its length; mentum sub-trapezoid, anterior angles slightly produced, anterior margin shallowly emarginate medially, with shallow median notch (Fig. 117), with several long setae; disc of mentum with sparse short setae; cardo of maxilla laterally with several short setae; stipes triangular, with three longer setae; terminal maxillary palpomere elongated, its width about one-fourth its length, about 2.5 times as penultimate.

Clypeus (Fig. 322) rounded laterally, with round punctures, separated about twice their own diameter; frontal, supraorbital striae absent; postorbital stria vaguely impressed; frontal disc flat, with regular round punctures, separated by about their own to several times their diameter; eyes convex, well visible from above.

Pronotum (Fig. 318) conspicuously narrower than elytra; pronotal sides on apical half almost straight, thence slightly convergent forwardly, on basal fourth strongly convergent; apical angles blunt; marginal pronotal stria well impressed, complete; pronotal disc slightly convex, with slight lateral depressions, pronotal foveae absent, disc laterally covered with coarse punctures, punctation weakened medially; pronotal hypomeron smooth; scutellum small, well visible.

Elytral epipleuron with regular round dense punctation; marginal epipleural stria complete, continued along elytral apex as incomplete apical stria; marginal elytral stria well impressed, obliterated near elytral apex. Humeral elytral stria weakly impressed on basal third, someti-



Figs. 328–338. *Euspilotus* (*Neosaprinus*) *perrisi* (Marseul, 1872), male terminalia: 328 – 8th sternite and tergite, ventral view; 329 – ditto, dorsal view; 330 – ditto, lateral view; 331 – ditto, frontal view; 332 – 9th tergite and 10th tergite, dorsal view; 333 – ditto, lateral view; 334 – aedeagus, dorsal view; 335 – ditto, lateral view; 336 – apex of aedeagus, frontal view; 337 – spiculum gastrale, ventral view; 338 – ditto, lateral view

mes double; inner subhumeral stria present as short median fragment; elytra with four well impressed dorsal striae 1–4, in small punctures, all about the same length, reaching about half of elytral length apically; fourth dorsal elytral stria curved towards sutural elytral stria, but not connected with it; sutural elytral stria shortened on basal third and apical sixth, in round punctures, not continuous with apical elytral stria; between sutural elytral stria and elytral suture a row of minute punctures present. Elytral disc entirely punctate, on apical half punctures denser and coarser, separated by about their own diameter; on basal half the punctation much finer and sparser.

Propygidium almost completely exposed, transverse, with deep coarse punctures; pygidium with sparser oblong punctures separated by about their own diameter, becoming smaller and sparser apically. Sexually dimorphic species, female with deeply impressed curious pygidial sulci (Figs. 162–167).

Anterior margin of median portion of prosternum (Fig. 323) rounded, densely punctate; pre-apical foveae vaguely impressed, linked by vague transverse sulcus; prosternal process distinctly convex, with sparse punctures; lateral prosternal striae straight, parallel, terminating on two-thirds of process' length apically; carinal prosternal striae on prosternal apophysis subparallel, thence strongly divergent anteriorly, parallel, terminating in vague pre-apical foveae.

Anterior margin of mesoventrite (Fig. 325) shallowly emarginate medially; discal marginal mesoventral stria well impressed, carinate; disc of mesoventrite flat, with sparse punctures separated up to several times their own diameter; meso-metaventral suture vaguely impressed; meso-metaventral sutural stria absent.

Intercoxal disc of metaventrite (Fig. 325) with a shallow longitudinal median depression in male, disc medially almost smooth, along posterior margin several rows of scattered punctures present; lateral metaventral stria well impressed, carinate, straight, almost reaching metacoxa; lateral disc of metaventrite (Fig. 324) with setiferous punctures separated about their own diameter; metepisternum + fused metepimeron (Fig. 324) evenly covered with much coarser and denser punctation, punctures separated less than half time their own diameter; metepisternal stria deeply impressed.

Intercoxal disc of first abdominal sternite broad, lateral stria vaguely impressed; disc with dense punctation, becoming finer and sparser medially.

Protibia (Fig. 326) slightly dilated, outer margin with about ten low teeth topped with short thin denticle, diminishing in size in proximal direction; setae of outer row regular, short; protarsal groove deep; anterior protibial stria shortened apically; setae of median row shorter but denser than those of outer row, terminating in several tarsal denticles; protibial spur well developed, bent, growing out from apical margin of protibia; outer part of posterior surface (Fig. 326) obscurely variolate, separated from substrigulate median part of posterior surface by vague boundary and row of minute denticles present on basal half; posterior protibial stria complete, with tiny sclerotized setae turning into three inner posterior denticles; inner row of setae double.

Mesotibia (Fig. 327) slender, outer margin with two rows of short denticles; setae of outer row regular, sparse, about as long as denticles themselves; median row of setae double, setae shorter but denser than those of outer row; posterior mesotibial stria almost complete; anterior surface of mesotibia coriarious-punctate; anterior mesotibial stria complete, terminating

in two tiny sclerotized setae; mesotibial spur short; claws of apical tarsomere slightly bent, longer than half its length; metatibia slenderer than mesotibia, in all aspects similar to it, but denticles on outer margin even sparser.

Male genitalia. Eighth sternite (Figs. 328–331) completely fused, laterally with dense rows of long setae, apically with large inflatable membrane (velum) (Fig. 331); eighth tergite and eighth sternite not fused laterally (Fig. 330); eighth tergite comparably short. Ninth tergite (Figs. 332–333) conspicuously broader than small tenth tergite; spiculum gastrale (Figs. 337–338) widely expanded on apical end, on basal end not expanded; basal end dilated from ventral view. Aedeagus (Figs. 334–336) slender; basal piece of aedeagus rather long, ratio of its length : length of parameres 1 : 2.10; parameres fused almost along their entire length with a small circular slit for ejaculatory duct of median lobe; aedeagus apically slightly curved ventrad (Fig. 335).

Exaesiopus Reichardt, 1926

Exaesiopus Reichardt, 1926: 14. Type species: *Saprinus grossipes* Marseul, 1855, original designation.
Exaesiopus: Reichardt (1941): 156, 329; Peyerimhoff (1936): 226; Kryzhanovskij & Reichardt (1976): 112, 232; Mazur & Kaszab (1980): 7, 61; Vienna (1980): 117, 195; Mazur (1984): 101; Mazur (1997): 263; Yélamos (2002): 245, 338; Mazur (2004): 92.

Diagnosis. Frontal stria carinate; frontal disc impunctate, with irregular deeply impressed longitudinal rugae (as in several species of *Hypocaccus*); pronotum rounded laterally; pronotal hypomeron setose; elytral epipleuron glabrous; metepisternum, lateral disc of metaventrite and lateral parts of all visible abdominal sternites setose, setae on abdominal sternites very short; protibia on outer margin with several low teeth, topped by rounded denticle, followed by three to four short denticles; meso- and metatibiae thickened and dilated, metafemora conspicuously thickened.

When composing the diagnosis of this genus the morphological characters of the species *Exaesiopus grosclaudei* Normand, 1935 have not been taken into account since this species belongs to genus *Hypocacculus* (*Nessus*) (see also the diagnosis of this subgenus).

Differential diagnosis. *Exaesiopus* is superficially strikingly similar to the genus *Hypocaccus*, differing from it chiefly by the setose lateral disc of metaventrite, lateral parts of all visible abdominal sternites (as well as setose pronotal hypomeron) and dilated and thickened meso- and metatibiae. Several species of *Hypocaccus* have also underside of their bodies with short setae (e.g. *Hypocaccus* (*Hypocaccus*) *crassipes* (Erichson, 1834)), but their pronotal hypomeron is always asetose, whereas it is setose in *Exaesiopus*.

Biology. Although the species of the genus *Exaesiopus* are mostly collected on beaches, they are, unlike most members of the similar genus *Hypocaccus*, found also further inland. Their biology is generally poorly understood. Species *Exaesiopus atrovirens* Reichardt, 1926 and *E. torvus* Reichardt, 1926 from Central Asia are occasionally found under *Tamarix* spp.

Distribution. *Exaesiopus* is predominantly a Palaearctic genus, occurring on the sandy soils from the Canary Islands throughout northern Africa, southern Europe and southern parts of Central Europe (reaching the northernmost point of its distribution in southern Slovakia) eastwards through Turkey and Caucasus as far as Central Asia (up to Afghanistan). One species, *Exaesiopus laevis* Thérond, 1964 has been described from Somalia.

Species examined. *Exaesiopus atrovirens* Reichardt, 1926, *E. grossipes berberus* Peyerimhoff, 1936, *E. grossipes grossipes* (Marseul, 1855), *E. henoni* (Schmidt, 1896), *E. torvus* Reichardt, 1926.

Discussion. This taxon is most likely not monophyletic and its relationship with the genus *Hypocaccus* should be the focus of the future studies. It is supported by only a few weak synapomorphies, e.g. shape of the protibia, thickened meso- and metatibiae or vestiture of the underside of body, but these may be simply results of the convergent evolution and do not present valuable taxonomic characters. Revision of the species of *Exaesiopus* is in progress.

Exaesiopus grossipes (Marseul, 1855)

(Figs. 19, 54, 89, 118, 339–359)

Saprinus grossipes Marseul, 1855: 718, t. XX, Fig. 153.
Saprinus grossipes: Schmidt (1885a): 315.
Saprinus rugicollis: Schmidt 1890: 19 (*nomen nudum*, given as synonym).
Pachylopus grossipes: Schmidt (1896): 296; G. Müller (1931): 102.
Hypocaccus grossipes: Ganglbauer (1899): 393.
Styphrus grossipes: Jakobson (1911): 651.
Exaesiopus grossipes: Reichardt (1926): 16; Reichardt (1941): 329, 330, Fig. 117; Peyerimhoff (1936): 227; Kryzhanovskij & Reichardt (1976): 232, Figs. 455–458; Vienna (1980): 196, Fig. 69; Mazur & Kaszab (1980): 61, Figs. 31, 34D–F; Mazur (1984): 101; Mazur (1997): 263; Yélamos (2002): 338, Figs. 12E, 161G, 169, 170A; Mazur (2004): 92.
Exaesiopus grossipes berberus Peyerimhoff, 1936: 227.
Exaesiopus grossipes berberus: Kryzhanovskij & Reichardt (1976): 232; Mazur (1984): 101; Mazur (1997): 263; Mazur (2004): 92.

Note. Sensory structures of the antennal club were studied by De Marzo & Vienna (1982a).

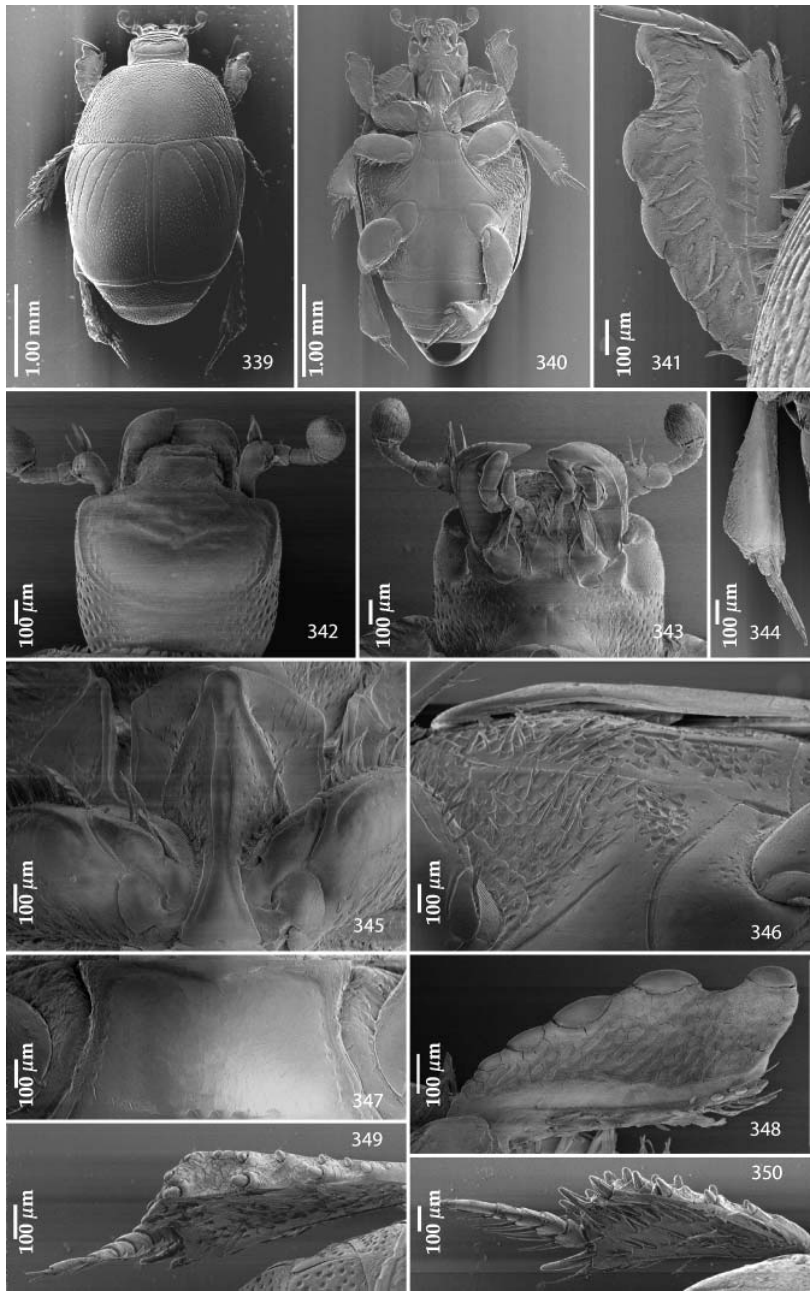
Type locality. *E. grossipes grossipes*: Spain, France: Bayeux, Marseille. *E. grossipes berberus*: Algeria.
Type material examined. *Saprinus grossipes grossipes*. Syntype: 1 spec. 'tiny pink square label // 153 / *Saprinus* / *grossipes* / m. / Marseul / Baron [illegible] [round label, written] // TYPE [red-printed label] // Museum Paris / Coll. / De Marseul 1890 [light-blue label]' (MNHN).
Additional material examined. *Exaesiopus grossipes grossipes*: **BULGARIA:** Asenovgrad, vi.1963, 1 ♀, A. Olexa lgt. **SLOVAKIA:** Čenkov, 24.vi.1987, 1 ♂, Vít Kubáň lgt. **ITALY:** Lagnola [illegible], xi.1910, 1 ♂ 1 ♀, Sekera lgt. **SERBIA:** Veliko Gradište, 2.ix.1955, 1 spec., Stančić lgt. (TLAN).
Exaesiopus grossipes berberus: **TUNISIA:** Kairuan, 6.–8.xi.1982, 1 ♂ 1 ♀, A. Olexa lgt. (TLAN).

Redescription. Body length: PEL: 2.10–2.75 mm; APW: 0.825–1.00 mm; PPW: 1.625–2.25 mm; EL: 1.25–2.00 mm; EW: 1.875–2.50 mm.

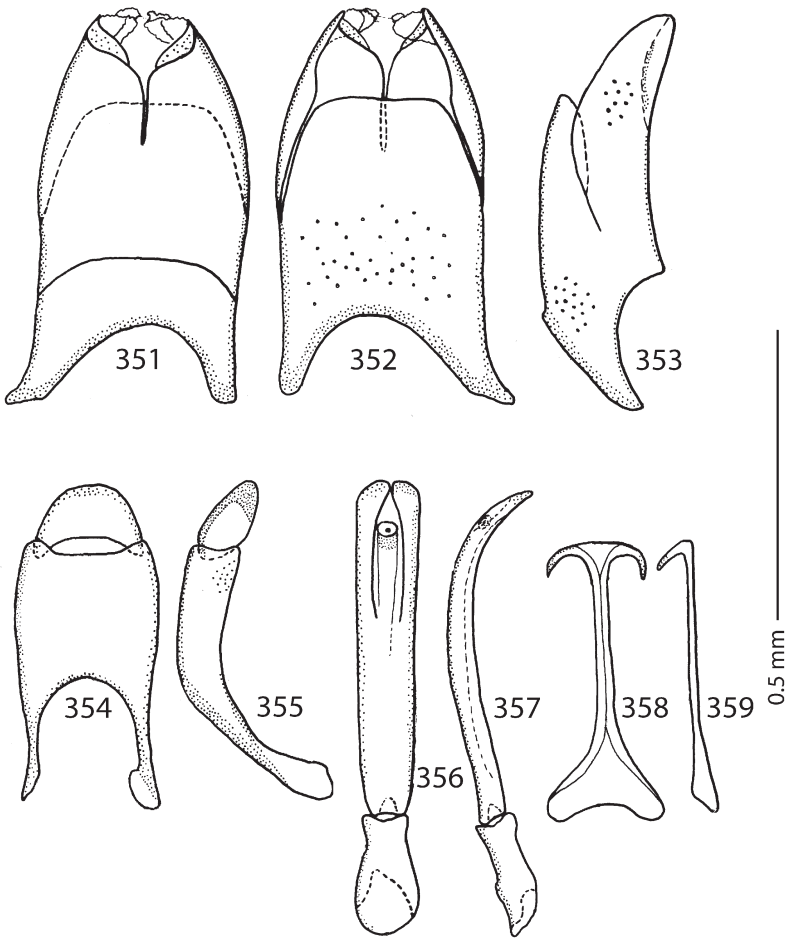
Body (Figs. 339–340) oval, convex, cuticle dark brown to black, sometimes with feeble bronze or greenish metallic tinge; legs, mouthparts and antennae reddish-brown.

Antennal scape (Fig. 342) with few short setae; club round, without visible articulation, entire surface with thick short yellow sensilla intermingled with sparser slightly longer erect sensilla; sensory structures of antennal club (Fig. 19) in form of stipe-shaped vesicle situated under circular sensory area on internal distal margin of the ventral side of antennal club.

Mouthparts. Mandibles (Fig. 89) stout, outer margin slightly curved; mandibular apex bluntly pointed; sub-apical tooth of left mandible large, almost perpendicular; labrum (Fig. 54) sparsely punctate, shallowly depressed medially, with two labral pits, two setae arising from each; epipharynx almost completely hidden under labral fold; terminal labial palpomere elongated, its width less than half its length; mentum square-shaped, with deep antero-median emargination (Fig. 118); anterior margin with few long setae, lateral margins with single row



Figs. 339–350. *Exaesiopus grossipes grossipes* (Marseul, 1855), SEM micrographs: 339 – habitus, dorsal view; 340 – ditto, ventral view; 341 – protibia, dorsal view; 342 – head, dorsal view; 343 – ditto, ventral view; 344 – mesotibia, ventral view; 345 – prosternum; 346 – lateral disc of metaventrite, metepisternum and fused metepimeron; 347 – mesoventrite; 348 – protibia, ventral view; 349 – metatibia, dorsal view; 350 – mesotibia, dorsal view



Figs. 351–359. *Exaesiopus grossipes grossipes* (Marseul, 1855), male terminalia: 351 – 8th sternite and tergite, ventral view; 352 – ditto, dorsal view; 353 – ditto, lateral view; 354 – 9th tergite, 10th tergite, dorsal view; 355 – ditto, lateral view; 356 – aedeagus, dorsal view; 357 – ditto, lateral view; 358 – spiculum gastrale, ventral view; 359 – ditto, lateral view.

of much shorter sparse setae; cardo of maxilla with few short setae on lateral margin; stipes triangular, with three much longer setae; terminal maxillary palpomere somewhat thickened, its width less than half its length, about twice as long as penultimate.

Clypeus (Fig. 342) rectangular, almost smooth, anterior margin slightly elevated, somewhat depressed medially; frontal stria well impressed, almost straight (occasionally somewhat curved outwardly), carinate, continued as carinate supraorbital and postorbital striae; frontal disc with several irregularly shaped carinate longitudinal rugae; eyes flattened, inconspicuous from above.

Pronotal sides (Fig. 339) slightly convergent forwards; apical angles blunt; marginal pronotal stria complete; pronotal disc convex, with dense round punctation, forming longitudinal rugae laterally, postero-median part of disc in most cases smooth, at times entire pronotal disc punctate (punctation can also be stopping short of lateral pronotal margin); pronotal base with a double row of round dense punctures; pronotal hypomeron with amber setae; scutellum small, visible.

Elytral humeri slightly prominent, elytra broad, almost as broad as long at its widest point; elytral epipleura with microscopic punctures, almost smooth; marginal epipleural stria complete; marginal elytral stria deeply impressed, continued as well impressed apical elytral stria; along elytral marginal stria a regular row of round punctures present. Humeral elytral stria weakly impressed on basal third, sometimes double; inner subhumeral stria present medially, deep and rather long, rarely joining marginal elytral stria; elytra with four dorsal elytral striae 1–4, in punctures, all striae approximately reaching elytral half apically (occasionally slightly surpassing it), fourth stria connected with sutural elytral stria; sutural stria well impressed, in deep punctures, apically joining apical elytral stria. Elytral punctation variable, often confined to apical half, along elytral suture reaching almost two-thirds of elytral length anteriorly, punctures regular and deep, separated by about half to their own diameter, occasionally covering most part of elytral disc (elytral flanks and humeri almost always smooth).

Propygidium almost completely exposed, with coarse and dense regular punctation; punctation of pygidium sparser and finer, punctures separated by about 1–3 times their diameter.

Anterior margin of median portion of prosternum (Fig. 345) regularly rounded; pre-apical foveae well impressed; prosternal process slightly concave, impunctate dorsally, laterally substrigulate-punctate, few microscopic setae present; carinal prosternal striae divergent on prosternal apophysis, subparallel, vaguely united in front; lateral prosternal striae carinate, convergent anteriorly, united in front of apices of carinal prosternal striae.

Anterior margin of mesoventrite (Fig. 347) slightly emarginate medially; discal marginal mesoventral stria deeply impressed; disc somewhat convex, almost smooth; meso-metaventral sutural stria well impressed, in several punctures; intercoxal disc of metaventrite with longitudinal depression in male, smooth, basally with irregular sparse shallow fine punctures; lateral metaventral stria well impressed, carinate, obliquely arcuate, apically almost reaching metacoxa; lateral disc of metaventrite (Fig. 346) concave, with shallow setiferous punctures of various sizes, separated approximately by their own diameter, punctures fringed with setae; metepisternum with even denser and coarser punctation and setae, on apical third + fused metepimeron punctation much finer and sparser; metepisternal stria deeply impressed, present on fused metepimeron and approximately apical third of metepisternum.

Intercoxal disc of first abdominal sternite almost completely striate laterally; disc almost smooth, with sparse punctures along apical margin; lateral disc of all visible abdominal sternites with short setae laterally.

Protibia on outer margin (Fig. 348) with three low teeth topped with rounded blunt denticle followed by another two inconspicuous rounded denticles; setae of outer row sparse, moderately long; setae of median row shorter than those of outer row, sparse; anterior protibial stria shortened apically; protibial groove shallow; protibial spur minuscule, growing out from apical margin of protibia; outer part of posterior surface of protibia (Fig. 348) with irregular

rugae; vaguely separated from comparatively narrower median part; posterior protibial stria complete, terminating in two minute inner posterior denticles; inner margin of protibia with double row of short dense ramose setae.

Mesotibia (Fig. 350) moderately dilated and thickened, outer margin with two rows of sparse short denticles; setae of outer row well sclerotized, comparatively short; setae of median row shorter and sparser, covering most part of posterior surface; posterior mesotibial stria vaguely impressed, shortened apically; mesotibial spur stout prominent and long; anterior surface of mesotibia smooth; anterior mesotibial stria shortened apically; claws of last tarsomere bent, shorter than half its length.

Metatibia (Fig. 349) triangularly dilated and thickened apically, two rows of tiny sparse denticles diverge on apical third creating glabrous free space in-between them; metatibia otherwise similar to mesotibia.

Male genitalia. Eighth sternite (Figs. 351–352) on apical half longitudinally separated medially, vela of the apical part asetose (Figs. 351–352); eighth tergite and eighth sternite fused laterally (Fig. 353). Morphology of ninth tergite (Figs. 354–355) typical for the subfamily; spiculum gastrale (Fig. 358) expanded on both ends. Aedeagus (Figs. 356–357) slender; basal piece of aedeagus rather short, ratio of its length : length of parameres 1 : 3.5; parameres fused along their basal two-thirds; aedeagus apically slightly curved ventrad (Fig. 357).

Remarks. This species has two described subspecies: *Exaesiopus grossipes grossipes* (Marseul, 1855), distributed in southern Europe and southern parts of central Europe as far north as southern Slovakia and as far east as southern Russia, reaching Morocco and Canary Islands on its south-western distributional border; and *Exaesiopus grossipes berberus* Peyerimhoff, 1936 found in north Africa, from Morocco to Tunisia. Subspecies *E. g. berberus* differs from the nominotypical subspecies largely by the elytral punctation, which covers almost the entire elytral disc. *Exaesiopus grossipes grossipes* exhibits some degree of variation, especially regarding dorsal and ventral punctation, two sets of prosternal striae and other characteristics.

Gnathoncus Jacquelin-Duval, 1858

Gnathoncus Jacquelin-Duval, 1858: 112. Type species: *Hister rotundatus* Kugelann, 1792, designated by C. Thomson (1859: 75).

Gnathoncus: Thomson (1867): 391; Schmidt (1885a): 283, 317; Reitter (1896): 306; Ganglbauer (1899): 378; Reitter (1904): 35; Reitter (1909): 290; Jakobson (1911): 641, 648; Bickhardt (1916–1917): 104; Auzat (1917): 206; Horion (1935): 238; Reichardt (1941): 154, 157; McGrath & Hatch (1941): 54; Stockmann (1957): 67–76; Wenzel (1962): 374, 380; Hatch (1962): 258; Halstead (1963): 9, 11–13; Hansen (1968): 295, 315; Witzgall (1971): 166; Mazur (1973): 27; Kryzhanovskij & Reichardt (1976): 110, 113; Mazur & Kaszab (1980): 6, 42; Vienna (1980): 115, 117; Mazur (1981a): 71, 87; Mazur (1984): 103; Ôhara (1994): 215; Downie & Arnett (1996): 607, 612; Mazur (1997): 213; Bousquet & Laplante (1999): 141, 142; Mazur (2001): 19, 30; Kovarik & Caterino (2001): 221, 224; Yélamos (2002): 245, 246; Mazur (2004): 92; Bousquet & Laplante (2006): 79–81.

Diagnosis. Cuticle brown to black, never metallic; frontal, supraorbital striae absent; pronotum flattened; pronotal hypomeron glabrous; pronotal foveae absent; punctures of pronotum often forming longitudinal rugae laterally (in *Gnathoncus kiritshenkoi* pronotal disc medially with curious tubercle); elytra often imbricate, punctures on apical part of elytra often forming longitudinal rugae; marginal epipleural stria usually double; fourth dorsal elytral stria never connected with sutural stria; apical elytral stria often shortened. In most species there is a

characteristic hooked appendix between fourth dorsal and sutural striae at elytral base; anterior ends of fourth dorsal elytral and sutural elytral striae form a small hook. Prosternum without pre-apical foveae; median fossa often present; carinal prosternal striae strongly convergent anteriorly, often united under sharp angle; lateral prosternal striae shortened, strongly convergent anteriorly; prosternal process flattened, broad; outer-lateral costa reaches prosternal process, its basal margin distinctly elevated; metaventrite of males often longitudinally concave; ninth tergite of male genitalia divided longitudinally.

Differential diagnosis. *Gnathoncus* is most similar to the presumably related genera *Eremosaprinus* and *Myrmetes* sharing with them several putative synapomorphies: absent frontal and supraorbital striae, body without metallic luster and longitudinally divided ninth tergite of male genitalia. *Gnathoncus* differs from *Eremosaprinus* chiefly by the presence of lateral prosternal striae (absent in *Eremosaprinus*) and shorter meso- and metatibiae. From *Myrmetes*, it differs by the presence of sutural elytral stria (absent in *Myrmetes*), punctate dorsal surface (impunctate, matt in *Myrmetes*), outer margin of protibia with teeth (only short denticles present in *Myrmetes*) and the characteristic hooked appendix between the fourth dorsal elytral and sutural elytral striae (absent in *Myrmetes*). Superficially also similar the sole Palaearctic representative of the subgenus *Neosaprinus* of the genus *Euspilotus*, *E.* (*Neosaprinus*) *perrisi*, but the species of *Gnathoncus* differ from it by absent preapical foveae and flattened and broad prosternal process (distinctly convex in *E.* (*Neosaprinus*) *perrisi*). Female specimens of *E.* (*Neosaprinus*) *perrisi* also possess curious pygidial sulci (Figs. 162–167) that are always absent in *Gnathoncus*.

Biology. Predominantly inquilinous genus, its representatives are found within nests of birds or mammals; some species are found exclusively inside these nests where they are an active and important part of the local communities (Kryzhanovskij & Reichardt 1976: 114). They presumably prey upon larvae of fleas and other tiny arthropods thus reducing their number within the nests. Some species, however, are occasionally collected also on carrion. At least one species (*Gnathoncus cerberus* Auzat, 1923) lives cavernicolously, probably feeding on flies and other arthropods developing in guano. Several species of *Gnathoncus* (e.g. *Gnathoncus rotundatus*) are typical synanthropes and are often collected in pigsties, dovecotes or chicken coops.

Distribution. Twenty-four species and subspecies are known to occur world-wide (Mazur 1997); several species were possibly distributed over the globe by human activity. However, most of the species are found in the Holarctic Region.

Species examined. *Gnathoncus baeckmanni* Reichardt, 1941, *G. brevisternus* Lewis, 1907, *G. buyssoni* Auzat, 1917, *G. cerberus* Auzat, 1923, *G. communis* (Marseul, 1862), *G. disjunctus disjunctus* Solskij, 1876, *G. disjunctus suturifer* Reitter, 1896, *G. kiritshenkoi* Reichardt, 1930, *G. nannetensis* (Marseul, 1862), *G. nidorum* Stockmann, 1957, *G. potanini* Reitter, 1896, *G. pygmaeus* Kryzhanovskij, 1976, *G. rotundatus* (Kugelann, 1792), *G. semimarginatus* Bickhardt, 1920, *G. turkmenicus transcaucasianus* Olexa, 1992, *G. turkmenicus turkmenicus* Olexa, 1992, *G. wassiliefi* Normand, 1935, *Gnathoncus* spec. nov.

Discussion. This is most likely a monophyletic taxon, well delineated by the presence of at least two synapomorphies, e.g, short hooked appendix between the fourth dorsal elytral and sutural elytral striae and double marginal epipleural stria. The longitudinally divided tenth abdominal tergite of males can be accounted among synapomorphies shared also with taxa

Eremosaprinus, and *Myrmetes*. As mentioned above, together with *Eremosaprinus* and *Myrmetes*, these three taxa constitute the most basal 'grade' of the Palaearctic Saprininae (see Diagnosis of *Eremosaprinus* for details).

Gnathoncus rotundatus (Kugelann, 1792)

(Figs. 36, 55, 90, 119, 360–378)

Hister nanus: Scriba (1790): 73, nec Piller & Mitterpacher (1783): 34 (misidentification).
Hister rotundatus Kugelann, 1792: 304.
Saprinus deletus J. E. LeConte, 1844: 186. Synonymized by Marseul (1855): 503.
Saprinus rotundatus: J. E. LeConte (1845): 70; Marseul (1855): 348, 503; Horn (1873): 314; Blatchey (1910): 618, 619.
Gnathoncus rotundatus: Schmidt (1885a): 317; Mazur & Kaszab (1980): 45, Figs. 22A,I–J, 23A; Mazur (1981a): 88, Figs. 111–114; Mazur (1984): 105; Davies (1991): 138; Laplante et al. (1991): 44; Ôhara (1994): 215, 220, Figs. 130, 131, 133, 135; Downie & Arnett (1996): 612; Mazur (1997): 215; Bousquet & Laplante (1999): 144; Yélamos (2002): 246, 248, Figs. 124A,B, 126A,B; Mazur (2004): 92; Bousquet & Laplante (2006): 87, 90, Figs. 64, 65.
Gnathoncus ovulatus Casey, 1916: 256. Synonymized by Mazur (1997): 215.
Gnathoncus nanus Reichardt, 1941: 159, 161. Synonymized by Hoffmann (1803): 87.
Gnathoncus nanus: McGrath & Hatch (1941): 64; Hinton (1945): 322; Stockmann (1957): 67; Hatch (1962): 265; Halstead (1963): 13; Hansen (1968): 317; Witzgall (1971): 166; Mazur (1973): 27, Figs. 25–28, 37; Kryzhanovskij & Reichardt (1976): 114, 116, Figs. 125, 130, 135, 140, 145; Vienna (1980): 120, Fig. 47.
Gnathoncus rotundatus var. *pygidialis* Ganglbauer, 1899.
Gnathoncus rotundatus var. *subsuturalis* Reitter, 1896.
Note. Larva was described by Perris (1877): 21. Sensory structures of the antennal club and spermatheca were studied by De Marzo & Vienna (1982a,b).

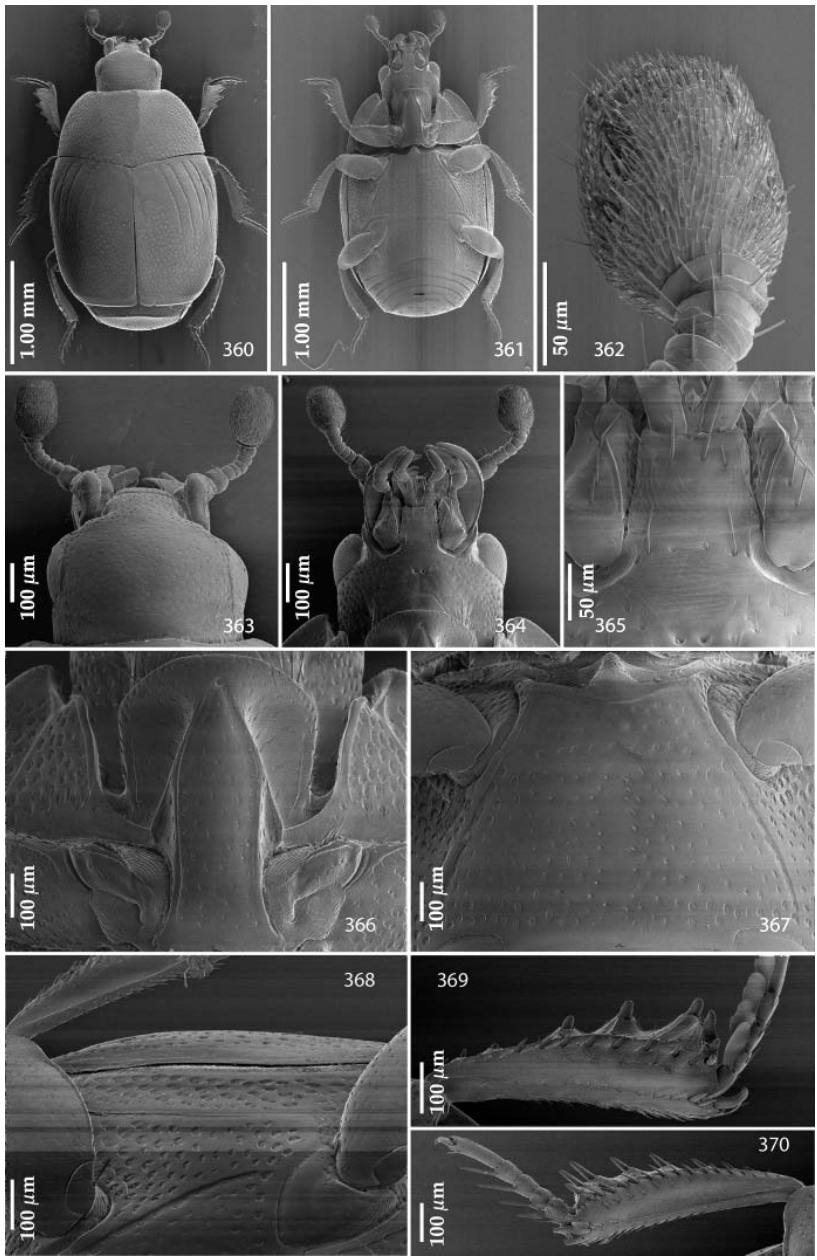
Type locality. Poland, East Prussia, Ostróda.
Material examined. CZECH REPUBLIC: Bohemia: Čelákovice, vi.1955, 1 ♂ 1 ♀, A. Olexa lgt. **JAPAN: Hokkaido:** Shimohoro, Tsurui, Kushiro moor, 1.vi.1992, 1 spec., M. Ôhara lgt. **KAZAKHSTAN:** Jambol Akkul, 8.v.1979, 2 ♀♀, A. Olexa lgt. **UKRAINE:** Odessa, vi.1957, 1 ♂ 1 ♀, A. Olexa lgt. (TLAN).

Redescription. Body length: PEL: 1.75–2.50 mm; APW: 0.625–0.825 mm; PPW: 1.20–1.725 mm; EL: 1.175–1.675 mm; EW: 1.375–2.00 mm.

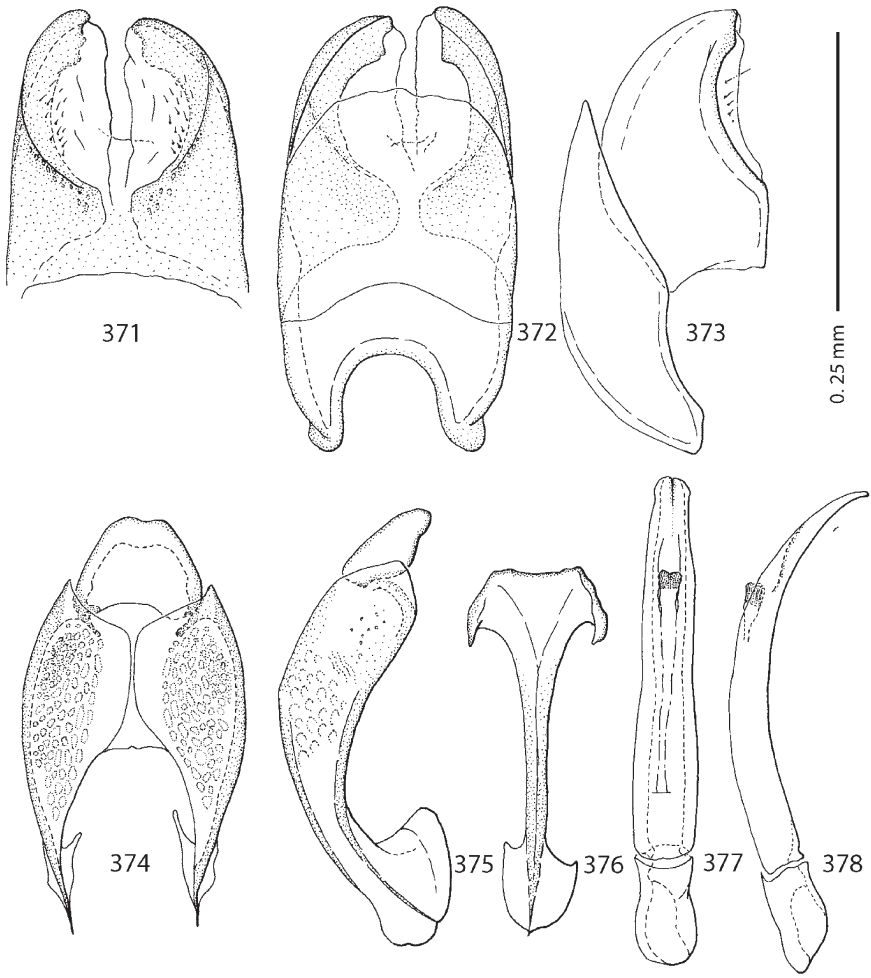
Body (Figs. 360–361) oval, moderately convex, slightly flattened from above, cuticle dark brown to black without metallic luster; legs, mouthparts and antennae rufous.

Antennal scape (Fig. 363) not thickened, with very few short setae; club (Fig. 362) comparatively large, oval, without visible articulation, entire surface covered in dense short sensilla, intermingled with sparse somewhat longer erect sensilla; sensory structures of antennal club (Fig. 36) in form of two sensory areas on ventral side and five vesicles; one of them is larger than other four; vesicles arranged in two pairs on ventral and dorsal side respectively.

Mouthparts. Mandibles (Fig. 90) with rounded outer margin curved inwardly, acutely pointed, subapical tooth on inner margin of left mandible very small; labrum (Fig. 55) flattened, punctate, with very shallow median excavation; labral fold significantly less developed; labral pits very small, one short seta present in each pit; terminal labial palpomere elongated, its width about one-third its length; palpal organ present on both labial and maxillary palpi; mentum (Fig. 365) sub-trapezoid, anterior angles slightly produced, anterior margin with a shallow medial notch (Fig. 119), surface around it with two long setae, lateral margins with



Figs. 360–370. *Gnathoncus rotundatus* (Kugelann, 1792), SEM micrographs: 360 – habitus, dorsal view; 361 – ditto, ventral view; 362 – antennal club, ventral view; 363 – head, dorsal view; 364 – ditto, ventral view; 365 – mentum, ventral view; 366 – prosternum; 367 – mesoventrite and metaventrite; 368 – lateral disc of metaventrite, metepisternum and fused metepimeron; 369 – protibia, ventral view; 370 – mesotibia, ventral view.



Figs. 371–378. *Gnathoncus rotundatus* (Kugelann, 1792), male terminalia (after Ôhara 1994): 371 – 8th sternite and tergite, ventral view; 372 – ditto, dorsal view; 373 – ditto, lateral view; 374 – 9th tergite, 10th tergite, dorsal view; 375 – ditto, lateral view; 376 – spiculum gastrale, ventral view; 377 – aedeagus, dorsal view; 378 – ditto, lateral view.

a single one row of much shorter sparse ramose setae, disc glabrous; cardo of maxilla with few short setae on lateral margin; stipes triangular, with three short setae; lacinia with lacinial hook; terminal labial palpomere elongated, its width about one-third its length, about three times as long as penultimate palpomere.

Clypeus (Fig. 363) large, rectangular, rounded laterally, with sparse fine punctures, separated several times their own diameter; frontal and supraorbital striae absent; frontal disc (Fig. 363) with sparse fine round punctures; eyes convex, well visible from above.

Pronotal sides (Fig. 360) feebly convergent anteriorly, apical angles obtuse, marginal pronotal stria complete, thin, slightly carinate, somewhat weakened behind head; disc entirely covered with deep, round punctation, becoming coarser and denser laterally; pronotal base with ante-scutellar depression; pronotal hypomeron glabrous; scutellum very small.

Elytral epipleura with scattered punctures of various sizes; marginal epipleural stria double, both striae weakly impressed but complete; marginal elytral stria well impressed, continuous along elytral apex as apical elytral stria, stopping short of sutural elytral stria; humeral elytral stria impressed on basal fourth; inner subhumeral stria present medially, very short; elytral disc with four dorsal elytral striae 1–4, first the longest, almost complete, becoming very fine and almost invisible on apical half, second to fourth striae well impressed, reaching about elytral half; between fourth dorsal elytral and sutural striae a characteristic hooked appendix present; sutural elytral stria present usually only on basal fourth to basal sixth. Entire elytral disc with regular dense round punctation, becoming sparser anteriorly and especially around scutellum; punctures separated by about their own to twice their own diameter; around apical elytral stria with longitudinal rugae.

Propygidium transverse, about four times as broad as long, partly concealed by elytra, with dense and coarse punctures; pygidium with dense elliptic punctures, separated by about their own diameter, becoming sparser towards apex.

Anterior margin of median portion of prosternum (Fig. 366) rounded; marginal prosternal stria present only laterally; prosternal process flattened, broad, dorso-laterally with sparse punctures, intermingled with alutaceous microsculpture; carinal prosternal striae carinate, parallel on basal two-thirds, thence strongly convergent anteriorly, vaguely united under a sharp angle terminating in shallow tiny prosternal apical fossa; lateral prosternal striae strongly convergent anteriorly, attaining carinal striae in middle of prosternal process.

Anterior margin of mesoventrite (Fig. 367) moderately emarginate medially; discal marginal mesosternal stria well impressed, somewhat carinate; disc flattened, with round punctures separated about their own to three times their diameter; meso-metaventral suture indistinct, meso-metaventral sutural stria marked as a sinuate row of large punctures; intercoxal disc of metaventrite (Fig. 368) laterally and along apical margin with deep round punctures of various sizes; in male longitudinally somewhat concave, with narrowly-defined longitudinal area along median line bordered with microscopic setae; surface mesad of it glabrous. Lateral metaventral stria well impressed, carinate, almost straight, reaching metacoxa; lateral disc of metaventrite (Fig. 368) flattened, with round shallow large punctures fringed with microscopic setae; metepisternum + fused metepimeron (Fig. 368) evenly covered with even coarser and denser punctation, punctures without setae.

Intercoxal disc of first abdominal sternite with lateral depressions, almost completely striate laterally; surface of disc with dense oblong punctation, punctures becoming sparser and finer medially.

Protibia (Fig. 369) flattened and somewhat dilated, outer margin with three low teeth topped with short denticle (first tooth topped with double denticle) followed by three minuscule denticles; setae of outer row rather dense, regular and short; setae of median row similarly dense and regular, but even shorter than those of outer row; protarsal groove deep; anterior protibial stria ridge-like; two thin, rather long tarsal denticles present apically; protibial spur

large, bent, growing out from apical protibial margin; apical margin of protibia posteriorly with two tiny apical denticles; outer part of posterior surface of protibia (Fig. 369) finely imbricate, with a row of about 10 minute denticles; delimitation from median part of posterior surface vague, marked by a row of sparse minuscule setae; posterior protibial stria complete, with rather dense sclerotized setae that become thicker towards apical margin; inner margin with double row of short setae.

Mesotibia (Fig. 370) slender, outer margin with a single row of thin denticles growing in size apically; setae of outer row sparse, regular, rather dense but short; setae of median row irregular, much shorter than those of outer row; posterior mesotibial stria complete; anterior surface of mesotibia (Fig. 370) with dense row of well sclerotized short setae, with another similar row of much shorter and finer setae situated below it; anterior mesotibial stria complete, terminating in three tiny inner anterior denticles; mesotibial spur stout, short; apical margin with two tiny denticles; mesotarsus shorter than mesotibia; claws of apical tarsomere about one-third its length; metatibia basically similar to mesotibia, but denticles of outer margin much sparser than those of mesotibia; claws of apical tarsomere somewhat longer, about half its length.

Male genitalia. Eighth sternite (Figs. 371–372) separated medially, vela with sparse microscopic setae (Fig. 371); eighth tergite and eighth sternite not fused laterally (Fig. 373). Ninth tergite (Figs. 374–375) longitudinally divided medially; spiculum gastrale (Fig. 376) expanded on both ends. Aedeagus (Figs. 377–378) slender; basal piece of aedeagus short, ratio of its length : length of parameres 1 : 5; parameres fused along their basal three-fourths; aedeagus curved ventrad (Fig. 378).

Hypocacculus Bickhardt, 1914

Hypocacculus Bickhardt, 1914: 311. Type species: *Saprinus metallescens* Erichson, 1834, designated by Bickhardt (1916: 96).

Hypocacculus: Reichardt (1926): 14; Reichardt (1932): 28, 96; Reichardt (1941): 156, 280; Peyerimhoff (1936): 228; Witzgall (1971): 173; Mazur (1973): 27, 37; Kryzhanovskij & Reichardt (1976): 111, 201; Mazur & Kaszab (1980): 7, 52; Vienna (1980): 116, 171; Mazur (1981a): 71, 96; Mazur (1984): 83; Mazur (1997): 249; Yélamos (2002): 245, 308; Mazur (2004): 93.

Diagnosis. Cuticle often metallic, elytra never with red maculae; body size between 1.20–3.00 mm, in most cases smaller than 2.5 mm. Antennal scape never extremely dilated and/or thickened; antennal club without visible articulation. Frontal stria never interrupted; supraorbital stria at times lacking; frontal disc punctate, never smooth and/or with several deep rugae (as in *Hypocaccus*). Eyes always visible from above. Pronotum without pronotal foveae, pronotal disc usually with punctation at least laterally, never entirely smooth. Marginal pronotal stria usually complete, lateral pronotal stria always absent; disc of pronotum very convex, so that lateral margins are not observable along their entire length (seen from dorsal view). Prosternum in most cases with pre-apical foveae (apart from *Hypocacculus* (*Colpellus*) *solieri* (Marseul, 1862)); both sets of prosternal striae present. Basal area of metaventrite rarely (e.g. *Hypocacculus* (*Nessus*) *baudii* (Schmidt, 1890) or *Hypocacculus* (*Nessus*) *balux* Reichardt, 1932) with two large tubercles. Protibia usually moderately dilated, outer margin with 6–16 teeth; mesotibia and metatibia usually not particularly thickened.

Differential diagnosis. *Hypocacculus* is most similar to the presumably closely related genera *Chalcionellus*, *Pholioxenus* and *Paravolvulus*. Actually, *Pholioxenus* and *Paravolvulus* were once included in *Hypocacculus* and in several cases the delimitations between several species included in them and *Hypocacculus* are not clear-cut. *Chalcionellus* differs from *Hypocacculus* mainly by the well-developed pronotal foveae; however, not all taxa included in *Chalcionellus* possess them. In cases, where there are no pronotal foveae present in *Chalcionellus*, frontal stria is prolonged onto the clypeus (occasionally clypeus and/or anterior part of frontal disc are depressed) and the body is metallic. From *Pholioxenus* this genus differs chiefly by the shape of protibia and number of teeth on its outer margin: protibia in *Pholioxenus* is more dilated than in *Hypocacculus* and it is usually furnished with 4–6 low, broad teeth, topped with tiny slender denticle (whereas the outer margin of protibia in *Hypocacculus* is furnished with 6–15 low teeth topped with short denticle) and the pronotum in *Pholioxenus* is only slightly convex so that its lateral margins are visible along their entire length (seen from dorsal view). Furthermore, the eyes in *Pholioxenus* are more convex than in *Hypocacculus* and the elytral surface is often imbricate. Pre-apical foveae are also considerably less developed in *Pholioxenus* and in several species they are even absent. Sutural elytral stria, especially on its apical half is strongly carinate in many species of *Pholioxenus* and it is rarely basally connected with fourth dorsal elytral stria (in *Hypocacculus* the sutural elytral stria is rarely carinate and it is often connected with the fourth dorsal elytral stria). *Pholioxenus* is a typical inquilinous taxon with all of its known Palaearctic species inhabiting burrows of rodents – this behavior is more an exception than a rule in *Hypocacculus*. Another presumably closely related genus *Paravolvulus* differs from the species of *Hypocacculus* with usually interrupted frontal stria and often present lateral pronotal stria; in several cases the species of *Paravolvulus* possess red maculae on their elytra (e.g. *Paravolvulus fausti* Schmidt, 1885a), which is unseen in *Hypocacculus*. The cuticle of *Paravolvulus* is usually not metallic, whereas in *Hypocacculus* it often is, and eyes in *Paravolvulus* are more convex than in *Hypocacculus*.

There are several more genera that could also be confused with *Hypocacculus*: *Zorius*, *Axelinus*, *Saprinillus*, and in the case of subgenus *Nessus* even with species of the genus *Hypocaccus*. Species of the genus *Zorius* generally differ from *Hypocacculus* by the larger body size and elevated anterior margin of clypeus, furthermore, the pre-apical foveae in *Zorius* are absent, whereas they are almost universally present in *Hypocacculus.* The sole taxon included in genus *Axelinus*, *A. ghilarovi*, differs from all species of *Hypocacculus* by widely interrupted frontal stria, rugulose-lacunose frontal disc and by the shape of protibia: in *Axelinus ghilarovi* it is with three triangular teeth topped with short broad denticle, followed by two minute denticles and in *Hypocacculus* the teeth of protibia are usually more numerous. Another very similar genus, *Saprinillus*, differs from *Hypocacculus* likewise by the widely interrupted frontal stria, more cylindrical body and the shape of protibia that in the case of *Saprinillus* bears only denticles and never articulated teeth. Taxa included in the subgenus *Nessus* of the genus *Hypocacculus* possess similarly structured frontal disc as some species of *Hypocaccus* (frontal disc with numerous coarse rugae), but their body size is generally smaller than that of the most *Hypocaccus* species, and the frontal stria of subgenus *Nessus* is similarly strongly carinate and straight. According to Mazur (pers. comm. 2008), *Nessus* ought to be synonymized with *Hypocaccus*; however, the two taxa should be first compared

using modern phylogenetical methods at the species level, something that is beyond the scope of this paper.

Biology. The species of *Hypocacculus* are typically collected on carrion and in dung in dry and arid places. Several species (e.g. *Hypocacculus* (*Nessus*) *eremobius* Reichardt, 1932) appear to be true psammophiles with their corresponding morphological adaptations.

Distribution. This genus is distributed mostly in the Palaearctic and Afrotropical Regions, with several representatives known also from Indo-Malayan Subregion. *Hypocacculus* (*Hypocacculus*) *hyla* (Marseul, 1864) has been recorded as far as New Guinea, enriching thus the Australopacific Region; *Hypocacculus* (*Hypocacculus*) *interpunctatus* (Schmidt, 1885a) has been introduced into Australia (Mazur 1997). This genus consists of five subgenera, two of which (*Nannolepidius* Reichardt, 1932 and *Toxometopon* Reichardt, 1932) are monotypic and confined to the Afrotropical Region. *Hypocacculus* is absent in New World. This genus contains around 76 species worldwide (1 species is regarded *incertae sedis*) (Mazur 1997).

Discussion. As mentioned earlier, monophyly of this taxon is probably questionable (see Diagnosis of *Axelinus* or *Chalcionellus*), with only a few weak supporting synapomorphies, most likely homoplasies. This is possibly a paraphyletic genus with several smaller genera deeply nested within *Hypocacculus*. The daunting task for the future researchers would be to revise this taxon and establish groupings of monophyletic taxa that it contains. This, however is a challenging task given the number of species that *Hypocacculus* contains, including many undescribed ones. The taxonomical value of its subgenera, artificial in authors' opinion, must be likely tested using modern phylogenetic methods.

Key to the Palaearctic subgenera of the genus *Hypocacculus*

1 (4) Frontal disc with fine punctation.

2 (3) Frontal stria medially almost straight (Fig. 400); supraorbital stria elevated above eyes, forming carina. ..... subgenus ***Colpellus*** Reichardt, 1932

3 (2) Frontal stria usually curved outwardly (Fig. 382); supraorbital stria mostly absent, never forming carina; frontal disc with fine to moderately coarse punctation. .... subgenus ***Hypocacculus*** s. str.

4 (1) Frontal disc usually coarsely and very densely punctate (Fig. 420); often with short numerous rugae; body slightly convex. ..... subgenus ***Nessus*** Reichardt, 1932

Subgenus *Hypocacculus* Bickhardt, 1914

Hypocacculus (*Hypocacculus* s. str.): Reichardt (1926): 14; Reichardt (1932): 28, 96; Reichardt (1941): 156, 280; Peyerimhoff (1936): 228; Kryzhanovskij & Reichardt (1976): 202, 205; Mazur & Kaszab (1980): 52; Vienna (1980): 171, 174; Mazur (1984): 84; Mazur (1997): 250; Yélamos (2002): 308, 314; Mazur (2004): 93.

Diagnosis. The subgenus *Hypocacculus* differs from the subgenera *Colpellus* and *Nessus* by the usually absent supraorbital striae, outwardly curved frontal stria, never forming acute angles above eyes and in general slightly coarser frontal punctation, never being rugulose-lacunose. Pronotal hypomeron is with short setae; elytra in most cases without apical elytral stria, usually with punctation that is becoming denser towards elytral apex. Protibia usually with 6–8 teeth on outer margin, becoming progressively smaller apically.

Biology. See Biology of *Hypocacculus* s. l.

Distribution. About 12 species are known, most of them from the Palaearctic and Afrotropical Regions; *Hypocacculus* (*Hypocacculus*) *spretulus* is spread in the Palaearctic Region and Indo-Malayan Subregion and *Hypocacculus* (*Hypocacculus*) *hyla* reaches as far as New Guinea (Mazur 1997).

Species examined. *Hypocacculus* (*Hypocacculus*) *atrocyaneus* (Schmidt, 1888), *H.* (*H.*) *elongatulus elongatulus* (Rosenhauer, 1856), *H.* (*H.*) *elongatulus portusmagni* (Coquerel, 1859), *H.* (*H.*) *metallescens* (Erichson, 1834), *H.* (*H.*) *spretulus* (Erichson, 1834), *H.* (*H.*) *virens* Dahlgren, 1973.

Hypocacculus (*Hypocacculus*) *metallescens* (Erichson, 1834)

(Figs. 22, 57, 92, 122, 379–397)

Hister virens: Dejean (1821): 48 (*nomen nudum*). Synonymized by Dejean (1837): 142.
Hister metallescens: Dejean (1821): 48 (*nomen nudum*).
Saprinus metallescens Erichson, 1834: 192.
Hister sardeus Dejean, 1837: 142 (unnecessary new name for *S. metallescens* Erichson, 1834).
Saprinus metallescens: Marseul (1855): 686, t. XIX, Fig. 128; Schmidt (1885a): 310; Ganglbauer (1899): 388; Jakobson (1911): 650.
Saprinus geminatus Wollaston, 1867: 86. Synonymized by Bickhardt (1913): 701.
Saprinus arachnidarum Marseul, 1876: 39. Synonymized by Schmidt (1885a): 310.
Hypocaccus metallescens: Ragusa (1892): 265.
Hypocacculus metallescens: Reichardt (1932): 35, 105; Reichardt (1941): 282, 289; Hinton (1945): 316, 327, Fig. 46; Horion (1949): 338; Kryzhanovskij & Reichardt (1976): 202, 206, Figs. 411, 412; Vienna (1980): 174, 177; Mazur (1984): 85; Mazur (1997): 251; Yélamos (2002): 315, 316, Figs. 156D, 157D; Mazur (2004): 93.
Saprinus (*Hypocacculus*) *metallescens* var. *marqueti* Thérond, 1948: 124.

Type locality. Italy, Sardinia.

Material examined. ALGERIA: Ain Sefra, 26.iv.1987, 2 spec., A. Olexa lgt.; Bèni Abbés, 11.iv.1988, 1 ♂, A. Olexa lgt. **SYRIA:** Palmyra env., 25.–27.iv.1982, 1 ♂, A. Olexa lgt. **TUNISIA:** Monastir, 12.–15.vi.1982, 3 ♂♂, A. Olexa lgt.; Msaken, 8.vi.1982, 1 ♂, A. Olexa lgt. **TURKEY:** Kahramanmaras, 25 km SW K. Maras, Yesilyöre, 600 m, 37º27′18″N, 36°46′55″E, 18.iii.2005, 1 ♂, V. Assing lgt. (TLAN).

Redescription. Body length: PEL: 1.625–2.05 mm; APW: 0.50–0.75 mm; PPW: 1.25–1.575 mm; EL: 1.00–1.375 mm; EW: 1.30–1.75 mm.

Body (Figs. 379–380) oval, moderately convex; cuticle brown, shining, with brassy luster; legs, antennae and mouthparts light brown.

Antennal scape (Fig. 382) moderately dilated with few short setae; club (Fig. 388) rounded, without visible articulation, entire surface imbricate, basal sixth of club glabrous, apical two-thirds with dense short sensilla, intermingled with sparse somewhat longer sensilla; sensory structures of antennal club (Fig. 22) in form of stipe-shaped vesicle situated under circular sensory area on internal distal margin of the ventral side of antennal club.

Mouthparts. Mandibles (Fig. 92) with rounded outer margin curved inwardly, acutely pointed; sub-apical tooth on inner margin of left mandible moderately large, almost perpendicular; labrum convex (Fig. 57) with two well-impressed labral pits, with two well-sclerotized setae present in each pit; anterior margin of labrum with shallow concavity interrupting convexity; terminal labial palpomere elongated, its width about one-third its length; mentum sub-trapezoid, with tiny notch in middle of anterior margin (Fig. 122); antero-lateral corners

with few ramose setae, lateral margins with two rows of much shorter ramose setae; disc of mentum imbricate, with scattered microscopic setae; cardo of maxilla with few short setae on outer margin; stipes triangular, with three much longer setae; terminal maxillary palpomere elongate, its width shorter than half its length, approximately twice as long as penultimate.

Clypeus (Fig. 382) rounded laterally; disc punctate; frontal stria curved outwardly, somewhat weakened medially; supraorbital stria absent; frontal disc (Fig. 382) with scattered punctation, punctures separated by 2–4 times their diameter; eyes moderately convex, visible from above.

Pronotal sides (Fig. 379) feebly arcuate; apical angles inconspicuous; marginal pronotal stria complete, anteriorly somewhat carinate; disc laterally covered with coarse and dense punctation, medially punctation weakens and becomes sparser; along pronotal base a row of coarse punctures present; pronotal hypomeron with very short, almost invisible amber setae.

Elytral epipleura almost smooth, with fine scattered punctures; marginal epipleural stria complete, rather thin; marginal elytral stria well impressed, apically attaining elytral apex and shortly continued along it, apical stria absent. Humeral elytral stria weakly impressed on basal third; inner subhumeral stria shortly present medially in a form of a short row of coarse punctures; elytra with four dorsal elytral striae 1–4, in punctures, first dorsal elytral stria the longest, reaching about three-fourths of elytral length apically; slightly curved inwardly; second and third striae about the same length, surpassing half of elytral length apically; fourth dorsal elytral stria the shortest, not reaching half of elytral length apically, basally connected with complete sutural elytral stria; between it and elytral suture a row of very fine punctures present. Elytral disc punctate, punctures on basal half fine, almost invisible, apical half with coarse punctures separated about 1–3 times their diameter, punctation becomes coarser and denser towards elytral apex; extreme elytral apex impunctate.

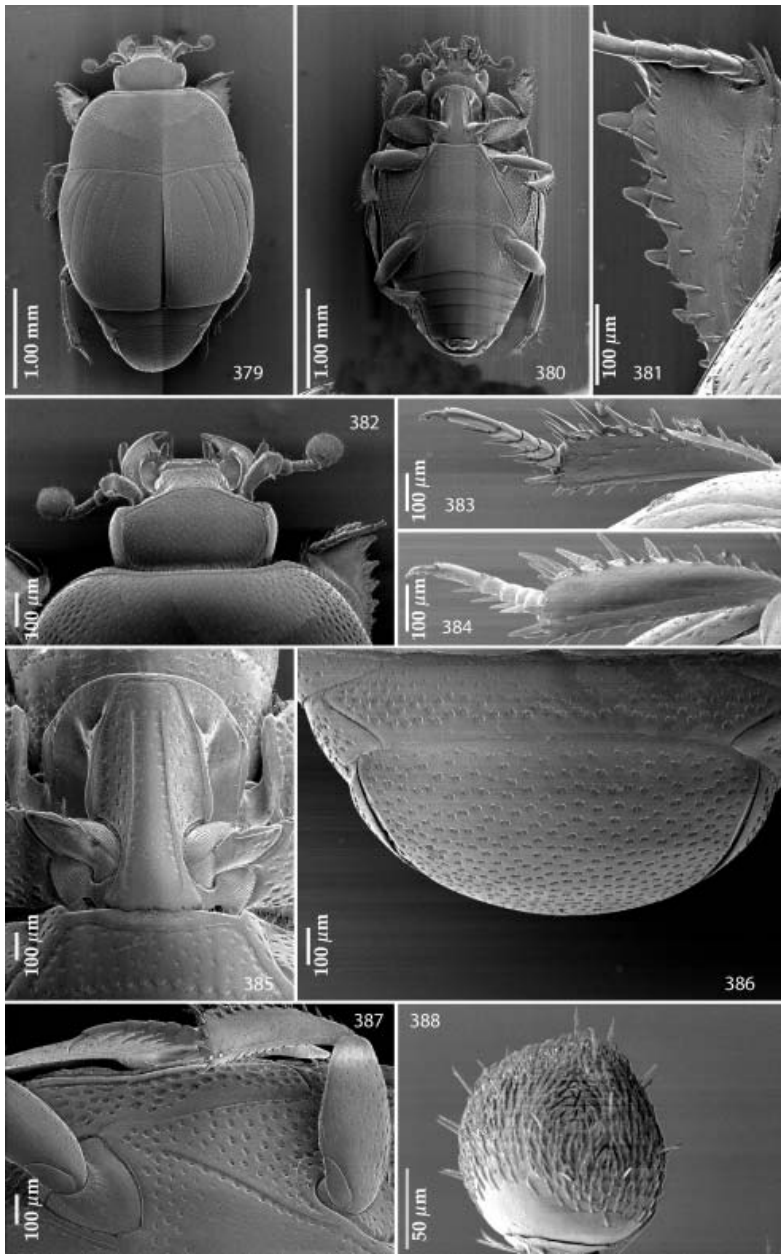
Propygidium and pygidium (Fig. 386) coarsely and densely punctate, punctures separated by about their own to twice their diameter.

Anterior margin of median portion of prosternum (Fig. 385) almost straight; marginal prosternal stria present laterally; pre-apical foveae deep; prosternal process slightly concave, laterally finely strigulate-coarsely punctate, dorsally smooth, with scattered fine punctation; lateral prosternal striae strongly carinate, united in front of not united sub-parallel carinal prosternal striae.

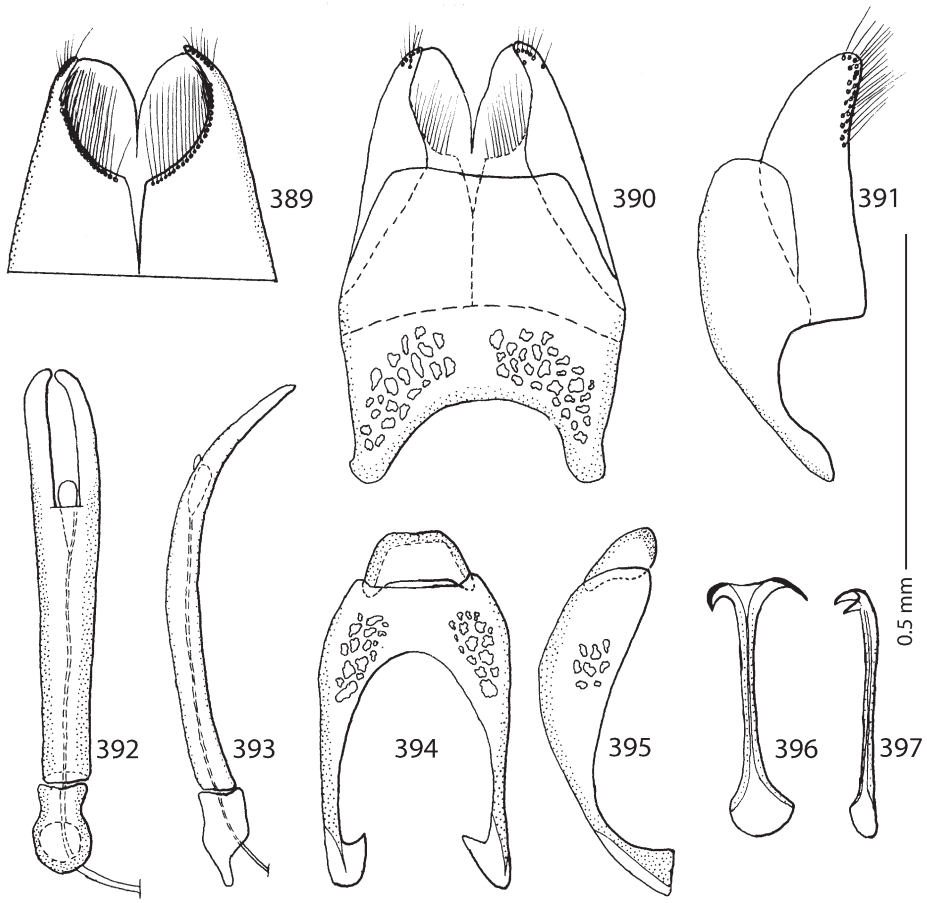
Anterior margin of mesoventrite (Fig. 385) feebly emarginate medially, discal marginal mesoventral stria well impressed; carinate; disc of mesoventrite with scattered fine punctures; meso-metaventral sutural stria well impressed, undulate; intercoxal disc of metaventrite with very fine, scattered punctation, along apical margin punctures become coarser and denser. Lateral metaventral stria (Fig. 387) deeply impressed, in punctures, almost reaching hind coxa; lateral disc of metaventrite with coarse deep punctures separated by about their own diameter; metepisternum + fused metepimeron (Fig. 387) with even coarser punctures; metepisternal stria present on basal half; along metaventral-metepisternal suture short thin curious parallel stria present basally.

Intercoxal disc of first abdominal sternite completely striate laterally, with sparse round punctures, medially punctures becoming sparser and finer.

Protibia (Fig. 381) flattened and somewhat dilated, outer margin with four very low teeth



Figs. 379–388. *Hypocacculus* (*Hypocacculus*) *metallescens* (Erichson, 1834), SEM micrographs: 379 – habitus, dorsal view; 380 – ditto, ventral view; 381 – protibia, dorsal view; 382 – head, dorsal view; 383 – mesotibia, dorsal view; 384 – ditto, ventral view; 385 – prosternum and mesoventrite; 386 – propygidium and pygidium; 387 – lateral disc of metaventrite, metepisternum and fused metepimeron; 388 – antennal club, ventral view.



Figs. 389–397. *Hypocacculus* (*Hypocacculus*) *metallescens* (Erichson, 1834), male terminalia: 389 – 8th sternite, ventral view; 390 – 8th sternite and tergite, dorsal view; 391 – ditto, lateral view; 392 – aedeagus, dorsal view; 393 – ditto, lateral view; 394 – 9th tergite, 10th tergite, dorsal view; 395 – ditto, lateral view; 396 – spiculum gastrale, ventral view; 397 – ditto, lateral view.

topped with short denticle followed by two minuscule denticles; setae of outer row rather sparse, regular and short; setae of median row similarly dense and regular, but much shorter than those of outer row; protarsal groove shallow; anterior protibial stria curved, shortened apically; two tarsal denticles present apically; protibial spur tiny, inconspicuous; apical margin of protibia posteriorly with two tiny widely separated apical denticles; outer part of posterior surface of protibia microscopically punctate; distinctly separated from substrigulate median part of posterior surface by a row of about 7 tiny denticles; posterior protibial stria complete, with very sparse weakly sclerotized setae, near apical margin turning into several sclerotized inner posterior denticles; inner margin with double row of short setae.

Mesotibia (Figs. 383–384) slender, outer margin with two sparse rows of thin denticles

growing in size apically; setae of outer row regular, well sclerotized; setae of median row irregular, much shorter than those of outer row; posterior mesotibial stria complete; anterior surface of mesotibia imbricate (Fig. 384) with scattered minuscule punctures with microscopic setae; anterior mesotibial stria complete, terminating in two tiny inner anterior denticles; mesotibial spur stout, moderately long; apical margin with two tiny denticles; claws of apical tarsomere shorter than half its length; metatibia basically similar to mesotibia, but more slender and denticles of outer margin much sparser than those of mesotibia.

Male genitalia. Eighth sternite (Figs. 389–390) on apical half longitudinally separated medially, inflatable membrane (velum) with dense row of long setae; apex with few much shorter and sparser setae; eighth tergite and eighth sternite not fused laterally (Fig. 391). Morphology of 9th tergite (Figs. 394–395) typical for the subfamily; spiculum gastrale (Fig. 396) expanded on both ends. Basal piece of aedeagus (Figs. 392–393) short, ratio of its length : length of parameres 1 : 4; parameres fused along their basal two-thirds; aedeagus curved ventrad (Fig. 393).

Subgenus *Colpellus* Reichardt, 1932

Colpellus Reichardt, 1932: 32, 33. Type species *Saprinus praecox* Erichson, 1834, original designation.
Colpellus: Reichardt (1941): 282, 286; Kryzhanovskij & Reichardt (1976): 201, 204; Vienna (1980): 171; Mazur (1984): 84; Mazur (1997): 250; Yélamos (2002): 308; Mazur (2004): 93.

Diagnosis. The subgenus *Colpellus* differs from the subgenus *Hypocacculus* and subgenus *Nessus* by the straight carinate frontal stria elevated above eyes continuous as a strongly carinate supraorbital stria. Clypeus often carinate laterally. Frontal disc with scattered fine punctation; punctation of elytra does not form a band of dense punctures before elytral apex. Protibia on outer margin with 6–7 low teeth, topped with short denticle.
Biology. See Biology of *Hypocacculus* s. l.
Distribution. This subgenus includes 6 species, distributed in Afrotropical and Palaearctic Regions, with *Hypocacculus* (*Colpellus*) *biskrensis* (Marseul, 1876) reaching as far as India and *Hypocacculus* (*Colpellus*) *praecox* (Erichson, 1834) to Afghanistan (Mazur 1997).
Species examined. *Hypocacculus* (*Colpellus*) *biskrensis* (Marseul, 1876), *H.* (*C.*) *infensus* G. Müller, 1937, *H.* (*C.*) *praecox* (Erichson, 1834), *H.* (*C.*) *solieri* (Marseul, 1862).

Hypocacculus (*Colpellus*) *praecox* (Erichson, 1834)

(Figs. 23, 58, 93, 123, 398–416)

Saprinus praecox Erichson, 1834: 193.
Saprinus praecox: Marseul (1855): 685, t. XIX, Fig. 127; Schmidt (1885a): 311.
Saprinus minyops Wollaston, 1864: 174. Synonymized by Schmidt (1895): 177.
Saprinus novellus Marseul, 1876: xxxv. Synonymized by Peyerimhoff (1917): 139.
Hypocaccus praecox: Ragusa (1892): 265.
Hypocacculus novellus: Bickhardt (1916): 97.
Hypocacculus praecox: Reichardt (1932): 33, 97, t. I, Fig. 7; Reichardt (1941): 282, 287; Théröond (1963b): 68; Kryzhanovskij & Reichardt (1976): 202, 205, Fig. 401; Vienna (1980): 172, 173, Fig. 63a; Mazur (1984): 84; Mazur (1997): 250; Yélamos (2002): 309, 313, Figs. 156B, 157B; Mazur (2004): 93.

Type locality. Egypt.
Material examined. ALGERIA: Ain Sefra, 26.iv.1987, 2 ♂♂ 3 spec., A. Olexa lgt. **EGYPT:** Mamura, x.1967, 1 spec., A. Olexa lgt. (TLAN).

Redescription. Body length: PEL: 1.575–2.375 mm; APW: 0.625–0.75 mm; PPW: 1.125–1.675 mm; EL: 0.925–1.375 mm;

Body (Figs. 398–399) oval, moderately convex, cuticle dark-brown with metallic luster; legs, antennae and mouthparts rufopiceous.

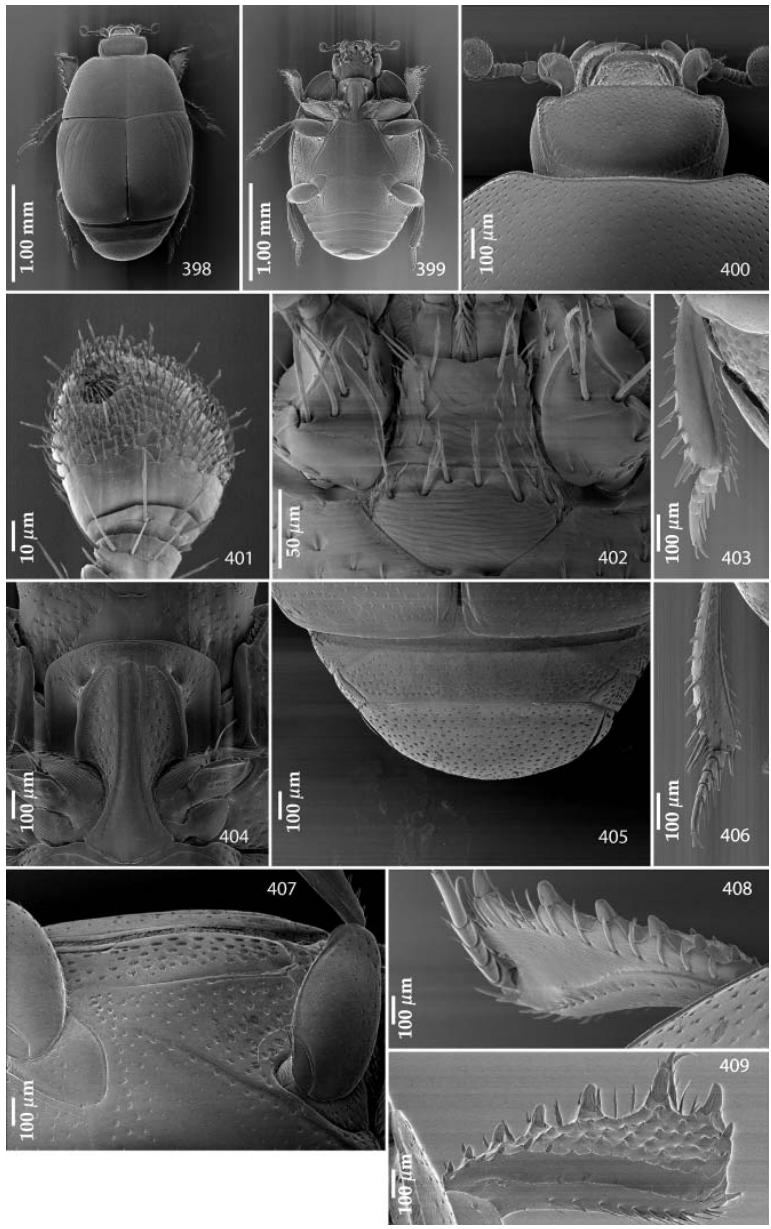
Antennal scape (Fig. 400) not thickened, with few short setae; club (Fig. 401) oval, without visible articulation, entire surface imbricate, basal third of club glabrous, apical two-thirds with dense short sensilla, intermingled with sparse somewhat longer sensilla; sensory structures of antennal club (Fig. 23) in form of stipe-shaped vesicle situated under circular sensory area on internal distal margin of the ventral side of antennal club, supplemented by another large sensory area under apical surface of club.

Mouthparts. Mandibles (Fig. 93) with rounded outer margin curved inwardly, acutely pointed, sub-apical tooth on inner margin of left mandible moderately large, almost perpendicular; labrum (Fig. 58) strongly convex with two well-impressed labral pits, with two well-sclerotized setae in each pit; anterior margin of labrum without concavity interrupting convexity; terminal labial palpomere elongated, its width about half its length; mentum (Fig. 402) sub-trapezoid, with shallow emargination in middle of anterior margin (Fig. 123); antero-lateral corners with few ramose setae, lateral margins with two rows of much shorter ramose setae; disc of mentum imbricate, medially glabrous; cardo of maxilla with few short setae on outer margin; stipes triangular, with three much longer setae; terminal maxillary palpomere elongate, its width shorter than half its length, approximately twice as long as penultimate.

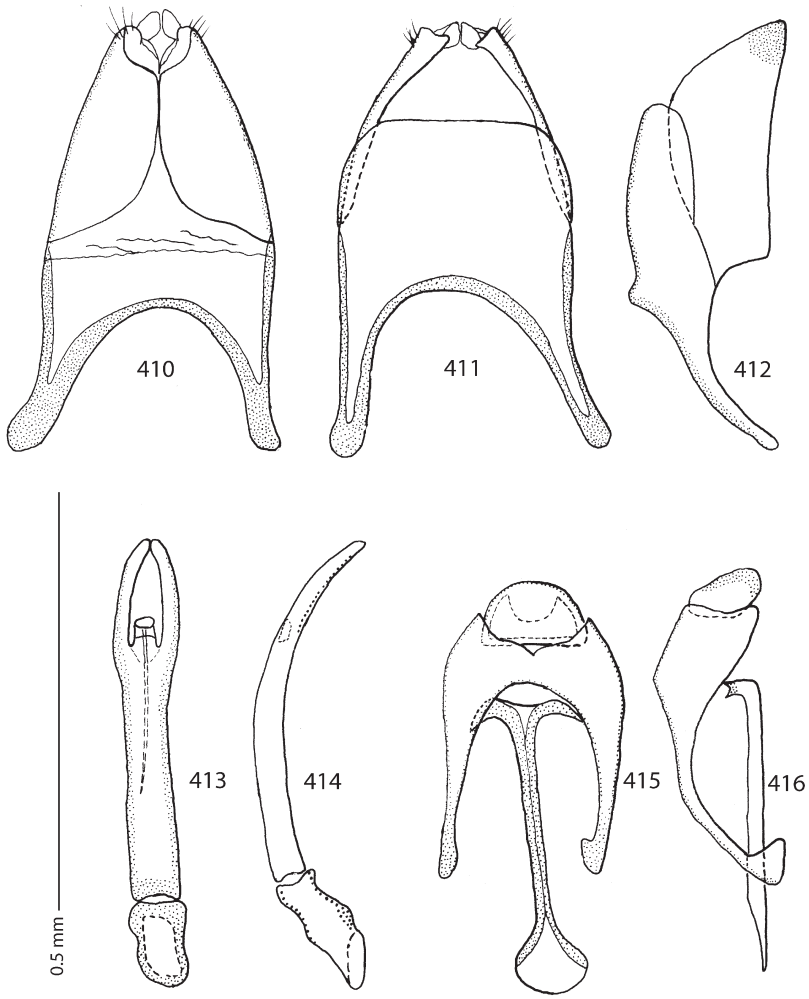
Clypeus (Fig. 400) laterally carinate; disc rugulose-lacunose; frontal stria carinate, straight, elevated above of eyes, continued as carinate supraorbital stria; frontal disc (Fig. 400) with fine shallow punctation, punctures separated by 2–4 times their diameter becoming sparser and finer posteriorly; eyes rather flat, visible from above.

Pronotal sides (Fig. 398) feebly arcuate anteriorly, apical angles rather blunt; disc with round punctures, separated by 1–3 times their diameter; medially punctation weakens; pronotal base with a row of coarse round punctures; marginal pronotal stria complete, carinate; pronotal hypomeron with very short, almost invisible amber setae.

Elytral epipleura with fine scattered punctures, almost smooth; marginal epipleural stria complete, rather thin, marginal elytral stria well impressed, its apical end attaining near the posterior third of elytron; apical elytral stria obliterated. Humeral elytral stria weakly impressed, present on basal third; inner subhumeral stria very short, present only as a medial fragment. Elytral disc with four dorsal elytral striae 1–4; first the longest, reaching about three-fourths of elytral length apically; second and third dorsal elytral striae about the same length, reaching elytral half apically, second stria somewhat longer than third; fourth dorsal elytral stria the shortest, not reaching elytral half posteriorly, basally well connected with sutural elytral stria; sutural stria thin but complete, in sparse moderately large punctures; between sutural stria and elytral suture a row of very fine punctures present. Entire elytral disc punctate; punctation coarser and denser on apical half, basal half with only scattered fine punctation; punctation weakens apically, stopping just short of elytral apex.



Figs. 398–409. *Hypocacculus* (*Colpellus*) *praecox* (Erichson, 1834), SEM micrographs: 398 – habitus, dorsal view; 399 – ditto, ventral view; 400 – head, dorsal view; 401 – antennal club, ventral view; 402 – mentum, submentum, cardines and stipites of maxilla, ventral view; 403 – mesotibia, ventral view; 404 – prosternum; 405 – propygidium and pygidium; 406 – metatibia, dorsal view; 407 – lateral disc of metaventrite, metepisternum + fused metepimeron; 408 – protibia, dorsal view; 409 – ditto, ventral view.



Figs. 410–416. *Hypocacculus* (*Colpellus*) *praecox* (Erichson, 1834), male terminalia: 410 – 8th sternite and tergite, ventral view; 411 – dito, dorsal view; 412 – ditto, lateral view; 413 – aedeagus, dorsal view; 414 – ditto, lateral view; 415 – 9th tergite, 10th tergite (dorsal view) and spiculum gastrale (ventral view); 416 – 9th tergite, 10th tergite and spiculum gastrale, lateral view.

Propygidium (Fig. 405) transverse, with sparse fine punctures, separated by 2–4 times their diameter; punctation becoming denser apically; pygidium (Fig. 405) with similar punctation, becoming sparser and finer towards the apex.

Anterior margin of median portion of prosternum (Fig. 404) almost straight; marginal prosternal stria fragmentally present anteriorly and laterally; pre-apical foveae deep; prosternal

process slightly concave, laterally finely strigulate-coarsely punctate, dorsally substrigulate, with scattered fine punctation; lateral prosternal striae strongly carinate, not united in front of united parallel carinal prosternal striae.

Anterior margin of mesoventrite deeply emarginate medially; discal marginal mesoventral stria complete; disc of mesoventrite with dense and coarse punctures separated about by 2–3 times their diameter; meso-metaventral sutural stria well impressed, undulate; intercoxal disc of metaventrite with very fine scattered punctation; punctures becoming coarser near hind coxa. Lateral metaventral stria carinate on outer side, reaching just short of hind coxa; lateral disc of metaventrite (Fig. 407) with sparse setiferous punctures; metepisternum + fused metepimeron (Fig. 407) evenly covered with coarser and denser punctation than that of lateral disc of metaventrite; along metaventral-metepisternal suture short curious parallel stria present basally.

Intercoxal disc of the first abdominal sternite completely striate laterally, with scattered sparse punctation; punctures becoming denser and coarser along lateral and apical margins.

Protibia (Figs. 408–409) flattened and somewhat dilated, outer margin with six low teeth topped with short denticle followed by two minuscule denticles; setae of outer row rather sparse, regular and short; setae of median row similarly dense and regular, but much shorter than those of outer row; protarsal groove shallow; anterior tibial stria shortened apically; single, rather long tarsal denticle present apically; protibial spur tiny, bent, growing out from apical protibial margin; apical margin of protibia posteriorly with two tiny apical denticles; outer part of posterior surface of protibia (Fig. 409) rugulose-lacunose; distinctly separated from glabrous median part of posterior surface, basally with row of about 5 minuscule denticles; posterior protibial stria complete, with very sparse weakly sclerotized setae, apical margin with two tiny inner-posterior denticles present; inner margin with double row of short setae.

Mesotibia (Fig. 403) slender, outer margin with two sparse rows of thin denticles growing in size apically; setae of outer row regular, well sclerotized; setae of median row irregular, much shorter than those of outer row; posterior mesotibial stria complete; anterior surface of mesotibia imbricate (Fig. 403) with scattered minuscule punctures with microscopic setae; anterior mesotibial stria complete, terminating in single tiny inner ventral denticle; mesotibial spur stout, short; apical margin with two tiny denticles; claws of apical tarsomere shorter than half its length; metatibia (Fig. 406) basically similar to mesotibia, but denticles of outer margin much sparser than those of mesotibia.

Male genitalia. Eighth sternite (Figs. 410–411) longitudinally separated medially, apically with small inflatable membrane (velum) fringed with few sparser setae; eighth tergite and eighth sternite not fused laterally (Fig. 412). Morphology of 9th tergite (Figs. 415–416) typical for the subfamily; spiculum gastrale (Fig. 415) expanded on both ends. Basal piece of aedeagus (Figs. 413–414) rather short, ratio of its length : length of parameres 1 : 3; parameres fused along their basal three-fourths; aedeagus gently curved ventrad (Fig. 414).

Remarks. A variable species, elytral striae (including the first dorsal elytral stria) can be shortened apically, reaching just elytral half; alternatively, they can surpass elytral half apically and reach as far as three fourths of elytral length. Punctation on elytral disc can be sparser; punctures can be separated by 3.0–3.5 times their diameter.

Subgenus *Nessus* Reichardt, 1932

Nessus Reichardt, 1932: 32. Type species: *Saprinus rubripes* Erichson, 1834, original designation.
Nessus: Reichardt (1941): 293; Kryzhanovskij & Reichardt (1976): 202, 207; Vienna (1980): 171, 178; Mazur & Kaszab (1980): 45; Mazur (1984): 86; Mazur (1997): 252; Yélamos (2002): 308, 318; Mazur (2004): 93.

Diagnosis. The subgenus *Nessus* differs from the subgenera *Hypocacculus* and *Colpellus* by densely and usually coarsely punctated frontal disc, often with shallow irregular rugae (frontal disc occasionally coarsely granulate, especially in several species from the Afrotropical Region); frontal stria usually well impressed, curved or straight, in most cases interrupted behind eyes; supraorbital stria usually absent.
Biology. As it is common with this genus, members of this subgenus are mostly found on carrion and in dung, excrements, etc. Several species are apparently psammophilous (e.g. *Hypocacculus* (*Nessus*) *eremobius* Reichardt, 1932).
Distribution. This subgenus includes the bulk (about 54 species) of representatives of the genus *Hypocacculus*, and is especially species-rich in the Afrotropical Region. Several species occur as far east as India and Sri Lanka. *Hypocacculus* (*Nessus*) *interpunctatus* has been introduced into Australia (Mazur 1997).
Species examined. *Hypocacculus* (*Nessus*) *ascendens* Reichardt, 1932, *H.* (*N.*) *balux* Reichardt, 1932, *H.* (*N.*) *baudii* (Schmidt, 1890), *H.* (*N.*) *controversus* G. Müller, 1937, *H.* (*N.*) *eremobius* Reichardt, 1932, *H.* (*N.*) *grosclaudei* (Normand, 1935), *H.* (*N.*) *hosseinus* (Théry, 1921), *H.* (*N.*) *interpunctatus* (Schmidt, 1885a), *H.* (*N.*) *kiseritzkyi* Reichardt, 1932, *H.* (*N.*) *occator* Reichardt, 1932, *H.* (*N.*) *orbus* Reichardt, 1932, *H.* (*N.*) *oxytropis* Reichardt, 1932, *H.* (*N.*) *rubripes* (Erichson, 1834), *H.* (*N.*) *rufipes* (Kugelann, 1792), *H.* (*N.*) *tigris araxis* Reichardt, 1932, *H.* (*N.*) *tigris tigris* (Marseul, 1862), *H.* (*N.*) *vethi* (Bickhardt, 1912), *H.* (*N.*) *vlasovi* Kryzhanovskij, 1966.
Notes on the taxonomic status of *Hypocacculus* (*Nessus*) *grosclaudei*. *Hypocacculus* (*N.*) *grosclaudei* has been originally described in the genus *Exaesiopus*. However, Peyerimhoff (1936) proposed to include it in the genus *Hypocacculus*, subgenus *Nessus*. Although Kryzhanovskij & Reichardt (1976) likewise objected placing it in *Exaesiopus*, Mazur (1984, 1997) left its taxonomic status unchanged. After examining several specimens of this species (one of them has been compared with the type species by Peyerimhoff (MNHN)) the opinion of Peyerimhoff (1936) is upheld in this work.

Hypocacculus (*Nessus*) *rubripes* (Erichson, 1834)

(Figs. 24, 59, 94, 124, 175, 415–430)

Hister arenarius: Dejean (1821): 48 (*nomen nudum*).
Saprinus rubripes Erichson, 1834: 193.
Saprinus granarius Erichson, 1834: 191. Synonymized by Fauvel in Gozis (1886): 202.
Saprinus granarius: Schmidt (1885a): 313.
Saprinus corsicus Marseul, 1855: 688. Synonymized by Bickhardt (1910): 104.
Saprinus corsicus: Schmidt (1885a): 312.
Saprinus arenarius Marseul, 1855: 691. Synonymized by Reitter (1909): 293.
Hypocaccus rubripes: Ganglbauer (1899): 390; Reitter (1909): 393; Jakobson (1911): 651; Reichardt (1925): 113.
Saprinus rubripes var. *granarius*: Ganglbauer (1899): 390.

Hypocaccus corsicus: Lewis (1905): 77.
Saprinus rubripes var. *corsicus*: Bickhardt (1910): 104.
Saprinus rubripes var. *clermonti* Auzat, 1920: 4.
Hypocacculus rubripes: Reichardt (1932): 50, 125, Figs. 3v, 16; t. II, Fig. 4; t. III, Figs. 17, 35; Reichardt (1941): 286, 301, Figs. 147R, 148, 149B, 153; Horion (1949): 338; Witzgall (1971): 173; Kryzhanovskij & Reichardt (1976): 204, 211, Figs. 404, 406, 410, 416, 417, 418; Vienna (1980): 179, 180, Fig. 65; Mazur & Kaszab (1980): 56, Figs. 28A–D; Mazur (1981a): 96, 97, Figs. 132, 133; Mazur (1984): 90; Mazur (1997): 255; Yélamos (2002): 320, 322, Figs. 154C, 156H; Mazur (2004): 93.
Hypocacculus rubripes corsicus: Reichardt (1932): 128.
Note. Sensory structures of the antennal club and spermatheca were studied by De Marzo & Vienna (1982a,b).

Type locality. Portugal.
Material examined. ALGERIA: Bèni Abbés, 20.x.1980, 1 ♂, A. Olexa lgt. **BULGARIA:** Stranzha, vii.1934, 2 ♂♂, Dr. Purkyně lgt.; Sozopol, vi.1965, 1 spec., A. Olexa lgt.; Kamchiya, vii.73, 1 ♂, A. Olexa lgt. **IRAN:** Talysch, Haktpar [illegible], 25.vii.1976, 1 ♂, collector unknown. **ITALY:** Grado, date unknown, 1 spec., Dr. Jureček lgt.; Alessio, Alb., date unknown, 1 spec., Matzenauer lgt. (TLAN).

Redescription. Body length: PEL: 1.70–2.175 mm; APW: 0.60–0.75 mm; PPW: 1.275–1.625 mm; EL: 1.05–1.40 mm; EW: 1.40–1.825 mm.

Body (Figs. 417–418) roundly oval, convex; cuticle shining, castaneous brown; legs, antennae and mouthparts rufopiceous.

Antennal scape (Fig. 420) somewhat dilated, with few short setae; club without visible articulation, entire surface imbricate, with short dense sensilla intermingled with sparse somewhat longer erect sensilla; sensory structures of antennal club (Fig. 24) in form of stipe-shaped vesicle situated under circular sensory area on internal distal margin of the ventral side of antennal club.

Mouthparts. Mandibles (Fig. 94) with rounded outer margin curved inwardly, acutely pointed, sub-apical tooth on inner margin of left mandible moderately large, almost perpendicular; labrum (Fig. 59) punctate, convex with two well-impressed labral pits, with two well-sclerotized setae in each pit; anterior margin of labrum with small concavity interrupting convexity; terminal labial palpomere elongated, its width about one-third its length; mentum sub-trapezoid, with shallow median notch (Fig. 124); anterior margin with few ramose setae, lateral margins with one row of much shorter ramose setae; disc of mentum imbricate, with scattered microscopic setae; cardo of maxilla with few short setae on outer margin; stipes triangular, with three much longer setae; terminal maxillary palpomere elongate, its width shorter than half its length, approximately twice as long as penultimate.

Clypeus (Fig. 420) with elevated anterior margin, somewhat margined laterally, rugulose-lacunose; frontal stria well impressed, straight, carinate; continued as a well-impressed carinate supraorbital stria; frontal disc (Fig. 420) with irregular longitudinal rugae intermingled with sparse microscopic punctation; eyes flat, inconspicuous from above.

Pronotal sides (Fig. 417) moderately convergent anteriorly; apical angles conspicuous; marginal pronotal stria complete, carinate; disc laterally with coarse punctation, between it and pronotal margin a smooth longitudinal band present; medially punctation much finer and sparser; pronotal base with two rows of coarse round punctures; pronotal hypomeron glabrous.

Elytral epipleura with microscopic punctation; marginal epipleural stria complete, well impressed; marginal elytral stria well impressed, continued for a short distance along apical margin. Humeral elytral stria weakly impressed on basal third; inner subhumeral stria deeply impressed medially; elytra with four dorsal elytral striae 1–4, in punctures; first dorsal elytral stria the longest, reaching approximately three-fourths of elytral length apically, on apical half somewhat curved inwardly; second, third and fourth dorsal elytral striae about the same length, reaching approximately elytral half apically; fourth dorsal elytral stria basally connected with sutural elytral stria; sutural stria well impressed, in shallow punctures, shortened on its apical tenth. Elytral disc on apical half (except for elytral flanks) with coarse and dense punctation, punctures separated by about their own diameter, anteriorly reaching about half of elytral length; basal half with only fine microscopic punctation; extreme apex of elytra with an impunctate band.

Propygidium completely exposed, with even denser punctures than those of elytra; pygidium with much sparser and finer punctation, becoming sparser and finer towards the apex.

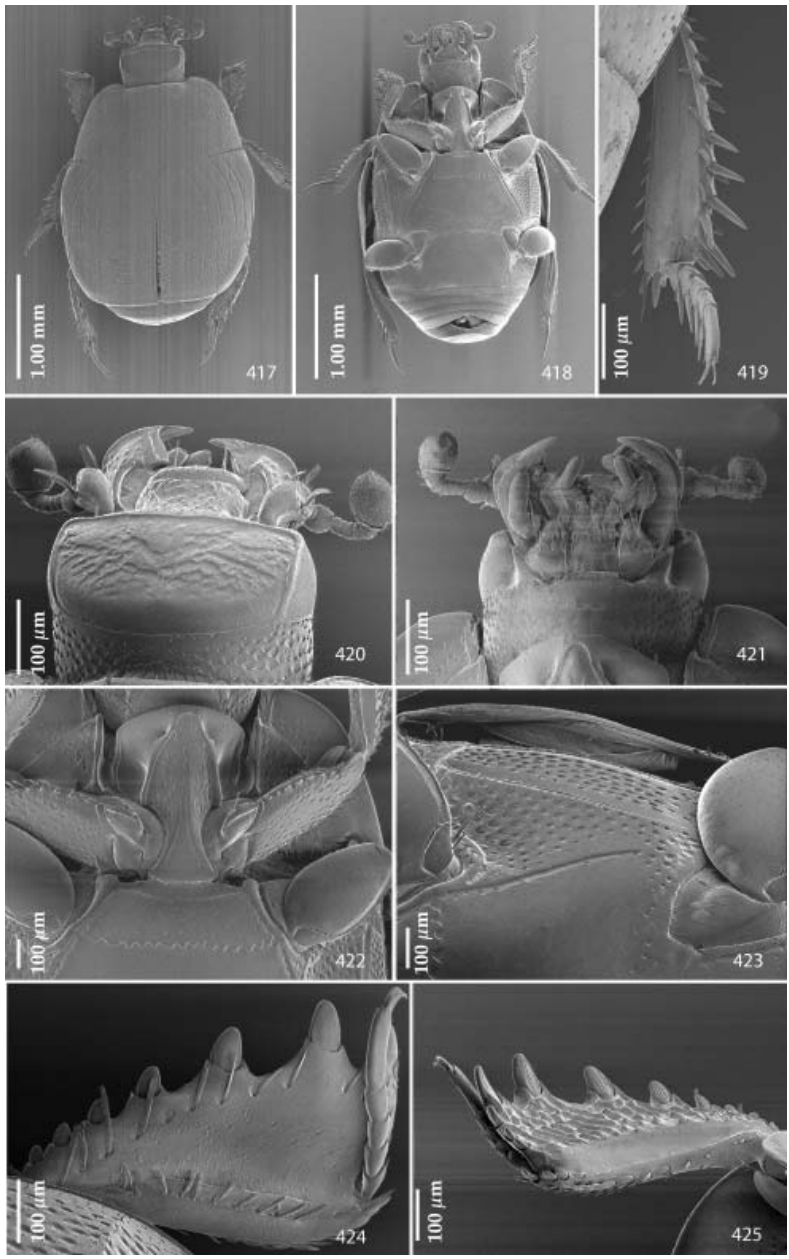
Anterior margin of median portion of prosternum (Fig. 422) evenly rounded; marginal prosternal stria present laterally and as a tiny anterior fragment; pre-apical foveae well impressed, deep; prosternal process rather narrow, slightly concave, dorsally almost smooth, laterally substrigulate, with large coarse punctures; carinal prosternal striae weakly impressed, divergent between procoxae, subparallel, vaguely united anteriorly; lateral prosternal striae carinate, united in front of carinal prosternal striae.

Anterior margin of mesoventrite (Fig. 422) moderately emarginate medially, discal marginal mesoventral stria well impressed, somewhat carinate laterally, anteriorly slightly weakened; disc with scattered round punctation, punctures separated about 3–5 times their diameter; meso-metaventral sutural stria (Fig. 422) well impressed, undulate; intercoxal disc of metaventrite almost smooth; only area near hind coxa and along apical margin covered with fine scattered punctation; lateral metaventral stria (Fig. 423) well impressed, stopping short of hind coxa; lateral disc of metaventrite with shallow setiferous punctures, separated by about their own diameter; metepisternum + fused metepimeron (Fig. 423) with even denser and coarser punctation, punctures not setiferous.

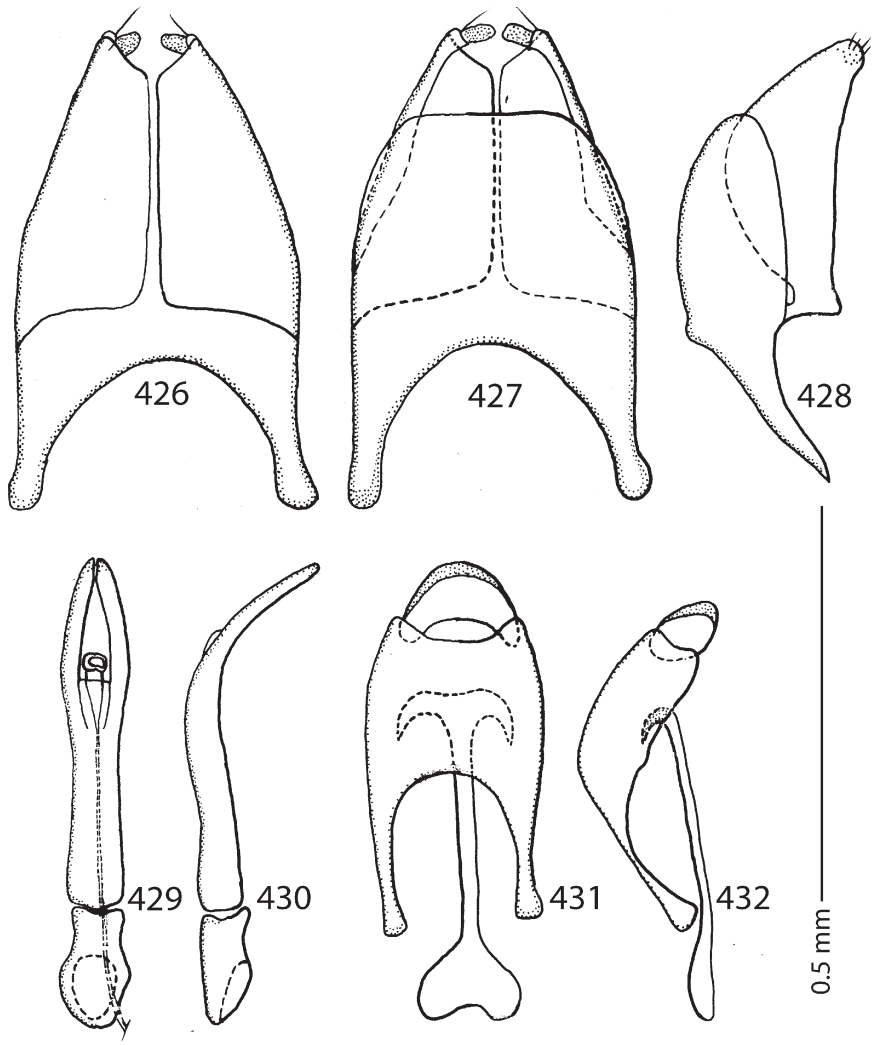
Intercoxal disc of first abdominal sternite completely striate laterally, almost smooth, only along apical and lateral margins a short band of fine punctures present.

Protibia (Figs. 424–425) flattened and somewhat dilated, outer margin with four low teeth topped with short denticle followed by three minuscule denticles; setae of outer row sparse, regular and short; setae of median row similarly sparse and regular, even shorter than those of outer row; protarsal groove moderately deep; anterior protibial stria almost complete, shortened apically; single, rather long tarsal denticle present apically; protibial spur tiny, bent, growing out from apical protibial margin; apical margin of protibia posteriorly with three tiny apical denticles; outer part of posterior surface of protibia (Fig. 425) areolate-rugose; distinctly separated from glabrous median part of posterior surface, basally with row of about 5 minuscule denticles; posterior protibial stria complete, terminating in three tiny inner-posterior denticles; inner margin with double row of short setae.

Mesotibia (Fig. 419) slender, outer margin with two sparse rows of thin denticles growing in size apically; setae of outer row sparse, strongly sclerotized; setae of median row irregular,



Figs. 417–425. *Hypocacculus* (*Nessus*) *rubripes* (Erichson, 1834), SEM micrographs: 417 – habitus, dorsal view; 418 – ditto, ventral view; 419 – mesotibia, dorsal view; 420 – head, dorsal view; 421 – ditto, ventral view; 422 – prosternum and mesoventrite; 423 – lateral disc of metaventrite, metepisternum and fused metepimeron; 424 – protibia, dorsal view; 425 – protibia, oblique ventral view.



Figs. 426–432. *Hypocacculus* (*Nessus*) *rubripes* (Erichson, 1834), male terminalia: 426 – 8th sternite and tergite, ventral view; 427 – ditto, dorsal view; 428 – ditto, lateral view; 429 – aedeagus, dorsal view; 430 – ditto, lateral view; 431 – 9th tergite, 10th tergite (dorsal view) and spiculum gastrale (ventral view); 432 – 9th tergite, 10th tergite and spiculum gastrale, lateral view.

microscopic; posterior mesotibial stria complete; anterior surface of mesotibia imbricate, with scattered minuscule punctures with microscopic setae; anterior mesotibial stria shortened apically; mesotibial spur stout, rather long; apical margin with several tiny denticles; claws of apical tarsomere shorter than half its length; metatibia basically similar to mesotibia, but slenderer and denticles of outer margin much sparser than those of mesotibia.

Male genitalia. Eighth sternite (Figs. 426–427) longitudinally separated medially, apically with tiny inflatable membrane (velum); fringed with single short seta; eighth tergite and sternite not fused laterally (Fig. 428). Morphology of 9th tergite (Figs. 431–432) typical for the subfamily; spiculum gastrale (Fig. 431) expanded on both ends. Basal piece of aedeagus (Figs. 429–430) rather short, ratio of its length : length of parameres 1 : 3; parameres fused along their basal two-thirds; aedeagus curved ventrad (Fig. 430).

Remarks. A variable species, showing a high degree of variability concerning the coloration of its cuticle (which can be light metallic bronze, sometimes even with a greenish hue), the structure of elytral punctation (which can surpass elytral half anteriorly), the elytral striation (sutural elytral stria can be shortened apically; or it can also be interrupted), shape and punctation of pronotum, structure of prosternal striation (striae can be very approximate, strongly convergent or almost parallel) and meso- and metaventral punctation. Perhaps this species forms a complex of closely related cryptic species.

Hypocaccus C. Thomson, 1867

Hypocaccus C. Thomson, 1867: 400. Type species: *Hister quadristriatus* Hoffmann, 1803, designated by Lewis (1899): 3.

Hypocaccus: Schmidt (1885a): 302; Ganglbauer (1899): 382; Lewis (1899): 3; Reitter (1909): 291; Bickhardt (1916–1917): 82, 98; Reichardt (1926): 14; Reichardt (1941): 156, 305; Peyerimhoff (1936): 226; McGrath & Hatch (1941): 54; Blackwelder & Blackwelder (1948): 11; Wenzel (1962): 374, 380; Hatch (1962): 257; Halstead (1963): 9; Dahlgren (1969): 64–66; Witzgall (1971): 173; Mazur (1973): 38; Kryzhanovskij & Reichardt (1976): 112, 217; Mazur & Kaszab (1980): 7, 57; Vienna (1980): 116, 182; Mazur (1981a): 72, 99; Mazur (1984): 92; Ôhara (1994): 215, 243; Downie & Arnett (1996): 607, 610; Kim & Lim (1997): 60; Mazur (1997): 257; Ôhara & Paik (1998): 28; Bousquet & Laplante (1999): 141, 164; Mazur (2001): 19, 33; Kovarik & Caterino (2001): 220, 223; Yélamos (2002): 245, 326; Mazur (2004): 94; Bousquet & Laplante (2006): 168, 169.

Rhytidoprinus Houlbert & Monnot, 1923: 46. Type species: *Hister rugiceps* Duftschmid, 1805, designated by Mazur (2004): 94. Synonymized by Cooman (1947): 428.

Diagnosis. Cuticle often metallic and lustrous, at times matt, black or dark-brown; frontal stria carinate, in most cases straight or only slightly curved outwardly (rarely weakened medially with traces prolonged onto clypeus); frontal disc marked by single or double chevron, sometimes with longitudinal rugae or granulose structures. Pronotal disc punctate (at times rugulose-lacunose) or entirely smooth (subgenus *Baeckmanniolus*), pronotal foveae absent, pronotal hypomeron glabrous. Prosternal process concave, compressed, carinal prosternal striae usually running parallel or subparallel, occasionally united in front; lateral prosternal striae united anteriorly under a sharp angle; pre-apical foveae present, usually moderately sized. Lateral sides of meso- and metaventrites occasionally shortly setose, often smooth. Outer margin of metatibia with two (subgenus *Hypocaccus*) or three (subgenus *Baeckmanniolus*) rows of short denticles.

Differential diagnosis. Representatives of this genus are most similar to the genus *Exaesiopus*, differing from it by the glabrous pronotal hypomeron (setose in *Exaesiopus*) as well as not particularly thickened metafemora (strongly thickened in *Exaesiopus*). The species *Hypocaccus* (*Hypocaccus*) *crassipes* (Erichson, 1834) which has slightly thickened metafemora, but a glabrous pronotal hypomeron, is probably externally most similar to the species of the

genus *Exaesiopus*. This species has been previously transferred between genera *Exaesiopus* and *Hypocaccus*, but can be viewed as a transitional form between them (Kryzhanovskij & Reichardt 1976: 228). Several smaller species of the subgenus *Hypocaccus* are externally very similar to the species of the subgenus *Nessus* of genus *Hypocacculus* and according to Mazur (pers. comm. 2008), *Nessus* ought to be synonymized with *Hypocaccus* (see also above).

Biology. Species of the subgenus *Hypocaccus* are found on the sandy shores of seas, lakes and rivers (sometimes also on inland sand dunes without the presence of water) where they prey upon dipteran larvae developing in various decomposing organic substances such as excrements, carcasses, seaweed, etc. Species of the subgenus *Baeckmanniolus* are confined to seashores with similar feeding habits.

Distribution. *Hypocaccus*, with around 65 described species and subspecies is a worldwide-distributed genus, with the bulk of its species known to occur in the Holarctic Region (Mazur 1997). Several species (e.g. *Hypocaccus* (*Hypocaccus*) *brasiliensis*) are widely distributed on the beaches around the globe; others (e.g. *Hypocaccus* (*Hypocaccus*) *ainu* Lewis, 1899 from Japan) are confined to mountain rivers and streams of geographically limited regions.

Discussion. *Hypocaccus* is probably a paraphyletic taxon with respect to several smaller genera e.g. *Exaesiopus*, or subgenus *Nessus* of the genus *Hypocacculus* (see above). It is supported only by several weak synapomorphies that include frontal disc with chevrons, longitudinal rugae or granulose structures. Subgenus *Baeckmanniolus* is supported by only two weak putative synapomorphies, most likely homoplasies. Revision of the members of both subgenera of *Hypocaccus* would be one of highly required tasks for the future research.

Key to the subgenera of the genus *Hypocaccus*

1 (2) Pronotum (at least laterally) with punctation; metatibia with two rows of denticles on outer margin. ..... subgenus ***Hypocaccus*** s. str.

2 (1) Pronotum (except for row of punctures along base) almost smooth*); metatibia with at least three rows of denticles on outer margin. ....subgenus ***Baeckmanniolus*** Reichardt, 1926

Subgenus *Hypocaccus* C. Thomson 1867

Hypocaccus C. Thomson, 1867: 400. Type species: *Hister quadristriatus* Hoffmann, 1803, subsequent designation by Lewis (1899: 3).

Hypocaccus: Schmidt (1885a): 302; Ganglbauer (1899): 382; Lewis (1899): 3; Reitter (1909): 291; Bickhardt (1916–1917): 82, 98; Reichardt (1926): 14; Reichardt (1941): 156, 305; Peyerimhoff (1936): 226; McGrath & Hatch (1941): 54; Blackwelder & Blackwelder (1948): 11; Wenzel (1962): 374, 380; Hatch (1962): 257; Halstead (1963): 9; Dahlgren (1969): 64–66; Witzgall (1971): 173; Mazur (1973): 38; Kryzhanovskij & Reichardt (1976): 112, 217; Mazur & Kaszab (1980): 7, 57; Vienna (1980): 116, 182; Mazur (1981a): 72, 99; Mazur (1984): 92; Ôhara (1994): 215, 243; Downie & Arnett (1996): 607, 610; Kim & Lim (1997): 60; Mazur (1997): 257; Ôhara & Paik (1998): 28; Bousquet & Laplante (1999): 141, 164; Mazur (2001): 19, 33; Kovarik & Caterino (2001): 220, 223; Yélamos (2002): 245, 326; Mazur (2004): 94; Bousquet & Laplante (2006): 168, 169.

Rhytidoprinus Houlbert & Monnot, 1923: 46. Type species *Hister rugiceps* Duftschmid, 1805, subsequent designation by Mazur (2004: 94). Synonymized by Cooman (1947): 428.

*) Rarely with fine punctation in the anterolateral corners of pronotum (e.g. *Hypocaccus* (*Baeckmanniolus*) *varians* (Schmidt, 1890).

Diagnosis. The subgenus *Hypocaccus* differs from the subgenus *Baeckmanniolus* by the punctate pronotum and the number of rows of denticles on metatibiae (two in the subgenus *Hypocaccus* versus at least three in the subgenus *Baeckmanniolus*). However, this last mentioned character has been discovered only recently (Bousquet & Laplante 2006: 196). These two authors studied only the taxa spread in the Nearctic Region (especially Canada) and their results need to be verified by examining taxa from other geographical regions. Bousquet & Laplante (2006) assign a generic rank to the subgenus *Baeckmanniolus*, stressing the above-mentioned differences between the two taxa. However, the more conservative view is adopted here, since these two taxa externally differ only minimally and their natural habitat is almost the same.

Biology. See Biology of *Hypocaccus* s. l.

Distribution. See Distribution of *Hypocaccus* s. l.

Species examined. *Hypocaccus* (*Hypocaccus*) *axeli* Kryzhanovskij, 1976, *H.* (*H.*) *brasiliensis* (Paykull, 1811), *H.* (*H.*) *crassipes* (Erichson, 1834), *H.* (*H.*) *dauricus* Reichardt, 1930, *H.* (*H.*) *fochi* (Auzat, 1921), *H.* (*H.*) *formosus* Reichardt, 1941, *H.* (*H.*) *lewisi* (Schmidt, 1890), *H.* (*H.*) *metallicus* (Herbst, 1792), *H.* (*H.*) *rugiceps* (Duftschmid, 1805), *H.* (*H.*) *rugifrons rugifrons* (Paykull, 1798), *H.* (*H.*) *rugifrons subtilis* (Schmidt, 1884), *H.* (*H.*) *sinae* (Marseul, 1862), *H.* (*H.*) *specularis* (Marseul, 1855), *H.* (*H.*) *speculum speculum* (Schmidt, 1884), *H.* (*H.*) *subaeneus* (Schmidt, 1890).

Hypocaccus (*Hypocaccus*) *rugiceps* (Duftschmid, 1805)

(Figs. 20, 56, 79, 120, 433–452)

Hister quadristriatus: Hoffmann (1803): 85, nec Paykull (1798): 45 (misidentification).
Hister rugiceps Duftschmid, 1805: 125.
Saprinus quadristriatus: Erichson (1834): 194.
Saprinus rugiceps: Redtenbacher (1849): 238; Marseul (1855): 703, t. XIX, Fig. 141; C. Thomson (1862): 238; Ganglbauer (1899): 391; Reitter (1909): 294, t. 67, Fig. 12; Jakobson (1911): 651.
Hypocaccus quadristriatus: C. Thomson (1867): 401.
Saprinus (*Hypocaccus*) *quadristriatus*: Schmidt (1885a): 316.
Hypocaccus rugiceps: Bickhardt (1916): 100; Reichardt (1941): 308, 316, Fig. 165; Horion (1949): 342; Mazur (1973): 40, Fig. 80, Kryzhanovskij & Reichardt (1976): 218, 220, Figs. 428, 435, 436, 437, 442; Vienna (1980): 185, 190; Mazur & Kaszab (1980): 58, Figs. 26J, 28K, 29, 30F; Mazur (1981a): 100, 103, Fig. 135; Mazur (1984): 96; Mazur (1997): 260; Yélamos (2002): 328, 330, Figs. 163A, 164A, 166B; Mazur (2004): 94.

Type locality. Austria, Oerlander near Linz.

Material examined. CZECH REPUBLIC: Moravia: Bzenec env., vii.1948, 1 spec., L. Krejcárek lgt.; Velké Pavlovice, vii.1947, 1 ♂, collector unknown. **ITALY:** Les Vignes, a Millan, 16.v.1914, 1 spec., collector unknown. **GERMANY:** Markgratenheide, near Warnemünde, 12.vii.1976, 1 spec., J. Strejček lgt. **UKRAINE:** Kiev, v.1975, 1 ♂ 1 ♀, A. Olexa lgt. (TLAN).

Redescription. Body length: PEL: 3.10–3.50 mm; APW: 1.125–1.25 mm; PPW: 2.25–2.625 mm; EL: 2.00–2.25 mm; EW: 2.60–3.00 mm.

Body (Figs. 433–434) shortly oval, convex, cuticle dark brown to blackish-blue; pronotum occasionally with feeble bronze luster, elytra with greenish metallic tinge; legs, mouthparts and antennae dark brown to black.

Antennal scape (Fig. 436) slightly thickened, with few short setae; club (Fig. 440) round, without visible articulation, entire surface covered with thick short yellow sensilla intermingled

with sparse somewhat longer erect sensilla; sensory structures of antennal club (Fig. 20) in form of stipe-shaped vesicle situated under circular sensory area on internal distal margin of the ventral side of antennal club.

Mouthparts. Mandibles (Fig. 79) with almost straight outer margin, moderately curved inwardly, acutely pointed; sub-apical tooth on inner margin of left mandible large, perpendicular; labrum (Figs. 56, 437) microscopically punctate, medially convex, anterior margin with slight median projection; with two labral pits, with two setae arising from each; terminal labial palpomere elongated, its width about one-third its length; mentum sub-trapezoid, anterior margin medially with shallow notch (Fig. 120) surrounded with few moderately long setae; lateral margins with a single row of sparse much shorter ramose setae; cardo of maxilla with few short setae on lateral margin; stipes triangular, with three much longer setae; terminal maxillary palpomere elongated, its width about one-fourth its length, about twice as long as penultimate.

Clypeus (Fig. 437) rectangular, rounded laterally, rugulose-lacunose; frontal stria (Fig. 436) well impressed, almost straight (occasionally somewhat curved outwardly), carinate, continued as carinate supraorbital stria; frontal disc (Fig. 436) rugulose-lacunose, with several deeply impressed longitudinal rugae; eyes convex, observable from above.

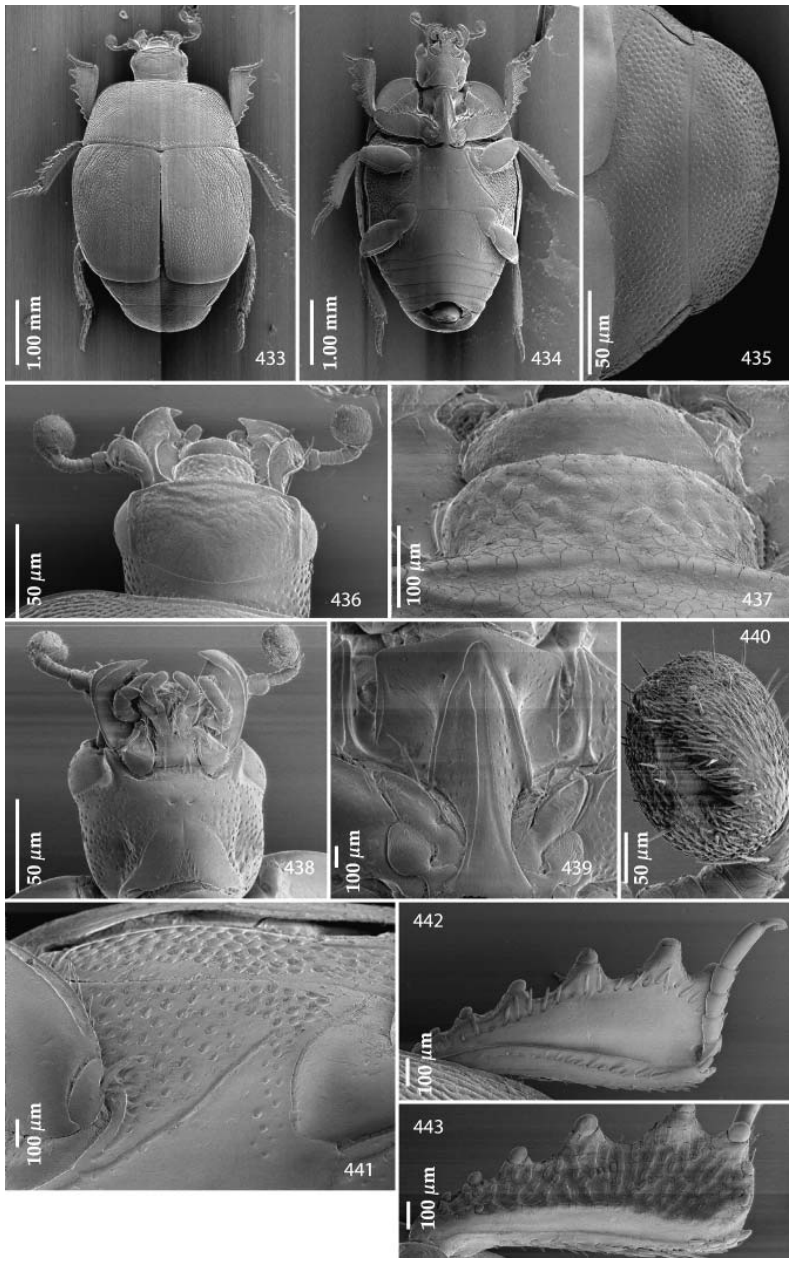
Pronotal sides (Fig. 433) almost parallel on apical two-thirds, thence curved inwardly; apical angles obtuse; marginal pronotal stria complete; pronotal disc convex, except for postero-median part entirely covered with dense punctation, punctures laterally form longitudinal rugae; postero-median part forming a well-defined triangular impunctate part; pronotal base with a double row of round dense punctures, with slight antero-scutellar depression; scutellum small, well visible.

Elytral humeri slightly prominent, epipleura with microscopic punctures; marginal epipleural stria complete; marginal elytral stria deeply impressed, continued as weakly impressed shortened apical elytral stria; along elytral marginal stria a regular row of round punctures present. Humeral elytral stria vaguely impressed on basal fifth; inner subhumeral stria present medially, deep and rather long, rarely joining humeral elytral stria; dorsal elytral striae almost unrecognizable beneath punctation; first dorsal elytral stria usually conspicuous, stopping short of elytral apex, apically slightly curved inwardly, second dorsal stria reaching approximately elytral half apically, third and fourth dorsal elytral striae do not reach elytral half apically, often unrecognizable beneath coarse elytral punctation; fourth dorsal elytral stria basally connected with sutural elytral stria; sutural elytral stria well impressed, in punctures, almost reaching elytral apex; between it and elytral suture a row of small round punctures present.

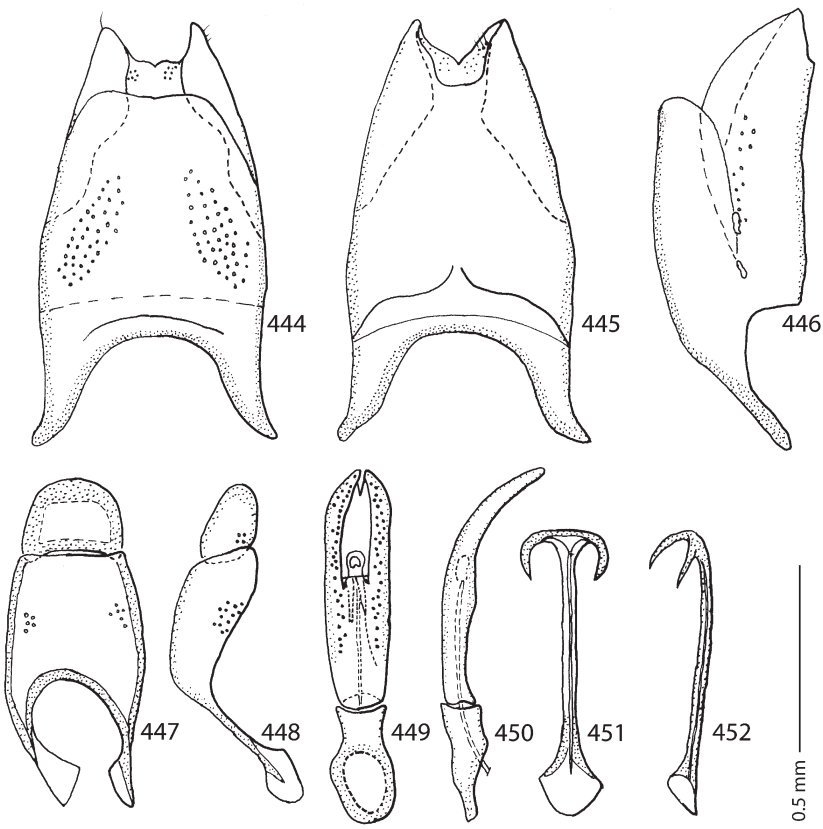
Elytral disc (with exception of elytral epipleura, humeri, smooth apical elytral band and a small 'mirror' between fourth dorsal elytral and sutural striae) completely covered with deep regular and very dense and coarse punctation; punctures separated by about half their diameter; elytral 'mirrors' between each other not divided by a band of punctation.

Propygidium (Fig. 435) almost completely exposed, about twice as broad as long, with dense and coarse punctation, punctures smaller than those of elytra; punctation of pygidium (Fig. 435) similar to that of propygidium, becoming somewhat sparser apically.

Anterior margin of median portion of prosternum (Fig. 439) obtuse-angulate; marginal prosternal stria present laterally; pre-apical foveae comparatively small; prosternal process



Figs. 433–443. *Hypocaccus* (*Hypocaccus*) *rugiceps* (Duftschmid, 1805), SEM micrographs: 433 – habitus, dorsal view; 434 – ditto, ventral view; 435 – propygidium and pygidium; 436 – head, dorsal view; 437 – clypeus + labrum, dorsal view; 438 – head, ventral view; 439 – prosternum; 440 – antennal club, ventral view; 441 – lateral disc of metaventrite, metepisternum and fused metepimeron; 442 – protibia, dorsal view; 443 – ditto, ventral view.



Figs. 444–452. *Hypocaccus* (*Hypocaccus*) *rugiceps* (Duftschmid, 1805), male terminalia: 444 – 8th sternite and tergite, dorsal view; 445 – ditto, ventral view; 446 – ditto, lateral view; 447 – 9th tergite, 10th tergite, dorsal view; 448 – ditto, lateral view; 449 – aedeagus, dorsal view; 450 – ditto, lateral view; 451– spiculum gastrale, ventral view; 452 – ditto, lateral view.

slightly concave, surface between carinal striae smooth, laterally substrigulate with sparse deep punctures; carinal prosternal striae slightly divergent on prosternal apophysis, sub-parallel, usually not united apically; lateral prosternal striae strongly carinate, convergent anteriorly, united in front of apices of carinal prosternal striae.

Anterior margin of mesoventrite slightly emarginate medially; discal marginal mesoventral stria well impressed, carinate; disc of mesoventrite flat, smooth (at times sparsely punctate); meso-metaventral sutural stria well impressed, undulate; intercoxal disc of metaventrite smooth, with a longitudinal depression in male, area behind hind coxa with sparse punctures; lateral metaventral stria well impressed, curved outwardly, stopping short of metacoxa; lateral disc of metaventrite (Fig. 441) slightly concave, with deep setiferous punctures of various sizes; metepisternum + fused metepimeron (Fig. 441) with much coarser and denser punctation, punctures without setae.

Intercoxal disc of the first abdominal sternite completely striate laterally; almost smooth, with sparse punctures along lateral, anterior and posterior margins.

Protibia (Figs. 442–443) flattened and somewhat dilated, outer margin with five moderately large triangular teeth topped with short rounded denticle followed by two minuscule denticles; setae of outer row moderately dense, regular and short; setae of median row similarly dense and regular, somewhat shorter than those of outer row; protarsal groove moderately deep; anterior protibial stria carinate, almost complete, shortened apically; one rather long and thin + one shorter but stouter tarsal denticle present apically; protibial spur tiny, straight, growing out from apical protibial margin; apical margin of protibia posteriorly with two tiny rounded apical denticles; outer part of posterior surface of protibia (Fig. 443) areolate-rugose; distinctly separated from glabrous median part of posterior surface, basally with two minuscule denticles; posterior protibial stria complete, terminating in three tiny inner-posterior denticles; inner margin with double row of short setae.

Mesotibia slender, outer margin with two sparse rows of thin denticles growing in size apically; setae of outer row sparse, strongly sclerotized; setae of median row irregular, microscopic; posterior mesotibial stria shortened apically; anterior surface of mesotibia glabrous; anterior mesotibial stria shortened apically; mesotibial spur stout, rather long; apical margin with several tiny denticles; claws of apical tarsomere shorter than half its length; metatibia basically similar to mesotibia, but slenderer and denticles of outer margin much sparser than those of mesotibia.

Male genitalia. Eighth sternite (Figs. 444–445) longitudinally entirely fused medially, apically with large inflatable membrane (velum); furnished with sparse microscopic setae; eighth tergite and eighth sternite fused laterally (Fig. 446). Morphology of 9th tergite (Figs. 447–448) typical for the subfamily; spiculum gastrale (Fig. 451) expanded on both ends. Basal piece of aedeagus (Figs. 449–450) rather long, ratio of its length : length of parameres 1 : 2.5; parameres fused approximately along their basal half; aedeagus curved ventrad (Fig. 450).

Subgenus *Baeckmanniolus* Reichardt, 1926

Baeckmanniolus Reichardt, 1926: 14. Type species *Hister dimidiatus* Illiger, 1807, original designation.

Baeckmanniolus: Peyerimhoff (1936): 225; Reichardt (1941): 157, 222; Wenzel (1962): 374, 380; Halstead (1963): 9; Dahlgren (1969): 66; Witzgall (1971): 165, 1974; Kryzhanovskij & Reichardt (1976): 219, 229; Vienna (1980): 115, 193; Mazur & Kaszab (1980): 60; Mazur (1981a): 99, 104; Mazur (1984): 99; Ôhara (1994): 243, 258; Kim & Lim (1997): 60; Ôhara & Paik (1998): 29; Bousquet & Laplante (1999): 141, 172; Mazur (2001): 19, 34; Yélamos (2002): 326, 336; Mazur (2004): 94; Bousquet & Laplante (2006): 81, 196.

Diagnosis. Species of this subgenus differ from those of the subgenus *Hypocaccus* chiefly by the almost completely smooth pronotum; occasionally there is fine punctation in the anterior angles.

Bousquet & Laplante (2006: 196) state that metatibia is on the outer-lateral margin with at least three rows of denticles, as opposed to two that are present in the subgenus *Hypocaccus*. However, this character must be verified by further studies based on more material.

Biology and Distribution. Typical littoral taxon, with 13 species and 3 subspecies distributed worldwide on beaches (Mazur 1997). Absent in the interior.

Species examined. *Hypocaccus* (*Baeckmanniolus*) *dimidiatus dimidiatus* (Illiger, 1807), *H.* (*B.*) *dimidiatus maritimus* (Stephens, 1830), *H.* (*B.*) *varians varians* (Schmidt, 1890).

Hypocaccus (*Baeckmanniolus*) *dimidiatus* (Illiger, 1807)

(Figs. 21, 45, 91, 121, 453–470)

Hister dimidiatus Illiger, 1807: 41.
Hister dimidiatus: Paykull (1811): 73, t. VI, Fig. 8.
Hister semiaeneus Brullé, 1832: 159. Synonymized by Gemminger & Harold (1868): 785.
Saprinus dimidiatus: Erichson (1834): 195; Marseul (1855): 730, t. XX, Fig. 162; Schmidt (1885a): 317; Ganglbauer (1899): 393; Jakobson (1911): 651.
Hister tauricus: Dejean (1837): 142 (*nomen nudum*, given as synonym).
Saprinus semiaeneus: Kraatz (1858): 131.
Saprinus lobatus Wollaston, 1864: 178. Synonymized by Marseul (1870): 134.
Pachylopus dimidiatus: Zimmermann in J. L. LeConte (1869): 253.
Pachylopus lobatus: Lewis (1905): 76.
Saprinus dimidiatus var. *hummleri* J. Müller, 1899: 154.
Saprinus dimidiatus hummleri: Jakobson (1911): 651.
Hypocaccus (*Baeckmanniolus*) *dimidiatus*: Reichardt (1926): 14; G. Müller (1931): 101; Peyerimhoff (1936): 229; Reichardt (1941): 323, Figs. 168, 169; Horion (1949): 344; Dahlgren (1969): 66, 70, Figs. 3E, F; Kryzhanovskij & Reichardt (1976): 220, 231, Figs. 451, 454; Vienna (1980): 194, Fig. 68; Mazur (1981a): 104, Fig. 139; Mazur (1984): 99; Mazur (1997): 262; Yélamos (2002): 336, Figs. 161F, 163F, 166H, 168; Mazur (2004): 94.
Baeckmanniolus convexicollis G. Müller, 1937: 118. Synonymized by Mazur (1997): 262.
Hypocaccus (*Baeckmanniolus*) *dimidiatus* var. *camarguensis* Thérond, 1948: 126.
Hypocaccus convexicollis: Mazur (1984): 98.
Note. Sensory structures of the antennal club and spermatheca were studied by De Marzo & Vienna (1982a,b).

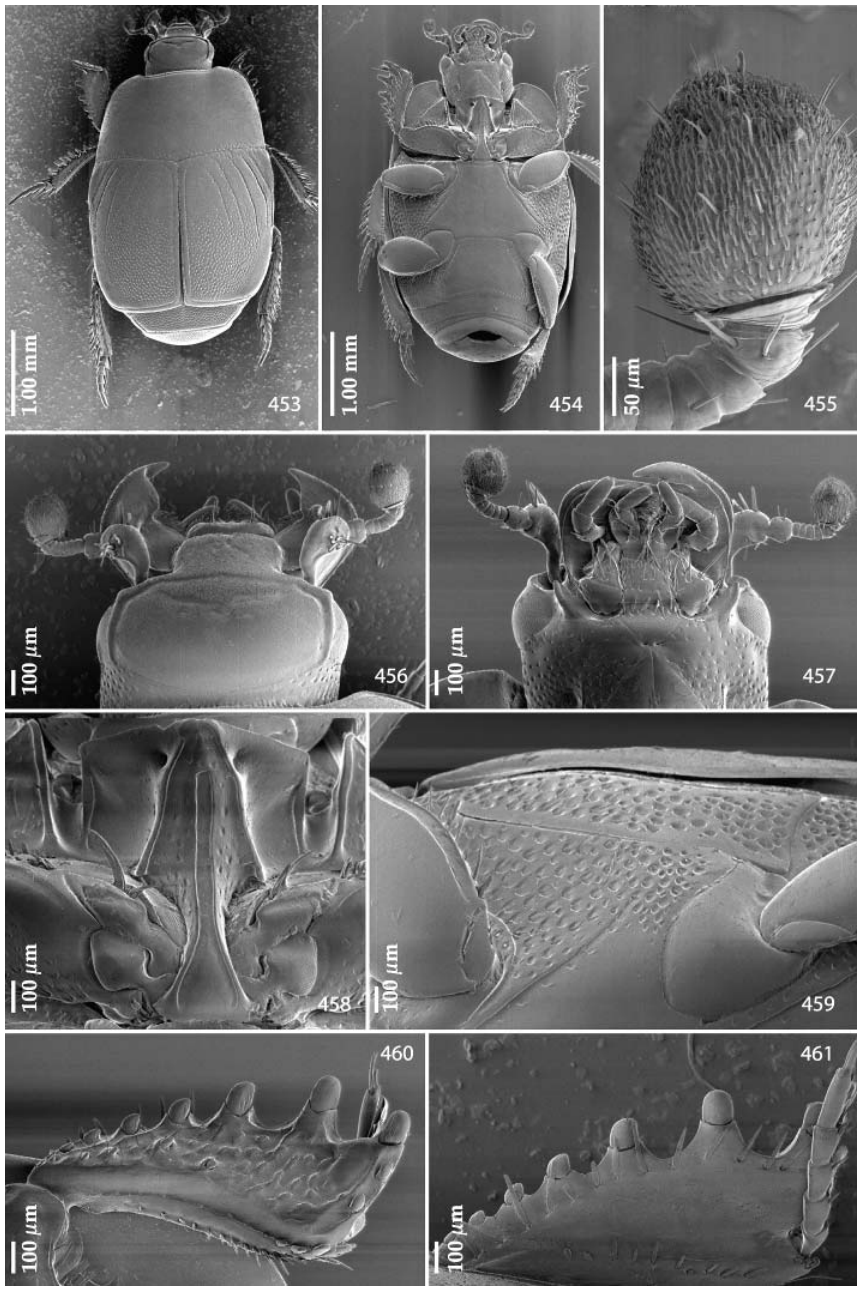
Type locality. Portugal.
Material examined. MOROCCO: Bouknadel, vi.1976, 1 ♂ 2 spec., Z. Táborský lgt.; ditto, but 27.ix.1975, 1 ♂ (TLAN).

Redescription. Body length: PEL: 2.75–3.65 mm; APW: 1.125–1.375 mm; PPW: 1.875–2.75 mm; EL: 1.625–2.25 mm; EW: 2.00–3.00 mm.

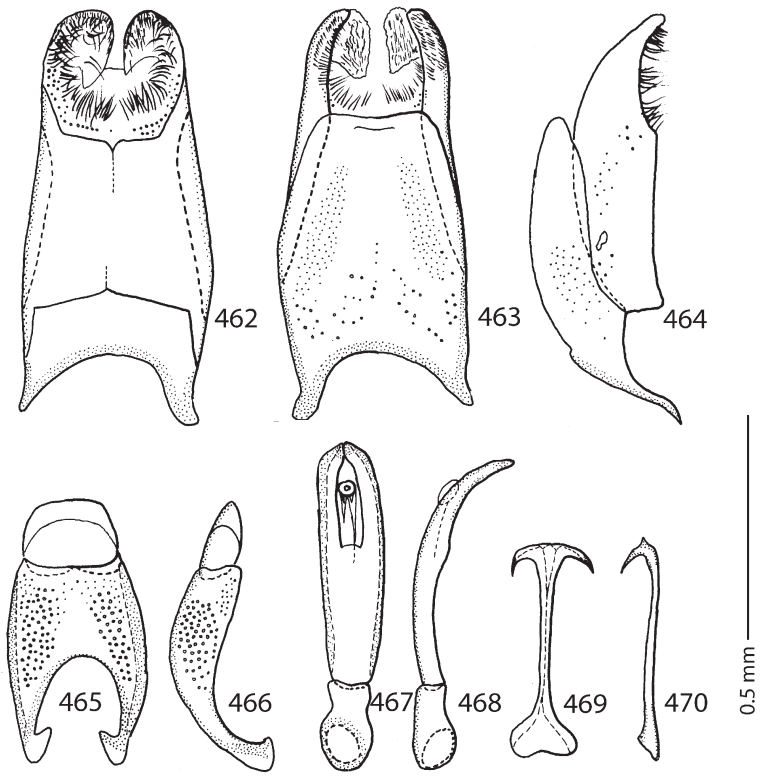
Body (Figs. 453–454) rectangular oval, convex, cuticle dark brown to black; pronotum sometimes with feeble bronze hue; legs, mouthparts and antennae castaneous to dark brown.

Antennal scape (Fig. 456) somewhat thickened, with numerous well sclerotized moderately long setae; club (Fig. 455) round, without visible articulation, its entire surface with thick short yellow sensilla intermingled with sparse longer sensilla; sensory structures of antennal club (Fig. 21) in form of stipe-shaped vesicle situated under circular sensory area on internal distal margin of the ventral side of antennal club, supplemented by another sensory area situated opposite to it.

Mouthparts. Mandibles (Fig. 91) with rounded outer margin, strongly curved inwardly, acutely pointed; sub-apical tooth on inner margin of left mandible large, almost perpendicular; labrum (Fig. 45) with scattered microscopic punctation, somewhat convex, with a slight median depression and a tiny median convexity interrupting concavity; two well impressed labral pits present, with two well-sclerotized setae arising from each pit; terminal labial palpomere elongate, its width about one-third its length; mentum square-shaped, anterior margin (Fig. 121) medially with shallow emargination, surface around it with several moderately long setae; posterior angles somewhat produced; lateral margins with a single row of much shorter setae; disc of mentum with sparse short setae; cardo of maxilla with two short setae on lateral margin; stipes triangular, with three much longer setae; terminal maxillary palpomere elongated, its width about one-fourth its length, approximately twice as long as penultimate.



Figs. 453–461. *Hypocaccus* (*Baeckmanniolus*) *dimidiatus dimidiatus* (Illiger, 1807), SEM micrographs: 453 – habitus, dorsal view; 454 – ditto, ventral view; 455 – antennal club, dorsal view; 456 – head, dorsal view; 457 – ditto, ventral view; 458 – prosternum; 459 – lateral disc of metaventrite, metepisternum and fused metepimeron; 460 – protibia, ventral view; 461 – ditto, dorsal view.



Figs. 462–470. *Hypocaccus* (*Baeckmanniolus*) *dimidiatus dimidiatus* (Illiger, 1807), male terminalia: 462 – 8th sternite and tergite, ventral view; 463 – ditto, dorsal view; 464 – ditto, lateral view; 465 – 9th tergite, 10th tergite, dorsal view; 466 – ditto, lateral view; 467 – aedeagus, dorsal view; 468 – ditto, lateral view; 469 – spiculum gastrale, ventral view; 470 – ditto, lateral view.

Clypeus (Fig. 456) rectangular, slightly rounded laterally, with irregular shallow impressions; frontal stria (Fig. 456) well impressed, almost straight (sometimes somewhat curved outwardly), carinate, continued as carinate supraorbital stria. Frontal disc smooth, with single deeply marked chevron, rarely with minute fragments of rugae; eyes somewhat flattened, conspicuous from above.

Pronotal sides (Fig. 453) almost parallel, apical angles somewhat produced; marginal pronotal stria complete; disc (except for a double row of round punctures along base) smooth; scutellum small, visible.

Elytral epipleura with microscopic punctures, almost smooth; marginal epipleural stria complete; marginal elytral stria deeply impressed, continued as well impressed complete apical elytral stria; along elytral marginal stria regular row of round punctures present. Humeral elytral stria well impressed on basal fourth; inner subhumeral stria present medially, rather short. Elytral disc with four variably long dorsal elytral striae 1–4, usually reaching elytral half, occasionally shortened, fourth dorsal elytral stria basally connected with sutural elytral

stria. Sutural elytral stria well impressed and complete, apically connected with complete apical elytral stria. Punctation of elytral disc round, coarse and dense, punctures separated by about half to their own diameter; punctation variable, usually reaches about two-thirds of elytral length anteriorly, punctures along elytral apex aciculate; lateral elytral margins, elytral humeri and usually first and second interval between dorsal striae as well as interspace between sutural and fourth dorsal elytral striae impunctate.

Punctation of propygidium and pygidium less dense and coarse than that of elytra, punctures separated by about their own diameter.

Anterior margin of median portion of prosternum (Fig. 458) obtuse-angulate, pre-apical foveae small, deep. Prosternal process slightly concave; surface between carinal prosternal striae smooth, laterally substrigulate, intermingled with sparse large punctures; carinal prosternal striae slightly carinate, divergent on prosternal apophysis, almost parallel, united in front (at times not united); lateral prosternal striae well impressed, strongly carinate, convergent anteriorly, united in front of apices of carinal prosternal striae.

Anterior margin of mesoventrite slightly emarginate medially; discal marginal mesoventral stria deeply impressed, carinate; meso-metaventral sutural stria vaguely impressed in shallow punctures; disc of mesoventrite flat, smooth; intercoxal disc of metaventrite smooth, basally with irregular sparse shallow fine punctures with a longitudinal median excavation in male; lateral metaventral stria (Fig. 459) well impressed, carinate, curved outwardly, stopping short of metacoxa; lateral disc of metaventrite (Fig. 459) slightly concave, with shallow dense setiferous punctures of various sizes; metepisternum + fused metepimeron (Fig. 459) with even coarser and denser setiferous punctures.

Intercoxal disc of the first abdominal sternite completely striate laterally, almost smooth, only with sparse punctures along basal and lateral margins; basally with a shallow concavity.

Protibia (Figs. 460–461) flattened and somewhat dilated, outer margin with four moderately large triangular teeth topped with short rounded denticle followed by three minuscule denticles; setae of outer row moderately dense, regular and short; setae of median row similarly dense and regular, somewhat shorter than those of outer row; protarsal groove moderately deep; anterior protibial stria shortened, present only as basal fragment; two tiny tarsal denticles present apically; protibial spur tiny, straight, growing out from apical protibial margin; apical margin of protibia posteriorly with two tiny rounded, widely separated apical denticles; outer part of posterior surface of protibia (Fig. 460) areolate-rugose, with four irregularly situated minuscule denticles; distinctly separated from glabrous median part of posterior surface; posterior protibial stria complete, somewhat carinate, terminating in three tiny inner-ventral denticles; inner margin with single row of short setae.

Mesotibia slender, outer margin with three dense rows of moderately thick denticles abutting each other, growing in size apically; setae of outer row rather sparse, but strongly sclerotized and as long as denticles themselves; setae of median row regular, much thinner and shorter than those of outer row; posterior mesotibial stria shortened apically; anterior surface of mesotibia glabrous; anterior mesotibial stria shortened apically; mesotibial spur stout, rather long; apical margin with several rather stout and moderately long denticles; claws of apical tarsomere shorter than half its length; metatibia basically similar to mesotibia, but slenderer and rows of denticles much sparser than those of mesotibia.

Male genitalia. Eighth sternite (Figs. 462–463) longitudinally entirely fused medially, apically with large inflatable membrane (velum) covered with moderately long dense setae; eighth tergite and eighth sternite not fused laterally (Fig. 464). Morphology of 9th tergite (Figs. 465–466) typical for the subfamily; spiculum gastrale (Fig. 469) expanded on both ends. Basal piece of aedeagus (Figs. 467–468) rather short, ratio of its length : length of parameres 1 : 4; parameres fused approximately along their basal half; aedeagus curved ventrad (Fig. 468).

Remarks. This species consists of two subspecies: *Hypocacculus* (*Baeckmanniolus*) *dimidiatus dimidiatus* and *Hypocacculus* (*Baeckmanniolus*) *dimidiatus maritimus*. They differ in elytral punctation, length of the dorsal elytral striae, size, color of the cuticle and variously thickened metacoxa and metafemora. Their geographical distribution is also separate: the nominotypical subspecies lives on the shores of Mediterranean and Black Seas and on the Atlantic coast of North Africa (including the Canary Islands and Azores) and the subspecies *maritimus* is spread along the coasts of the north-western Europe (including England and Ireland) as far north-east as Bornholm Island (Denmark) (Mazur 1997).

Microsaprinus Kryzhanovskij, 1976, stat. nov.

Microsaprinus Kryzhanovskij, 1976 in Kryzhanovskij & Reichardt (1976): 126, 184 (as a subgenus of *Saprinus*). Type species: *Saprinus therondianus* Dahlgren, 1973, original designation.

Microsaprinus: Mazur (1984): 63; Secq & Secq (1995): 30; Mazur (1997): 231; Yélamos (2002): 260, 292; Mazur (2004): 96.

Diagnosis. Body conspicuously small for the subfamily (1.40–2.00 mm), roundly oval, cuticle light brown to yellow without metallic luster; eyes inconspicuous; frontal stria widely interrupted medially (occasionally shortly present); pre-apical foveae absent; protibiae slightly dilated, outer margin with row of short denticles, teeth absent; meso- and metatibiae slender. Aedeagi of *Microsaprinus therondianus* (Dahlgren, 1973) and *M. bonnairei* (Fairmaire, 1884) with parameres dorsally not fused almost along its entire length; eighth sternite of males of all known species widely separated, sickle-shaped.

Differential diagnosis. By its small size the species of this genus could be confused with several small species of the genus *Hypocacculus*, but by the absence of pre-apical foveae and widely interrupted frontal stria they are easily separated from them.

Taxonomy. This genus has formerly been a subgenus of the genus *Saprinus* Erichson, 1834. However, already Kryzhanovskij (Kryzhanovskij & Reichardt 1976: 184) suggested that it might be elevated to generic rank. I fully agree with this opinion and elevate here *Microsaprinus* to generic rank.

Biology. *Microsaprinus* is a poorly studied genus, absent in many large collections of the Histeridae. According to Kryzhanovskij & Reichardt (1976), specimens of *M. therondianus* were collected in the burrows of rodents, mainly ground squirrels (*Spermophilus* spp.); one specimen was even collected on the flower of *Chondrilla* sp. (Asteraceae). The holotype of *M. gomyi* Secq & Secq, 1995 was found in an empty swimming pool (Secq & Secq 1995). *Microsaprinus* is probably an inquilinous taxon, rarely reported in the literature.

Distribution. Palaearctic taxon, with four described species. Three species occur in the Mediterranean basin and fourth is distributed across Central Asia to Mongolia (Mazur 1997).

Species examined. *Microsaprinus bonairii* (Fairmaire, 1884) **comb. nov.**, *M. gomyi* (Secq & Secq, 1995) **comb. nov.**, *M. pastoralis* (Jacquelin-Duval, 1852) **comb. nov.**, *M. therondianus* (Dahlgren, 1973) **comb. nov.**

Discussion. *Microsaprinus* is probably a monophyletic taxon well supported by two putative autapomorphies, e.g. special form of the sensory structures of the antenna, and the peculiar form of the 8th sternite of males. The widely separated parameres of the aedeagi of the two of its species suggest that it might be an ancestral taxon (separated parameres are presumably a plesiomorphic condition).

Microsaprinus therondianus (Dahlgren, 1973) comb. nov.

(Figs. 38, 60, 80, 125, 176, 471–490)

Saprinus therondianus Dahlgren, 1973: 193, Figs. A, B.

Saprinus (*Microsaprinus*) *therondianus*: Kryzhanovskij & Reichardt (1976): 127, 185, Figs. 365, 366; Mazur (1984): 63; Secq & Secq (1995): 30; Mazur (1997): 232; Mazur (2004): 97.

Type locality. Mongolia, Bajanchongor aimak.

Type material. Paratypes: ♂, 'MONGOLIA: Bajanchongor / aimak, 22 km N von Pass / des Gebirges Ongon Ulaan / ul, 890–920 m / Exp. Dr. Z. KASZAB, 1967 [printed] // Nr. 865 / 29.VI.1967 [printed] // Paratypus 1971. / *Saprinus* / *therondianus* / G. Dahlgren [red-margined label, printed-written]' (MNHN); ♀, with identical labels, except Nr. 864 instead of 'Nr. 865' (MNHN).

Additional material examined. IRAN: Yousef-Abad, Tazeh-Kand, 9.ix.1967, 1 ♂, M. Daniel lgt., by a trap on a lorry; Mashad, Fariman, 4.ix.1967, 1 spec., M. Daniel lgt., by a trap on a lorry. **TURKMENISTAN:** Kara-Kum, Orta Kuyu, 19.v.1953, 1 ♂, Kiryakova lgt., in the burrow of gerbil *Rhombomys opimus* Wagner, 1841 (TLAN). Kara-Kum Orta-Kuju, 17.v.[1]953, 1 ♂, Kirjakova lgt., bearing a paratype label of an unpublished species *Saprinus steinbergi* Kryzhanovskij, 1967 (MNHN).

Redescription. Body length: PEL: 1.575–1.625 mm; APW: 0.475–0.55 mm; PPW: 1.20–1.25 mm; EL: 1.00–1.05 mm; EW: 1.375–1.45 mm.

Body (Figs. 471–472) roundly oval, convex, cuticle yellow to light brown, without metallic luster, shining; legs, mouthparts and antennae yellow-brown.

Antennal scape (Fig. 475) with carinate margins, with two weakly sclerotized short setae; club (Figs. 473–474) elongate, apical surface with sensory area with very short sparse erect sensilla, remaining surface of club glabrous, only with very sparse minute sensilla; sensory structures of antennal club (Fig. 38) in form of two thin, slit-like pits situated on ventral side in vague sutures between antennomeres IX, X and XI and four vesicles situated in two pairs on the ventral side.

Mouthparts. Mandibles (Fig. 80) with straight outer margin, curved inwardly, mandibular apex acutely pointed; prostheca unusually wide, with dense row of minute prosthecal setae; labrum (Fig. 60) microscopically punctate, slightly depressed medially; labral pits inconspicuous, with single short weakly sclerotized seta; cardo of maxilla with few minute setae, stipes triangular, with two very short setae; terminal labial palpomere somewhat thickened, its width less than half its length; mentum (Fig. 478) sub-trapezoid, anterior margin (Fig. 125) asetose, slightly projected, with microscopic median notch; lateral margins with one row of sparse short ramose setae, disc of mentum glabrous; terminal maxillary palpomere elongated, its width about one-third its length; about twice as long as penultimate.

Clypeus flat, rounded laterally, rugulose-lacunose; frontal stria (Fig. 475) vaguely impressed, widely interrupted medially; supraorbital stria absent, frontal disc coriarious-punctate; eyes somewhat flattened, visible from above.

Pronotal sides (Fig. 471) weakly convergent anteriorly, apical angles obtuse, anterior incision for head shallow, pronotal foveae absent; marginal pronotal stria complete; disc punctate, punctures separated by about their own to twice their diameter, laterally forming tiny wrinkles; pronotal hypomeron glabrous; scutellum very small, inconspicuous.

Elytral epipleura with scattered microscopic punctures, area between marginal epipleural stria and elytral margin smooth; marginal epipleural stria fine, complete; marginal elytral stria straight, fine, continued as weakened complete apical elytral stria. Humeral elytral stria well impressed on basal third, occasionally doubled; inner subhumeral stria present medially as a short median fragment; elytral disc with four weakly impressed thin dorsal elytral striae 1–4, striae about the same length, approximately reaching elytral half apically, first dorsal elytral stria somewhat longer, fourth dorsal elytral stria basally connected with sutural elytral stria; sutural elytral stria fine, in shallow punctures, complete, apically connected with apical elytral stria; entire elytral disc with fine shallow punctures separated by about 2–3 times their own diameter, extreme elytral apex smooth.

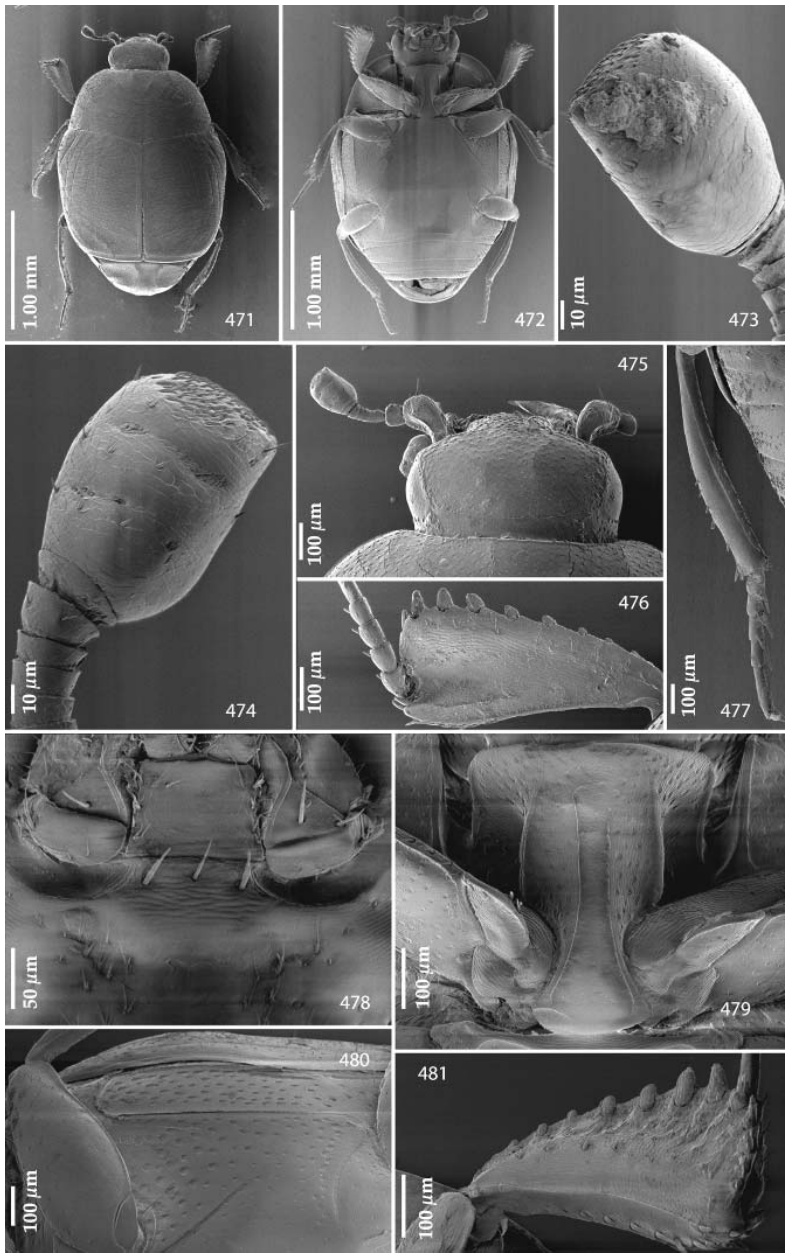
Propygidium almost entirely concealed by elytra, pygidium about as long as wide, with even sparser and finer punctation than that of elytra.

Anterior margin of median portion of prosternum (Fig. 479) almost straight, rounded laterally; marginal prosternal stria weakly impressed anteriorly as a short fragment; prosternal process flattened, surface between carinal prosternal striae slightly imbricate with very sparse microscopic punctation, laterally prosternal process imbricate-punctate; pre-apical foveae absent; carinal prosternal striae well-impressed, divergent on prosternal apophysis, thence subparallel, slightly divergent on anterior end, not united in front; lateral prosternal striae well-impressed, subparallel, strongly carinate, widely ‘open’ anteriorly.

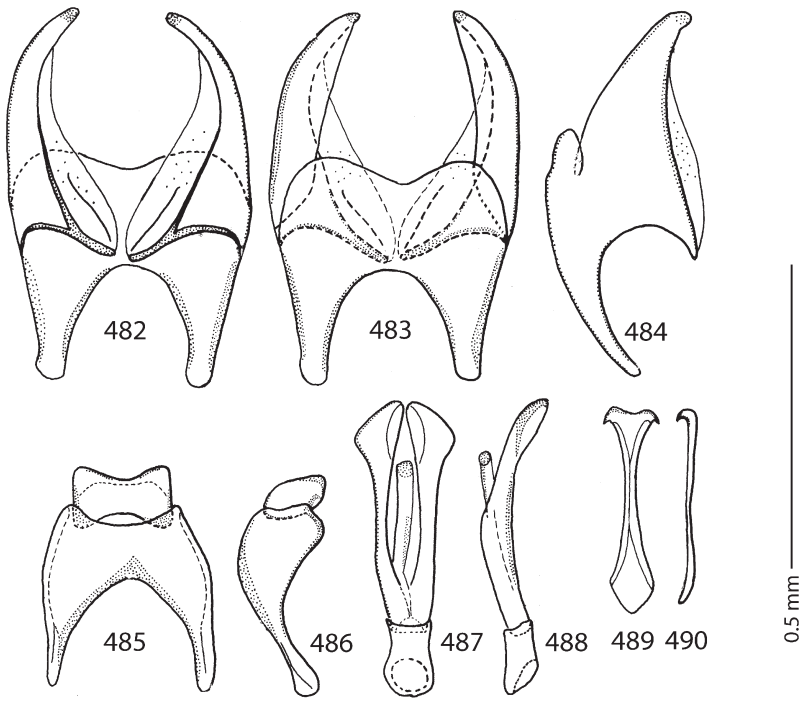
Anterior margin of mesoventrite deeply emarginate medially; discal marginal mesoventral stria thin, slightly carinate, complete; disc of mesoventrite with sparse fine punctation; meso-metaventral sutural stria slightly undulate; intercoxal disc of metaventrite somewhat convex, with scattered microscopic punctures; lateral metaventral stria well impressed, slightly carinate on outer margin, almost straight, shortened apically; lateral disc of metaventrite (Fig. 480) slightly concave, imbricate-punctate, next to metaventral-metepisternal suture a short carinate stria present basally; metepisternum + fused metepimeron (Fig. 480) on basal two-thirds imbricate-punctate, punctures separated about twice their own diameter, on apical third almost glabrous, punctation much sparser; metepisternal stria intermittent.

Intercoxal disc of the first abdominal sternite almost completely striate laterally; with scattered microscopic punctation, interspaces finely imbricate.

Protibia (Figs. 476, 481) flattened and slightly dilated, outer margin with about ten short denticles gradually decreasing in size in proximal direction, denticles continue ventrally along apical margin; setae of outer row extremely sparse and short; setae of median row likewise very sparse and short; protarsal groove deep; anterior protibial stria inconspicuous; single tiny tarsal denticle present apically; protibial spur tiny, growing out from apical protibial margin; outer part of posterior surface of protibia (Fig. 481) imbricate-punctate, distinctly



Figs. 471–481. *Microsaprinus therondianus* (Dahlgren, 1973), SEM micrographs: 471 – habitus, dorsal view; 472 – ditto, ventral view; 473 – antennal club, ventral view; 474 – ditto, dorsal view; 475 – head, dorsal view; 476 – protibia, dorsal view; 477 – metatibia, ventral view; 478 – mentum, stipites and cardines, ventral view; 479 – prosternum; 480 – lateral disc of metaventrite, metepisternum and fused metepimeron; 481 – protibia, ventral view.



Figs. 482–490. *Microsaprinus therondianus* (Dahlgren 1973), male terminalia: 482 – 8th sternite and tergite, ventral view; 483 – ditto, dorsal view; 484 – ditto, lateral view; 485 – 9th tergite, 10th tergite, dorsal view; 486 – ditto, lateral view; 487 – aedeagus, dorsal view; 488 – ditto, lateral view; 489 – spiculum gastrale, ventral view; 490 – ditto, lateral view.

separated from imbricate median part of posterior surface, along basal two-thirds with sparse row of about six microscopic denticles; posterior protibial stria complete, thin, terminating in two tiny, well separated inner-posterior denticles; inner margin with single sparse row of short setae.

Mesotibia slender, outer margin with two sparse rows of thin short denticles, growing in size apically; setae of outer row very sparse; setae of median row inconspicuous; posterior mesotibial stria shortened apically; anterior surface of mesotibia imbricate; anterior mesotibial stria shortened apically; mesotibial spur thin, short; apical margin with three thin short denticles; claws of apical tarsomere longer than half its length; metatibia (Fig. 477) basically similar to mesotibia, but longer and slenderer and denticles on outer margin extremely sparse.

Male genitalia. Eighth sternite (Figs. 482–483) sickle-shaped, widely longitudinally separated medially, mesally with thin short velum without setae; eighth tergite and eighth sternite not fused laterally (Fig. 484). Morphology of 9th tergite (Figs. 485–486) typical for

the subfamily; spiculum gastrale (Fig. 489) thickened on basal half, expanded on both ends. Basal piece of aedeagus (Figs. 487–488) rather short, ratio of its length : length of parameres 1 : 4; parameres separated medially almost along their entire length; aedeagus slightly curved ventrad (Fig. 488).

Myrmetes Marseul, 1862

Myrmetes Marseul, 1862: 511. Type species: *Hister piceus* Paykull, 1809, by monotypy.

Myrmetes: Thomson (1867): 402; Schmidt (1885a): 283, 318; Ganglbauer (1899): 378; Reitter (1909): 290; Jakobson (1911): 641, 648; Bickhardt (1916–1917): 105; Reichardt (1941): 154, 157; Witzgall (1971): 165; Mazur (1973): 41; Kryzhanovskij & Reichardt (1976): 111, 121; Mazur & Kaszab (1980): 6, 62; Vienna (1980): 112; Mazur (1981a): 71, 93; Mazur (1984): 107; Mazur (1997): 217; Yélamos (2002): 245, 254; Mazur (2004): 95.

Diagnosis. Cuticle rufous, silky metallic; frontal and supraorbital striae absent; frontal disc microscopically imbricate-punctate; pronotal foveae absent; pronotal disc impunctate; pronotal hypomeron glabrous; elytra almost entirely smooth, only on apical part with shallow scattered punctures; sutural elytral stria absent; inner subhumeral stria almost complete; carinal prosternal striae united in front with lateral prosternal striae, continued onto the anterior margin of prosternum; pre-apical foveae absent; meso-metaventral sutural stria absent. All tibiae slender and flattened; protibia on outer margin with one row of short denticles, teeth absent; protarsal groove absent.

Differential diagnosis. This taxon is most similar to the genera *Gnathoncus* and *Eremosaprinus*, which are presumably its closely related taxa. From *Eremosaprinus* it differs by the absent sutural elytral stria, absent protibial groove and the strongly reduced, but present lateral prosternal striae. Likewise, the pronotal punctation is lacking in *Myrmetes*, whereas it is well developed in *Eremosaprinus*. By the aforementioned characters (except for the strongly reduced lateral prosternal striae that are present in both taxa) this taxon differs likewise from the genus *Gnathoncus*; furthermore in *Gnathoncus* there is a characteristic short hooked appendix between the fourth dorsal elytral and sutural elytral striae, absent in *Myrmetes*.

Biology. The genus *Myrmetes* contains one myrmecophilous species, *Myrmetes paykulli* Kanaar, 1979. It is found within the nests of *Formica rufa* and more rarely in the nests of several other *Formica* species. Very occasionally it is also found on carcasses.

Distribution. Distribution of *Myrmetes* covers a large part of the Palaearctic Region, from Spain to Siberia. Its presence in Central Asia reported by Kryzhanovskij & Reichardt (1976) was later refuted (Tishechkin 2002).

Species examined. *Myrmetes paykulli* Kanaar, 1979.

Discussion. *Myrmetes* is a well-defined monophyletic taxon, supported by several autapomorphies: silky metallic rufous cuticle, absent sutural elytral stria, absent protibial groove, and peculiar shape of the sensory structures of antennal club. It shares several putative synapomorphies with genera *Eremosaprinus* and *Gnathoncus*, as mentioned earlier (see Diagnosis of the aforementioned genera for details), e.g. absent frontal and supraorbital striae and longitudinally divided tenth tergite of males. Possibly, this taxon branched off the common ancestor of these three taxa and the above-mentioned autapomorphies are simply result of the convergence of its lifestyle within ant nests. A molecular study of these three genera would be highly desirable and would undubtedly yield interesting results.

Myrmetes paykulli Kanaar, 1979

(Figs. 11, 61, 95, 126, 160–161, 491–507)

Hister piceus: Paykull (1809): 231, nec Marsham (1802): 97 (misidentification).
Saprinus piceus: Erichson (1839): 676; Marseul (1855): 505, t. XIX, Fig. 122.
Gnathoncus piceus: Jacquelin-Duval (1858): 112.
Myrmetes piceus: Marseul (1862): 515, t. XIII, Figs. 1, 1a; Thomson (1862): 243; Schmidt (1885a): 318; Ganglbauer (1899): 378; Reitter (1909): 290, t. 67, Fig. 4; Bickhardt (1916–1917): t. IV, Fig. 35; Reichardt (1941): 172, Fig. 82; Horion (1949): 346; Mazur (1973): 41, Fig. 88; Kryzhanovskij & Reichardt (1976): 122, Fig. 164.
Myrmetes paykulli Kanaar, 1979: 24. New substitute name for *Hister piceus* Paykull, 1809, nec Marsham, 1802).
Myrmetes paykulli: Vienna (1980): 113, Fig. 42; Mazur & Kaszab (1980): 63, Fig. 32; Mazur (1981a): 94, Fig. 128; Mazur (1984): 107; Mazur (1997): 217; Yélamos (2002): 254, Figs. 122D, 128; Mazur (2004): 95.
Note. Sensory structures of the antennal club were studied by De Marzo & Vienna (1982a).

Type locality. Sweden, near Uppsala.
Material examined. CZECH REPUBLIC: Bohemia: Liberec, Ruprechtice, xii.1997, nest of *Formica rufa*, 1 ♂, M. Švarc lgt.; Horní Jelení, 19.x.2001, 1 ♂, V. Zieris lgt. **Moravia:** Hnanice env., Na Fládnici, 30.iv.2003, 1 spec., Jiří Hájek lgt.; Srbce env., 28.xi.2001, 1 spec., V. Zieris lgt. (TLAN).

Redescription. Body length: PEL: 1.70–1.775 mm; APW: 0.525–0.625 mm; PPW: 1.375–1.425 mm; EL: 1.175–1.25 mm; EW: 1.575–1.675 mm.

Body (Figs. 491–492) shortly oval, rounded, dorsally moderately convex, flattened ventrally, cuticle reddish-brown to dark brown with silk metallic luster; legs, mouthparts and antennae reddish.

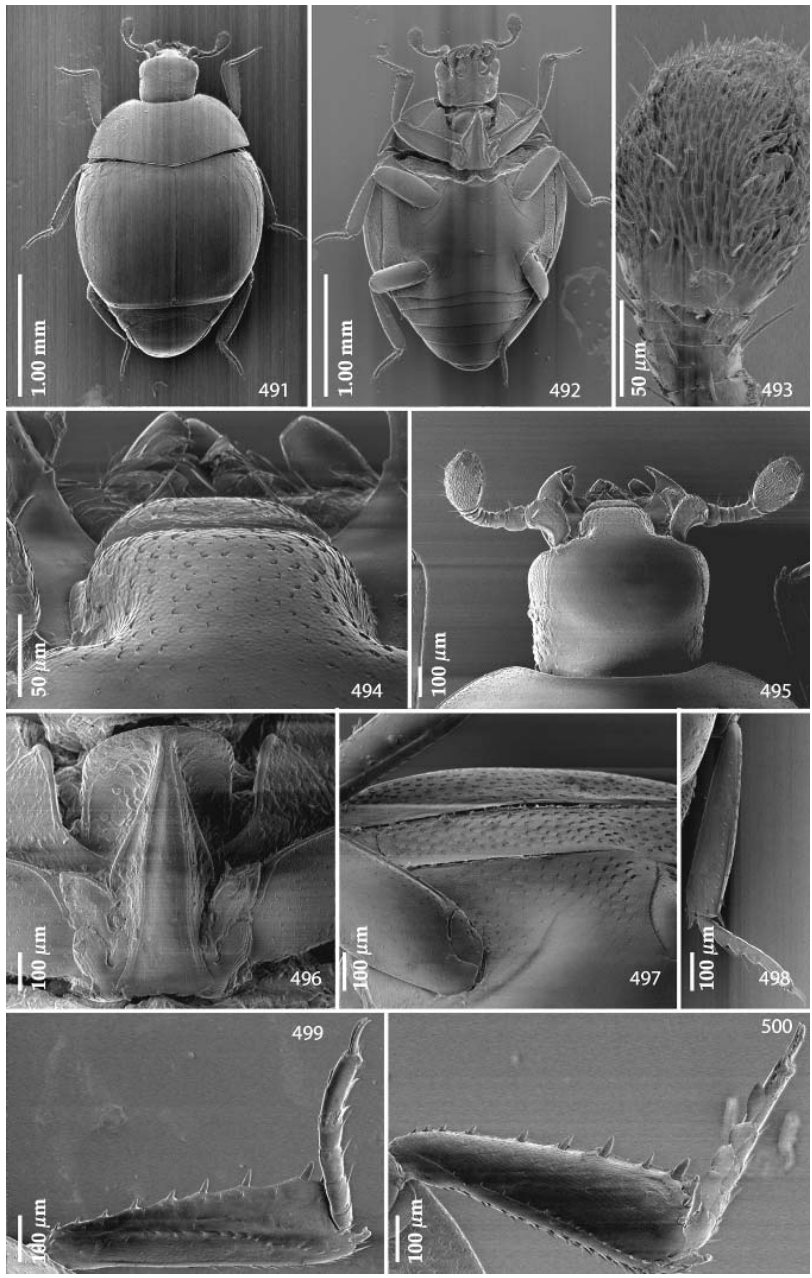
Antennal scape (Fig. 495) slender, surface imbricate, with few short setae, club (Fig. 493) elongated, flattened, without visible articulation, entire surface with dense short sensilla intermingled with sparse somewhat longer erect sensilla; sensory structures of antennal club (Fig. 11) in form of four rather small round circular sensory areas on ventral side and one large round vesicle on internal distal margin of ventral side.

Mouthparts. Mandibles (Fig. 95) with curved outer margin, acutely pointed; sub-apical tooth on inner margin of left mandible minute; disc of labrum (Fig. 61) imbricate, flattened; labral pits tiny, single weakly sclerotized seta present in each pit; labral fold significantly less developed; terminal labial palpomere thickened, its width about half its length; mentum sub-trapezoid, anterior angles (Fig. 126) somewhat produced; anterior margin shallowly emarginate, with sparse, moderately long setae; lateral margins with one row of short ramose setae; disc of mentum glabrous; cardo of maxilla on lateral margin with few short setae; stipes triangular, with three short weakly sclerotized setae; terminal maxillary palpomere elongated, its width about one third its length, about three times as long as penultimate.

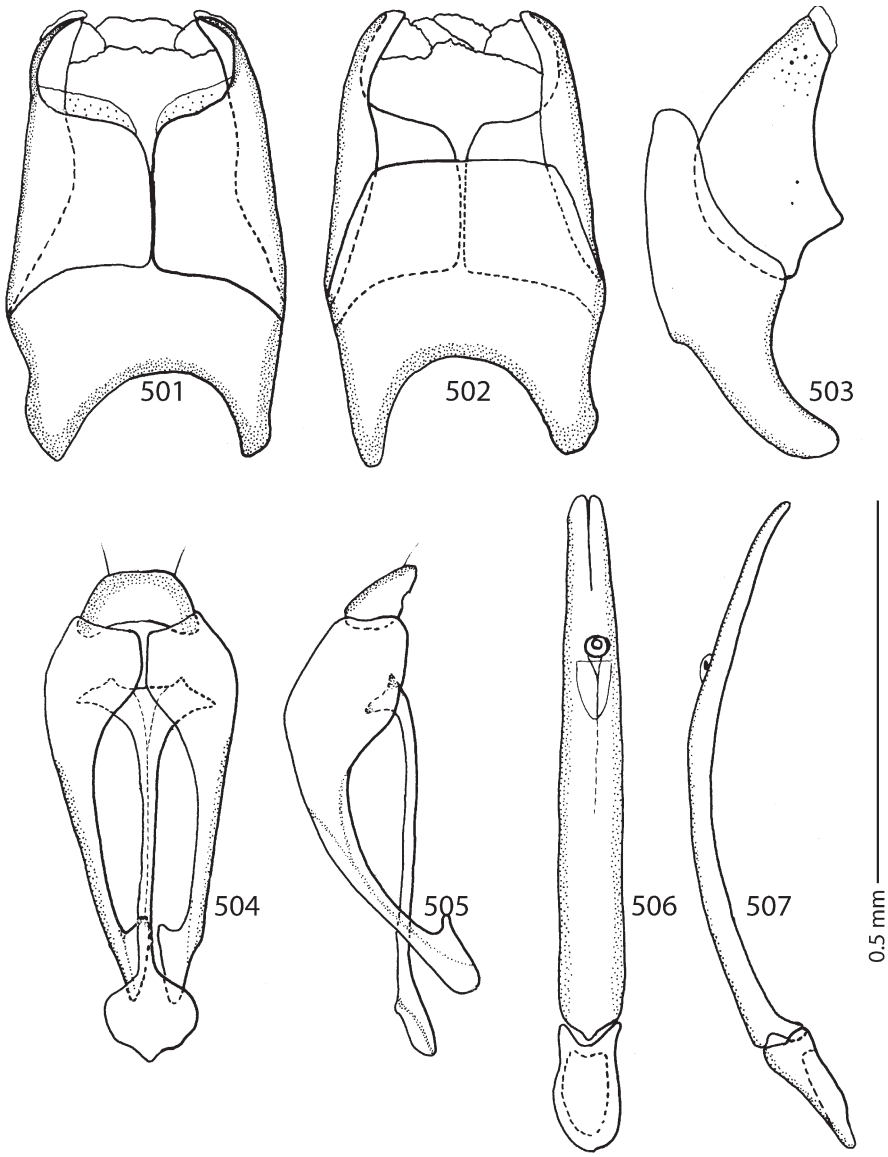
Clypeus (Fig. 494) rectangularly rounded laterally, imbricate-punctate; frontal and supraorbital striae absent; frontal disc (Fig. 495) microscopically imbricate-punctate; eyes flattened, visible from above.

Pronotum (Fig. 491) transverse, about twice as broad as long; pronotal sides strongly narrowed anteriorly; apical angles conspicuous; marginal pronotal stria weakly impressed but complete; pronotal disc smooth; pronotal hypomeron glabrous; scutellum extremely small.

Elytral epipleura finely imbricate-punctate; marginal epipleural stria weakly impressed, complete; marginal elytral stria well impressed, slightly carinate, continued as shortened apical elytral stria, next obliterated; humeral elytral stria weakly impressed on basal fourth; inner subhumeral stria well impressed, carinate and almost complete, abbreviated on apical sixth;



Figs. 491–500. *Myrmetes paykulli* Kanaar, 1979, SEM micrographs: 491 – habitus, dorsal view; 492 – ditto, ventral view; 493 – antennal club, ventral view; 494 – clypeus and labrum, dorsal view; 495 – head, dorsal view; 496 – prosternum; 497 – lateral disc of metaventrite, metepisternum + fused metepimeron; 498 – metatibia, dorsal view; 499 – protibia, dorsal view; 500 – ditto, ventral view.



Figs. 501–507. *Myrmetes paykulli* Kanaar, 1979, male terminalia: 501 – 8th sternite and tergite, ventral view; 502 – ditto, dorsal view; 503 – ditto, lateral view; 504 – 9th tergite, 10th tergite (dorsal view) and spiculum gastrale (ventral view); 505 – 9th tergite, 10th tergite and spiculum gastrale, lateral view; 506 – aedeagus, dorsal view; 507 – ditto, lateral view.

elytral disc with four thin dorsal elytral striae 1–4, abbreviated basally, apically surpassing half of elytral length, fourth dorsal elytral stria slightly shortened apically, sutural elytral stria absent; elytral disc microscopically punctate, punctation becomes more prominent in postero-lateral corners.

Propygidium almost completely exposed, with lateral depressions, imbricate-punctate, punctures separated by about their own diameter; pygidium likewise imbricate-punctate, punctures becoming sparser medio-apically.

Anterior margin of median portion of prosternum (Fig. 496) rounded, pre-apical foveae absent; prosternal process flat, substrigulate; carinal prosternal striae narrowing anteriorly; lateral prosternal striae carinate, narrowing anteriorly; both sets of striae apically attaining anterior margin of prosternal process.

Anterior margin of mesoventrite deeply emarginate medially; discal marginal mesoventral stria anteriorly carinate, weakened laterally; disc of mesoventrite transverse, smooth; meso-metaventral sutural stria absent. Intercoxal disc of metaventrite slightly convex, smooth; lateral metaventral stria weakly impressed, obliquely arcuate, shortened; lateral disc of metaventrite (Fig. 497) concave, imbricate-punctate; metepisternum + fused metepimeron (Fig. 497) likewise imbricate-punctate, but punctation coarser and denser.

Intercoxal disc of the first abdominal sternite laterally depressed, completely striate laterally; imbricate-punctate.

Protibia (Figs. 499–500) slender, flattened, outer margin with sparse row of short thin denticles; setae of outer row extremely short and sparse; setae of median row similarly short and sparse, irregular; protarsal groove absent; anterior protibial stria inconspicuous; two thin short tarsal denticles present apically; protibial spur large, bent, growing out from apical protibial margin; apical margin of protibia posteriorly with two tiny apical denticles; outer part of posterior surface of protibia (Fig. 500) imbricate, with two scattered irregular rows of microscopic sclerotized setae; delimitation from median part of posterior surface vague; posterior protibial stria complete, with rather dense sclerotized setae that become thicker towards apical margin; inner margin with double row of short setae.

Mesotibia (Figs. 160–161) slender, outer margin with a single row of sparse thin denticles growing in size apically; setae of outer row extremely short and minute; setae of median row inconspicuous; posterior mesotibial stria inconspicuous; anterior surface of mesotibia imbricate, with two rows of well sclerotized short setae; anterior mesotibial stria complete, terminating in single tiny inner anterior denticle; mesotibial spur stout, short; apical margin with two tiny denticles; mesotarsus shorter than mesotibia; claws of apical tarsomere longer than half its length; metatibia (Fig. 498) basically similar to mesotibia, but denticles of outer margin almost absent, only near tarsal insertion two minute denticles present; claws of apical tarsomere about half its length.

Male genitalia. Eighth sternite (Figs. 501–502) not fused medially, vela without setae; eighth tergite and eighth sternite not fused laterally (Fig. 503). Ninth tergite (Figs. 504–505) longitudinally divided medially, tenth tergite (Fig. 504) with two moderately long thin setae (styli?); spiculum gastrale (Fig. 504) expanded on both ends. Aedeagus (Figs. 506–507) slender, conspicuously long, approximately 1.5 times as long as 8th sternite; basal piece of aedeagus short, ratio of its length : length of parameres 1 : 6; parameres fused along their basal three-fourths; aedeagus apically slightly curved ventrad (Fig. 507).

Paravolvulus Reichardt, 1932

Paravolvulus Reichardt, 1932: 31, 36, 109 (as subgenus of *Hypocacculus*). Type species: *Saprinus ovillum* Solskij, 1876, original designation.

Paravolvulus: Reichardt (1941): 272, 290 (as subgenus of *Hypocacculus*); Kryzhanovskij & Reichardt (1976): 112, 234; Mazur (1984): 102; Mazur (1997): 264; Mazur (2004): 95.

Diagnosis. Cuticle usually dark brown to black, at times with feeble bronze luster; elytra in some species with red maculae; frontal stria almost straight, often interrupted in middle, never strongly carinate on outer side, in few cases prolonged onto clypeus, never acutely angulate above eyes; pronotum often with lateral pronotal stria shortened anteriorly and posteriorly; marginal pronotal stria complete and carinate; pronotal foveae always absent; pre-apical foveae weakly impressed.

Differential diagnosis. *Paravolvulus* is most similar to members of the genus *Hypocacculus*, differing from its representatives by (in most cases) medially interrupted frontal stria and often present lateral pronotal stria that is always absent in *Hypocacculus*. Likewise, elytra are occasionally with red maculae in this genus whereas in *Hypocacculus* they are never so.

Biology. The biology of *Paravolvulus* is poorly documented. Its representatives seem to inhabit arid and semi-desert biotopes, from lowlands to higher elevations (some species were found above 1500 m in Kyrgyzstan and Afghanistan) and are generally rare in collections. They are often found in very small series, and are not typically found in dung or on carrion, although sometimes can be found there, too. Several species (*Paravolvulus binaevulus* (Reitter, 1887), *P. refector* (Reitter, 1904)) have been collected in larger series in the nests of gerbils (*Pachyuromys* sp.) (Kryzhanovskij & Reichardt 1976). *Paravolvulus assimilis* Kryzhanovskij, 1987 has been collected in a large series by pitfall traps in the wheat fields of southeastern Kazakhstan (Kryzhanovskij 1987).

Distribution. The genus *Paravolvulus* currently comprises 11 species, all found in Central Asia and the Middle East (Jordan, Iraq, Iran), with one species (*P. fausti* (Schmidt, 1885a) reaching as far west as southeastern Turkey (Mazur 1997). *Paravolvulus syphax* (Reitter, 1904) occurring in the Sahara and recorded also from Saudi Arabia most likely belongs to another genus and its taxonomic status will be clarified in a later paper.

Species examined. *Paravolvulus assimilis* Kryzhanovskij, 1987, *P. binaevulus* (Reitter, 1887), *P. fausti* (Schmidt, 1885a), *P. lateristrius* (Solskij, 1876), *P. occidentalis* Mazur, 1981b, *P. ovillum* (Solskij, 1876), *P. refector* (Reitter, 1904), *P. syphax* (Reitter, 1904).

Discussion. This taxon is weakly supported in the preliminary phylogenetic analysis of Palaearctic Saprininae (Lackner, in prep.) and it is possible that it is deeply nested within poly- or paraphyletic *Hypocacculus*.

Paravolvulus ovillum (Solskij, 1876)

(Figs. 5, 127, 508–524)

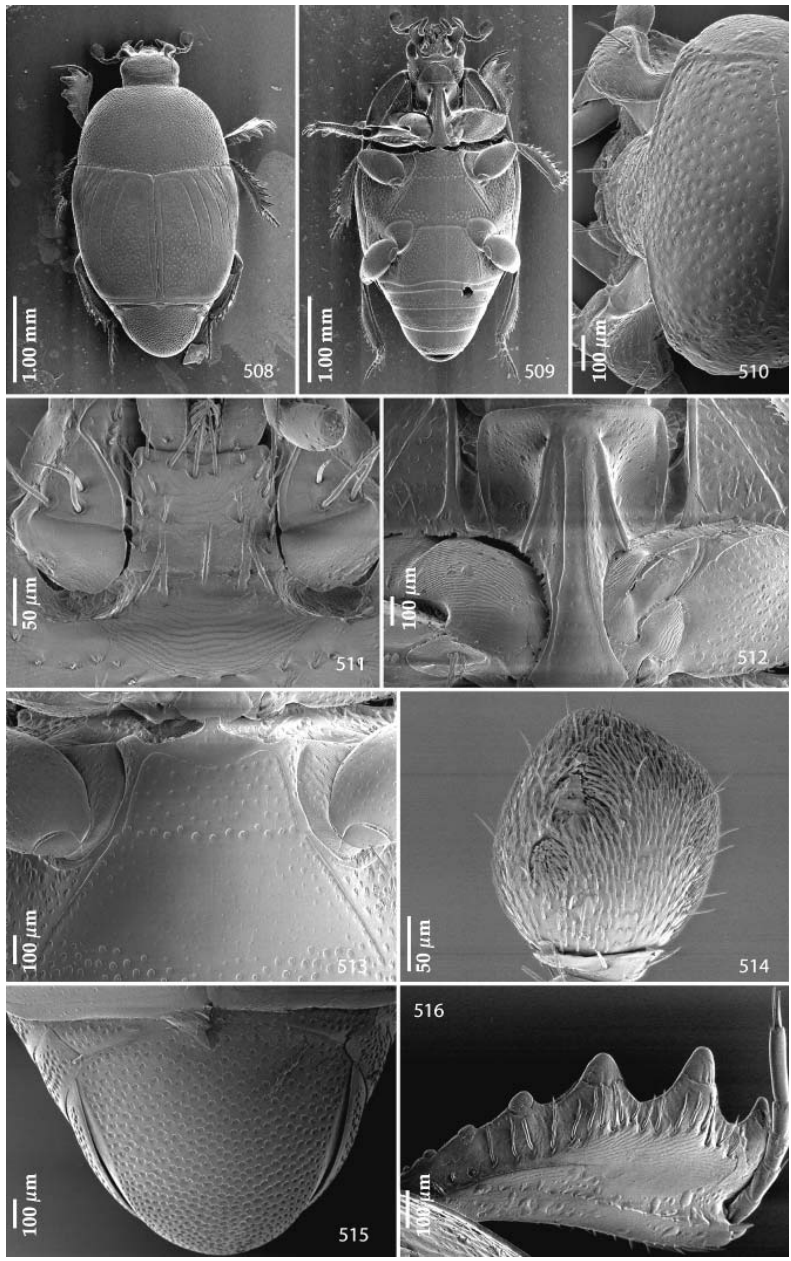
Saprinus ovillum Solskij, 1876: 240.

Saprinus ovillum: Lewis (1907): 484; Jakobson (1911): 651.

Hypocacculus ovillum: Bickhardt (1916): 97.

Hypocacculus (*Paravolvulus*) *ovillum*: Reichardt (1932): 38, 112; Reichardt (1941): 283, 293.

Paravolvulus ovillum: Kryzhanovskij & Reichardt (1976): 235, 236; Mazur (1984): 103; Mazur (1997): 264; Mazur (2004): 95.



Figs. 508–516. *Paravolvulus ovillum* (Solskij, 1876), SEM micrographs: 508 – habitus, dorsal view; 509 – ditto, ventral view; 510 – clypeus and frontal disc; 511 – mentum, submentum and cardines and stipites of maxilla, ventral view; 512 – prosternum; 513 – mesoventrite and metaventrite; 514 – antennal club, ventral view; 515 – pygidium; 516 – protibia, dorsal view.

Type locality. Uzbekistan, Katty-Kurgan.
Material examined. KAZAKHSTAN: Dshulek [= Zhulek], 8.vi.1911, 1 ♀, Koshantshikov lgt.; Perovsk Syr-Darijsk. Obl., 27.iv.[1]928, 1 ♂, V. Popov lgt. (ZIN). **TURKMENISTAN:** Bajram Ali, 23.iv.1981, 1 ♀, A. Olexa lgt. (TLAN).
Note. The type specimen of this species has not been found in the Solskij's collection, housed at ZMUM. According to N. Nikitsky (ZMUM) the type specimen should be housed at ZIN since Axel Reichardt personally examined it. However, no type specimen has been found during the visit at ZIN and its whereabouts are unknown. Since it is possible that the type specimen may re-emerge in the future the neotype is not designated herein.

Redescription. Body length: PEL: 2.425–2.50 mm; APW: 0.75 mm; PPW: 1.75–1.85 mm; EL: 1.45–1.50 mm; EW: 1.875 mm.

Body (Figs. 508–509) elongate oval, convex; cuticle shining, dark brown with a feeble bronzy luster; pronotum darker; legs, antennae and mouthparts castaneous.

Antennal scape (Fig. 510) slightly thickened, surface imbricate; with two short setae; club (Fig. 514) without visible articulation, entire surface covered with short sensilla intermingled with sparser longer erect sensilla; sensory structures of antennal club not examined.

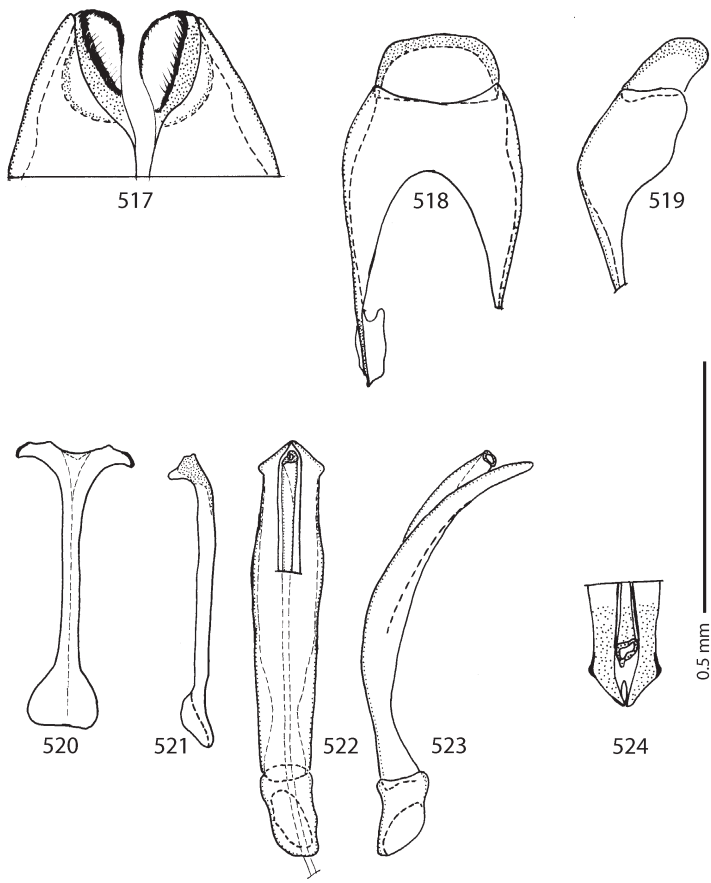
Mouthparts. Mandibles with rounded outer margin curved inwardly, acutely pointed. Labrum coarsely punctate, underside not examined; disc of labrum with two well impressed labral pits; two setae arising from each one; terminal labial palpomere elongated, its width about one-third its length; mentum (Fig. 511) square-shaped; anterior margin (Fig. 127) medially with a small acute notch surrounded by four moderately long setae; lateral margins with single row of shorter ramose setae, several sparse short setae present also on finely imbricate disc of mentum; cardo of maxilla on outer margin with few short setae; stipes (Fig. 511) triangular, with three longer setae; terminal maxillary palpomere elongated, its width about one-third its length, about 2.5 times as long as penultimate; remaining mouthparts not examined.

Clypeus (Fig. 510) rounded laterally, rugulose-punctate, punctures umbilicate; frontal stria weakly impressed, slightly carinate, medially interrupted, continued as a weakly impressed supraorbital stria; frontal disc (Fig. 510) on anterior third verrucose-punctate; rest of disc with fine punctures separated about twice their own diameter; eyes moderately convex, well visible from above.

Pronotal sides (Fig. 508) evenly rounded, almost parallel on basal two-fifths, thence convergent apically, strongly convergent on apical fourth; apical angles rather blunt; marginal pronotal stria complete, slightly carinate; disc with coarse and dense punctation, laterally forming elongate wrinkles, becoming finer and sparser medially; pronotal hypomeron glabrous.

Elytral epipleura punctate; marginal epipleural stria complete, well impressed; marginal elytral stria well impressed, carinate, continued as complete, if slightly weakened apical elytral stria; humeral elytral stria vaguely impressed on basal fourth, doubled; inner subhumeral stria well impressed as short medial fragment; elytra with four dorsal elytral striae 1–4, about the same length, apically surpassing elytral half; fourth stria basally connected with sutural elytral stria; sutural elytral stria well impressed, complete, continued as complete, somewhat weakened apical elytral stria; entire elytral disc covered with punctation, on basal half punctures sparser and finer; denser and coarser on apical half; extreme apex of elytra with a very narrow impunctate band.

Propygidium almost entirely concealed by elytra; pygidium (Fig. 515) about as long as broad, with coarse and dense punctation, interspaces finely imbricate.



Figs. 517–524. *Paravolvulus ovillum* (Solskij, 1876), male terminalia: 517 – 8th sternite (apical half), ventral view; 518 – 9th tergite, 10th tergite (dorsal view); 519 – ditto, lateral view; 520 – spiculum gastrale, ventral view; 521 – ditto, lateral view; 522 – aedeagus, dorsal view; 523 – ditto, lateral view; 524 – apex of aedeagus, frontal view.

Anterior margin of median portion of prosternum (Fig. 512) straight; marginal prosternal stria fragmentally present anteriorly and laterally; pre-apical foveae small; prosternal process moderately concave; between carinal prosternal striae finely punctulate, laterally substrigulate; carinal prosternal striae well impressed, slightly carinate, sub-parallel, not connected in front; lateral prosternal striae carinate, convergent anteriorly, not connected in front.

Anterior margin of mesoventrite (Fig. 513) deeply emarginate medially, discal marginal mesoventral stria well impressed, slightly weakened anteriorly; disc of mesoventrite with scattered punctation, punctures separated several times their diameter; meso-metaventral sutural stria in form of a row of deep round punctures; intercoxal disc of metaventrite (Fig. 513) with fine scattered punctures, along apical margin a band of coarse scattered punctures

appears; lateral metaventral stria well impressed, carinate, straight, stopping near metacoxa; lateral disc of metaventrite with shallow round setiferous punctures; interspaces substrigulate; metepisternum + fused metepimeron on basal two-thirds with similar setiferous punctation, but punctures deeper, interspaces substrigulate; apical third (especially fused metepimeron) with much sparser punctation.

Intercoxal disc of the first abdominal sternite completely striate laterally; mesad to marginal stria with deep round punctures laterally, punctation medially weaker and sparser; along apical margin row of fine punctures present.

Protibia (Fig. 516) moderately dilated, outer margin with three moderately large triangular teeth topped with triangular denticle becoming progressively smaller in proximal direction, followed by three minute round denticles; setae of outer row moderately dense, regular and short; setae of median row much shorter than those of outer row, inconspicuous; protarsal groove rather deep; anterior tibial stria present on basal half; single, rather short tarsal denticle present apically; protibial spur tiny, bent, growing out from apical protibial margin; apical margin of protibia posteriorly with two minute apical denticles; outer part of posterior surface of protibia coriarious-punctate; vaguely separated from glabrous median part of posterior surface, boundary between outer and median part of posterior surface marked by row of about 10 minute sclerotized setae; posterior protibial stria complete, in sparse weakly sclerotized setae apically turning into several short well sclerotized denticles; inner margin with single row of short setae.

Mesotibia slender, outer margin with two sparse rows of thin denticles growing in size apically; setae of outer row regular, rather dense, well sclerotized; setae of median row regular, much shorter and finer than those of outer row; posterior mesotibial stria almost complete; anterior surface of mesotibia imbricate with scattered minuscule punctures with microscopic setae; anterior mesotibial stria shortened apically, terminating in three tiny inner anterior denticles; mesotibial spur stout, short; apical margin with three tiny denticles; claws of apical tarsomere shorter than half its length; metatibia basically similar to mesotibia, slightly more slender.

Male genitalia. Apex of 8th sternite (Fig. 517) with large inflatable velum, resembling a suction cup fringed with microscopic setae; ninth tergite, tenth tergite and spiculum gastrale typical for the subfamily (Figs. 518–521); apex of aedeagus pointed (Fig. 524), aedeagus somewhat narrowed before apex (Fig. 522), median lobe conspicuously protruding (Fig. 523); basal piece rather short, ratio of basal piece : length of parameres 1 : 6, aedeagus strongly curved ventrad (Fig. 523).

Philothis Reichardt, 1930

Philothis Reichardt, 1930: 293. Type species: *Philothis arcanus* Reichardt, 1930, original designation.
Philothis: Reichardt (1941): 157, 337; Peyerimhoff (1936): 224; Kryzhanovskij & Reichardt (1976): 112, 243; Mazur (1984): 109; Olexa (1990): 146; Mazur (1997): 268; Mazur (2004): 96.

Diagnosis. Body strongly vaulted, especially ventrally, cuticle castaneous to dark brown, often with metallic luster; eyes inconspicuous from above; clypeus and frontal disc smooth, frontal stria usually broadly interrupted medially, rarely complete; supraorbital stria usually present, rarely absent; labrum smooth, flattened, labral pits and setae absent; pronotum usually

conspicuously narrowed anteriorly with deep anterior incision for head, pronotal angles prominent; pronotal hypomeron setose, pronotal disc rarely with vague bulges in postero-median part; pronotal foveae absent. Elytral epipleura glabrous; inner subhumeral stria usually well developed; marginal elytral stria complete, apical elytral stria at times erased by punctation; sutural elytral stria on basal half distanced from elytral suture (in some species doubled) and at times continuous as basal elytral stria surrounding large transverse bulge situated on median part of elytral base; in subgenera *Philothis* and *Farabius* only first and sometimes second dorsal elytral striae developed; in subgenus *Atavinus* all four, or even five dorsal striae developed; disc of elytra usually entirely punctate, punctures very dense, shallow, often confluent, occasionally leathery at apex; scutellum very small. Propygidium and pygidium with large, shallow and very dense punctures, rarely lateral sides of pygidium glabrous; pygidium (and partly also propygidium) of at least one species, *Philothis* (*Atavinus*) *pierrei* (Thérond, 1963), setose. Prosternum without pre-apical foveae, with long yellow setae; lateral prosternal striae absent, carinal prosternal striae usually absent as well (in subgenus *Farabius* present on prosternal apophysis), in some cases marginal prosternal stria complete. Mesoventrite of at least one species, *Philothis* (*Philothis*) *alsiosus* Peyerimhoff, 1936, setose; lateral metaventral stria shortened (in some species extremely). Lateral striae of first abdominal sternite weakened, often shortened apically. Lateral parts of pleura and sterna with long yellow setae. Protibia anteriorly truncated, anterior margin of protibia formed by apical margin of most-distal large triangular tooth; outer margin of protibia with two large triangular teeth, topped with tiny round denticle, occasionally followed by several indistinct minuscule denticles; protarsi shortened, at times rudimentary, in subgenus *Atavinus* completely absent; apical protarsomere occasionally with single long, thin straight claw. Meso- and metatarsi with basal-most tarsomere the thickest, tarsomeres gradually diminishing in diameter apically; each tarsomere of mesotarsus with two strongly sclerotized lamelliform setae, one posteriorly and one anteriorly; mesotarsal claws thin, hair-like, several times as long as fifth tarsomere itself. Outer margin of metatibia with one double row of morphologically different sets of denticles: denticles of the first type short, thick-set with rounded apices, denticles of the second type much longer and thinner, with pointed apices; another row markedly shifted from outer margin, situated on anterior side of metatibia, observable only from ventral view.

Differential diagnosis. Species of this genus could be confused with the genera *Ctenophilothis*, *Xenophilothis*, *Xenonychus*, and perhaps also with *Styphrus* or *Ammostyphrus*. From *Ctenophilothis* they differ chiefly by the shape of protibia that is with two large distal triangular teeth instead of numerous long movable denticles; furthermore in *Ctenophilothis* the elytral epipleuron is setose, whereas in *Philothis* it is glabrous. From the genus *Xenophilothis* the members of this genus differ also chiefly by the shape of protibia, that is with two rounded teeth each topped with a triangular denticle, followed by the two shorter triangular teeth topped with a denticle (whereas in *Philothis* it is with two large triangular distal teeth, see above), as well as the shape of mentum (sub-trapezoid to square-shaped in *Philothis* and broadening anteriorly in *Xenophilothis*); furthermore, the lateral prosternal striae are well developed, straight in *Xenophilothis* (whereas they are absent in *Philothis*) and the elytral epipleuron is likewise setose (glabrous with *Philothis*). From the genus *Xenonychus* they differ by the usually reduced dorsal elytral striae, whereas they are well developed and almost complete

in *Xenonychus* (in the subgenus *Atavinus* these striae are likewise well developed, but they rarely surpass the elytral half apically, whereas they are almost complete in *Xenonychus*); furthermore, *Xenonychus* has a setose elytral epipleuron, whereas in *Philothis* it is glabrous. From the genus *Styphrus* the members of *Philothis* differ chiefly by present both sets of prosternal striae (absent in *Philothis*) as well as the shape of protibia and different chaetotaxy of the antennal club and differently shaped pro-, meso- and metatibiae. *Ammostyphrus* possesses lateral pronotal stria, which is absent in *Philothis*; furthermore, *Ammostyphrus* has lateral prosternal striae well developed, whereas they are absent in *Philothis*.

Biology. A strictly psammophilous genus. The biology and distribution of *Philothis* was elaborated by Olexa (1990). Beetles burrow deep in sand, often near roots of various desert plants or shrubs recently entombed by shifting sands and still having faded leaves buried in the sand where they prey on larvae of various arthropods, like other Histeridae (Olexa 1990). They are extremely well adapted to the psammophilous way of life.

Distribution. This genus has 14 described species from Algerian and Egyptian Sahara, Iranian and Omani deserts and desert regions of Central Asia (Kazakhstan, Uzbekistan and Turkmenistan) as far west as Azerbaijan (Mazur 1997).

Discussion. *Philothis* ranks among most derived psammophilous Saprininae, containing most of the peculiar morphological adaptations linked with its special habits. It is probably monophyletic and sister to *Ctenophilothis*. The monophyly of *Philothis* is supported by several synapomorphies e.g. vesicle of the antennal club situated under apical surface (instead of internal distal margin), peculiar shape of prosternal process, flattened smooth labrum without labral pits or setae and cupuliform 8th antennomere.

Key to the subgenera of the genus *Philothis* Reichardt, 1930

1 (2) Protarsi absent (Fig. 551); elytra with four (rarely even five) dorsal elytral striae. ..... subgenus ***Atavinus*** Olexa, 1990

2 (1) Protarsi present.

3 (4) Prosternal apophysis large, triangular; carinal prosternal striae present, convergent anteriorly (Fig. 564). ..... subgenus ***Farabius*** Reichardt, 1930

4 (3) Prosternal apophysis faintly triangular, carinal prosternal striae absent (Fig. 531). ..... subgenus ***Philothis*** s. str.

Subgenus *Philothis* Reichardt, 1930

Philothis Reichardt, 1930: 293. Type species: *Philothis arcanus* Reichardt, 1930, original designation.

Philothis: Reichardt (1941): 157, 337; Peyerimhoff (1936): 224; Kryzhanovskij & Reichardt (1976): 112, 243; Mazur (1984): 109; Olexa (1990): 146; Mazur (1997): 268; Mazur (2004): 96.

Diagnosis. Characters of this subgenus are given in the determination key and in the general diagnosis of the genus.

Differential diagnosis. This subgenus differs from the other two subgenera by the following characters: from the subgenus *Atavinus* by the present (if at times reduced) pretarsi and reduced dorsal elytral striae (usually only dorsal elytral striae 1–2 are present, often abbreviated at base or apex); and from the subgenus *Farabius* by the smaller prosternal apophysis devoid of carinal prosternal striae.

Biology. See biology of *Philothis* s. l.

Distribution. Seven species of this subgenus are known hitherto, five of them from Central Asia (mostly from the Kara-kum and Kyzyl-kum Deserts located in Uzbekistan and Turkmenistan) and two species from Algerian Sahara (Olexa 1990, Mazur 1997).

Species examined. *Philothis* (*Philothis*) *alsiosus* Peyerimhoff, 1936, *P.* (*P.*) *arcanus* Reichardt, 1930, *P.* (*P.*) *asper* Kryzhanovskij, 1982, *P.* (*P.*) *bidens* (Peyerimhoff, 1900), *P.* (*P.*) *generator* Reichardt, 1930, *P.* (*P.*) *medvedevi* Kryzhanovskij, 1966, *P.* (*P.*) *suturalis* Reichardt, 1930.

Philothis (*Philothis*) *arcanus* Reichardt, 1930

(Figs. 32, 44, 63, 97, 128, 525–542)

Philothis (*Philothis*) *arcanus* Reichardt, 1930: 295, Figs. 8, 11, 12, 13.

Philothis (*Philothis*) *arcanus*: Reichardt (1941): 339, 342, Figs. 73, 175A; Kryzhanovskij & Reichardt (1976): 244, 246, Fig. 475; Mazur (1984): 109; Olexa (1990): 153, Fig. 19; Mazur (1997): 268; Mazur (2004): 96.

Type locality. Uzbekistan, Farab.

Type material examined. Holotype: spec., 'Buchara occ. / Farab. / 3.iv.[1]911 / A. Hohlbeck // *Philothis* / *arcanus* sp. n. / Holotyp / Reichardt det. [printed-written] // Coll. Semenov-Tian-Shansky [printed] // with another golden round label' (ZIN). Paratype: 1 spec., 'Buchara occ. / Farab. / 16.iv.[1]912 / A. Hohlbeck [printed-written] // Coll. Semenov-Tian-Shansky [printed] // *Philothis* / *arcanus* sp. n. / P-typ / Reichardt det [printed-written] // with another golden round label' (MNHN).

Additional material examined. UZBEKISTAN: Buchara, Shafrikan, 29.iv.1979, 1 ♂, A. Olexa lgt.; Karakum, Chiva [= Khiva], 3.v.1978, 1 ♂, A. Olexa lgt.; ditto, but 1.–5.v.1979, 4 spec.; Kyzylkum, Buchara, 30.iv.1979, 1 ♂, A. Olexa lgt. (TLAN).

Redescription. Body length: PEL: 1.975–2.175 mm; APW: 0.75–0.80 mm; PPW: 1.50–1.75 mm; EL: 1.225–1.425 mm; EW: 1.925–2.00 mm.

Body (Figs. 525–526) roundly oval, moderately convex from above, underside very convex, cuticle light to dark brown, shining; legs, mouthparts and antennal scape rufopiceous.

Antennal scape (Fig. 529) thickened, imbricate, with numerous long setae; club (Fig. 528) comparatively small, round, without visible articulation, apical third imbricate, with thick dense short erect yellow sensilla concealing apical sensory area; basal surface glabrous; sensory structures of antennal club (Fig. 32) in form of one doubled apical sensory area and one stipe-shaped vesicle situated under it.

Mouthparts. Mandibles (Fig. 97) with straight outer margin strongly curved inwardly, mandibular apex sharply pointed; sub-apical tooth on inner margin of left mandible moderately large, perpendicular; labrum (Figs. 44, 63, 527) smooth, flattened, slightly depressed medially; labral pits and setae absent; labral process significantly developed; terminal labial palpomere elongated, its width about one-third its length; mentum sub-trapezoid, finely imbricate, with shallow emargination in middle of anterior margin (Fig. 128), surrounded with numerous moderately long ramose setae, lateral margins with single row of much shorter ramose setae; cardo of maxilla on lateral margin with numerous short setae; stipes triangular, with numerous much longer setae; terminal maxillary palpomere thickened, apically truncate, its width about half its length, approximately twice as long as penultimate.

Clypeus (Fig. 527) rectangular, rounded laterally, smooth; frontal stria (Fig. 529) broadly interrupted medially, continued as well impressed and carinate supraorbital stria; frontal disc smooth; eyes flattened, invisible from above.

Pronotal sides (Fig. 525) moderately convergent anteriorly; apical angles obtuse; marginal pronotal stria well impressed, laterally carinate, broadly interrupted behind head; pronotal disc convex, entirely smooth, except for a row of small round punctures along base; posteromedian part with two vague bulges; pronotal hypomeron with long yellow setae; scutellum very small, almost invisible.

Elytra with prominent elytral humeri, elytral epipleura almost smooth, only with microscopic punctation; marginal epipleural stria complete; marginal elytral stria well impressed, carinate, continued as complete apical elytral stria. Humeral elytral stria distinctly impressed on basal third, occasionally doubled; inner subhumeral stria present medially, at times joining humeral elytral stria; outer subhumeral stria shortly present on basal fifth; first dorsal elytral stria shortened on basal third and apical fourth, on both ends bent inwardly, second dorsal elytral stria vaguely impressed as short fragment on apical half (at times completely absent); other dorsal elytral striae absent. Sutural elytral stria well impressed, apically connected with complete apical elytral stria, on basal half somewhat distanced from elytral suture, continuous as basal elytral stria surrounding large transverse bulge situated at median part of elytral base, vaguely connected with first dorsal elytral stria; elytral suture depressed; interspace between elytral suture and sutural elytral stria smooth. Elytral disc with dense, shallow obscurely-variolate punctation, interspaces with microsculpture, punctation becomes leathery apically; area around scutellum, elytral humeri, flanks and transverse basal bulge glabrous.

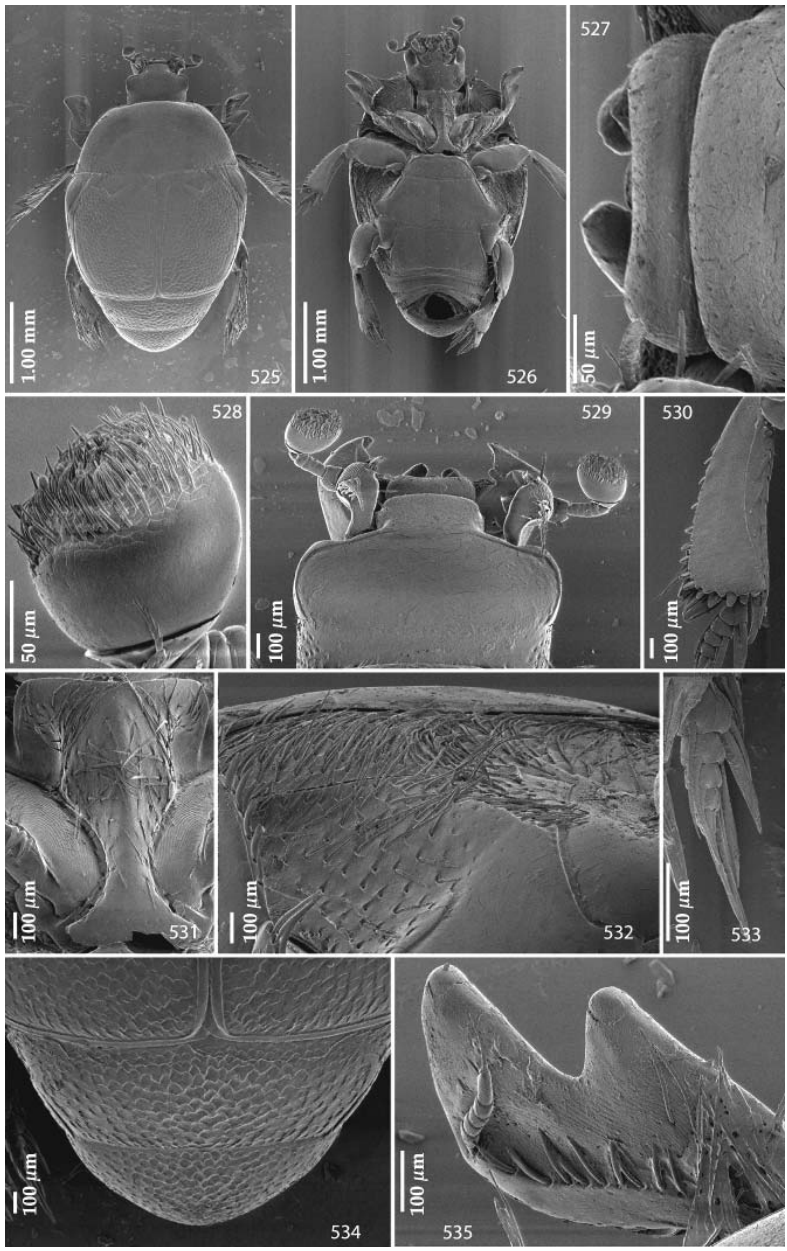
Propygidium (Fig. 534) completely exposed, almost twice as broad as long, areolate-rugose; pygidium (Fig. 534) almost as long as broad, convex, medially areolate-rugose, laterally almost glabrous, slightly obscurely-variolate.

Anterior margin of median portion of prosternum (Fig. 531) almost straight, slightly emarginate medially; marginal prosternal stria present only laterally; prosternal process concave, setose, substrigulate; both sets of prosternal striae absent.

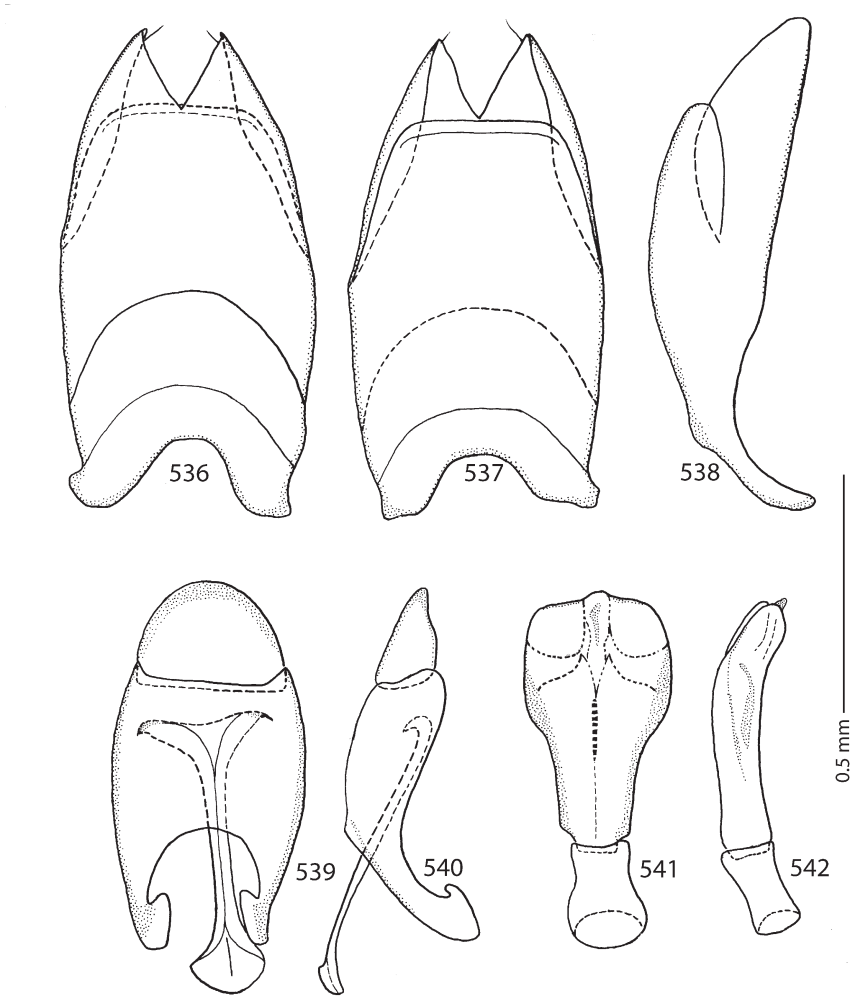
Anterior margin of mesoventrite with large shallow emargination; discal marginal mesoventral stria well impressed, carinate; disc with scattered shallow elongate punctures separated about their own to twice their own diameter; meso-metaventral sutural stria well impressed, almost straight, carinate; intercoxal disc of metaventrite medially with shallow scattered punctures, laterally smooth; posterior margin with coarser punctation; in male with shallow longitudinal depression; lateral metaventral stria well impressed, carinate, obliquely arcuate, shortened; lateral disc of metaventrite (Fig. 532) concave, with shallow round punctures fringed with long setae; metepisternum + fused metepimeron (Fig. 532) setose, punctation almost unrecognizable beneath setae; area of fused metepimeron depressed, setae less dense than on metepisternum.

Intercoxal disc of the first abdominal sternite almost completely striate laterally, with scattered microscopic punctation; lateral disc of all visible abdominal sternites setose laterally.

Protibia (Fig. 535) dilated, anterior margin truncate, formed by anterior margin of distalmost large triangular tooth; outer margin of protibia apart from this tooth with another, slighty shorter triangular tooth, both teeth topped with short rounded blunt denticle; setae of outer row confined to basal third, thin, sparse and moderately long; setae of median row thicker, more regular and dense; protarsal groove moderately deep; apical margin of protibia posteriorly without denticles; outer part of posterior surface of protibia smooth, distinctly



Figs. 525–535. *Philothis* (*Philothis*) *arcanus* Reichardt, 1930, SEM micrographs: 525 – habitus, dorsal view; 526 – ditto, ventral view; 527 – clypeus and labrum, dorsal view; 528 – antennal club, dorsal view; 529 – head, dorsal view; 530 – mesotibia, ventral view; 531 – prosternum; 532 – lateral disc of metaventrite, metepisternum and fused metepimeron; 533 – mesotarsus, ventral view; 534 – propygidium and pygidium; 535 – protibia, dorsal view.



Figs. 536–542. *Philothis* (*Philothis*) *arcanus* Reichardt, 1930, male terminalia: 536 – 8th sternite and tergite, ventral view; 537 – ditto, dorsal view; 538 – ditto, lateral view; 539 – 9th tergite, 10th tergite (dorsal view) and spiculum gastrale (ventral view); 540 – 9th tergite, 10th tergite and spiculum gastrale, lateral view; 541 – aedeagus, dorsal view; 542 – ditto, lateral view.

separated from smooth median part of posterior surface by thin complete stria; posterior protibial stria shortened apically; inner margin of protibia with long lamelliform dense setae; protibial spur rudimentary, almost invisible, entombed in apical margin of protibia; protarsus rudimentary, apical tarsomere with single thin claw, approximately twice as long as apical tarsomere itself.

Mesotibia (Fig. 530) somewhat dilated, not particularly thickened, outer margin with one double row of sparse, morphologically different short denticles significantly growing in size and density near tarsal insertion, denticles continuous anteriorly along apical margin; setae of outer row growing out near inner mesotibial margin, dense and long, covering almost entire posterior mesotibial surface; setae of median row absent; posterior mesotibial stria shortened, present only on basal half; mesotibial spur conspicuously long and stout; outer part of median surface of mesotibia almost smooth, only with scattered microscopic punctation, anterior mesotibial stria thin, almost complete; inner margin of mesotibia with dense row of long lamelliform setae; mesotarsus (Fig. 533) telescope-like, diameter of tarsomeres diminishing apically, each tarsomere with two long lamelliform, strongly sclerotized setae, one dorsally and one ventrally; claws of apical mesotarsomeres thin, hair-like, several times as long as mesotarsomeres itself. Metatibia conspicuously dilated, outer margin with double row (short rounded and dense, thinner, longer denticles) of morphologically different denticles, another row of short sparser round denticles markedly shifted from it, present on anterior surface of metatibia and only observable from ventral view. Posterior surface of metatibia with dense rows of short setae, distinction between outer and median row unclear; posterior metatibial stria inconspicuous (absent?); metatibia otherwise similar to mesotibia.

Male genitalia. Eighth sternite (Figs. 536–537) longitudinally fused medially, apically with large inflatable membrane (velum); fringed with single thin short seta; eighth tergite and eighth sternite fused laterally (Fig. 538). Morphology of 9th tergite (Figs. 539–540) typical for the subfamily; spiculum gastrale (Fig. 539) expanded on both ends. Basal piece of aedeagus (Figs. 541–542) rather short, ratio of its length : length of parameres 1 : 3.5; parameres fused along their basal three-fourths; aedeagus conspicuously dilated apically and gently curved ventrad (Fig. 542).

Subgenus *Atavinus* Olexa, 1990

Atavinus Olexa, 1990: 148. Type species: *Philothis atavus* Reichardt, 1931, original designation.
Atavinus: Mazur (1997): 269; Mazur (2004): 96.

Diagnosis. Elytra without basal bulge and basal elytral stria; with four (or even five) well developed dorsal elytral striae, fourth dorsal elytral stria connected with sutural elytral stria; protarsi absent.

Differential diagnosis. Members of this subgenus differ from the subgenera *Philothis* and *Farabius* by the totally absent protarsi, and well developed 4th and in case of some species even 5th dorsal elytral striae.

Biology. See the biology of *Philothis* s. l.

Distribution. This subgenus is distributed from Sahara through the deserts of Oman and Iran into Central Asia (Turkmenistan, Uzbekistan, Kazakhstan) (Mazur 1997).

Species examined. *Philothis* (*Atavinus*) *arnoldii* Kryzhanovskij, 1976 in Kryzhanovskij & Reichardt (1976), *P.* (*A.*) *atavus* Reichardt, 1931, *P.* (*A.*) *olexai* Gomy, 1992, *P.* (*A.*) *pierrei* Thérond, 1963.

Philothis (*Atavinus*) *atavus* (Reichardt, 1931)

(Figs. 6, 33, 40, 64, 98, 129, 543–558)

Philothis atavus Reichardt, 1931: 308, Figs. 1–4.
Philothis atavus: Reichardt (1941): 338, 340, 409, Figs. 176 A,B; Kryzhanovskij & Reichardt (1976): 248, Fig. 484; Mazur (1984): 109.
Philothis (*Atavinus*) *atavus*: Olexa (1990): 148, Figs. 2, 32–33; Mazur (1997): 269; Mazur (2004): 96.

Type locality. Uzbekistan, Termez.
Type material examined. Holotype: spec., 'Termes, Buchara / 31.v.1926 / Shestoperov [written] // Termez / 31.v.[19]26 [written] // *Philothis* / *atavus* / sp. n. / Monotypus / A. Reichardt det [printed-written] // Holotypus [red label, printed] // golden round label' (ZIN).
Additional material examined. TURKMENISTAN: Ashgabat, 16.iv.1980, 1 spec., A. Olexa lgt. **UZBEKISTAN:** Buchara, Kyzylkum, 28.iv.1978, 2 ♂♂, A. Olexa lgt.; Chiva [= Khiva], Karakum, 1.–5.v.1979, 1 spec., A. Olexa lgt. (TLAN).

Redescription. Body length: PEL: 1.875–2.25 mm; APW: 0.75–1.0 mm; PPW: 1.7–1.875 mm; EL: 1.375–1.5 mm; EW: 1.875–2.075 mm.

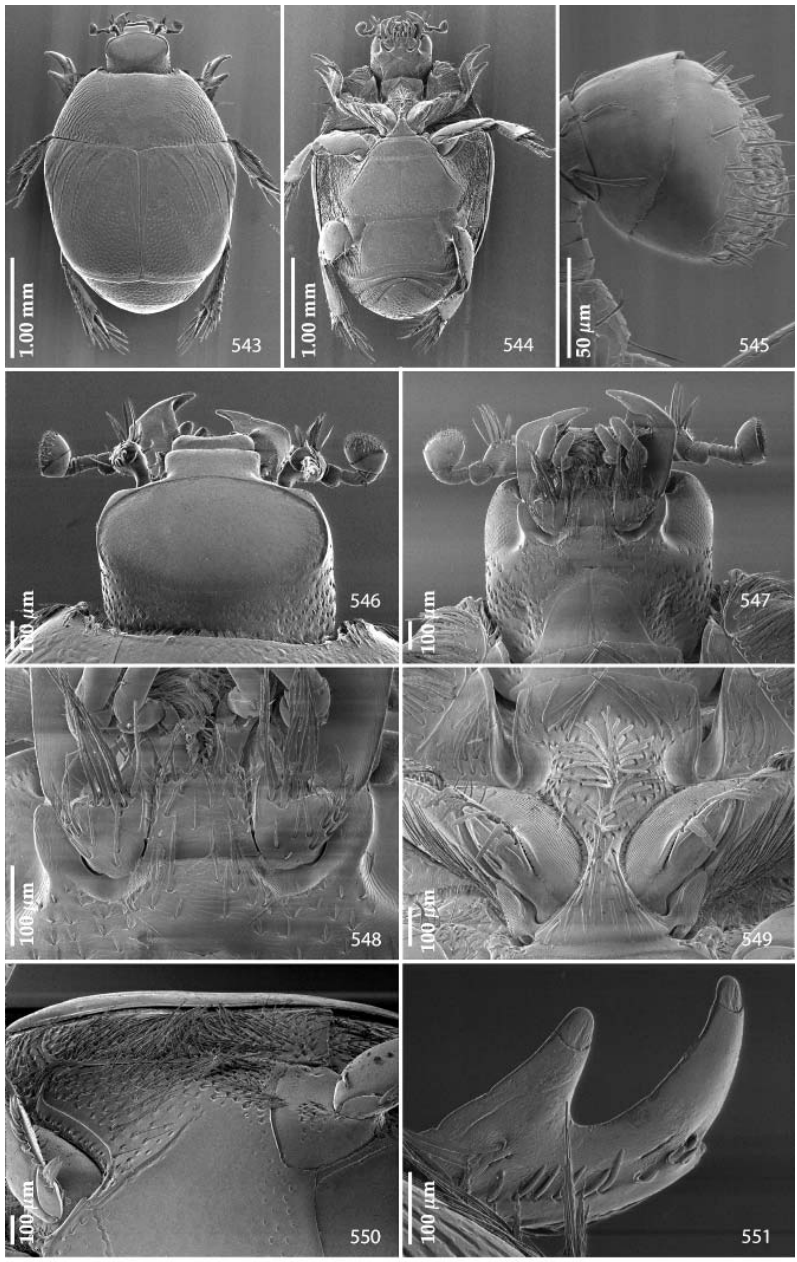
Body (Figs. 543–544) roundly oval, moderately convex from above, underside very convex, cuticle dark brown with conspicuous greenish-bronze metallic luster; legs, mouthparts rufous, antennal club yellow.

Antennal scape (Fig. 546), with numerous long setae; 8th segment (Figs. 6, 545) cupuliform, surrounding basal half of the club; club (Fig. 545) comparatively small, without visible articulation, apical third (roughly) imbricate with dense curved short sensilla intermingled with somewhat sparser straight thicker sensilla, concealing two round apical sensory areas; basal two-thirds (roughly) glabrous; sensory structures of antennal club (Fig. 33) in form of one apical sensory area and one stipe-shaped vesicle situated under it, supplemented by another vague sensory area under apical surface of club.

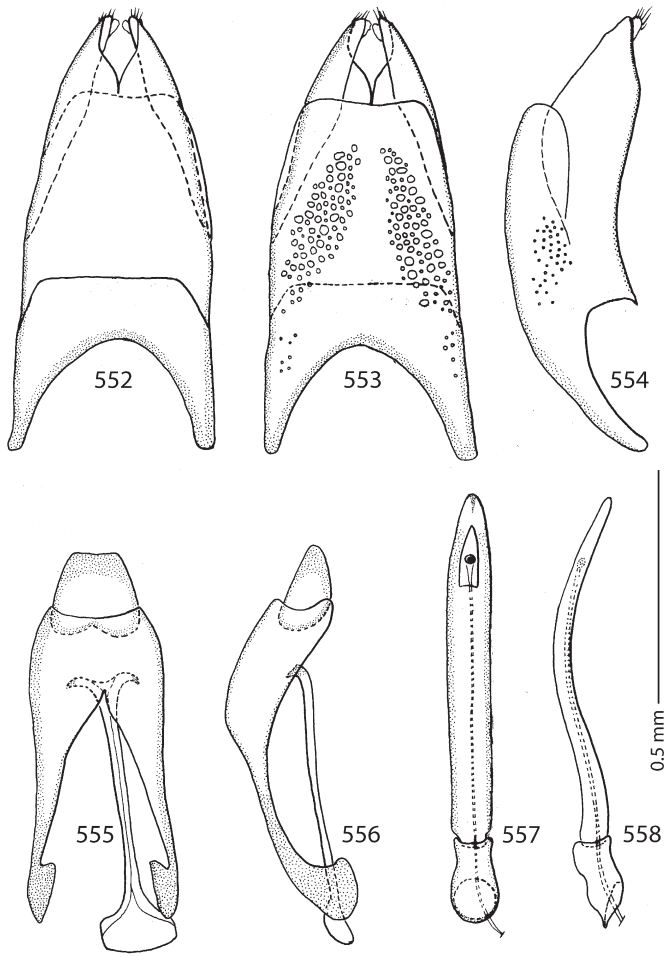
Mouthparts. Mandibles (Fig. 98) with straight outer margin strongly curved inwards; mandibular apex acute; sub-apical tooth on left mandible moderately large, almost perpendicular; disc of labrum (Fig. 64) slightly emarginate medially, almost smooth; epipharynx almost completely hidden under labral fold (Fig. 40); terminal labial palpomere elongated, its width about one-third its length; mentum (Fig. 548) sub-trapezoid, finely imbricate with tiny median notch (Fig. 129); anterior margin with dense brush of long ramose setae, lateral margins with a row of slightly shorter setae, disc of mentum with several ramose setae, approximately as long as those of anterior margin; cardo of maxilla (Fig. 548) on lateral margin with numerous short ramose setae; stipes (Fig. 548) triangular, with numerous much longer ramose setae; terminal maxillary palpomere elongated, its width about one-third its length, approximately twice as long as penultimate.

Clypeus (Fig. 546) rectangular, rounded laterally, smooth; frontal stria complete, slightly weakened medially, continued as complete and carinate supraorbital stria; frontal disc (Fig. 546) almost smooth, only with scattered microscopic punctation; eyes very flattened, invisible from above.

Pronotal sides (Fig. 543) strongly convergent anteriorly, apical angles acute, anterior pronotal margin with a shallow incision for head, straight almost medially; marginal pronotal stria well impressed, carinate laterally, broadly interrupted behind head; pronotal disc moderately convex, with irregular wrinkles and curved lines becoming coarser laterally, wrinkles



Figs. 543–551. *Philothis* (*Atavinus*) *atavus* (Reichardt, 1931), SEM micrographs: 543 – habitus, dorsal view; 544 – ditto, ventral view; 545 – antennal club, ventral view; 546 – head, dorsal view; 547 – ditto, ventral view; 548 – mentum, submentum, cardines and stipites of maxilla, ventral view; 549 – prosternum; 550 – lateral disc of metaventrite, metepisternum and fused metepimeron; 551 – protibia, dorsal view.



Figs. 552–558. *Philothis* (*Atavinus*) *atavus* (Reichardt, 1931), male terminalia: 552 – 8th sternite and tergite, ventral view; 553 – ditto, dorsal view; 554 – ditto, lateral view; 555 – 9th tergite, 10th tergite (dorsal view) and spiculum gastrale (ventral view); 556 – 9th tergite, 10th tergite and spiculum gastrale, lateral view; 557 – aedeagus, dorsal view; 558 – ditto, lateral view.

intermingled with shallow scattered punctures; lateral and anterior margins of pronotum with narrow smooth band; pronotal base with a row of dense elongate punctures; pronotal hypomeron with long yellow setae; scutellum small, but visible.

Elytral humeri weakly developed, glabrous, elytral epipleura with sparse fine punctures, almost smooth; marginal epipleural stria complete, thin; marginal elytral stria well impressed, slightly carinate on outer side, continued as complete apical elytral stria. Humeral elytral stria finely impressed on basal third, occasionally doubled; inner subhumeral stria short, present medially, sometimes basally joining humeral elytral stria; elytral base without bulge; disc

with five developed dorsal elytral striae 1–5, striae (except for the 5th stria) in shallow round punctures; first dorsal elytral stria the longest, reaching about three-fourths of elytral length apically, striae 2–5 about the same length, reaching about elytral half apically; fourth dorsal elytral stria basally connected with complete sutural elytral stria, which is apically connected with the apical elytral stria and on basal half somewhat distanced from elytral suture. Elytral disc with dense round, shallow punctation, punctures separated by about their own to twice their diameter, becoming confluent apically, punctation becomes sparser anteriorly and laterally, elytral flanks almost smooth; interspace between sutural elytral stria and elytral suture impunctate; a complementary thin stria runs along elytral suture, reaching about half of elytral length apically.

Propygidium completely exposed, about half as long as broad, with dense, large, confluent shallow punctures becoming sparser and smaller laterally; pygidium slightly convex, about as long as broad, medially with confluent shallow punctation, similar to that of propygidium, punctures become much sparser and smaller laterally.

Anterior margin of prosternum (Fig. 549) obtuse-angulate; marginal prosternal stria anteriorly absent; prosternal process substrigulate, densely setose, gradually sloping down anteriorly; both sets of prosternal striae absent.

Anterior marginal stria of mesoventrite slightly emarginate medially, discal marginal mesoventral stria complete, carinate, slightly weakened medially; disc of mesoventrite with scattered shallow punctures; meso-metaventral sutural stria well impressed, carinate, undulate; intercoxal disc of metaventrite convex, with scattered microscopic punctures, along posterior margin a band of coarser and denser punctation appears; lateral metaventral stria (Fig. 550) shortened, carinate, almost straight; lateral disc of metaventrite concave, with dense round moderately deep punctures, fringed with long setae; metepisternum + fused metepimeron (Fig. 550) very setose, punctation almost unrecognizable beneath the setae.

Intercoxal disc of first abdominal sternite completely striate laterally; disc smooth; lateral disc of all visible abdominal sternites setose laterally.

Protibia (Fig. 551) moderately dilated, anterior margin truncate, formed by anterior margin of distal-most large triangular tooth; outer margin of protibia apart from this tooth with another, somewhat shorter triangular tooth, both teeth topped with short rounded blunt denticle; setae of outer row confined to basal third, thick, sparse and moderately long; setae of median row much shorter than those of outer row but more regular; protarsal groove inconspicuous; apical margin of protibia posteriorly without denticles; outer part of posterior surface of protibia with carinate rugae, distinctly separated from smooth median part of posterior surface by costiform stria; posterior protibial stria shortened apically; inner margin of protibia with long lamelliform dense setae; protibial spur rudimentary, almost invisible, entombed in apical margin of protibia; protarsus absent.

Mesotibia somewhat dilated, not particularly thickened, outer margin with one double row of sparse, morphologically different short denticles significantly growing in size and density near tarsal insertion, denticles continuous ventrally along apical margin; setae of outer row moderately long, dense, thickened; setae of median row dense and long, covering almost entire posterior mesotibial surface; posterior mesotibial stria shortened, present only on basal half; mesotibial spur conspicuously long and stout; outer part of median surface of mesotibia

almost smooth, only with scattered microscopic punctation; anterior mesotibial stria carinate, almost complete; inner margin of mesotibia with moderately dense row of long lamelliform setae; mesotarsus telescope-like, diameter of tarsomeres diminishing apically, each tarsomere with two long lamelliform strongly sclerotized setae, one posteriorly and one anteriorly; claws of apical mesotarsomeres thin, hair-like, several times as long as mesotarsomeres itself. Metatibia conspicuously triangularly dilated, outer margin with double row (short, blunt, dense and sparser, much longer denticles) of morphologically different denticles, another row of short sparser round denticles markedly shifted from it, present on anterior surface of metatibia and only observable from ventral view. Posterior surface of metatibia with dense rows of short setae, distinction between outer and median row unclear; posterior metatibial stria inconspicuous (absent?); metatibia otherwise similar to mesotibia.

Male genitalia. Eighth sternite (Figs. 552–553) conspicuously narrowing apically, longitudinally fused medially, apically with tiny inflatable membrane (velum); fringed with few short setae; eighth tergite and eighth sternite fused laterally (Fig. 546). Morphology of 9th tergite (Figs. 555–556) typical for the subfamily; spiculum gastrale (Fig. 555) expanded on both ends; tenth tergite conspicuously small. Basal piece of aedeagus (Figs. 557–558) rather short, ratio of its length : length of parameres ca 1 : 5; aedeagus slender along its entire length; parameres fused along their basal four-fifths; aedeagus gently sinuate from lateral view (Fig. 558).

Subgenus *Farabius* Reichardt, 1930

Farabius Reichardt, 1930: 299. Type species: *Philothis* (*Farabius*) *hexeris* Reichardt, 1930, by monotypy.
Farabius: Reichardt (1941): 340, 343; Kryzhanovskij & Reichardt (1976): 245, 249; Mazur (1984): 109; Mazur (1997): 268; Mazur (2004): 96.

Diagnosis. Species of this subgenus are most similar to species of the nominotypical subgenus and differ from them chiefly by the well-developed carinal prosternal striae (see below and Key to subgenera).
Differential diagnosis. Species of the subgenus *Farabius* differ from the subgenus *Philothis* by the larger triangular prosternal apophysis with well-developed, strongly convergent carinal prosternal striae (absent in the subgenus *Philothis*). From the subgenus *Atavinus* they differ by the absent dorsal elytral striae 3–5 as well as by developed rudimentary protarsi.
Biology. Biology of this subgenus is similar to the other two subgenera.
Distribution. Species of this subgenus occur in the deserts of Central Asia (Kara Kum and Kyzyl Kum in Turkmenistan and Uzbekistan).
Species examined. *Philothis* (*Farabius*) *hexeris* Reichardt, 1930, *P.* (*F.*) *reichardti* Kryzhanovskij, 1966.

Philothis (*Farabius*) *hexeris* Reichardt, 1930

(Figs. 34, 39, 65, 99, 130, 174, 559–576)

Philothis (*Farabius*) *hexeris* Reichardt, 1930: 299.
Philothis (*Farabius*) *hexeris*: Reichardt (1941): 340, 343, 409, Fig. 175B; Kryzhanovskij & Reichardt (1976): 245, 249, Fig. 485; Mazur (1984): 110; Olexa (1990): 153, Figs. 4, 13, 20, 26, 48, 49; Mazur (1997): 268; Mazur (2004): 96.

Type locality. Turkmenistan, Farab.
Type material examined. Holotype: spec., 'Buchara occ. / Farab 2.iv.[1]911 / A Hohlbeck [printed-written] // *Philothis* (*Farabius*) / *hexeris* sp. n. / Holotypus / Reichardt det. [printed-written] // Coll. Semenov-Tian-Shansky [printed] // Holotypus [red lablel, printed] // two golden round labels' (ZIN).
Additional material examined. UZBEKISTAN: Chiva [= Khiva], Karakum, 1.–5.v.1979, 1 ♂ 2 spec., A. Olexa lgt.; Buchara, Kyzylkum, 30.iv.1979, 1 ♂, A. Olexa lgt.; ditto, but 27.iv.1979, 1 ♂ 1♀ 1 spec. (TLAN).

Redescription. Body length: PEL: 2.25–2.50 mm; APW: 0.875–1.00 mm; PPW: 1.75–1.875 mm; EL: 1.375–1.50 mm; EW: 1.875–2.075 mm.

Body (Figs. 559–560) shortly oval, moderately convex from above, underside very convex, cuticle reddish brown, shiny; legs, mouthparts and antennal scape rufopiceous.

Antennal scape (Fig. 562), with numerous long setae; club comparatively small, round, without visible articulation, apical third imbricate, with thick dense short yellow sensilla concealing apical sensory area; basal surface glabrous; sensory structures of antennal club (Fig. 34) in form of one apical sensory area and one stipe-shaped vesicle situated under it.

Mouthparts. Mandibles (Fig. 99) stout, slightly curved, mandibular apex blunt; sub-apical tooth on inner margin of left mandible moderately large, perpendicular; disc of labrum (Fig. 65) slightly depressed medially, almost smooth; labral process and labral fold significantly developed, completely concealing epipharynx; terminal labial palpomere elongated, its width about one-third its length; mentum almost square-shaped, imbricate, anterior margin (Fig. 130) slightly shallowly emarginate medially with tiny median notch surrounded with few long setae; lateral margins with one row of sparse shorter ramose setae; disc of mentum with several long setae, almost as long as those of anterior margin. Cardo of maxilla with several short setae on lateral margin; stipes triangular, with numerous much longer setae; terminal maxillary palpomere elongated, its width about one-third its length, approximately three times as long as penultimate.

Clypeus (Fig. 562) rectangular, smooth, rounded laterally; frontal stria represented by short vague fragments above antennal insertions; supraorbital stria absent; frontal disc (Fig. 562) smooth; eyes flattened, invisible from above.

Pronotal sides (Fig. 559) with a shallow longitudinal excavation, weakly convergent anteriorly; apical angles prominent, anterior pronotal margin with a deep incision for head, almost straight medially; marginal pronotal stria well impressed, carinate, shortly interrupted behind head (at times complete); disc moderately convex, entirely smooth except for a row of small round punctures along pronotal base; disc with shallow depressions and bulges, in medio-lateral part with a single deep fovea on each side; pronotal hypomeron with long yellow setae; scutellum very small, almost invisible.

Elytral humeri weakly developed, elytral epipleura smooth; marginal epipleural stria complete, thin; marginal elytral stria well impressed, carinate, continued as complete apical elytral stria. Humeral elytral stria vaguely impressed, surrounded by tiny strioles, at times indistinguishable; inner subhumeral stria rather well developed, at times parallel to first dorsal elytral stria; outer subhumeral stria shortly impressed on basal fourth (at times absent). Only first dorsal elytral stria developed, shortened on basal fourth, almost reaching elytral apex, apically bent inwardly; other dorsal elytral striae absent; sutural elytral stria vaguely impressed, apically connected with apical elytral stria, on basal half slightly distanced from

elytral suture, interspace between it and elytral suture on basal third forming a longitudinal bulge, continued along elytral base as a bisinuate basal elytral stria surrounding a vague low bulge, occasionally obliterated. Elytral disc with dense, round, deep punctation, interspaces smooth, punctation becomes sparser towards elytral suture; area around scutellum and on transverse basal bulge smooth; along elytral apex punctures confluent.

Propygidium completely exposed, approximately 1.5 times as broad as long, with dense shallow confluent punctures; pygidium distinctly longer than broad, convex, with similar punctation.

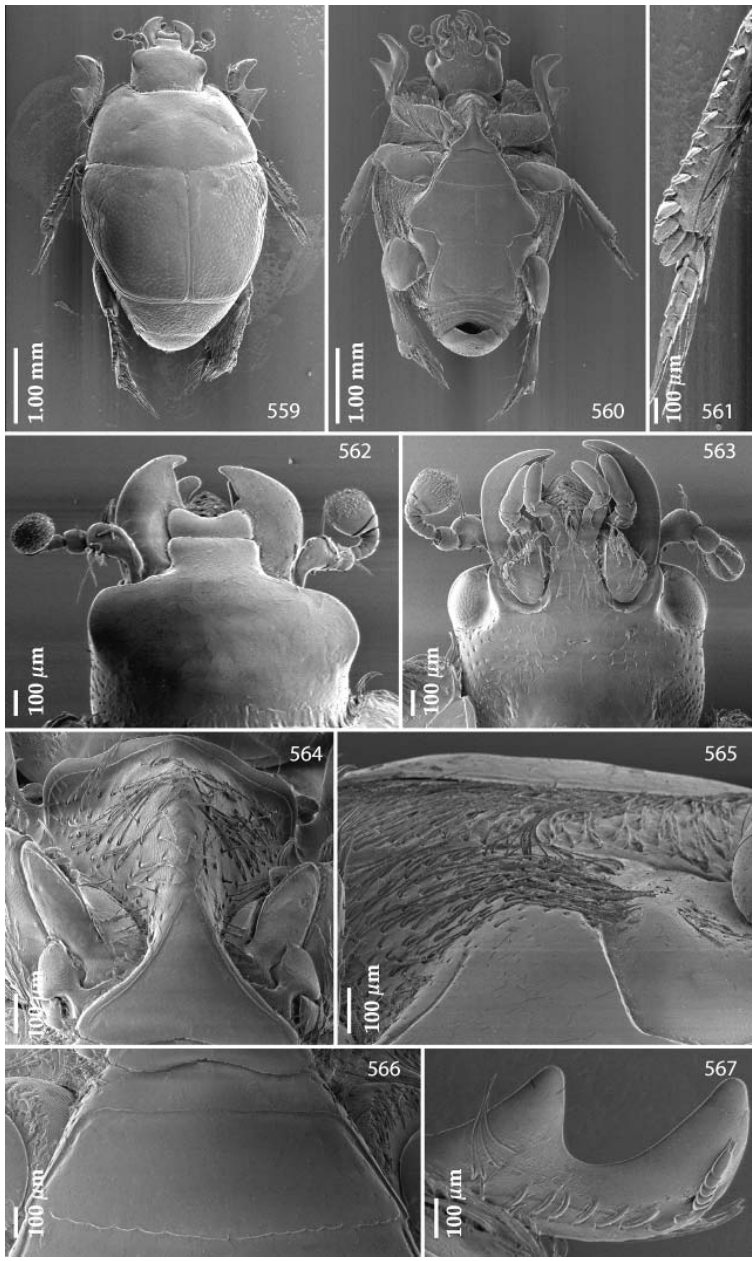
Anterior margin of median portion of prosternum (Fig. 564) obtuse-angulate; marginal prosternal stria well impressed, complete; prosternal process substrigulate, with dense long setae, gradually sloping down anteriorly; carinal prosternal striae present only on prosternal apophysis, strongly convergent anteriorly; lateral prosternal striae absent.

Anterior margin of mesoventrite (Fig. 566) bisinuate; discal marginal mesoventral stria well impressed, anteriorly almost straight, slightly carinate, distanced from anterior margin of mesoventrite; laterally deeply impressed, carinate; disc of mesoventrite with scattered microscopic punctures; meso-metaventral sutural stria (Fig. 566) well impressed, almost straight, slightly projected outwardly. Intercoxal disc of metaventrite with scattered microscopic punctures, almost smooth; lateral metaventral stria (Fig. 565) well impressed, carinate, obliquely arcuate, shortened apically; lateral disc of metaventrite (Fig. 565) concave, with oblong shallow punctures, fringed with long dense setae; metepisternum + fused metepimeron (Fig. 565) densely setose, punctation almost unrecognizable beneath the setae.

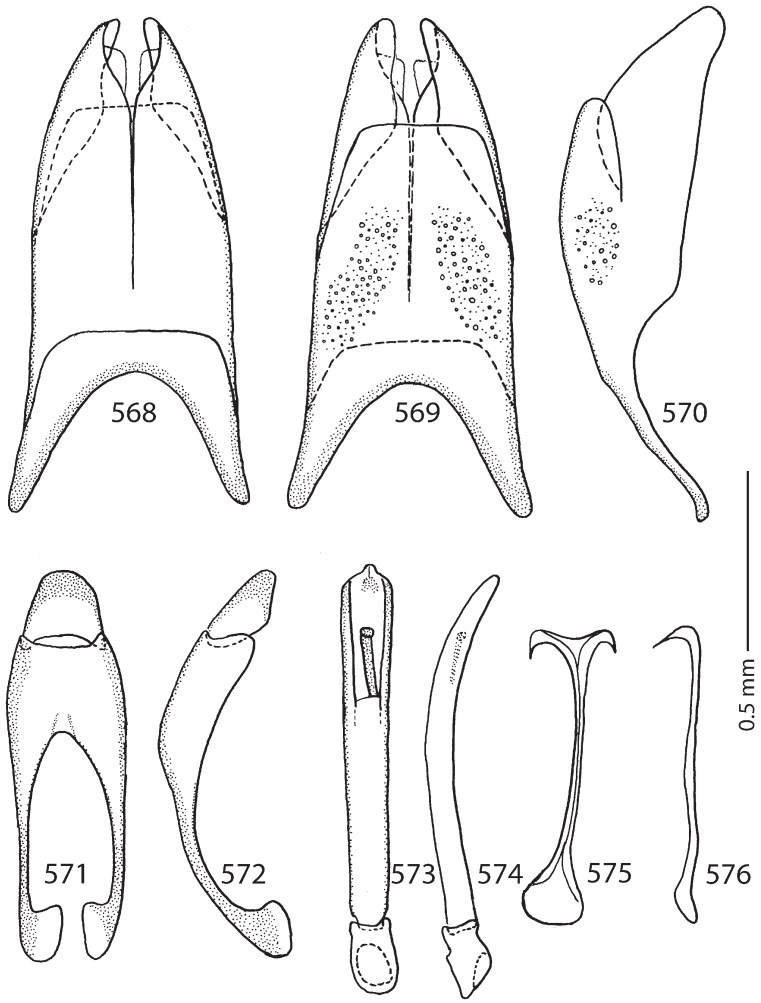
Intercoxal disc of the first abdominal sternite almost completely striate laterally, with scattered microscopic punctation, becoming more prominent along apical margin; lateral discs of all visible abdominal sternites setose laterally.

Protibia (Fig. 567) moderately dilated, anterior margin truncate, formed by anterior margin of distal-most large triangular tooth; outer margin of protibia apart from this tooth with one more, somewhat shorter triangular tooth, topped with short rounded blunt denticle; setae of outer row confined to basal third, thin, sparse, moderately long; setae of median row thicker, more regular; protarsal groove and anterior protibial stria inconspicuous; apical margin of protibia posteriorly without denticles; outer part of posterior surface of protibia smooth, vaguely separated from smooth median part of posterior surface by indistinct ridge with few obliterated rudimentary microscopic denticles; posterior protibial stria inconspicuous; inner margin of protibia with long lamelliform dense setae, apical third of inner margin of protibia with one row of shorter, morphologically different setae; protibial spur microscopic, entombed in apical margin of protibia; protarsus rudimentary, apical tarsomere with two short thin claws, approximately half as long as apical tarsomere itself.

Mesotibia (Fig. 561) slender, outer margin with one double row of sparse, morphologically different short denticles significantly growing in size and density near tarsal insertion, denticles continuous anteriorly along apical margin; setae of outer row growing near inner mesotibial margin, dense and long, covering almost entire posterior mesotibial surface; setae of median row absent; posterior mesotibial stria inconspicuous; mesotibial spur conspicuously long, slender; anterior surface of mesotibia smooth; anterior mesotibial stria thin, shortened apically; inner margin of mesotibia with rather sparse row of long lamelliform setae;



Figs. 559–567. *Philothis* (*Farabius*) *hexeris* Reichardt, 1930, SEM micrographs: 559 – habitus, dorsal view; 560 – ditto, ventral view; 561 – mesotibia, dorsal view; 562 – head, dorsal view; 563 – ditto, ventral view; 564 – prosternum; 565 – lateral disc of metaventrite, metepisternum and fused metepimeron; 566 – mesoventrite; 567 – protibia, dorsal view.



Figs. 568–576. *Philothis* (*Farabius*) *hexeris* Reichardt, 1930, male terminalia: 568 – 8th sternite and tergite, ventral view; 569 – ditto, dorsal view; 570 – ditto, lateral view; 571 – 9th tergite and 10th tergite, dorsal view; 572 – ditto, lateral view; 573 – aedeagus, dorsal view; 574 – ditto, lateral view; 575 – spiculum gastrale, ventral view; 576 – ditto, lateral view.

mesotarsus telescope-like, diameter of tarsomeres diminishing apically, each tarsomere with two long lamelliform strongly sclerotized setae, one posteriorly and one anteriorly; claws of apical mesotarsomeres thin, hair-like, several times as long as mesotarsomeres itself. Metatibia conspicuously dilated, thickened apically; outer margin (especially on thickened apical third) with up to three rows (two rows of short rounded and thick, dense, much longer denticles) of morphologically different denticles, another row of conspicuously short round regular denticles markedly shifted from it, present on anterior surface of metatibia and only

observable from ventral view. Posterior surface of metatibia entirely covered with dense rows of rather long setae, distinction between outer and median rows unclear; posterior metatibial stria inconspicuous; anterior surface of metatibia and metatarsus otherwise similar to mesotibia and mesotarsus.

Male genitalia. Eighth sternite (Figs. 568–569) moderately narrowing apically, longitudinally separated medially almost along its entire length, apically with tiny inflatable membrane (velum), without setae; eighth tergite and eighth sternite fused laterally (Fig. 570). Morphology of 9th tergite (Figs. 571–572) typical for the subfamily; spiculum gastrale (Fig. 575) expanded on both ends. Basal piece of aedeagus (Figs. 573–564) short, ratio of its length : length of parameres ca. 5.30; aedeagus slender; parameres fused along their basal two-thirds; aedeagus gently curved ventrad (Fig. 574).

Pholioxenus Reichardt, 1932

Pholioxenus Reichardt, 1932: 16, 26. Type species: *Hypocacculus phoenix* Reichardt, 1929, original designation.
Pholioxenus: Reichardt (1941): 156, 275; Porta (1939): 151, 152; Kryzhanovskij & Reichardt (1976): 111, 197; Olexa (1984): 113; Mazur & Kaszab (1980): 7, 51; Vienna (1980): 116, 168; Mazur (1984): 83; Mazur (1997): 245; Yélamos (2002): 245, 305; Mazur (2004): 96.

Diagnosis. Body rather flattened dorsally, cuticle light to dark brown, occasionally with greenish or bronze metallic tinge, surface often imbricate-punctate; eyes moderately to strongly convex; anterior margin of clypeus not elevated; frontal stria weakly impressed, at times weakened or even interrupted; pronotum only slightly convex so that both lateral margins are visible along their entire length (seen from dorsal view), lateral pronotal margins evenly arcuate; pronotal foveae absent; pronotal hypomeron usually glabrous. Sutural elytral stria especially on apical half often strongly carinate, in large round punctures; inner subhumeral stria often long, basally sometimes connected with humeral elytral stria forming an additional fifth dorsal elytral stria. Pre-apical foveae small and inconspicuous (occasionally absent); meso-metaventral sutural stria occasionally sinuate, distanced from meso-metaventral suture; protibia rather dilated, outer margin with up to six low teeth topped with tiny thin denticle; protarsal groove shallow; meso- and metatibiae slender, long, tarsal claws long, usually longer than apical tarsomere itself.

Differential diagnosis. Species of *Pholioxenus* are most similar to the members of the genus *Hypocacculus*, chiefly differing from them by the more dilated protibiae, more flattened pronotum, more convex (often almost semi-spherical) eyes, and usually imbricate-punctate dorsal and ventral body surface. Also, the meso- and metatibiae are longer and slenderer with *Pholioxenus* than with *Hypocacculus*, and sutural elytral stria is often strongly carinate (especially on its apical half) and in large punctures.

Biology. All species of *Pholioxenus* live as inquilines of various mammals (e.g. *Spermophilopsis*, *Jaculus*, *Rhombomys*, etc.) and birds. *Pholioxenus schawalleri* Mazur, 1987 has been recorded near the colony of Northern Bald Ibis (*Geronticus eremita* (Linnaeus, 1758)), or even in burrows of tortoises (e.g. *Testudo horsfeldi* Gray, 1844) (Olexa 1984). *Pholioxenus* species occur especially in the arid, semidesert or desert biotopes. They are occasionally also collected on dung, carrion, etc., but can be primarily collected in the nests of animals, where they most probably prey upon dipteran or siphonapteran larvae.

Distribution. Twenty-five species, distributed in the Palaearctic and Afrotropical Regions, have been hitherto described (Mazur 1997, 2006; Yélamos 2001).
Species examined. *Pholioxenus krali* Olexa, 1984, *P. kodymi* Olexa, 1984, *P. mesopotamicus* Olexa, 1984, *P. normandi* Olexa, 1984, *P. orichalceus* Reichardt, 1941, *P. phoenix* (Reichardt, 1929), *P. pickai* Olexa, 1984, *P. quedenfeldti* (Schmidt, 1887), *P. rutilus* (Erichson, 1834), *P. schatzmayri* (Müller, 1910).
Discussion. *Pholioxenus* is probably a monophyletic taxon that is supported by few synapomorphies, e.g. imbricate-punctate surface of body, long and slender metatibiae, very small (occasionally even absent) pre-apical foveae and carinate sutural elytral stria. It can be regarded as an evolutionary branch of its presumably related sister taxon *Hypocacculus* that became adapted to nidicolous way of life, speciated there and its members have probably been a part of this niche for a long time. Large convex eyes and a rather small vesicle of the sensory structures of antennal club could be listed among the possible morphological adaptations to the inquilinous way of life.

Pholioxenus phoenix (Reichardt, 1930)

(Figs. 26, 66, 100, 131, 577–592)

Hypocacculus phoenix Reichardt, 1930: 291.
Pholioxenus phoenix: Reichardt (1932): 28, 95, t. III, Fig. 29 (partim); Reichardt (1941): 276, 277; Kryzhanovskij & Reichardt (1976): 197, 198, Figs. 396, 397; Mazur (1984): 82; Mazur (1997): 248; Mazur (2004): 96.

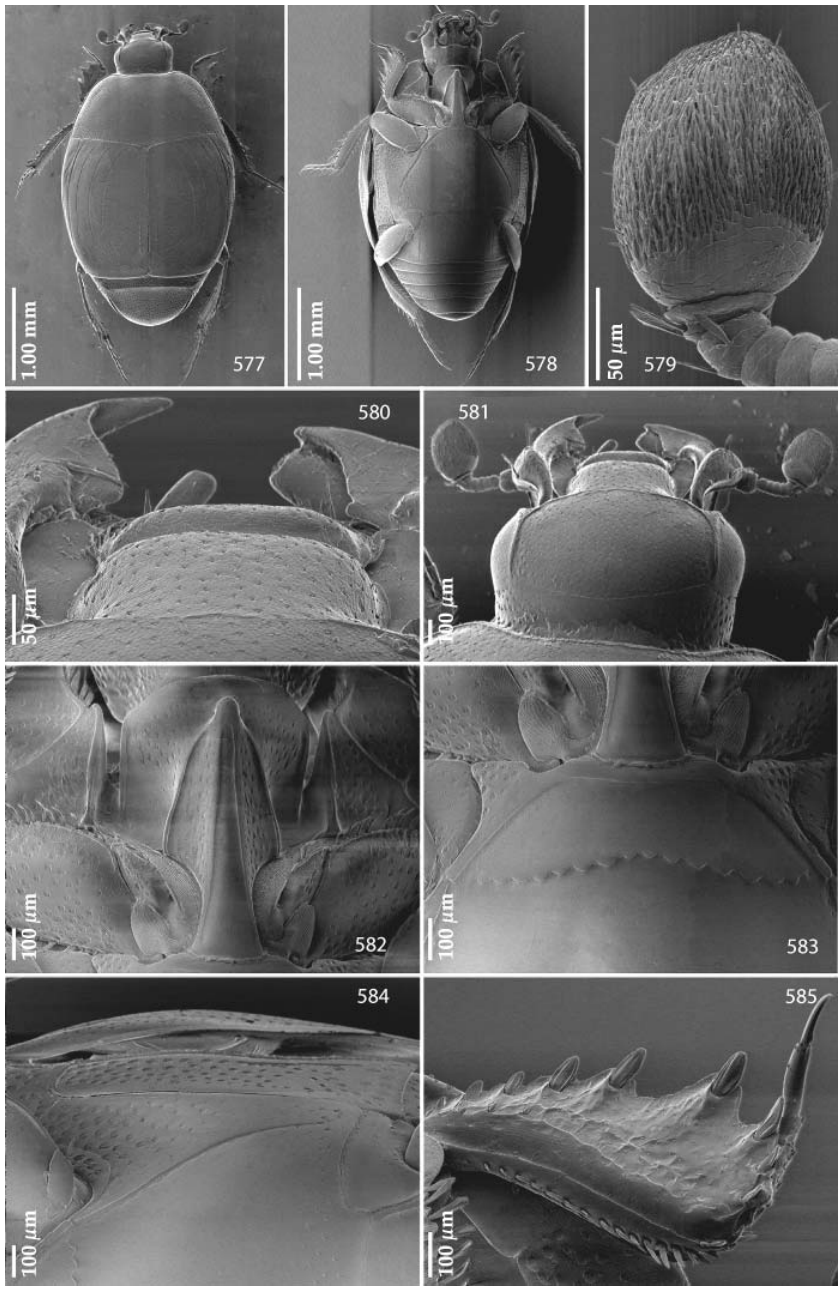
Type locality. Kazakhstan, Dzhulek.
Material examined. KAZAKHSTAN: Akzher, Jambol, 10.v.1979, 3 spec., A. Olexa lgt. **UZBEKISTAN:** Khiva, Karakum, 1.v.1980, 1 ♀, A. Olexa lgt.; Buchara, Shafrikan, 29.iv.1980, 1 ♀, A. Olexa lgt.; Buchara, Kyzylkum, 27.iv.1980, 1 ♂, A. Olexa lgt. (TLAN).

Redescription. Body length: PEL: 2.15–2.50 mm; APW: 0.675–0.875 mm; PPW: 1.65–1.90 mm; EL: 1.375–1.625 mm; EW: 1.75–2.15 mm.

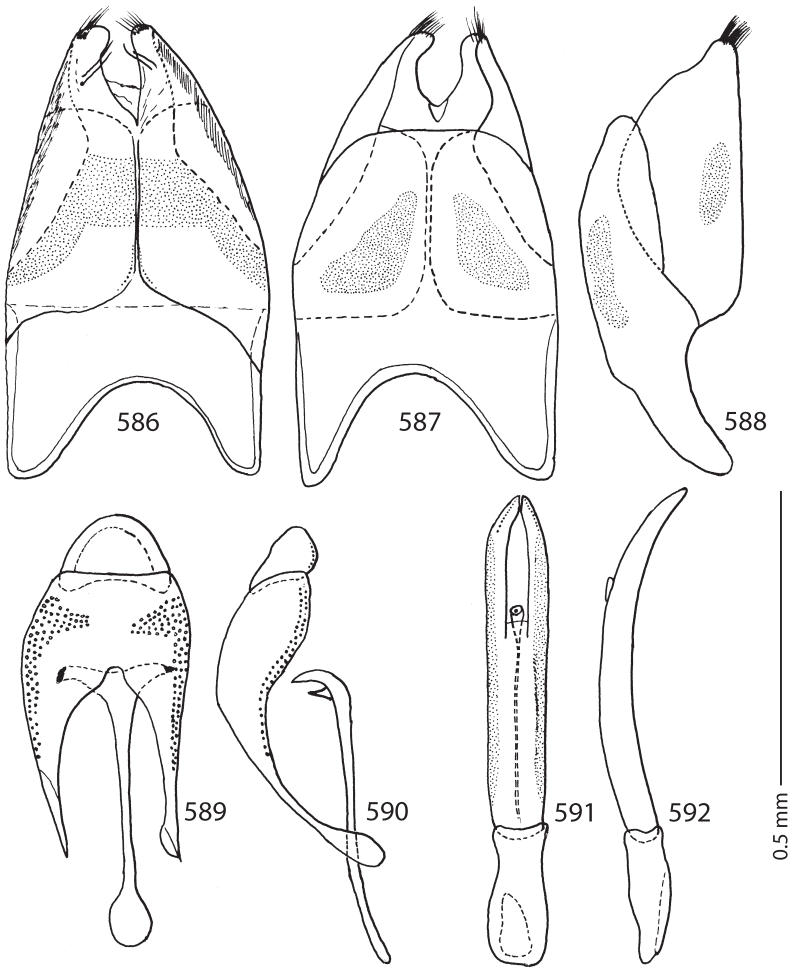
Body (Figs. 577–578) shortly oval, moderately convex; cuticle shining, castaneous brown with greenish hue; elytra often somewhat translucent; ventral surface slightly lighter-colored with hazy metallic luster; legs, antennae and mouthparts rufopiceous.

Antennal scape (Fig. 581) not particularly dilated; with two short setae; club (Fig. 579) without visible articulation, apical two-thirds with thick short yellow sensilla intermingled with sparse erect longer sensilla, basal third imbricate, without sensilla; sensory structures of antennal club (Fig. 26) in form of stipe-shaped vesicle situated under circular sensory area on internal distal margin of the ventral side of antennal club.

Mouthparts. Mandibles (Fig. 100) with slightly curved outer margin, mandibular apex acute; sub-apical tooth on left mandible moderately large, almost perpendicular; labrum (Figs. 66, 580) finely punctate, somewhat flattened; with two weakly impressed labral pits, two thin labral setae arising from each one; terminal labial palpomere elongated, about one-fourth its length; mentum sub-trapezoid, anterior margin shallowly emarginate medially, with tiny median notch (Fig. 131), surrounded with several long setae; lateral margins with one row of shorter ramose setae; disc of mentum imbricate, with sparse short ramose setae; cardo of maxilla on outer margin with several short setae; stipes triangular, with three much longer setae; terminal maxillary palpomere truncate apically, elongated, its width about one-fourth its length, approximately 2.5 times as long as penultimate.



Figs. 577–585. *Pholioxenus phoenix* (Reichardt, 1930), SEM micrographs: 577 – habitus, dorsal view; 578 – ditto, ventral view; 579 – antennal club, dorsal view; 580 – clypeus and labrum, dorsal view; 581 – head, dorsal view; 582 – prosternum; 583 – mesoventrite; 584 – lateral disc of metaventrite, metepisternum and fused metepimeron; 585 – protibia, ventral view.



Figs. 586–592. *Pholioxenus phoenix* (Reichardt, 1930), male terminalia: 586 – 8th sternite and tergite, ventral view; 587 – ditto, dorsal view; 588 – ditto, lateral view; 589 – 9th tergite, 10th tergite (dorsal view) and spiculum gastrale (ventral view); 590 – 9th tergite, 10th tergite and spiculum gastrale, lateral view; 591 – aedeagus, dorsal view; 592 – ditto, lateral view.

Clypeus (Fig. 580) flat, rounded laterally, imbricate-punctate; frontal stria complete, curved outwardly (occasionally weakened anteriorly), supraorbital stria well developed, slightly carinate; frontal disc (Fig. 581) with fine regular punctation, punctures separated by 1–3 times their diameter; eyes convex, well visible from above.

Pronotal sides (Fig. 577) moderately convergent anteriorly; apical angles inconspicuous; disc with sparse microscopic punctures, antero-laterally a band of coarser and denser punctures appears; pronotal base with a row of moderate punctures; marginal pronotal stria well impressed, complete, carinate; pronotal hypomeron glabrous.

Elytral epipleura almost smooth, only with scattered punctures; marginal epipleural stria complete, weakly impressed; marginal elytral stria deeply impressed, in round punctures; its apical end attaining elytral apex; apical elytral stria present only as a short fragment, next evanescent. Humeral elytral stria well impressed on basal third, occasionally doubled; inner subhumeral stria present as rather long median fragment. Elytra with four thin dorsal striae 1–4; first the longest, almost reaching elytral apex; second and third dorsal elytral striae about the same length, surpassing three-fourths of elytral length apically; fourth dorsal elytral stria only slightly shorter, basally vaguely connected with sutural elytral stria (at times interrupted); sutural elytral stria on apical half slightly elevated, costiform, in large round punctures, reaching about four-fifths of elytral length apically. Elytral disc imbricate-punctate, punctures becoming coarser and denser on apical third; between sutural elytral stria and elytral suture a row of fine punctures present.

Propygidium transverse, partially covered by elytra, coarsely and densely punctate, interspaces imbricate; pygidium with similar, but (especially medially) much sparser punctation, interspaces imbricate.

Anterior margin of median portion of prosternum (Fig. 582) evenly rounded, marginal prosternal stria present laterally and as a short anterior fragment; pre-apical foveae small, inconspicuous; prosternal process almost flat, surface between carinal prosternal striae with scattered microscopic punctures; laterally imbricate-punctate; carinal prosternal striae convergent anteriorly, vaguely connected apically; lateral prosternal striae carinate, attaining near apices of carinal striae, not united apically. Anterior margin of mesoventrite (Fig. 583) slightly emarginate medially; discal marginal mesoventral stria (Fig. 583) well impressed, carinate; disc with scattered microscopic punctation; meso-metaventral sutural stria well impressed, slightly sinuate, distanced from actual meso-metaventral suture, carinate and undulate.

Intercoxal disc of metaventrite convex, with scattered microscopic punctures, along apical margin and in the area near hind coxa punctation becoming coarser; lateral metaventral stria (Fig. 584) well-impressed, bisinuate, carinate, almost reaching hind coxa; lateral disc of metaventrite (Fig. 584) with coarser and denser punctures separated by about their own diameter, interspaces finely imbricate; metepisternum + fused metepimeron (Fig. 584) with similar punctation, punctures becoming finer and sparser on fused metepimeron; metepisternal stria present on apical half of metepisternum as well as on fused metepimeron, intermittent.

Intercoxal disc of the first abdominal sternite completely striate laterally, with scattered fine punctures, along apical margin row of fine punctures present.

Protibia (Fig. 585) flattened and dilated, outer margin apically with two approximate low teeth topped with short denticle followed by two low triangular teeth of which the first one is conspicuously larger than the second one, both teeth topped with moderately long thin denticle, followed by 4 short denticles becoming progressively shorter in proximal direction; setae of outer row sparse, short; setae of median row inconspicuous; protarsal groove moderately deep; anterior protibial stria inconspicuous; two rather short tarsal denticles present apically; protibial spur tiny, bent, growing out from apical protibial margin; apical margin of protibia posteriorly with two tiny apical denticles; outer part of posterior surface of protibia (Fig. 585) finely punctate-variolate; separated from imbricate median part of posterior surface by a vague thin stria, basally with a row of three minuscule denticles; posterior protibial stria

complete, terminating in two tiny inner-posterior denticles; inner margin with single row of short setae, becoming more sclerotized and longer apically.

Mesotibia slender, outer margin with two sparse rows of thin denticles growing in size apically; setae of outer row sparse, strongly sclerotized; setae of median row regular, much shorter than those of outer row; posterior mesotibial stria shortened apically; anterior surface of mesotibia imbricate with scattered minuscule punctures with microscopic setae; anterior mesotibial stria shortened, carinate; mesotibial spur thin, moderately long; apical margin of mesotibia anteriorly with several tiny denticles; claws of apical tarsomere longer than half its length; metatibia basically similar to mesotibia, but slenderer and longer and denticles of outer margin much sparser than those of mesotibia.

Male genitalia. Eighth sternite (Figs. 586–587) longitudinally separated medially, apically with tiny inflatable membrane (velum); fringed with tiny brush of short setae; eighth tergite and eighth sternite not fused laterally (Fig. 588). Morphology of 9th tergite (Figs. 589–590) typical for the subfamily; spiculum gastrale (Fig. 589) expanded on both ends. Basal piece of aedeagus (Figs. 591–592) rather short, ratio of its length : length of parameres 1 : 3; parameres fused along their basal two-thirds; aedeagus slightly curved ventrad (Fig. 592).

Reichardtiolus Kryzhanovskij, 1959

Reichardtiolus Kryzhanovskij, 1959: 217 (as a subgenus of *Exaesiopus*). Type species: *Saprinus duriculus* Reitter, 1904, original designation.

Reichardtiolus: Kryzhanovskij & Reichardt (1976): 112, 238; Mazur (1984): 103; Mazur (1997): 265; Mazur (2004): 96.

Diagnosis. Cuticle dark brown, only with slight metallic tinge; clypeus and frontal disc rugulose-lacunose; frontal stria well impressed, occasionally weakened medially; pronotal hypomeron with short amber setae; pronotal disc coarsely and densely punctate; pronotal foveae absent; elytral surface entirely punctate; pre-apical foveae rather small; lateral disc of metaventrite, parts of metepisternum and lateral parts of abdominal sternites with short amber setae. Anterior margin of protibia formed by the anterior margin of the distal-most tooth; outer margin of protibia with two large teeth topped with large triangular denticle, followed by another low tooth topped by small triangular denticle; hind femur conspicuously thickened; metatibia triangularly dilated and thickened, outer margin with two widely separated sparse rows of short denticles of which the outer row only observable from ventral view (similar to *Ammostyphrus* or several species of *Philothis*).

Diagnosis of this taxon is based solely on the species *R. duriculus*, since the other species, *R. pavlovskii* has not been examined and, based on its description, there is reason to believe that it belongs to a different genus.

Differential diagnosis. Most similar to the species of the genus *Exaesiopus* (originally described as a subgenus of *Exaesiopus*), but differing from them by the absence of deep longitudinal rugae and otherwise rugulose-lacunose frontal disc, as well as the entirely punctate elytra (usually partly glabrous in *Exaesiopus*). Protibia is also different between these two taxa: in *Reichardtiolus* its anterior margin is formed by the anterior margin of the distal-most tooth while in *Exaesiopus* it is normally formed. *Reichardtiolus* could be further

confused with several species of the genus *Paravolvulus* or *Hypocacculus*. From *Paravolvulus* it differs by the thickened hind femora and thickened and dilated metatibia with two widely separated rows of short denticles, as well as the setose lateral disc of metaventrite, metepisternum and lateral parts of abdominal sternites. From the members of *Hypocacculus* this genus differs chiefly by the rugulose-lacunose frontal disc, thickened hind femora and metatibia (with widely separated two rows of short denticles) as well as by the setose pronotal hypomeron, lateral disc of metaventrite, parts of the metepisternum and lateral parts of abdominal sternites (usually glabrous in *Hypocacculus*). *Reichardtiolus* can be also confused with *Axelinus*, with which it shares the rugulose-lacunose frontal disc and similar structure of protibia, but *Axelinus* is generally smaller and frontal stria is widely interrupted medially in this taxon (whereas it is in most cases complete, only slightly weakened medially in *Reichardtiolus*). Furthermore, the hind femora are not particularly thickened with *Axelinus* and eyes are flattened, almost invisible dorsally, while they are well visible from dorsal view in *Reichardtiolus*.

Biology. *Reichardtiolus* is a psammophilous genus, occurring in the desert regions. Its biology is poorly documented.

Distribution. *Reichardtiolus* contains two described species: *Reichardtiolus pavlovskii* (Kryzhanovskij, 1959) that is only known from two specimens found in Turkmenistan, and *R. duriculus* known from the following countries: Kazakhstan, Uzbekistan, Turkmenistan, Iran and West China (Mazur 1997). It is newly recorded from Jordan here.

Species examined. *Reichardtiolus duriculus* (Reitter, 1904).

Discussion. The monophyly of this taxon is questionable as it is supported by only few weak synapomorphies that are most likely homoplasies. Its relationship with the presumably related taxa (e.g. *Hypocaccus*, *Exaesiopus*, *Paravolvulus* or *Ammostyphrus*) must be tested by further studies based on the modern phylogenetic methods.

Reichardtiolus duriculus (Reitter, 1904)

(Figs. 27, 67, 132, 593–610)

Saprinus duriculus Reitter, 1904: 31.
Styphrus duriculus: Jakobson (1911): 651.
Hypocacculus duriculus: Bickhardt (1916): 97.
Exaesiopus duriculus: Reichardt (1926): 17; Reichardt (1941): 330, 333, Fig. 172.
Reichardtiolus duriculus: Kryzhanovskij & Reichardt (1976): 239, Figs. 465, 466, 468; Mazur (1984): 103; Mazur (1997): 265; Mazur (2004): 96.

Type locality. Turkmenistan, Mary.
Type material examined. Holotype: 1 spec., last two metatarsomeres of right hind tibia broken off: 'Merw [printed] // Ahnger [printed] // coll. Reitter [printed] // Holotypus 1904 / Saprinus / duriculus / Reitter [red-framed printed-written] // 1960 / Exaesiopus / (Reichardtiolus) / duriculus Rchdt. [sic!] / Kryzhanovskij det.[printed-written]' (HNHM).
Additional material examined. JORDAN: 60 km N El Mudawwara, 1000 m, 29º20'N, 35º32'E, 5.iv.1994, 2 ♂♂ 3 spec., Bečvář J. & S. lgt. **TURKMENISTAN:** Annau, Karakum, 21.iv.1981, 1 ♂, A. Olexa lgt.; Repetek, 12.iv.1989, 1 spec., M. Nikodým lgt. (TLAN).

Redescription. Body length: PEL: 2.00–3.40 mm; APW: 0.65–1.05 mm; PPW: 1.375–2.40 mm; EL: 1.25–2.25 mm; EW: 1.50–2.70 mm.

Body (Figs. 593–594) elongate oval, strongly convex, cuticle dark brown with feeble metallic luster, legs, antennae and mouthparts rufous. Antennal scape (Fig. 596) slightly thickened, with several short setae; club (Fig. 595) rather large, without visible articulation, apical four-fifths covered with short sensilla intermingled with longer sparse erect sensilla, basal fifth glabrous; sensory structures of antennal club (Fig. 27) in form of stipe-shaped vesicle situated under circular sensory area on internal distal margin of the ventral side of antennal club.

Mouthparts. Mandibles (Fig. 101) with rounded outer margin, strongly curved inwardly, mandibular apex acutely pointed; sub-apical tooth on inner margin of left mandible blunt; labrum (Fig. 67) convex, coarsely punctate; with two labral pits, each with two well-sclerotized setae; terminal labial palpomere thickened, its width about half its length; mentum subtrapezoid, anterior margin shallowly emarginate medially (Fig. 132); antero-lateral corners with few short setae, lateral margins with a single row of short ramose setae; disc of mentum imbricate, asetose; cardo of maxilla with few short setae on lateral margin; stipes triangular, with three short setae; terminal maxillary palpomere thickened, its width about half its length, about twice as long as penultimate.

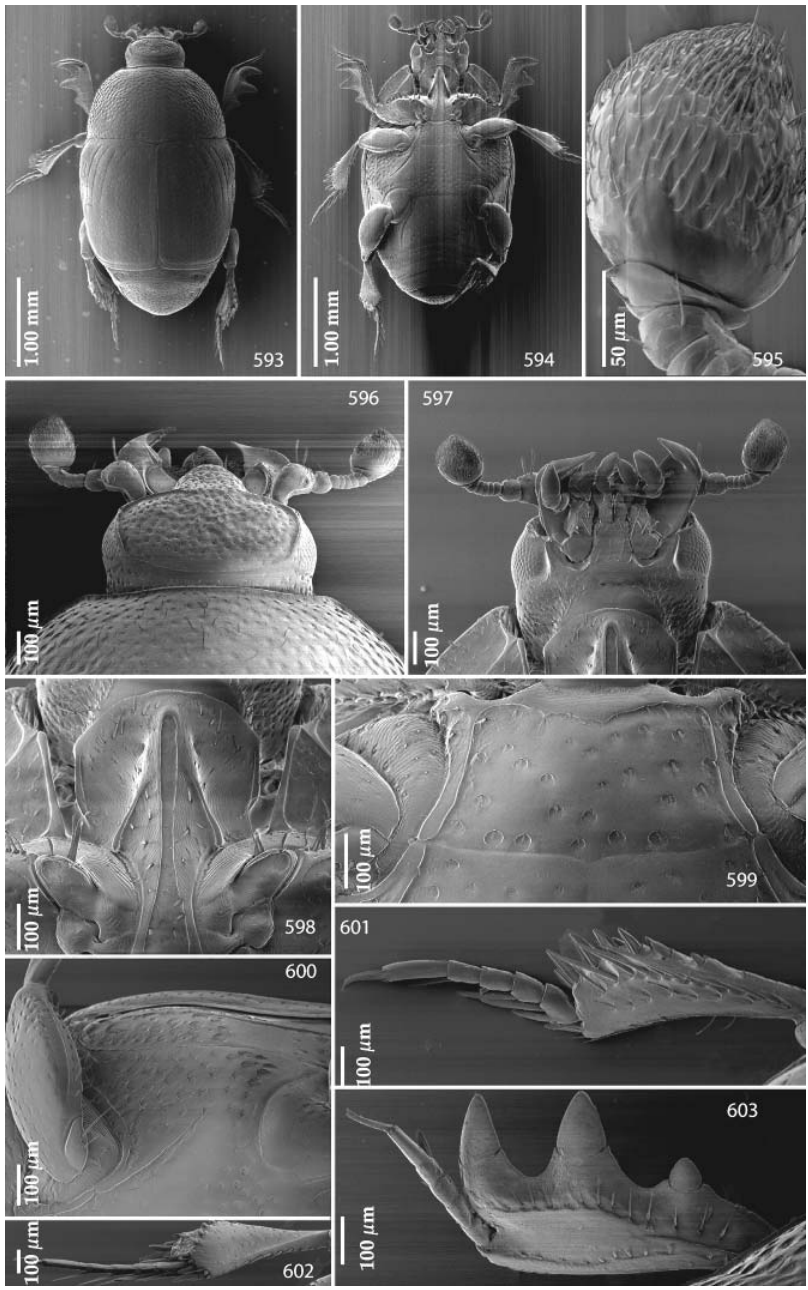
Clypeus (Fig. 596) slightly concave medially, rounded laterally, rugulose-lacunose; frontal stria well impressed, carinate, almost straight, somewhat weakened medially, continued as well-impressed, carinate supraorbital stria; frontal disc (Fig. 596) rugulose-lacunose; eyes slightly convex, visible from above.

Pronotum (Fig. 593) convex, pronotal sides rounded, strongly convergent anteriorly, apical angles inconspicuous; marginal pronotal stria complete, carinate; disc with very deep, dense and coarse punctures, laterally rugulose-lacunose, medially punctation weakens and becomes sparser; pronotal hypomeron with sparse short amber setae.

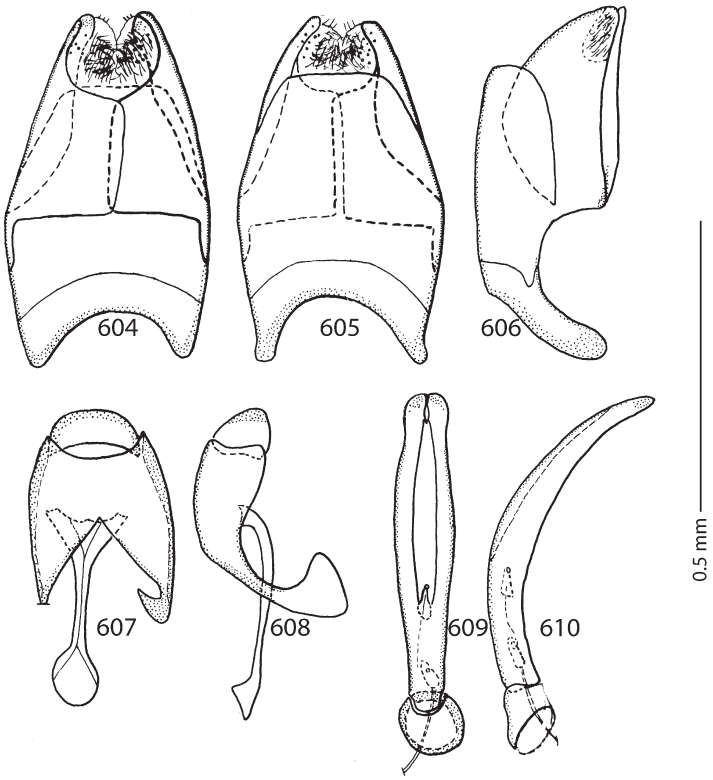
Elytral epipleura with a row of deep punctures; marginal epipleural stria well impressed, complete; marginal elytral stria complete, deeply impressed, carinate, continued as complete apical elytral stria. Humeral elytral stria weakly impressed on basal third, often doubled; inner subhumeral stria inconspicuous, present as tiny median fragment; elytra with four dorsal striae 1–4, bearing large punctures; first, second and third dorsal striae about the same length, reaching approximately elytral half apically, fourth dorsal elytral stria weakly impressed on basal third (occasionally longer apically), connected to complete sutural elytral stria. Elytral disc with deep round punctation, punctures separated by 2–4 times their diameter, becoming finer apically and laterally; between sutural elytral stria and elytral suture a row of regular fine punctures present.

Propygidium transverse, almost completely exposed, coarsely and densely punctate; pygidium almost as long as broad, with similar punctation; interspaces in both cases finely imbricate.

Anterior margin of median portion of prosternum (Fig. 598) rounded; marginal prosternal stria present laterally and as vague anterior fragment; pre-apical foveae rather small; prosternal process rather narrow, slightly concave; carinal prosternal striae slightly carinate, almost parallel, united in front of strongly carinate shortened lateral prosternal striae. Surface between carinal prosternal striae almost smooth, prosternal apophysis with several microscopic setae; lateral parts of prosternal process strigulate with scattered microscopic punctures fringed with tiny setae.



Figs. 593–603. *Reichardtiolus duriculus* (Reitter, 1904), SEM micrographs: 593 – habitus, dorsal view; 594 – ditto, ventral view; 595 – antennal club, dorsal view; 596 – head, dorsal view; 597 – ditto, ventral view; 598 – prosternum; 599 – mesoventrite; 600 – lateral disc of metaventrite, metepisternum and fused metepimeron; 601 – mesotibia, dorsal view; 602 – metatibia, ventral view; 603 – protibia, dorsal view.



Figs. 604–610. *Reichardtiolus duriculus* (Reitter, 1904), male terminalia: 604 – 8th sternite and tergite, ventral view; 605 – ditto, dorsal view; 606 – ditto, lateral view; 607 – 9th tergite, 10th tergite (dorsal view) and spiculum gastrale (ventral view); 608 – 9th tergite, 10th tergite and spiculum gastrale, lateral view; 609 – aedeagus, dorsal view; 610 – ditto, lateral view.

Anterior margin of mesoventrite (Fig. 599) feebly emarginate medially; discal marginal mesoventral stria well-impressed, carinate, slightly weakened anteriorly; disc of mesoventrite with scattered deep, round punctures, fringed with microscopic setae; meso-metaventral sutural stria absent; meso-metaventral suture well discernible.

Intercoxal disc of metaventrite longitudinally concave in male, with coarse scattered punctures, area around lateral metaventral stria smooth; lateral metaventral stria (Fig. 600) deeply impressed, carinate, extending obliquely and shortened apically; lateral disc of metaventrite (Fig. 600) with shallow large setiferous punctures; metepisternum on basal half with similar punctation, apical half of metepisternum (Fig. 600) almost smooth, fused metepimeron with few punctures; metepisternal stria present along entire fused metepimeron and metepisternum, basally intermittent.

Intercoxal disc of the first abdominal sternite completely striate laterally, with sparse coarse punctation.

Protibia (Fig. 603) flattened and somewhat dilated, anterior margin formed by anterior margin of large sub-triangular distal-most tooth topped with large triangular denticle, outer margin apart from this tooth with another similar tooth topped with large triangular denticle, followed by another, much lower tooth topped by much smaller triangular denticle and another microscopic denticle entombed in outer margin of protibia; setae of outer row sparse, regular and short; setae of median row similarly sparse and regular, much shorter than those of outer row; protarsal groove moderately deep; anterior protibial stria present only on basal third; tarsal denticles absent; protibial spur tiny, bent, growing out from apical protibial margin; apical margin of protibia posteriorly without denticles; outer part of posterior surface of protibia sparsely punctate, distinctly separated from glabrous median part of posterior surface by irregular costiform stria fringed with sparse microscopic setae; posterior protibial stria complete, deeply impressed, with sparse microscopic setae; inner-ventral denticles absent; inner margin with single row of well sclerotized setae.

Mesotibia (Fig. 601) slightly thickened, outer margin with two sparse rows of thin denticles growing in size apically; setae of outer row rather dense, strongly sclerotized and longer than denticles of outer margin; setae of median row sparse, microscopic; posterior mesotibial stria inconspicuous; anterior surface of mesotibia imbricate, with scattered minuscule punctures with microscopic setae; anterior mesotibial stria shortened apically, almost complete; mesotibial spur stout, rather short; apical margin with several tiny denticles; claws of apical tarsomere longer than half its length; metatibia basically similar to mesotibia, but much more thickened and dilated, rows of denticles of outer margin widely separated, outer row of denticles (Fig. 602) observable only from ventral view.

Male genitalia. Eighth sternite (Figs. 604–605) longitudinally separated medially, apically with large setose inflatable membrane (velum), with numerous dense short setae; eighth tergite and eighth sternite fused laterally (Fig. 606). Morphology of 9th tergite (Figs. 607–608) typical for the subfamily; spiculum gastrale (Fig. 607) expanded on both ends. Basal piece of aedeagus (Figs. 609–610) short, ratio of its length : length of parameres 1 : 5; parameres fused along their basal third; aedeagus conspicuously curved ventrad (Fig. 610).

Remarks. Mazur (1997: 265) erroneously stated the type locality for this species as 'Kazakhstan'. In fact, it is the city of Mary, which lies in Turkmenistan.

Saprinillus Kryzhanovskij, 1974

Saprinillus Kryzhanovskij, 1974: 106. Type species: *Saprinillus paromaloides* Kryzhanovskij, 1974, original designation.

Saprinillus: Kryzhanovskij in Kryzhanovskij & Reichardt (1976): 216; Mazur (1984): 83; Mazur (1997): 249; Mazur (2004): 96; Lackner (2009a): 108.

Diagnosis. Body very small for the subfamily (1.40–1.80 mm), cuticle without metallic luster, body sub-cylindrical to elongate oval, convex; clypeus and anterior third of frontal disc rugulose-lacunose, rest of frontal disc with sparse but coarse punctures; frontal stria largely interrupted, forming acute angles behind eyes; pronotal foveae absent; pronotal hypomeron glabrous (in case of *S. kryzhanovskyi* with extremely short sparse setae). Apical elytral stria absent, sutural stria complete; pre-apical foveae present, well impressed; prosternal process narrowed; both sets of prosternal striae well developed (in the case of *Saprinillus kryzhanov-*

skyi lateral prosternal striae interrupted by antennal cavity); protibia with 5–6 short denticles on outer margin, teeth absent.

This genus has been recently revised by Lackner (2009a). For the sake of consistency its diagnosis, biology and distribution are repeated here, if slightly altered to fit the style used in this publication. Likewise, since this paper introduces some new terminology, this has also been taken into the account and the relevant parts are duly altered.

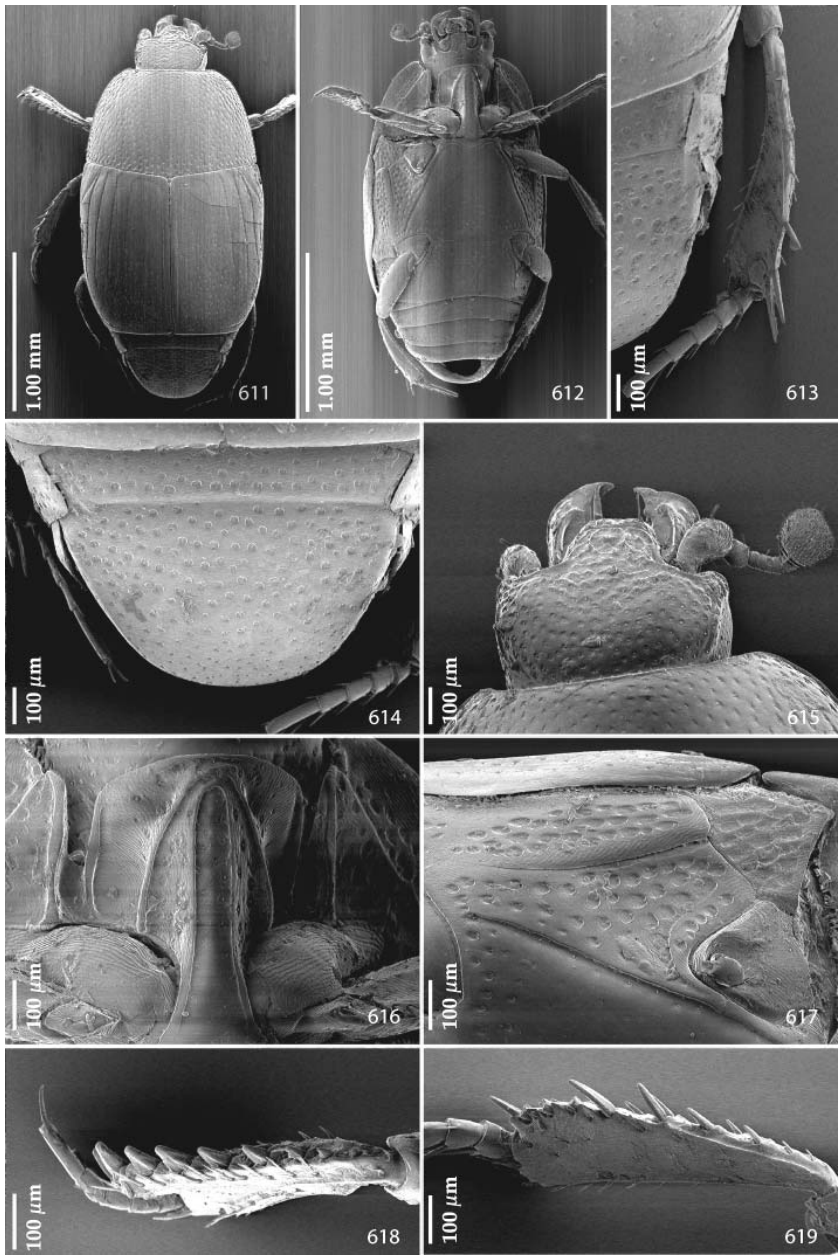
Differential diagnosis. Genus *Saprinillus* stands out from the other genera of Palaearctic Saprininae by its small body size, sub-cylindrical body, coarsely and rugosely granulate clypeus and anterior part of frontal disc, and by the shape of protibia which is without typical articulated triangular teeth and instead is adorned with denticles, growing out directly from the outer margin of protibia. Only few other genera of the Palaearctic Saprininae possess denticles (as opposed to articulated teeth) on the outer protibial margin, namely *Microsaprinus*, *Eremosaprinus*, *Myrmetes* and *Turanostyphrus*. However, *Saprinillus* differs significantly from all the above-mentioned genera: from the genus *Microsaprinus* by the rugulose-lacunose clypeus and anterior third of frontal disc, anteriorly united carinal and lateral prosternal striae (anteriorly 'open' in *Microsaprinus*), present pre-apical foveae (absent in *Microsaprinus*) and by the more elongate, almost cylindrical body; from *Eremosaprinus* it also differs by the rugulose-lacunose clypeus and anterior third of frontal disc (finely punctate in *Eremosaprinus*), present pre-apical foveae (absent in *Eremosaprinus*), by the sub-cylindrical body shape (roundly oval in *Eremosaprinus*), and the much shorter meso- and metatibiae; from *Myrmetes* it differs by the same characters as from *Eremosaprinus*; furthermore, *Myrmetes* has almost impunctate dorsal surface; and from the species of the genus *Turanostyphrus* it differs by the above-mentioned characters, plus asetose elytral epipleuron, bearing setae in *Turanostyphrus*. On the other hand, it superficially resembles the genus *Axelinus*, especially by the rugulose-lacunose anterior part of frontal disc, with largely interrupted frontal stria, but differing from it chiefly by the shape of protibia (bearing three large teeth topped with denticles in *Axelinus*), and by the more slender metatibiae (thickened in *Axelinus*).

Biology. The biology of this genus is poorly documented. The type series of both species were collected in debris under plant *Kalidium gracile* (Chenopodiaceae). The specimens from Turkmenistan and Kazakhstan were found in a burrow of a Giant Gerbil (*Rhombomys opimus* (Lichtenstein, 1823)) or trapped by a pitfall trap, respectively (Kryzhanovskij 1987). Lackner (2009a) speculated that this taxon might rank amongst inqulines rather than psammophiles, in accordance with Kryzhanovskij (1987) who discussed the shape of protibia as unfit for the psammophilous habits.

Distribution. Mongolia: South Gobi Aimak, Turkmenistan and Kazakhstan (Mazur 1997, Lackner 2009a).

Species examined. *Saprinillus kryzhanovskyi* Lackner, 2009, *S. paromaloides* Kryzhanovskij, 1974.

Discussion. *Saprinillus* belongs probably to the group of the genera (together with *Axelinus*, *Alienocacculus*, etc.) that are probably deeply nested within the paraphyletic genus *Hypocacculus*. It is supported by several 'weak' synapomorphies e.g. cylindrical body, rugulose-lacunose frons or interrupted frontal stria. Its monophyly should be tested in the future.



Figs. 611–619. *Saprinillus paromaloides* Kryzhanovskij, 1974, SEM micrographs: 611 – habitus, dorsal view; 612 – ditto, ventral view; 613 – metatibia, dorsal view; 614 – propygidium and pygidium; 615 – head, dorsal view; 616 – prosternum; 617 – lateral disc of metaventrite, metepisternum and fused metepimeron; 618 – protibia, dorsal view; 619 – mesotibia, dorsal view.

Saprinillus paromaloides Kryzhanovskij, 1974

(Figs. 133, 611–626)

Saprinillus paromaloides Kryzhanovskij, 1974: 107, Figs. 7–10.
Saprinillus paromaloides: Kryzhanovskij & Reichardt (1976): 216 (partim); Mazur (1984): 83; Mazur (1997): 249; Mazur (2004): 96; Lackner (2009a): 113, 117, Figs. 8–13, 14:A–G.

Type locality. Mongolia, Khushu Sayr, South Gobi Aimak.
Type material examined. Paratypes: 1 ♂ 1 ♀, 'MNR [= Mongolian People's Republic], Yu. [Yuzhno = Southern] Gob. [= Gobijskij] Khushu / Sayr, 25 km South of Khailastyn-Gobi / 21.vi.1971 / Kerzhner [written] //, Solonchak [= salt-marsh], v opade [in debris] / pod [= under] *Kalidium* [written] // Paratypus 1971 / *Saprinillus* / *paromaloides* sp.n. / Kryzhanovskyi det. [red label, printed-written] // St. Petersburg / Zool. Inst [yellow label, printed] // D07–070 [written pink label, added by the author] (ZIN)'.

Redescription. Body length: PEL: 1.50 mm; APW: 0.50 mm; PPW: 1.00 mm; EL: 1.00 mm; EW: 1.10 mm.

Body (Figs. 611–612) cylindrical, convex, without metallic luster; cuticle light brown, legs, antennae and mouthparts light brown. Antennal scape (Fig. 615) with two short setae; club without visible articulation, entire surface covered with short sensilla intermingled with much sparser erect sensilla; sensory structures of antennal club not examined.

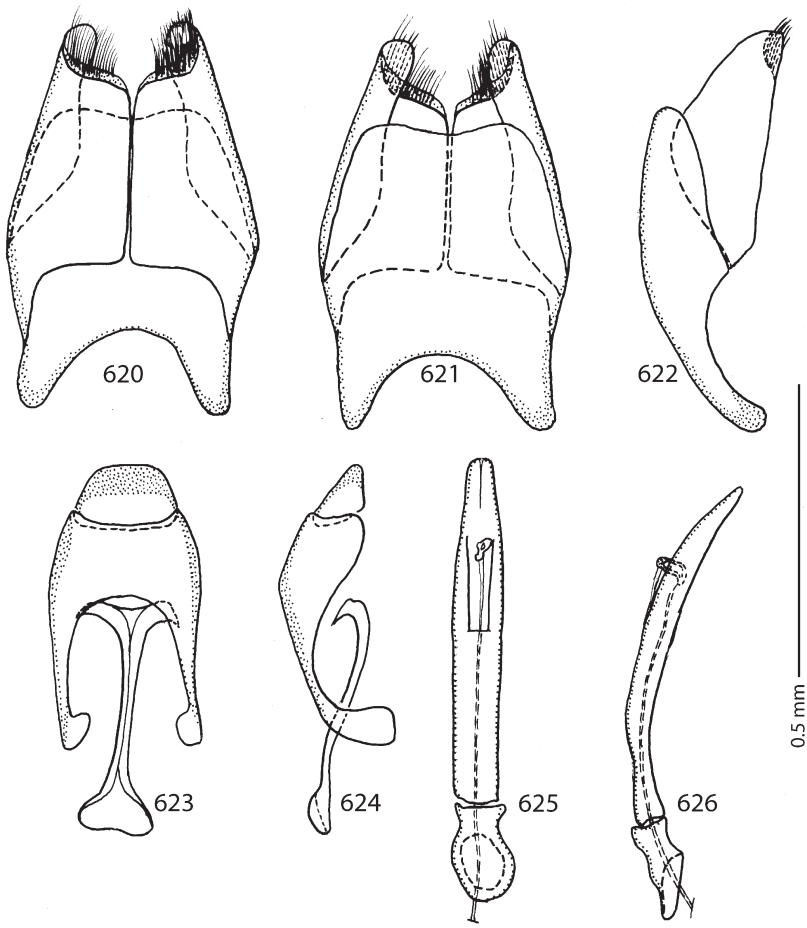
Mouthparts. Mandibles with almost straight outer margin, outer margin carinate, strongly curved inwardly, mandibular apex acutely pointed. Disc of labrum not examined, two well impressed labral pits present, with two well-sclerotized setae arising from each; terminal labial palpomere elongated, its width about one-third its length; mentum square-shaped, without emargination in middle of anterior margin (Fig. 133); antero-lateral corners with several short setae, lateral margins with a single row of short ramose setae; disc of mentum laterally covered with few short setae; medially imbricate, glabrous. Cardo of maxilla on lateral margin with few short setae; stipes triangular, with three much longer setae; terminal maxillary palpomere elongated, its width about one-third its length, approximately twice as long as penultimate; remaining mouthparts not examined.

Clypeus (Fig. 615) flat, rugulose-lacunose; frontal stria widely interrupted anteriorly, forming acute angles above eyes; supraorbital stria vaguely impressed; frontal disc (Fig. 615) anteriorly with a shallow depression, shallowly rugulose-lacunose, posteriorly with regular round moderate punctures; eyes flattened, visible from above.

Pronotum (Fig. 611) weakly convergent anteriorly; apical angles blunt; marginal pronotal stria complete, slightly carinate laterally; disc laterally with coarse and dense deep punctures becoming sparser and finer medially; antescutellar area with vague depression; pronotal hypomeron glabrous.

Elytral epipleuron with scattered fine punctures; marginal epipleural stria thin, complete; marginal elytral stria complete, slightly carinate, for short distance continuous along elytral apex; apical elytral stria absent.

Elytra with four well impressed dorsal elytral striae 1–4, in punctures, first three about the same length, reaching about two-thirds of elytral length apically, fourth dorsal elytral stria slightly shortened, reaching about elytral half apically, basally united with sutural elytral stria; sutural elytral stria well impressed, on basal half in sparse punctures, reaching elytral apex; between it and elytral suture a row of fine punctures present; humeral elytral stria finely



Figs. 620–626. *Saprinillus paromaloides* Kryzhanovskij, 1974, male terminalia: 620 – 8th sternite and tergite, ventral view; 621 – ditto, dorsal view; 622 – ditto, lateral view; 623 – 9th tergite, 10th tergite (dorsal view) and spiculum gastrale (ventral view); 624 – 9th tergite, 10th tergite and spiculum gastrale, lateral view; 625 – aedeagus, dorsal view; 626 – ditto, lateral view.

impressed on basal third; inner subhumeral stria present as short median fragment; elytral disc on apical half with deep scattered punctation, punctures separated by about 2–4 times their own diameter, becoming somewhat denser apically; basal half of elytral disc with much finer and sparser punctation.

Propygidium (Fig. 614) transverse, almost completely exposed, with several rows of punctures; pygidium (Fig. 614) with round regular punctures, separated by about their own to twice their diameter, becoming finer apically; interspaces in both cases imbricate.

Anterior margin of median portion of prosternum (Fig. 616) evenly rounded; marginal prosternal stria present laterally and as short vague anterior fragment; pre-apical foveae

well-impressed, deep; prosternal process flattened, surface between carinal prosternal striae shallowly imbricate-punctate; laterally coarsely imbricate-punctate; carinal prosternal striae carinate, slightly divergent on prosternal apophysis, subparallel, united anteriorly; lateral prosternal striae strongly carinate, convergent anteriorly, vaguely united in front of united carinal prosternal striae.

Anterior margin of mesoventrite deeply emarginate medially, discal marginal mesoventral stria well impressed, carinate; disc of mesoventrite with sparse fine punctures; meso-metaventral sutural stria inconspicuous, meso-metaventral suture well observable, thin.

Intercoxal disc of metaventrite almost smooth, with fine sparse punctures; area around hind coxae with few coarser punctures; lateral metaventral stria (Fig. 617) well impressed, straight, carinate, almost reaching hind coxa; lateral disc of metaventrite (Fig. 617) with shallow large punctures, interspaces imbricate; metepisternum (Fig. 617) with similar, even coarser and denser punctures, fused metepimeron smooth; surface around lateral margins of metepisternum imbricate.

Intercoxal disc of the first abdominal sternite completely striate laterally, lateral stria distinctly carinate, disc smooth, only in anterolateral corners with sparse round punctures of various sizes.

Protibia (Fig. 618) on outer margin with eight short denticles diminishing in size in proximal direction, teeth absent; setae of outer row sparse, regular and short; setae of median row not inspected; protarsal groove moderately deep; anterior protibial stria shortened apically, two tarsal denticles present apically; protibial spur not inspected. Apical margin of protibia not inspected; posterior surface of protibia not inspected.

Mesotibia (Fig. 619) slender, outer margin with two sparse rows of thin denticles growing in size apically; setae of outer row worn off; setae of median row inconspicuous; posterior mesotibial stria inconspicuous; anterior surface of mesotibia imbricate with scattered minuscule punctures with microscopic setae; anterior mesotibial stria complete, terminating in two tiny inner anterior denticles; mesotibial spur stout, moderately long; apical margin with several tiny denticles; claws of apical tarsomere shorter than half its length; metatibia (Fig. 613) basically similar to mesotibia, but slenderer and denticles of outer margin much sparser than those of mesotibia.

Male genitalia. Eighth sternite (Figs. 620–621) longitudinally separated medially, apically with tiny inflatable membrane (velum) with dense brush of moderately long setae; eighth tergite and eighth sternite not fused laterally (Fig. 622). Morphology of 9th tergite (Figs. 623–624) typical for the subfamily; spiculum gastrale (Fig. 623) expanded on both ends. Basal piece of aedeagus (Figs. 625–626) rather short, ratio of its length : length of parameres 1 : 4; parameres fused along their basal half; aedeagus slightly curved ventrad (Fig. 626).

Remarks. Redescription of this taxon has been recently published by the author (Lackner 2009a). For the sake of consistency and clarity of the terminology used it is repeated in the present paper. This re-description is likewise focused more in detail on several morphological structures omitted in the afore-mentioned publication, namely legs, mouthparts and male genitalia.

Saprinus Erichson, 1834

Saprinus Erichson, 1834: 172. Type species: *Hister nitidulus* Fabricius, 1801, designated by Westwood (1838): 22.

Saprinus: Lacordaire (1854): 274; J. E. LeConte (1845): 68; Marseul (1855): 327; Marseul (1857): 154; Jacquelin-Duval (1858): 111; Thomson (1862): 235; Horn (1873): 312; Schmidt (1885a): 283, 302; Ganglbauer (1899): 380; Reitter (1909): 290, 291; Blatchey (1910): 617; Jakobson (1911): 641; Bickhardt (1916): 82, 84; Germain (1917): 137; Bickhardt (1921): 109; Bradley (1930): 95; Peyerimhoff (1936): 223; Reichardt (1941): 156, 176; McGrath & Hatch (1941): 54; Blackwelder & Blackwelder (1948): 11; Wenzel (1962): 374; Dahlgren (1962): 237–248; Hatch (1962): 257; Halstead (1963): 9; Dahlgren (1964): 152–162; Dahlgren (1967): 213–224; Dahlgren (1968a): 82–94; Dahlgren (1968b): 255–268; Hansen (1968): 294, 320; Dahlgren (1969b): 257–269; Witzgall (1971): 168–172; Mazur (1973): 26, 29; Kryzhanovskij & Reichardt (1976): 111, 125; Vienna (1980): 116, 129; Mazur & Kaszab (1980): 6, 25; Mazur (1981a): 71, 72; Mazur (1984): 44; Ôhara (1994): 215, 226; Downie & Arnett (1996): 607; Secq & Secq (1997a): 10; Kim & Lim (1997): 60; Mazur (1997): 218; Ôhara & Paik (1998): 28; Bousquet & Laplante (1999): 141, 150; Mazur (2001): 19, 31; Kovarik & Caterino (2001): 220, 223; Yélamos (2002): 245, 255, 256; Mazur (2004): 96; Bousquet & Laplante (2006): 79, 81, 101.

Plesiosaprinus: Houlbert & Monnot (1923): 72 (*nomen nudum*). Synonymized by Cooman (1947): 428.

Diagnosis. Body usually moderately-sized to rather large for the subfamily (2.50–10.00 mm); cuticle often metallic, occasionally black or light brown. Antennal club round, usually without visible articulation, although in some species, e.g. *Saprinus* (*Phaonius*) *pharao*, ventrally with 4 slit-like pits and dorsally with 2 slit-like pits roughly corresponding to sutures between antennomeres. Surface of antennal club in most cases, except for slit-like pits that are with sensilla basiconica, entirely covered with short dense sensilla and sporadic longer erect sensilla, occasionally with a large sensory area on apical part of club; sensorial patches usually present on ventral surface of club, variously shaped. Eyes convex, normally well visible from above. Frontal stria in most cases interrupted, only rarely complete, never cariniform, at times prolonged onto clypeus; lateral pronotal stria never present, marginal pronotal stria usually complete, sometimes interrupted or weakened behind head; pronotal hypomeron in most cases glabrous; in psammophilous species setose. Elytral humeri usually slightly prominent; elytra often with 'mirrors'; dorsal elytral striae shortened, never reaching elytral apex (although in some species united inner subhumeral and humeral elytral striae can be almost nearing it); their configuration variable, but fifth dorsal elytral stria never present; humeral elytral stria in some taxa united with inner subhumeral stria creating thus a complimentary dorsal elytral stria parallel to first dorsal elytral stria; elytral disc in some cases with red or yellow maculae or transverse patch. Prosternal process with both sets of prosternal striae well developed, their configuration variable and useful in species determination, pre-apical foveae absent (present only in subgenus *Hemisaprinus*); surface between carinal prosternal striae usually convex, rarely flattened; metaventrite in males flattened, often with longitudinal depression; males of some species with two tubercles near or on posterior margin of metaventrite. Protibia, except for psammophilous taxa, not particularly dilated, outer margin with 5–12 moderately sized to short teeth topped with short denticle; anterior margin not truncate; meso- and metatibiae in most cases not thickened or dilated; males of some species possess brush-like long sclerotized setae on their mesotarsi. Shape and structure of male terminalia very useful (and in numerous cases the only possible way) in species recognition.

Differential diagnosis. Species of the genus *Saprinus* can be confused with several externally similar genera, especially *Styphrus*, *Zorius*, or *Euspilotus* (*Neosaprinus*) *perrisi*. They differ from the most other Palaearctic genera by the combination of widely interrupted frontal stria (only rarely complete), absent pre-apical foveae (but present in subgenus *Hemisaprinus*, see below) and usually present pronotal foveae. Likewise, species of this genus are larger in general than members of other genera. From the only Palaearctic representative of the genus *Styphrus*, *S. corpulentus*, they differ chiefly by the punctate frontal disc (impunctate in *Styphrus*) and shorter, curved meso- and metatarsal claws (longer and almost straight in *Styphrus*). Furthermore, lateral parts of all visible abdominal sternites are setose in *Styphrus* whereas they are normally asetose in *Saprinus*. From members of the genus *Zorius* the species of *Saprinus* differ chiefly by the form of the sensory structures of the antenna (see Lackner 2009b) and the complete frontal stria (in most cases widely interrupted in *Saprinus*), more flattened eyes, absent pronotal foveae (often present in *Saprinus*) as well as the elevated anterior margin of clypeus. From the sole Palaearctic representative of the subgenus *Neosaprinus* of the genus *Euspilotus*, *E.* (*Neosaprinus*) *perrisi*, the members of *Saprinus* chiefly differ by the present supraorbital stria and absent pre-apical foveae (present and vaguely connected with the marginal prosternal stria in *E.* (*N.*) *perrisi*); furthermore, females of *E.* (*N.*) *perrisi* possess curious pygidial sulci. Species of the subgenus *Hemisaprinus* possess pre-apical foveae and as such could be confused with several Palaearctic genera, e.g. *Hypocaccus*, *Chalcionellus* or *Pholioxenus*, but differs from them chiefly by the largely interrupted frontal stria (usually complete in the afore-mentioned taxa) and anteriorly divergent and 'open' carinal prosternal striae (usually anteriorly convergent and often united apically in *Hypocaccus*, *Chalcionellus* or *Pholioxenus*). Some species of the genus *Chalcionellus* have similarly widely interrupted frontal stria, but their carinal prosternal striae are usually convergent and not 'open' anteriorly.

Biology. Most species of this genus prefer open xerophilous landscapes; only few species inhabit mesic biotopes. They are most frequently collected on the carrion, less so in dung; in both cases they prey on eggs or larvae of soft-bodied insects, especially flies; according to Reichardt (1941) several central Asian species are even able to capture adult flies on dung. Some species are even attracted to flowers (Thérond 1931; Reichardt 1941; Kryzhanovskij & Reichardt 1976; Vienna 1980; Lackner, pers. observ.). Some species, e.g. *S.* (*Saprinus*) *rugifer* (Paykull, 1809), live in the nests of birds; another taxa are fond of rotting fungi where they probably prey on fly larvae (e.g. *S.* (*Saprinus*) *lautus* Erichson, 1839) (Kryzhanovskij & Reichardt 1976; Lackner, pers. observ.).

Distribution. With 150 species occurring around the world (Mazur 1997; Vienna 1996a,b; Gomy & Vienna 1998; Gomy 2000; Théry et al. 2009), the genus *Saprinus* is the most species-rich genus of the Saprininae; most of its species occur in the Palaearctic and Afrotropical Regions. Only about 10 species are known from the Nearctic Region (8 from Canada – Bousquet & Laplante (2006)), only 4 occur in South or Central America, 7–9 species occur in Australia, 1–2 species in New Caledonia, 4 in New Guinea, and 2 in New Zealand. Some species, e.g. *S.* (*Saprinus*) *chalcites* (Illiger, 1807), *S.* (*Saprinus*) *cupreus* Erichson, 1834 or *S.* (*Saprinus*) *splendens* (Paykull, 1811), are widespread, other species, like *S.* (*Saprinus*) *caerulescens* (Hoffmann, 1803) and *S.* (*Saprinus*) *subnitescens* Bickhardt, 1909, were probably introduced into Peru or North America, respectively (Mazur 1997).

Discussion. *Saprinus* is the most species-rich genus of the Palaearctic Saprininae, most likely polyphyletic with the respect to other smaller genera. Sensory strurctures of antennal club undergo remarkable transition among its subgenera (especially *Phaonius*), but also among the members of the nominotypical subgenus (for more details see De Marzo & Vienna (1980a)), and the task for the future research would be to delineate the phylogenetically most valuable characters and define the monophyly of this taxon, or monophyletic groupings within it. The current concept of this genus implies that it is not well defined by synapomophies and the characters that are currently used for the taxonomic classification of this taxon are merely phenetic. The task of revising this genus on species level is enormous, given the number of species and their geographical distribution. Many species are geographically scattered, but very similar morphologically, which may imply cryptic genetic variation. Among the putative synapomorphies that characterise this taxon can be listed the sensory structures of antennal club (but see above!), absence of pre-apical foveae (but present in the subgenus *Hemisaprinus*!), interrupted frontal stria (but occasionally complete, e.g. in *S.* (*S.*). *ruber* Marseul, 1855). The presence of slit-like pits on the ventral side of the antennal club present in several of its members (e.g. *S.* (*P.*) *pharao*) is considered a plesiomorphic character.

Key to the Palaearctic subgenera of the genus *Saprinus* Erichson, 1834

1 (4) Pre-apical foveae absent.

2 (3) Prosternal process convex between carinal prosternal striae, with very short setae; antennal club with large setose sensory area covering the apical part of club and four slit-like sensory pits on ventral side and two slit-like pits on dorsal side, respectively (Fig. 664). ..... subgenus ***Phaonius*** Kryzhanovskij, 1976

3 (2) Prosternal process usually flat or slightly convex between procoxae, asetose; dorsal surface of antennal club in most cases without slit-like sensory pits; ventral surface of antennal club in most cases with four large sensory areas (Fig. 9). .... subgenus ***Saprinus*** s. str.

4 (1) Pre-apical foveae present (Fig. 648). ..... subgenus ***Hemisaprinus*** Reichardt, 1941

Subgenus *Saprinus* Erichson 1834

Saprinus Erichson, 1834: 172. Type species: *Hister nitidulus* Fabricius, 1801, designated by Westwood (1838): 22.

Saprinus: Lacordaire (1854): 274; J. E. LeConte (1845): 68; Marseul (1855): 327; Marseul (1857): 154; Jacquelin-Duval (1858): 111; Thomson (1862): 235; Horn (1873): 312; Schmidt (1885a): 283, 302; Ganglbauer (1899): 380; Reitter (1909): 290, 291; Blatchey (1910): 617; Jakobson (1911): 641; Bickhardt (1916): 82, 84; Germain (1917): 137; Bickhardt (1921): 109; Bradley (1930): 95; Peyerimhoff (1936): 223; Reichardt (1941): 156, 176; McGrath & Hatch (1941): 54; Blackwelder & Blackwelder (1948): 11; Wenzel (1962): 374; Dahlgren (1962): 237–248; Hatch (1962): 257; Halstead (1963): 9; Dahlgren (1964): 152–162; Dahlgren (1967): 213–224; Dahlgren (1968): 82–94; Dahlgren (1968b): 255–268; Hansen (1968): 294, 320; Dahlgren (1969b): 257–269; Witzgall (1971): 168–172; Mazur (1973): 26, 29; Kryzhanovskij & Reichardt (1976): 111, 125; Vienna (1980): 116, 129; Mazur & Kaszab (1980): 6, 25; Mazur (1981): 71, 72; Mazur (1984): 44; Ôhara (1994): 215, 226; Downie & Arnett (1996): 607; Secq & Secq (1997a): 10; Kim & Lim (1997): 60; Mazur (1997): 218; Ôhara & Paik (1998): 28; Bousquet & Laplante (1999): 141, 150; Mazur (2001): 19, 31; Kovarik & Caterino (2001): 220, 223; Yélamos (2002): 245, 255, 256; Mazur (2004): 96; Bousquet & Laplante (2006): 79, 81, 101.

Plesiosaprinus: Houlbert & Monnot (1923): 72 (*nomen nudum*). Synonymized by Cooman (1947): 428.

Differential diagnosis. Differs from the subgenus *Hemisaprinus* by the absence of pre-apical foveae (well developed in *Hemisaprinus*) and from the subgenus *Phaonius* by the differntly structured antennal club and asetose flattened or only slightly convex prosternal process (see also Key to the subgenera).
Biology. See Biology of *Saprinus* s. l.
Distribution. See Distribution of *Saprinus* s. l.
Species examined. *Saprinus* (*Saprinus*) *acuminatus* (Fabricius, 1798), *S.* (*S.*) *aegialius* Reitter, 1884 in Brenske & Reitter (1884), *S.* (*S.*) *aegyptiacus aegyptiacus* Marseul, 1855, *S.* (*S.*) *aegyptiacus solskyi* Reiche, 1861, *S.* (*S.*) *aeneolus* Marseul, 1870, *S.* (*S.*) *aeneus* (Fabricius, 1775), *S.* (*S.*) *aeratus* Erichson, 1834, *S.* (*S.*) *apteli* Chobaut, 1922, *S.* (*S.*) *austerus* Reichardt, 1930, *S.* (*S.*) *bicolor* (Olivier, 1789), *S.* (*S.*) *biguttatus* (Steven, 1806), *S.* (*S.*) *bimaculatus* Dahlgren, 1964, *S.* (*S.*) *biplagiatus* Ballion, 1871, *S.* (*S.*) *beduinus* Marseul, 1862, *S.* (*S.*) *brenskei* Reitter, 1884 in Brenske & Reitter (1884), *S.* (*S.*) *buqueti* Marseul, 1855, *S.* (*S.*) *caerulescens* (Hoffmann, 1803) (= *semipunctatus* Fabricius, 1792), *S.* (*S.*) *chalcites* (Illiger, 1807), *S.* (*S.*) *calatravensis* Fuente, 1899, *S.* (*S.*) *concinnus* (Gebler, 1830), *S.* (*S.*) *confalonieri* G. Müller, 1933, *S.* (*S.*) *cupratus* Kolenati, 1846, *S.* (*S.*) *cupreus* Erichson, 1834, *S.* (*S.*) *cribellatus* Marseul, 1855, *S.* (*S.*) *cruciatus* (Fabricius, 1792), *S.* (*S.*) *delta* Marseul, 1862, *S.* (*S.*) *detersus* (Illiger, 1807), *S.* (*S.*) *divergens* Dahlgren, 1967, *S.* (*S.*) *dussaulti* Marseul, 1870, *S.* (*S.*) *externus* (Fischer de Waldheim, 1823), *S.* (*S.*) *fallaciosus* G. Müller, 1937, *S.* (*S.*) *figuratus* Marseul, 1855, *S.* (*S.*) *flexuosofasciatus* Motschulsky, 1845, *S.* (*S.*) *furvus* Erichson, 1834, *S.* (*S.*) *georgicus* Marseul, 1862, *S.* (*S.*) *gilvicornis* Erichson, 1834, *S.* (*S.*) *gilviqueti* Dégallier & Gomy, 1996, *S.* (*S.*) *graculus* Reichardt, 1930, *S.* (*S.*) *intractabilis* Reichardt, 1930, *S.* (*S.*) *immundus* (Gyllenhall, 1827), *S.* (*S.*) *lateralis* Motschulsky, 1849, *S.* (*S.*) *lautus* Erichson, 1839, *S.* (*S.*) *maculatus* (Rossi, 1792), *S.* (*S.*) *magnoguttatus* Reichardt, 1926, *S.* (*S.*) *melas* Küster, 1849, *S.* (*S.*) *moyses* Marseul, 1862, *S.* (*S.*) *muelleri* Mazur, 1997, *S.* (*S.*) *niger* Motschulsky, 1849, *S.* (*S.*) *niponicus* Dahlgren, 1962, *S.* (*S.*) *ornatus* Marseul, 1834, *S.* (*S.*) *pamiricus* Reichardt, 1930, *S.* (*S.*) *planiusculus* Motschulsky, 1849, *S.* (*S.*) *politus politus* (Brahm, 1790), *S.* (*S.*) *politus simillis* J. Müller, 1900, *S.* (*S.*) *prasinus* Erichson, 1834, *S.* (*S.*) *proximus simillimus* Wollaston, 1865, *S.* (*S.*) *punctatissimus* Erichson, 1834, *S.* (*S.*) *quadriguttatus* (Fabricius, 1798), *S.* (*S.*) *ruber ruber* Marseul, 1855, *S.* (*S.*) *sternifossa* G. Müller, 1937, *S.* (*S.*) *rugifer* (Paykull, 1809), *S.* (*S.*) *sedakovi* Motschulsky, 1860, *S.* (*S.*) *semiopacus* Schmidt, 1894 in Hauser (1894), *S.* (*S.*) *sinaiticus* Crotch, 1871, *S.* (*S.*) *schmidtianus* Reitter, 1887, *S.* (*S.*) *splendens* (Paykull, 1811), *S.* (*S.*) *steppensis* Marseul, 1862, *S.* (*S.*) *strigil* Marseul, 1855, *S.* (*S.*) *stussineri* Reitter, 1909, *S.* (*S.*) *submarginatus* Sahlberg, 1913b, *S.* (*S.*) *subnitescens* Bickhardt, 1909, *S.* (*S.*) *suturalis* Marseul, 1862, *S.* (*S.*) *tenuistrius tenuistrius* Marseul, 1876, *S.* (*S.*) *vermiculatus* Reichardt, 1923, *S.* (*S.*) *virescens* (Paykull, 1798), *S.* (*S.*) *viridicatus* Schmidt, 1894 in Hauser (1894).

Saprinus (*Saprinus*) *semistriatus* (Scriba, 1790)

(Figs. 9, 68, 102, 134, 142, 177, 627–642)

Hister semistriatus Scriba, 1790: 72.
Hister semistriatus: Hoffmann (1803): 77.
Hister nitidulus Fabricius, 1801: 85. Synonymized by Hoffmann (1803): 125.

Hister incrassatus Faldermann, 1832 in Ménétriés (1832): 170. Synonymized by Marseul (1855): 402.
Hister krynickii Krynicki, 1832: 113. Synonymized by Dejean (1837): 142.
Saprinus nitidulus: Erichson (1834): 179; Schmidt (1885a): 306.
Saprinus incrassatus: Motschulsky (1849): 97.
Saprinus uralensis Motschulsky, 1849: 98. Synonymized by Marseul (1855): 402.
Saprinus sparsipunctatus Motschulsky, 1849: 97. Synonymized by Marseul (1855): 402.
Saprinus punctatostriatus Marseul, 1862: 459. Synonymized by Schmidt (1885b): 444.
Saprinus krynickii: Marseul (1862): 718.
Saprinus rugipennis Hochhut, 1872: 225. Synonymized by Reitter (1906): 267.
Saprinus asphaltinus Hochhut, 1872: 226. Synonymized by Schmidt (1885a): 306.
Saprinus semistriatus: Ganglbauer (1899): 384; Reitter (1909): 292, t. 67, Fig. 6; Jakobson (1911): 649; Reichardt (1923): 24; Reichardt (1941): 181, 220, Figs. 111B, 112A, 115, 116; Horion (1949): 334; Ihssen (1949): 176; Dahlgren (1962): 238–242, Figs. 1, 6, 8, 9; Witzgall (1971): 171; Mazur (1973): 32, Figs. 50–53, 59; Kryzhanovskij & Reichardt (1976): 130, 156, Figs. 174, 255, 256, 265–268, 272, 273, 274; Vienna (1980): 132, 141, Fig. 54A; Mazur & Kaszab (1980): 32, Figs. 13, 15G, 16J, 17A–E.; Mazur (1981a): 73, 76, Figs. 79, 88, 91, 94; Mazur (1984): 59; Mazur (1997): 228; Secq & Secq (1997a): 13; Yélamos (2002): 265, 279, Figs. 18F, 136C, 140J–L; Mazur (2004): 100.
Saprinus semistriatus var. *hochhuti* Reitter, 1906: 267.
Saprinus semistriatus var. *punctatus* Kolbe, 1911: 10.
Saprinus semistriatus var. *simulans* Sahlberg, 1913b: 87.
Saprinus semistriatus ab. *pacoviensis* Roubal, 1926: 94 (unavailable name).
Note. Larva and life cycle were studied by Lindner (1967: 365, 366, Figs. 7a–d, 12, 21, 22, 29, 30a–d); biology was studied by Mattei (1906: 14). Spermatheca and sensory structures of antennal club were studied by De Marzo & Vienna (1982a,b).

Type locality. Germany, Rheinland-Pfalz, Darmstadt.
Material examined. BULGARIA: Sozopol, vi.1972, 1 ♀, A. Olexa lgt. **CZECH REPUBLIC: Bohemia:** Rychnov nad Kněžnou, 31.vii.1948, 1 ♂, A. Olexa lgt. **SLOVAKIA:** Košice, v.1949, 1 ♂, A. Olexa lgt. **RUSSIA: Primorskiy Region:** Lazo Nat. Reserve, 20.–25.vii.1993, 1 ♂, M. Trýzna lgt. (TLAN).

Redescription. Body length: PEL: 3.85–5.00 mm; APW: 1.25–1.75 mm; PPW: 3.00–3.50 mm; EL: 2.50–3.25 mm; EW: 3.40–3.50 mm.

Body (Figs. 627–628) broadly oval, convex, cuticle dark brown with bronze metallic luster, shining; legs, mouthparts and antennae castaneous brown; antennal scape and club dark brown.

Antennal scape (Fig. 630) imbricate-punctate, with few short setae; club round, without visible articulation, entire surface with dense short sensilla intermingled with sparse longer erect sensilla; sensory structures of antennal club (Fig. 9) in form of four rather large sensory areas on ventral side and one vesicle situated under internal distal margin.

Mouthparts. Mandibles (Fig. 102) punctate, with rounded outer margin, curved inwardly, mandibular apex rather obtuse; sub-apical tooth rather obtuse, inconspicuous; labrum (Fig. 68) convex, densely punctate, depressed medially, with two deep labral pits deep, each with two well-sclerotized long setae; labral fold significantly less developed; terminal labial palpomere (Fig. 142) elongated, its width about one-third its length; mentum (Fig. 631) sub-trapezoid, anterior margin medially with deep notch (Fig. 134) surrounded with several moderately long setae, lateral margins with several shorter setae; disc of mentum imbricate, with several sparse microscopic setae; cardo of maxilla on lateral margin with few short setae; stipes triangular, with three longer setae; terminal maxillary palpomere elongated, its width about one-third its length, approximately twice as long as penultimate.

Clypeus (Fig. 630) with deep dense punctures, lateral margins rounded; frontal stria usually largely interrupted medially, supraorbital stria rather weakly impressed; frontal disc (Fig. 630) with coarse and dense punctures; eyes convex, well visible from above.

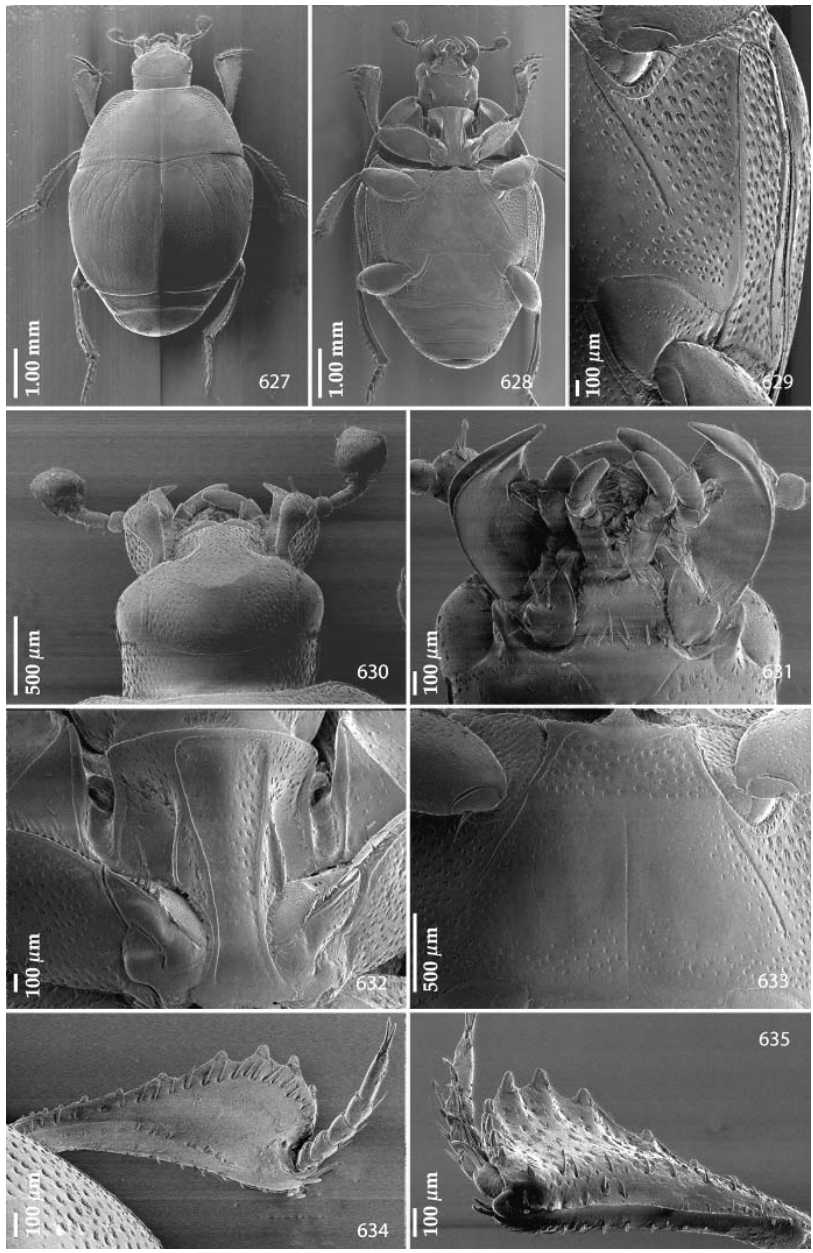
Pronotal sides (Fig. 627) moderately narrowing anteriorly, apical angles obtuse, pronotal foveae deep, rather large, anterior incision for head shallow; marginal pronotal stria complete, slightly carinate; disc of pronotum laterally with a band of coarse and dense punctation, not reaching posterior corners, between it and pronotal margin thin impunctate band present; pronotum medially almost smooth, with scattered microscopic punctation; along pronotal base two to three rows of coarse punctures present; pronotal hypomeron glabrous; scutellum well visible.

Elytral humeri prominent, impunctate; epipleura with scattered fine punctures; marginal epipleural stria fine, complete; marginal elytral stria nearly straight, in deep round punctures, continued as weakened complete apical elytral stria; along marginal elytral stria three rows of round dense punctures present. Humeral elytral stria well impressed on basal third, often joining inner subhumeral stria creating thus another complementary stria subparallel to first dorsal elytral stria; all four dorsal elytral striae 1–4 usually well impressed, in deep coarse punctures, usually reaching elytral half apically, third dorsal elytral stria in most cases not shorter than other striae, first dorsal elytral stria occasionally slightly shorter; fourth dorsal elytral stria basally curved inwardly, but not connected with sutural elytral stria (very occasionally connected with it); sutural elytral stria well-impressed, in punctures, abbreviated on basal third, apically connected with apical elytral stria. Punctation of elytral disc very variable, moderately dense and coarse, usually confined to apical half, along sutural elytral stria reaching basally in most cases further than along elytral lateral margins, rarely entire elytral disc coarsely and densely punctate, with exception of interval between sutural elytral and fourth dorsal elytral striae and elytral humeri; punctures on apical third sometimes confluent, carinulate or reticulate; towards elytral apex punctation becomes finer, reaching elytral apex.

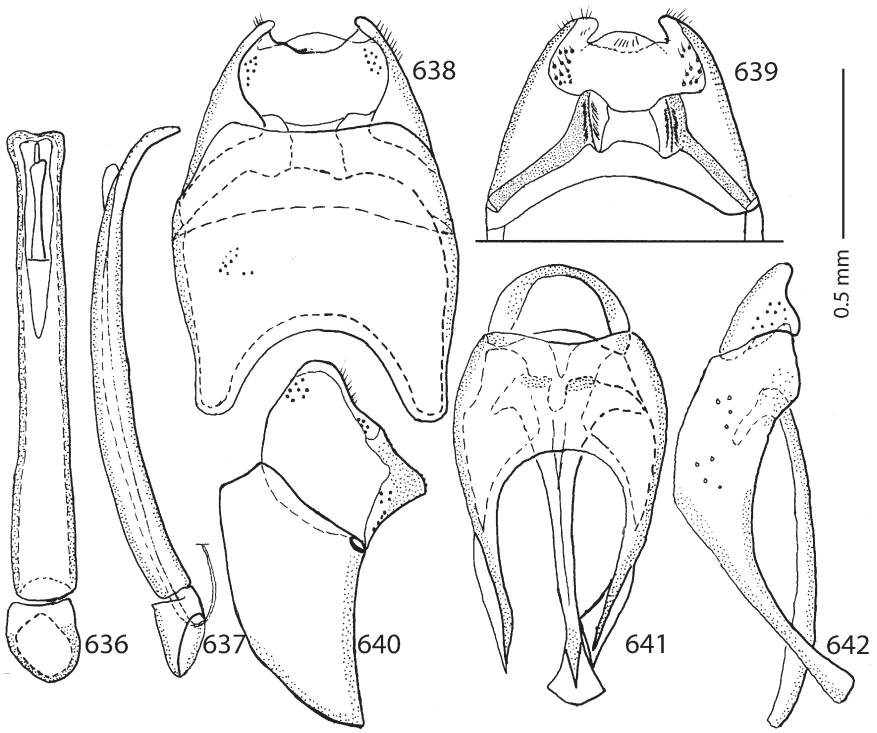
Propygidium almost completely exposed, laterally with depressions, with dense and coarse punctures; pygidium with sparser punctures, becoming even sparser and finer towards apex, antero-lateral corners of pygidium with shallow depressions.

Anterior margin of median portion of prosternum (Fig. 632) straight; prosternal process flattened, surface between carinal prosternal striae with coarse punctation, interspaces substrigulate; laterally punctures finer and sparser, interspaces substrigulate; carinal prosternal striae well-impressed, on prosternal apophysis parallel, strongly divergent anteriorly, anteriorly connected by marginal prosternal stria; lateral prosternal striae shortened, carinate, sub-parallel, apically attaining approximately two-thirds of length carinal prosternal striae.

Anterior margin of mesoventrite (Fig. 633) broadly emarginate medially; discal marginal mesoventral stria well impressed, complete, occasionally slightly weakened medially; disc of mesoventrite medially slightly depressed, with coarse and dense deep round punctures; meso-metaventral sutural stria absent; intercoxal disc of metaventrite (Fig. 633) flat (in males medially with a longitudinal excavation), smooth medially, area along lateral metaventral stria and posterior margin with fine scattered punctation; lateral metaventral stria well impressed, carinate, almost straight, shortened apically; lateral disc of metaventrite (Fig. 629) slightly concave, with dense shallow setiferous punctures of various sizes; metepisternum (Fig. 629)



Figs. 627–635. *Saprinus* (*Saprinus*) *semistriatus* (Scriba, 1790), SEM micrographs: 627 – habitus, dorsal view; 628 – ditto, ventral view; 629 – lateral disc of metaventrite, metepisternum and fused metepimeron; 630 – head, dorsal view; 631 – ditto, ventral view; 632 – prosternum; 633 – mesoventrite and metaventrite; 634 – protibia, dorsal view; 635 – ditto, ventral view.



Figs. 636–642. *Saprinus* (*Saprinus*) *semistriatus* (Scriba, 1790), male terminalia: 636 – aedeagus, dorsal view; 637 – ditto, ventral view; 638 – 8th sternite and tergite, dorsal view; 639 – 8th sternite, ventral view; 640 – 8th sternite and tergite, lateral view; 641 – 9th tergite, 10th tergite (dorsal view) and spiculum gastrale (ventral view); 642 – 9th tergite, 10th tergite and spiculum gastrale, lateral view.

with even denser and coarser punctures, punctures without setae, on fused metepimeron punctation sparser; metepisternum with complete metepisternal stria.

Intercoxal disc of the first abdominal sternite completely striate laterally, anteriorly with a broad deep depression, laterally and along anterior margin with fine scattered punctation.

Protibia (Figs. 634–635) slightly dilated, outer margin with about 5 low teeth topped with short thin denticle, diminishing in size in proximal direction, followed by about 5 tiny denticles; setae of outer row regular, short; protarsal groove deep; anterior protibial stria shortened apically; setae of median row shorter and sparser than those of outer row; two tarsal denticles present near tarsal insertion; protibial spur well developed, bent, growing out from apical margin of protibia; apical margin of protibia ventrally with 4 short denticles; outer part of posterior surface (Fig. 635) obscurely variolate, separated from glabrous median part of posterior surface by vague boundary and row of short sclerotized setae, several setae present also on median part of posterior surface; posterior protibial stria complete, basally with tiny sclerotized setae and apically with three inner posterior denticles; inner row of setae double, setae sparse and short.

Mesotibia slender, outer margin with two rows of short denticles; setae of outer row regular, dense, about as long as denticles themselves; setae of median row shorter, regular; posterior mesotibial stria shortened apically; anterior surface of mesotibia coriarious-punctate; anterior mesotibial stria complete, terminating in two tiny inner anterior denticles; mesotibial spur short; claws of apical tarsomere slightly bent, shorter than half its length, each mesotarsomere with two long well sclerotized setae, in males these setae are brush-like and even more sclerotized; metatibia slenderer and longer than mesotibia, in all aspects similar to it, but denticles on outer margin much sparser and metatersomeres without long setae.

Male genitalia. Eighth sternite (Figs. 638–639) widely separated medially, connected with membraneous 'bridge', apically with large inflatable membrane (velum) with several rows of short setae laterally; apex of eighth sternite laterally fringed with short brush of setae; eighth tergite and eighth sternite not fused laterally (Fig. 640). Ninth tergite (Figs. 641–642) typical for the subfamily; spiculum gastrale (Fig. 641) widely expanded on apical end, on basal end only slightly expanded. Aedeagus (Figs. 636–637) slender; basal piece of aedeagus short, ratio of its length : length of parameres 1 : 7.30; parameres fused almost along their apical two-thirds; aedeagus apically slightly curved ventrad (Fig. 637).

Remarks. This is a common and widely spread species exhibiting a considerable degree of variation, especially concerning the dorsal and ventral punctation, elytral striation and body luster.

Subgenus *Hemisaprinus* Kryzhanovskij, 1976

Hemisaprinus Kryzhanovskij, 1976 in Kryzhanovskij & Reichardt (1976): 111, 182. Type species: *Hister subvirescens* Ménétriés, 1832, original designation.

Hemisaprinus: Mazur (1984): 62; Mazur (1997): 231; Mazur (2004): 96.

Diagnosis. Species included in this subgenus differ from all other representatives of *Saprinus* by the presence of pre-apical foveae. All other characters as with subgenus *Saprinus*.

Biology. *Saprinus* (*Hemisaprinus*) *subvirescens* is found on carcasses, dung, etc. in arid regions and *S.* (*H.*) *lutshniki* (Reichardt, 1941) is found in decomposing vegetable matter, and has not been found on carcasses so far (Kryzhanovskij & Reichardt 1976: 184). The biology of *S.* (*H.*) *cyprius* Dahlgren, 1981, is virtually unknown.

Distribution. This subgenus includes three described species, all from the Palaearctic Region, with one species *S.* (*Hemisaprinus*) *subvirescens* (Ménétriés, 1832) occurring over a large area from Turkey in the west to Myanmar and China in the east. One species, *S.* (*H.*) *cyprius* Dahlgren, 1981 is endemic to the Cyprus (Mazur 1997).

Species examined. *Saprinus* (*Hemisaprinus*) *lutshniki* (Reichardt, 1941), *S.* (*H.*) *subvirescens* (Ménétriés, 1832).

Saprinus (*Hemisaprinus*) *subvirescens* (Ménétriés, 1832)

(Figs. 10, 69, 103, 135, 643–659)

Hister subvirescens Ménétriés, 1832: 171.

Hister subvirescens: Faldermann (1835): 230.

Saprinus subvirescens: Marseul (1855): 736; Reichardt (1922): 50; Reichardt (1941): 184, 240, Fig. 87; Dahlgren (1968): 87, 93, Figs. 2G, 5A; Kryzhanovskij & Reichardt (1976): 127, 183, Figs. 357–360; Mazur (1984): 62; Mazur (1997): 231; Mazur (2004): 96.

Saprinus syriacus Marseul, 1855: 469. Synonymized by Reichardt (1941): 240.
Saprinus viridulus Marseul, 1855: 468. Synonymized by Dahlgren (1968): 87.
Saprinus foveisternus Schmidt, 1884: 9. Synonymized by Auzat (1920): 3.

Type locality. Russia, Caucasus.
Type material. *Saprinus subvirescens*: Holotype: spec., '*subvirens* / Mén. Cauc (written) // Salian [red label, printed] // Holotypus [red label, printed] // round golden label' (ZIN).
Additional material examined. ISRAEL: Adullam, 17.v.2002, 2 ♂♂, Y. Mandelik & V. Chikatunov lgt. **TAJIKISTAN:** Aruk Tau Mts., 20.iv.1978, 2 ♂♂, A. Olexa lgt. **TURKMENISTAN:** Ashgabat, Nisa, 21.iv.1975, 4 ♂♂, A. Olexa lgt. (TLAN).

Redescription. Body length: PEL: 2.25–3.00 mm; APW: 0.75–1.00 mm; PPW: 1.75–2.325 mm; EL: 1.50–1.925 mm; EW: 1.875–2.50 mm.

Body (Figs. 643–644) roundly oval, convex, cuticle pitch-black with greenish hue, shining; legs, mouthparts and antennae dark brown; antennal club black.

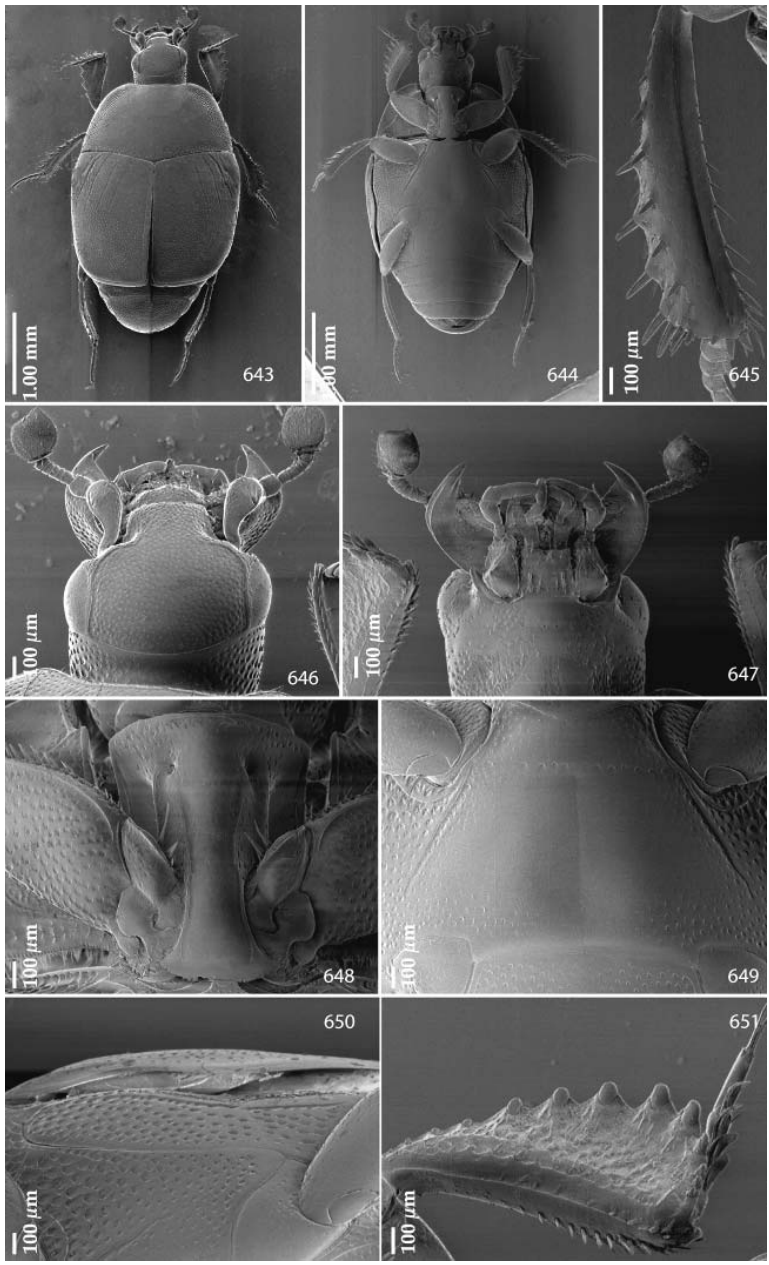
Antennal scape (Fig. 646) not particularly thickened, with shallow sparse punctures and two short setae; club round, without visible articulation, entire surface with dense short sensilla intermingled with sparser longer erect sensilla; sensory structures of antennal club (Fig. 10) in form of four ovoid sensory areas on ventral side and one vesicle situated under internal distal margin.

Mouthparts. Mandibles (Fig. 103) with rounded outer margin, laterally with deep dense punctures, moderately curved inwardly, mandibular apex apically pointed; sub-apical tooth obtuse, inconspicuous; labrum (Fig. 69) convex, densely punctate, anterior margin medially with a small convexity interrupting concavity; labral pits deep, each with two well-sclerotized long setae; terminal labial palpomere elongated, its width about one-third its length; mentum sub-trapezoid, anterior margin (Fig. 135) medially with deep notch surrounded with sparse short setae, lateral margins with single row of sparse shorter setae, several setae present also on disc of mentum; cardo of maxilla with few short setae; stipes triangular, with three short setae; terminal maxillary palpomere elongated, its width about one-fourth its length, approximately 2.5 times as long as penultimate.

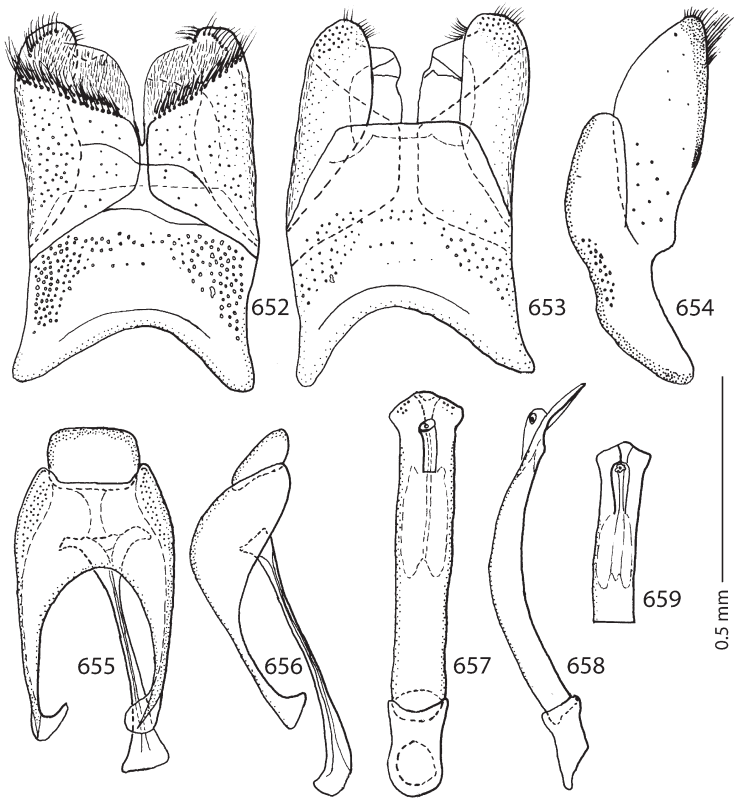
Clypeus (Fig. 646) flat, constricted laterally, with coarse and dense punctures; frontal stria largely interrupted medially, for short distance prolonged onto clypeus, supraorbital stria well impressed, carinate; frontal disc (Fig. 646) with coarse and dense punctures; eyes convex, well visible from above.

Pronotal sides moderately (Fig. 643) narrowing anteriorly, apical angles obtuse, pronotal foveae vaguely impressed, anterior incision for head shallow, almost straight in middle; marginal pronotal stria complete; pronotal disc laterally with longitudinal depression, with very coarse and dense punctures, punctures become finer and sparser medially; row of ovoid punctures present along pronotal base; pronotal hypomeron glabrous; scutellum small, but visible.

Elytral epipleura with scattered fine punctures, area between marginal epipleural stria and elytral margin smooth; marginal epipleural stria fine, complete; marginal elytral stria straight, well impressed and slightly carinate, continued as weakened complete apical elytral stria; along marginal elytral stria row of round dense punctures present. Humeral elytral stria weakly impressed on basal third; inner subhumeral stria present as short median fragment; all four dorsal elytral striae 1–4 weakly impressed, short, not reaching elytral half apically,



Figs. 643–651. *Saprinus* (*Hemisaprinus*) *subvirescens* (Ménétries, 1832), SEM micrographs: 643 – habitus, dorsal view; 644 – ditto, ventral view; 645 – mesotibia, ventral view; 646 – head, dorsal view; 647 – ditto, ventral view; 648 – prosternum; 649 – mesoventrite and metaventrite; 650 – lateral disc of metaventrite, metepisternum and fused metepimeron; 651 – protibia, ventral view.



Figs. 652–659. *Saprinus* (*Hemisaprinus*) *subvirescens* (Ménétries, 1832), male terminalia: 652 – 8th sternite and tergite, ventral view; 653 – ditto, dorsal view; 654 – ditto, lateral view; 655 – 9th tergite, 10th tergite (dorsal view) and spiculum gastrale (ventral view); 656 – 9th tergite, 10th tergite and spiculum gastrale, lateral view; 657 – aedeagus, dorsal view; 658 – ditto, lateral view; 659 – apex of aedeagus, dorsal view.

in shallow punctures; fourth dorsal elytral stria basally vaguely connected with sutural elytral stria; sutural elytral stria well-impressed and complete, in deep punctures, apically connected with apical elytral stria; entire elytral disc with punctation, punctures dense and coarse; along elytral margin, on elytral humeri and on interval between fourth dorsal and sutural elytral striae punctation weakens, extreme apex of elytra impunctate.

Propygidium and pygidium densely and coarsely punctate, punctures separated by about half their own diameter.

Anterior margin of median portion of prosternum (Fig. 648) almost straight; marginal prosternal stria present laterally and as short anterior fragment; prosternal process concave, surface between carinal prosternal striae with scattered fine punctation, laterally finely strigulate, punctures coarser and deeper; carinal prosternal striae well-impressed, parallel on prosternal

apophysis, slightly divergent anteriorly, not connected apically; pre-apical foveae deep; lateral prosternal striae carinate, sub-parallel, apically terminating in pre-apical foveae.

Anterior margin of mesoventrite (Fig. 649) deeply emarginate medially; discal marginal mesoventral stria well impressed, carinate, slightly weakened medially; disc of mesoventrite with scattered punctation; meso-metaventral sutural stria marked as straight row of coarse punctures; intercoxal disc of metaventrite (Fig. 649) flattened (in male with median longitudinal excavation), with fine punctures, becoming coarser and denser along posterior and lateral margins (especially behind hind coxa); lateral metaventral stria (Fig. 650) well impressed, carinate, almost straight, shortened; lateral disc of metaventrite (Fig. 650) slightly concave, with dense shallow setiferous punctures; metepisternum with even denser and coarser punctation, punctures not setiferous; fused metepimeron with somewhat sparser punctures; metepisternum + fused metepimeron with metepisternal stria, interrupted on fusion between metepimeron and metepisternum.

Intercoxal disc of the first abdominal sternite laterally with incomplete stria; except for median part with coarse round punctures, becoming finer along posterior margin.

Protibia (Fig. 651) slightly dilated, outer margin with 5 moderately large triangular teeth topped with short rounded denticle, diminishing in size in proximal direction, followed by 4 tiny denticles; setae of outer row regular, rather short; protarsal groove deep, strigulate; anterior protibial stria complete apically; setae of median row about as long as those of outer row, becoming more sclerotized apically; two tarsal denticles present near tarsal insertion; protibial spur short, bent, growing out from apical margin of protibia; apical margin of protibia posteriorly with 3 tiny denticles abutting each other; outer part of posterior surface (Fig. 651) obscurely variolate, separated from glabrous median part of posterior surface by vague boundary and row of short sclerotized setae; posterior protibial stria complete, with a row of tiny sclerotized setae becoming thicker apically; inner row of setae double, setae dense and short.

Mesotibia slender, outer margin with two rows of short denticles; setae of outer row regular, dense, shorter than denticles; setae of median row regular, shorter and finer than those of outer row; posterior mesotibial stria almost complete; anterior surface of mesotibia (Fig. 645) strigulate-punctate; anterior mesotibial stria complete, terminating in single tiny inner anterior denticle; mesotibial spur short; apical margin of mesotibia anteriorly with two short denticles; claws of apical tarsomere slightly bent, shorter than half its length; metatibia slenderer and longer than mesotibia, in all aspects similar to it, but denticles on outer margin much sparser and claws of apical tarsomere slightly longer than half its length.

Male genitalia. Eighth sternite (Figs. 652–653) widely separated medially, covered with pseudopores, apically with numerous close-set setae forming a conspicuous apical brush, velum with dense much shorter and finer setae; apex fringed with single row of longer setae; eighth tergite and eighth sternite fused laterally (Fig. 654). Ninth tergite (Figs. 655–656) typical for the subfamily; spiculum gastrale (Fig. 655) widely expanded on apical end, on basal end only slightly expanded. Aedeagus (Figs. 657–659) slender; basal piece of aedeagus short, ratio of its length : length of parameres 1 : 3.50; parameres fused almost along their apical three-fourths; aedeagus constricted apically, thence slightly dilated, curved ventrad (Fig. 658).

Subgenus *Phaonius* Reichardt, 1941

Phaonius Reichardt, 1941: 177, 188. Type species: *Saprinus pharao* Marseul, 1855, original designation.
Phaonius: Kryzhanovskij & Reichardt (1976): 126, 135; Mazur & Kaszab (1980): 26; Mazur (1984): 44; Mazur (1997): 218; Secq & Secq (1997a): 10; Yélamos (2002): 256, 257; Mazur (2004): 97.

Diagnosis. Body more rectangular shaped than in subgenus *Saprinus*, antennal club ventrally with four slit-like pits and dorsally with two slit-like pits roughly corresponding to sutures between antennomeres IX–XI; its surface furnished only with sparse erect long sensilla except for apical sensory area that is covered with dense short sensilla; prosternal process rather narrow, convex, with short sparse setae, propygidium long. Apical half of spiculum gastrale conspicuously dilated. The rest as with subgenus *Saprinus*.
Biology. Species of this subgenus are found on carcasses of mammals, birds, reptiles etc. (Lackner, pers. observ.).
Distribution. This subgenus contains three species distributed in the Afrotropical and Palaearctic Regions and one species occurring in Australia. *Saprinus* (*Phaonius*) *pharao* is distributed in Southern Europe (reaching its northernmost distribution limit in southern Slovakia), North Africa as far south as Senegal, Canary Islands, Asia Minor, South Russia, Central Asia, Iran, Afghanistan, West China and Mongolia (Mazur 1997). Two species with Afrotropical distribution, *S.* (*P.*) *erichsoni* Marseul, 1855 and *S.* (*P.*) *fulgidicollis* Marseul, 1855 are spread in Madagascar, Seychelles, Mauritius and Somalia (Mazur 1997). *Saprinus* (*P.*) *viridipennis* Lewis, 1901 is known only from Australia.
Species examined. *Saprinus* (*Phaonius*) *pharao* Marseul, 1855.

Saprinus (*Phaonius*) *pharao* Marseul, 1855

(Figs. 13, 41, 70, 104, 136, 660–676)

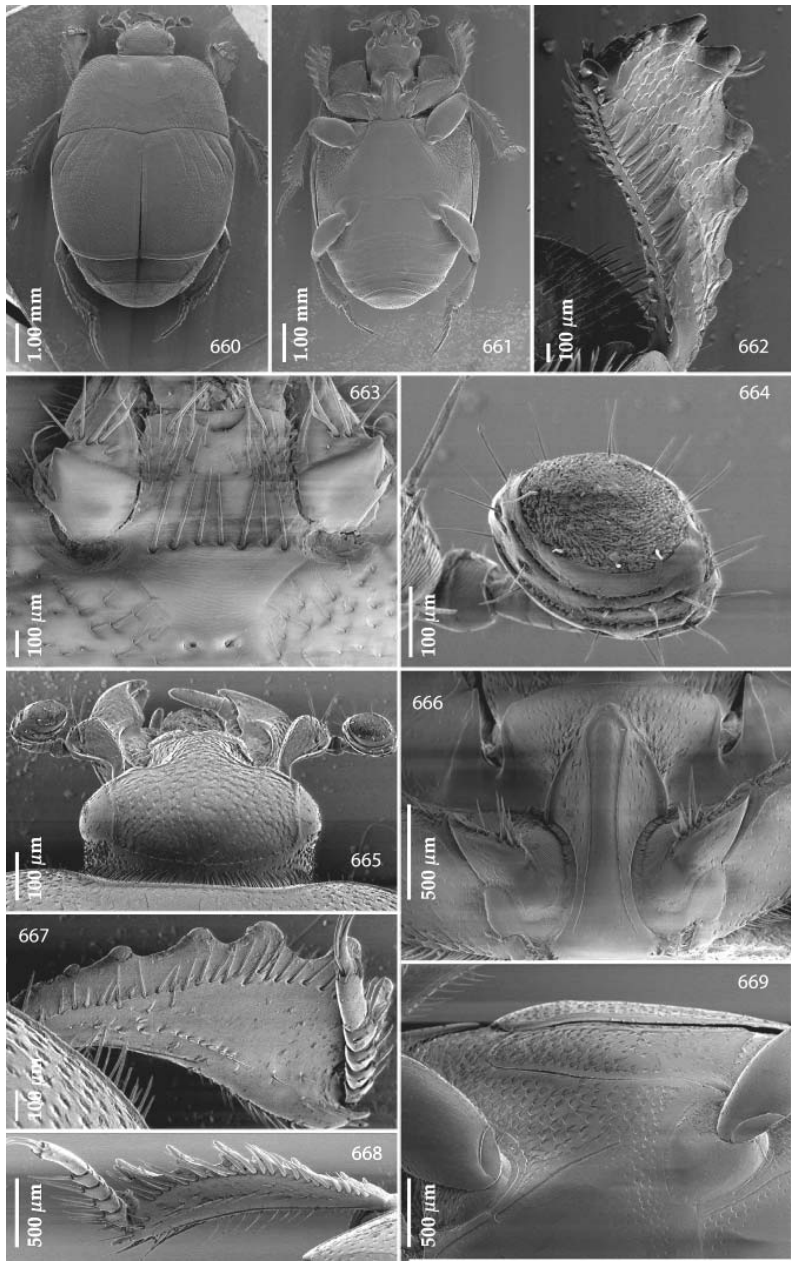
Saprinus pharao Marseul, 1855: 399, t. XVIII, Fig. 38.
Saprinus pharao: Schmidt (1885a): 304; Reichardt (1941): 177; Dahlgren (1968): 87, Figs. 1A, 3A; Kryzhanovskij & Reichardt (1976): 126, 135, Figs. 188–191; Mazur & Kaszab (1980): 27, Figs. 14C–G; Mazur (1984): 45; Mazur (1997): 218; Yélamos (2002): 257, Figs. 129A, 130, 131A, 132A–C; Mazur (2004): 97.
Saprinus aethiops: Gemminger & Harold (1868): 789 (*nomen nudum*, given as synonym).

Type locality. Egypt.
Type material examined. Syntype: 1 spec., '*Saprinus* / 38. *Pharao* / Aegypte / Deyrolle [round blue label] // Museum Paris / *pharao* / Coll. De Marseul / 2842-90 [printed-written label] // TYPE [red-printed label]' (MNHN).
Additional material examined. AZERBAIJAN: Zarat (Baku), Besh Barma, 19.v.1975, 1 ♂, A. Olexa lgt. **UZBEKISTAN: Ferghana prov.:** Chamza-Abad, 26.iv.1972, 1 ♂, A. Olexa lgt.; Kyzyl-Kum, Buchara, 30.vi.1976, 4 spec., A. Olexa lgt. (TLAN).

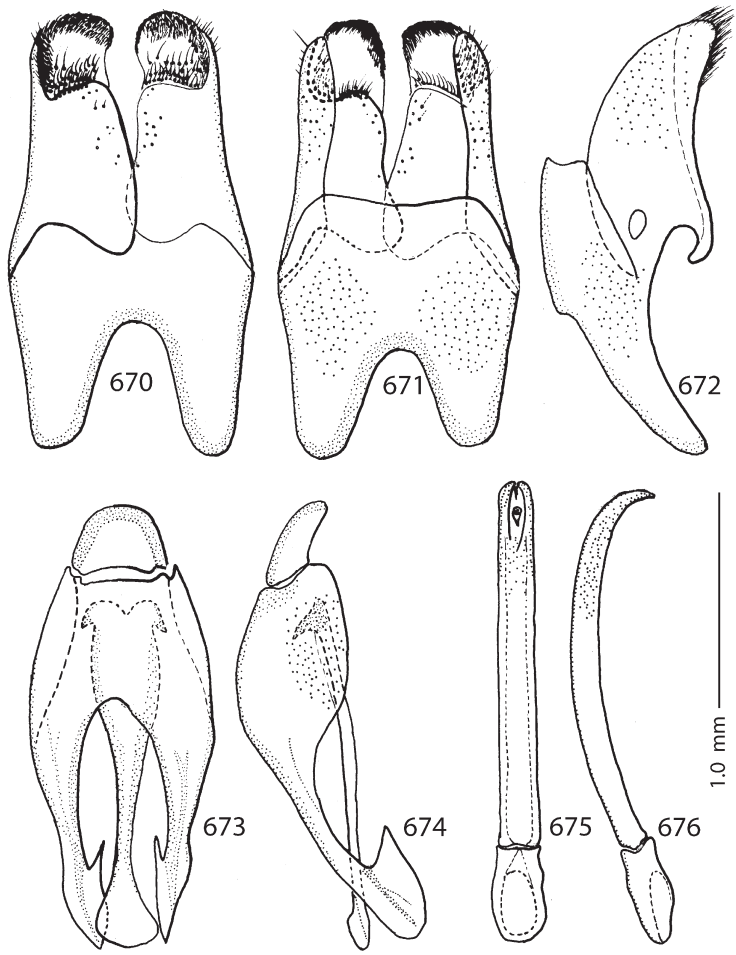
Redescription. Body length: PEL: 4.50–5.10 mm; APW: 1.65–1.75 mm; PPW: 3.55–3.85 mm; EL: 3.00–3.15 mm; EW: 3.80–4.20 mm.

Body (Figs. 660–661) rectangular oval, convex, cuticle pitch-black, shining, without metallic luster; legs, mouthparts and antennal scape castaneous brown; antennal funnicle rufopiceous.

Antennal scape (Fig. 665) slightly thickened, punctate, with several long setae; antennal club ventrally with 4 slit-like pits and dorsally with 2 slit-like pits roughly corresponding to sutures between antennomeres, furnished only with sparse long sensilla except for apical



Figs. 660–669. *Saprinus* (*Phaonius*) *pharao* (Marseul, 1855), SEM micrographs: 660 – habitus, dorsal view; 661 – ditto, ventral view; 662 – protibia, ventral view; 663 – mentum, submentum, cardines and stipites of maxilla, ventral view; 664 – antennal club, dorsal view; 665 – head, dorsal view; 666 – prosternum; 667 – protibia, dorsal view; 668 – mesotibia, dorsal view; 669 – lateral disc of metaventrite, metepisternum and fused metepimeron.



Figs. 670–676. *Saprinus* (*Phaonius*) *pharao* (Marseul, 1855), male terminalia: 670 – 8th sternite and tergite, ventral view; 671 – ditto, dorsal view; 672 – ditto, lateral view; 673 – 9th tergite, 10th tergite (dorsal view) and spiculum gastrale (ventral view); 674 – 9th tergite, 10th tergite and spiculum gastrale, lateral view; 675 – aedeagus, dorsal view; 676 – ditto, lateral view.

sensory area (Fig. 664) covered with dense short sensilla (presumably sensilla basiconica), sensory structures of antennal club (Fig. 13) in form of two slit-like pits on dorsal side and four slit-like pits on ventral side, with four vesicles, each under corresponding slit-like pit on ventral side.

Mouthparts. Mandibles (Fig. 104) laterally densely and coarsely punctate, rounded, mandibular apex acute; sub-apical tooth obtuse, inconspicuous; dorsolateral area of mandibles with few scattered short setae (presumably chemoreceptors); labrum (Fig. 70) punctate, emarginate

medially, labral pits deep, each with two well-sclerotized long setae; labral fold and process significantly less developed; terminal labial palpomere elongated, its width about one-fourth its length; mentum (Fig. 663) sub-trapezoid, anterior margin with deep conspicuous median notch (Fig. 136), surrounded with four long setae, disc of mentum (except for glabrous median part) with several rows of thick short setae; cardo of maxilla on lateral margin with few short setae; stipes (Fig. 663) triangular, with four to six longer setae; terminal maxillary palpomere elongated, its width about one-fourth its length, approximately 2.5 times as long as penultimate.

Clypeus (Fig. 665) slightly convex, constricted laterally, with coarse punctures and wrinkles; frontal stria largely interrupted medially, slightly prolonged onto clypeus, supraorbital stria well impressed, slightly carinate; frontal disc (Fig. 665) with coarse and dense punctures and wrinkles; eyes convex, well visible from above.

Pronotal sides (Fig. 660) almost straight on basal two-thirds, thence moderately narrowing anteriorly, apical angles rounded, pronotal foveae deeply impressed, anterior incision for head shallow; marginal pronotal stria complete; pronotal disc laterally with deep sparse punctures, becoming finer and sparser medially, median part of pronotal disc almost smooth; row of coarse ovoid punctures present along pronotal base; pronotal hypomeron with long yellow setae; scutellum very small, but visible.

Elytral epipleura on basal half with shallow ovoid punctures, on apical half punctation obliterated; marginal epipleural stria complete, continued as complete apical stria; marginal elytral stria slightly bisinuate, well impressed and carinate, apically nearly attaining marginal epipleural stria. Humeral elytral stria deeply impressed on basal third; inner subhumeral stria absent; all four dorsal elytral striae 1–4 weakly impressed, thin, not in punctures, apically not reaching elytral half; fourth dorsal elytral stria often apically slightly shortened, basally not connected with sutural elytral stria; sutural elytral stria well-impressed, thin, abbreviated on basal third, apically connected with apical elytral stria; elytral disc with moderately dense deep round punctures, separated by about their own to twice their diameter, surface between fourth dorsal and sutural striae with very fine, almost indistinguishable scattered punctation.

Propygidium with dense ellipsoid shallow punctures, interspaces imbricate; pygidium with deep round dense punctures, interspaces not imbricate, punctures becoming sparser apically.

Anterior margin of median portion of prosternum (Fig. 666) straight, rounded laterally; marginal prosternal stria present as lateral fragment; prosternal process convex, surface between carinal prosternal striae with sparse fine punctures, laterally substrigulate, punctures larger and denser, some fringed with sparse short setae; carinal prosternal striae well-impressed, slightly divergent on prosternal apophysis, thence parallel, slightly divergent anteriorly, united in front; lateral prosternal striae carinate, strongly convergent anteriorly, apically attaining near apices of united carinal prosternal striae.

Anterior margin of mesoventrite deeply emarginate medially; discal marginal mesoventral stria well impressed, complete; disc with sparse fine punctation; meso-metaventral sutural stria almost straight, impressed as a row of punctures; intercoxal disc of metaventrite flattened, with longitudinal depression in male, disc of metaventrite for the most part almost

smooth, only with scattered microscopic punctation, along posterior margin (especially in area behind hind coxa) denser and coarser punctation appears; lateral metaventral stria (Fig. 669) well impressed, carinate, almost straight, shortened; lateral disc of metaventrite (Fig. 669) slightly concave, with dense shallow large punctures, fringed with short thick yellow setae; metepisternum (Fig. 669) on basal three-fourths with similar punctation, punctures fringed with yellow setae, on apical fourth + fused metepimeron almost smooth; metepisternal stria present along entire metepisternum + fused metepimeron.

Intercoxal disc of the first abdominal sternite completely striate laterally; disc along lateral margins with scattered round punctures, apically with one row of dense punctures, median part almost smooth.

Protibia (Figs. 662, 667) slightly dilated, outer margin with about 5 low teeth topped with short rounded denticle, diminishing in size in proximal direction, followed by 2 tiny round denticles; setae of outer row regular, moderately long and dense; protarsal groove deep; anterior protibial stria present on basal third, next obliterated; setae of median row shorter and sparser than those of outer row; two tarsal denticles present near tarsal insertion; protibial spur well developed, bent, growing out from apical margin of protibia; apical margin of protibia posteriorly with 4 short denticles abutting each other; outer part of posterior surface (Fig. 662) obscurely variolate, separated from glabrous median part of posterior surface by vague boundary, basal third with row of microscopic setae; posterior protibial stria complete, along entire length with dense row of long well sclerotized setae almost completely covering median part of posterior surface of protibia; inner row of setae double, setae dense, shorter than those of posterior protibial stria.

Mesotibia (Fig. 668) slender, outer margin with two rows of short sparse denticles; setae of outer row very regular and dense, longer than denticles themselves; setae of median row shorter, irregular; posterior mesotibial stria shortened apically; anterior surface of mesotibia coriarious-punctate; anterior mesotibial stria almost complete, terminating in single tiny inner anterior denticle; mesotibial spur short; apical margin of mesotibia anteriorly with three short denticles; inner margin of mesotibia with sparse row of long setae; claws of apical tarsomere slightly bent, shorter than half its length; metatibia slenderer and longer than mesotibia, in all aspects similar to it, but denticles on outer margin much sparser and setae of median row denser.

Male genitalia. Eighth sternite (Figs. 670–671) widely separated medially, with pseudopores, several of them with microscopic setae, apically with numerous close-set setae forming a conspicuous apical brush, velum apically with a brush of dense much shorter and finer setae; apex of 8th sternite fringed with several rows of short setae; eighth tergite and eighth sternite fused laterally (Fig. 672). Ninth tergite (Figs. 673–674) typical for the subfamily; tenth tergite conspicuously small; spiculum gastrale (Fig. 673) conspicuously dilated on apical half. Aedeagus (Figs. 675–676) slender; basal piece of aedeagus short, ratio of its length : length of parameres 1 : 4.50; parameres fused almost along their entire length; aedeagus slightly curved ventrad (Fig. 676).

Styphrus Motschulsky, 1845

Styphrus Motschulsky, 1845: 54. Type species: *Styphrus corpulentus* Motschulsky, 1845, by monotypy.
Styphrus: Jakobson (1911): 641, 651 (partim); Reichardt (1925): 138; Reichardt (1926): 15; Reichardt (1941): 154, 174; Peyerimhoff (1936): 214, 223; Kryzhanovskij & Reichardt (1976): 111, 186; Mazur (1984): 78; Mazur (1997): 245; Mazur (2004): 101.

Diagnosis. Cuticle slightly metallic; frontal disc smooth; frontal stria straight, often interrupted medially; eyes convex; pronotal foveae vaguely impressed, often absent; disc of pronotum with sparse punctures along lateral margins, otherwise smooth; pronotal hypomeron setose; inner subhumeral stria linked basally with humeral elytral stria, long, reaching approximately four-fifths of elytral length apically; elytral epipleura glabrous. Prosternal process flattened, setose, pre-apical foveae absent; lateral prosternal striae shortened, 'open' apically, carinal prosternal striae subparallel, approximate; lateral sides of mesoventrite, metaventrite, metepisternum + fused meso- and metepimeron and all visible abdominal sternites setose. Claws of meso- and metatarsi only slightly curved, almost straight, thin, as long as or longer than apical-most tarsomere.
Biology. *Styphrus corpulentus* is found mostly on carcasses of gerbils, turtles etc., occasionally caught also at light (Kryzhanovskij & Reichardt 1976).
Distribution. *Styphrus corpulentus* is distributed across the deserts of Central Asia and southern Russia.
Species examined. *Styphrus corpulentus* Motschulsky, 1845.
Discussion. *Styphrus corpulentus* is most similar to the species of the genus *Saprinus*, but can be easily distinguished from them by the impunctate frontal disc as well as only slightly bent (almost straight), thin claws of apical-most meso- and metatarsomeres, that are as long (or slightly longer) than apical-most meso- and metatarsomeres. The sensory structures of the antennal club and absent pre-apical foveae indicate that this taxon is probably sister to *Saprinus*, as already indicated by Kryzhanovskij & Reichardt (1976: 186). Otherwise *Styphrus* is mostly characterised by homoplasies e.g. setose prosternal process, underside of body with vestiture or almost straight thin claws of meso- and metatarsi.
Remarks. The diagnosis of this genus is based only on species *Styphrus corpulentus* Motschulsky, 1845. The genus *Styphrus* contains another Palaearctic species, *S. peyerimhoffi* Chobaut, 1923 that belongs in fact to another genus and whose taxonomic status will be treated in a subsequent paper.

Styphrus corpulentus Motschulsky, 1845
(Figs. 12, 71, 105, 136, 677–693)

Styphrus corpulentus Motschulsky, 1845: 54.
Styphrus corpulentus: Jakobson (1911): 651; Reichardt (1941): 174, Figs. 83, 84; Kryzhanovskij & Reichardt (1976): 187, Figs. 367–372; Mazur (1984): 78; Mazur (1997): 245; Mazur (2004): 101.
Saprinus akinini Schmidt, 1890: 19. Synonymized by Jakobson (1910): 264.
Saprinus mimulus Reitter, 1904: 29. Synonymized by Jakobson (1910): 263.
Xenonychus akinini: Lewis (1905): 78.
Pachylopus akinini: Reitter (1906): 268.

Xenonychus laevidorsis Reitter, 1910: 13. Synonymized by BICKHARDT (1916): 103.
Styphrus laevidorsis: BICKHARDT (1910): 107.
Saprinus rugosipennis Dahlgren, 1971: 50. Synonymized by Kryzhanovskij in KRYZHANOVSKIJ & REICHARDT (1976): 187.

Type locality. Uzbekistan, Buchara.
Type material examined. *Styphrus corpulentus*. NEOTYPE (here designated): ♂, 'Buchara, Kyzyl Kum / Uzbekistan 28.–30.IV. / A. Olexa 1975 [printed] // D07-026 [pink label, written] // NEOTYPUS / *Styphrus* / *corpulentus* / Motschulsky 1845 / Des. T. Lackner 2009 [red label, written]' (ZIN).

Saprinus akinini. Paratype: 1 spec., '*Saprinus* / *akinini* / Schmidt / typ [written] // Paratypus [red label, written]' (ZIN).
Comment. Type specimen(s) of this species were not found in Motschulsky's collection, housed at ZMUM. According to N. Nikitsky (ZMUM), a part of the type specimens described by Motschulsky in 1845 has been destroyed and lost. Perhaps the type specimen(s) of *Styphrus corpulentus* were among those. The Motschulsky's collection is in a very poor state. Therefore, it is necessary to designate a neotype for this species to fix its identity as type species of *Styphrus*. The neotype will be housed at ZIN.
Additional material examined. UZBEKISTAN: Kyzylkum, Buchara, 28.–30.iv.1975, 1 ♂, A. Olexa lgt.; Kyzyk-Kum, Chiva [= Khiva], 25.iv.1972, 1 ♂ 1 ♀, A. Olexa lgt.; ditto, but 3.v.1978, A. Olexa lgt., 3 ♀♀; ditto, but 23.iv.1972, A. Olexa lgt. (TLAN).

Redescription. Body length: PEL: 2.50–3.45 mm; APW: 0.85–1.20 mm; PPW: 1.975–2.80 mm; EL: 1.55–2.25 mm; EW: 2.20–3.10 mm.

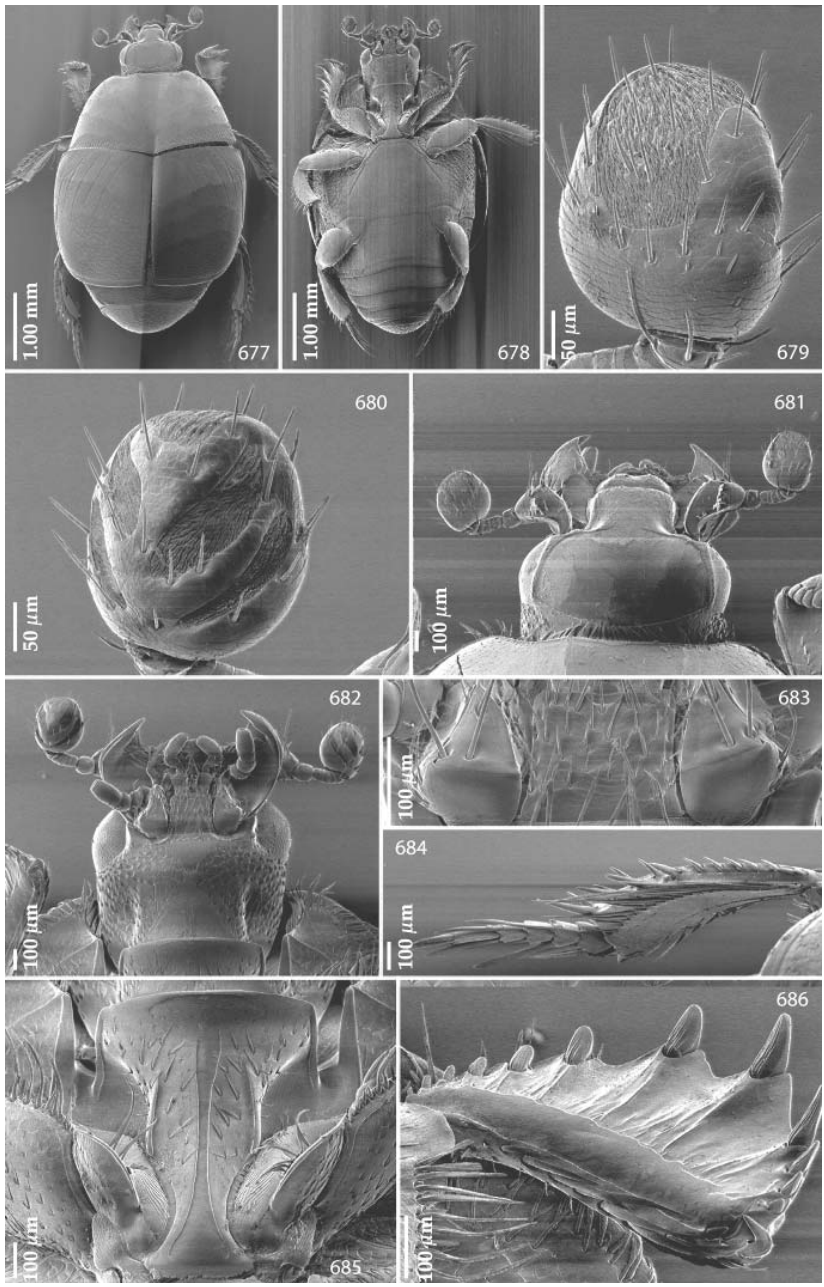
Body (Figs. 677–678) roundly oval, ventrally strongly convex, moderately convex dorsally; cuticle dark brown with slight metallic tinge, elytral apex rufous; legs, mouthparts and antennae rufopiceous.

Antennal scape (Fig. 681) substrigulate, with numerous well sclerotized long setae; club (Figs. 679–680) large, flattened dorso-ventrally, round, without visible articulation, dorsal surface with large apical sensory area with dense short sensilla, intermingled with longer, much sparser erect sensilla; surface of club otherwise imbricate, with sparse long erect sensilla (except for basal fourth); sensory structures of antennal club (Fig. 12) in form of one large apical sensory area and four rather large ventral sensory areas and one vesicle on internal distal margin of ventral side.

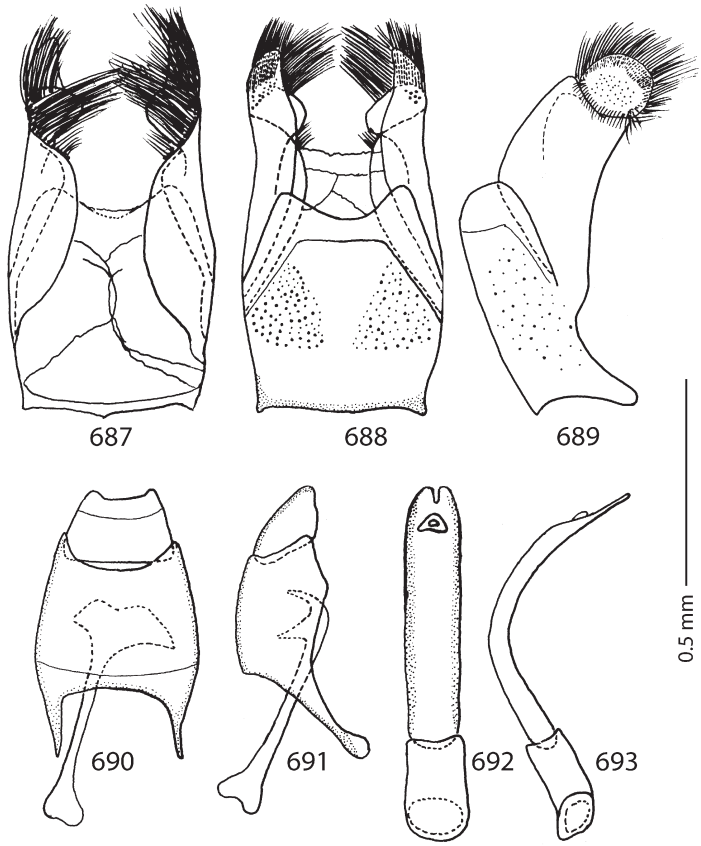
Mouthparts. Mandibles (Fig. 104) with rounded outer margin, mandibular apex acute; subapical tooth of left mandible moderately large; labrum (Fig. 70) with scattered microscopic punctation, convex, with a slight median depression; labral pits with two weakly sclerotized setae; terminal labial palpomere thickened, its width about half its length; mentum (Fig. 683) square-shaped, imbricate, anterior margin medially with conspicuous notch (Fig. 136), fringed with numerous long setae, lateral margins as well as disc of mentum with numerous much shorter setae; cardo of maxilla on lateral margin with several short setae; stipes triangular, with three much longer setae; terminal maxillary palpomere thickened, its width about half its length, approximately twice as long as penultimate.

Clypeus (Fig. 681) rectangular, basally constricted, depressed laterally, with shallow irregular punctures; frontal stria well impressed, usually interrupted medially, shortly prolonged onto clypeus; supraorbital stria well impressed, carinate; frontal disc (Fig. 681) smooth, only with scattered microscopic punctation; eyes convex, conspicuous from above.

Pronotal sides (Fig. 677) moderately narrowed anteriorly, apical angles obtuse; pronotal foveae vaguely impressed, often absent; marginal pronotal stria complete, slightly weakened behind head; pronotal disc (except for inconspicuous scattered punctation along lateral margins



Figs. 677–686. *Styphrus corpulentus* Motschulsky, 1845, SEM micrographs: 677 – habitus, dorsal view; 678 – ditto, ventral view; 679 – antennal club, dorsal view; 680 – ditto, ventral view; 681 – head, dorsal view; 682 – ditto, ventral view; 683 – mentum, cardines and stipites of maxilla, ventral view; 684 – metatibia, dorsal view; 685 – prosternum; 686 – protibia, ventral view.



Figs. 687–693. *Styphrus corpulentus* Motschulsky, 1845, male terminalia: 687 – 8th sternite and tergite, ventral view; 688 – ditto, dorsal view; 689 – ditto, lateral view; 690 – 9th tergite, 10th tergite (dorsal view) and spiculum gastrale (ventral view); 691 – 9th tergite, 10th tergite and spiculum gastrale, lateral view; 692 – aedeagus, dorsal view; 693 – ditto, lateral view.

and a double row of small ellipsoid punctures along pronotal base) entirely smooth; pronotal hypomeron setose; scutellum small, visible.

Elytral epipleura shiny, almost smooth, with scattered microscopic punctures; marginal epipleural stria weakly impressed, complete; marginal elytral stria well impressed, continued as weakly impressed complete apical elytral stria; inner subhumeral stria well impressed, rather long, apically reaching as far as four-fifths of elytral length, basally connected with weakly impressed humeral elytral stria; elytra with four rather thin dorsal elytral striae 1–4, apically reaching about elytral half, occasionally second dorsal elytral stria slightly longer; fourth dorsal elytral stria basally connected with complete sutural elytral stria; sutural elytral stria well impressed, complete, apically connected with apical elytral stria. Elytral disc on

apical half with dense, shallow, often confluent punctures, basal half with much finer and sparser punctation; elytral flanks and elytral humeri smooth.

Propygidium almost completely exposed; punctation of propygidium and pygidium shallow but dense, punctures confluent, becoming more granulose apically.

Anterior margin of median portion of prosternum (Fig. 685) almost straight, pre-apical foveae absent; marginal prosternal stria present laterally and as thin apical fragment; prosternal process flattened; surface between carinal prosternal striae smooth; laterally substrigulate, with sparse punctures fringed with setae; carinal prosternal striae on prosternal apophysis slightly divergent, approximate, sub-parallel, slightly divergent apically, not united; lateral prosternal striae well impressed, shortened, slightly carinate, anteriorly 'open'.

Anterior margin of mesoventrite straight; discal marginal mesoventral stria well impressed, slightly carinate; disc of mesoventrite flat, with shallow scattered punctation, few punctures with microscopic setae; meso-metaventral sutural stria well impressed, undulate; intercoxal disc of metaventrite convex, almost smooth, along posterior margin with irregular sparse fine punctures. Lateral metaventral stria well impressed, slightly carinate, almost straight, shortened apically; lateral disc of metaventrite concave, with scattered shallow punctures fringed with long setae; metepisternum on basal three-fourths with similar punctation and setae, on apical fourth + fused metepimeron punctation and setae sparser and finer.

Intercoxal disc of the first abdominal sternite completely striate laterally; surface of disc with sparse scattered punctation, interspaces imbricate, apically punctation sparser and finer; lateral sides of all visible abdominal sternites setose.

Protibia (Fig. 686) dilated, outer margin with three low teeth topped with rather long acute denticle, second and third teeth larger than first, followed by six short denticles diminishing in size in proximal direction; setae of outer row regular, rather sparse; protarsal groove deep; anterior protibial stria absent; setae of median row much shorter and sparser than those of outer row, present only on basal half; single tiny tarsal denticle present near tarsal insertion; protibial spur well developed, bent, growing out from apical margin of protibia; apical margin of protibia posteriorly with three short denticles; outer part of posterior surface of protibia (Fig. 686) broadly strigate, interspaces smooth, separated from glabrous median part of posterior surface by clear-cut boundary; posterior protibial stria complete, apically terminating in two tiny inner ventral denticles; inner row of setae lamelliform, strongly sclerotized, long.

Mesotibia slender, outer margin with single row of short thin denticles, only slightly growing in size in proximal direction; setae of outer row situated approximately in middle of posterior mesotibial surface, setae regular, dense, about as long as denticles themselves; setae of median row absent; posterior mesotibial stria shortened apically; anterior surface of mesotibia microscopically punctate; anterior mesotibial stria almost complete; inner anterior denticles absent; mesotibial spur rather long and stout; apical margin of mesotibia anteriorly with two tiny denticles; inner margin of mesotibia with long dense well sclerotized setae; claws of apical tarsomere almost straight, thin, almost as long as apical-most tarsomere itself; each mesotarsomere anteriorly with single long well sclerotized seta; metatibia (Fig. 684) similar to mesotibia, but slightly more thickened and another row of four sparse longer denticles appears on apical half of outer margin and posterior metatibial stria even shorter than posterior mesotibial stria.

Male genitalia. Eighth sternite (Fig. 687–688) widely separated along their entire length, apically with large inflatable membrane (velum) mesally and laterally with several rows of long close-set setae creating a conspicuous apical brush; eighth tergite and eighth sternite fused laterally (Fig. 689). Ninth tergite (Figs. 690–691) typical for the subfamily; spiculum gastrale (Fig. 690) expanded on both ends. Aedeagus (Figs. 692–693) slender; basal piece of aedeagus rather short, ratio of its length : length of parameres 1 : 3.50; parameres fused almost along their apical length, on apical tenth with opening for the median lobe (best seen from lateral view); aedeagus strongly curved ventrad (Fig. 693).

Turanostyphrus Tishechkin, 2005

Turanostyphrus Tishechkin, 2005: 348. Type species: *Turanostyphrus ignoratus* Tishechkin, 2005, original designation.

Diagnosis. Cuticle without prominent metallic luster; frontal and supraorbital striae absent; pronotal hypomeron setose; elytral epipleuron with short setae; both sets of prosternal striae present; pre-apical foveae absent. Protibia dilated, outer margin explanate, concealing numerous denticles (similar to *Eremosaprinus vlasovi*); metatibia with explanate outer margin almost entirely concealing two rows of numerous denticles observable only from ventral view.

This genus has been erected only recently and Tishechkin's (2005) diagnosis serves the purpose well. However, for the sake of consistency and clarity concerning the morphology used in this work it is repeated here. The concerning parts are duly modified and characters omitted by Tishechkin in his paper are supplemented.

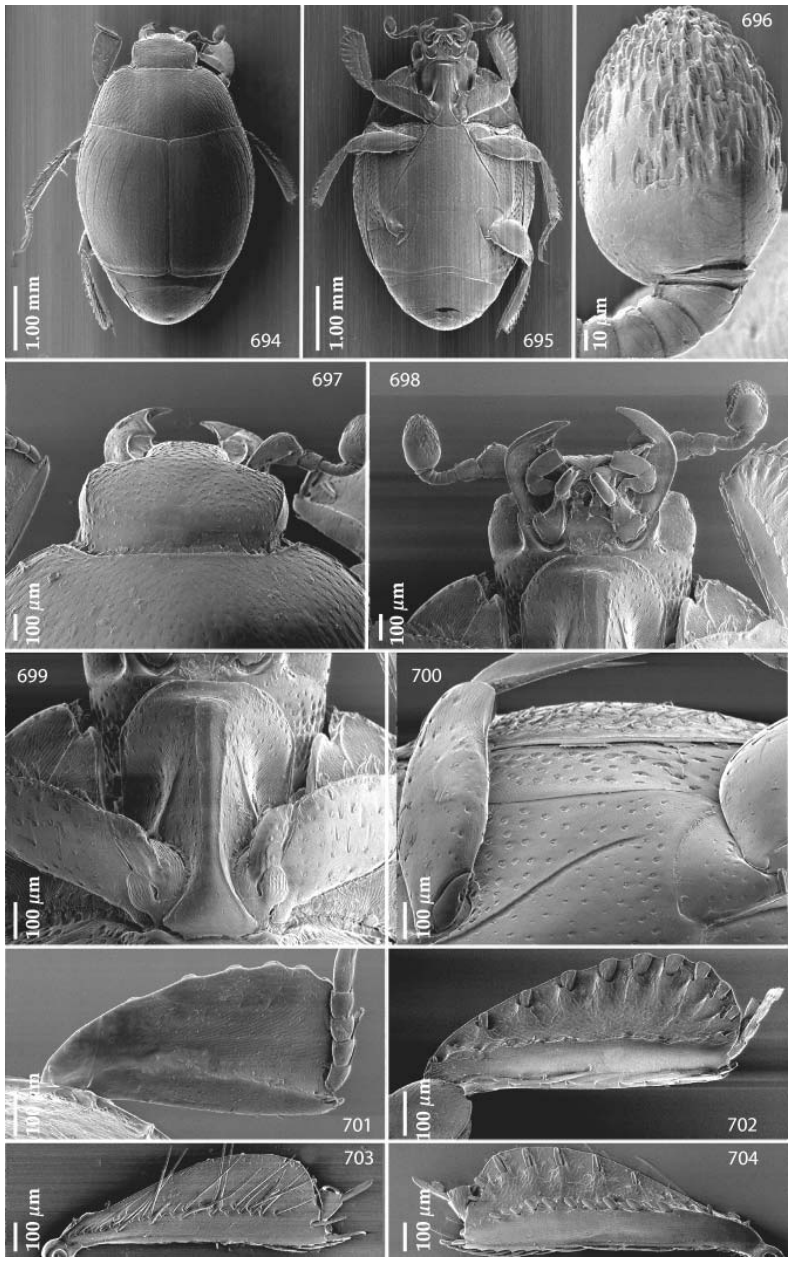
Differential diagnosis. This genus is one of the most peculiar among the Palaearctic Saprininae genera. The structure of protibia, and especially metatibia (with explanate outer margins almost completely concealing one or two rows of short denticles, respectively) and the setose elytral epipleuron does not allow it to be confused with any currently known taxon. By the absent frontal and supraorbital striae and pre-apical foveae, as well as the explanate outer margin of protibia it can be compared to the species *Eremosaprinus vlasovi*, but clearly differing from it by differently structured metatibia (long and slender, almost without denticles *versus* dilated and explanate concealing two rows of numerous denticles) as well as by the setose pronotal hypomeron and elytral epipleuron *versus* glabrous in *Eremosaprinus vlasovi*.

Biology. Virtually unknown; the only two described species (each known only from a holotype) were collected in a rodent burrow and trapped by a pitfall trap, respectively. Tishechkin (2005) hypothesized that this taxon probably leads psammophilous way of life, based on its external morphology.

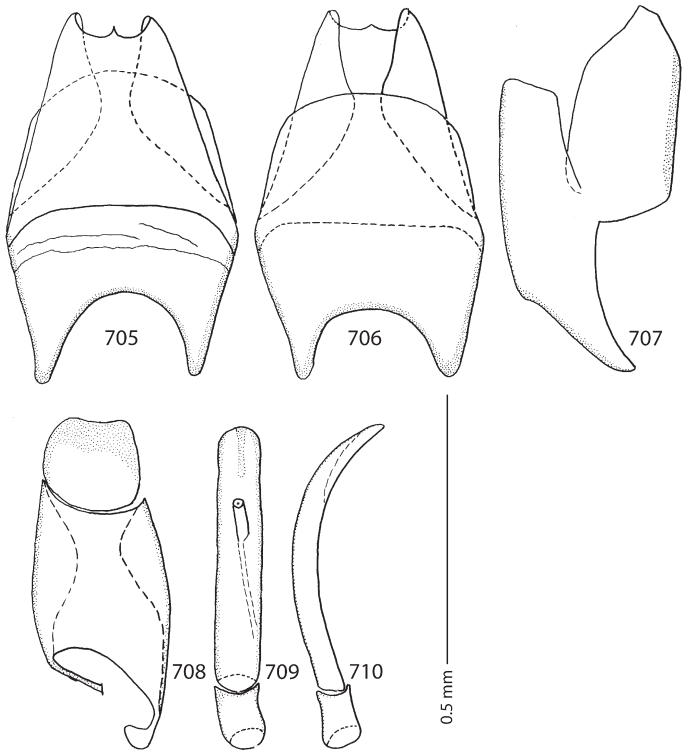
Distribution. Central Asian province of Turan: Turkmenistan and Uzbekistan.

Species examined. *Turanostyphrus ignoratus* Tishechkin, 2005, *T. kizilkumis* Tishechkin, 2005.

Discussion. Resolving the exact taxomonic position within the Palaearctic Saprininae of this genus is a puzzling task, which needs to be examined by further studies. In the preliminary studies on the phylogeny of Saprininae (Lackner, in prep.) it came out in several equally parsimonious trees on the bottom, close to the group '*Eremosaprinus – Myrmetes – Gnathoncus*'; weighted analysis, however, placed it near the most derived psammophilous taxa, as originally also indicated by Tishechkin (2005). It is probably a well-defined monophyletic



Figs. 694–704. *Turanostyphrus ignoratus* Tishechkin, 2005, SEM micrographs: 694 – habitus, dorsal view; 695 – ditto, ventral view; 696 – antennal club, dorsal view; 697 – head, dorsal view; 698 – ditto, ventral view; 699 – prosternum; 700 – lateral disc of metaventrite, metepisternum and fused metepimeron; 701 – protibia, dorsal view; 702 – ditto, ventral view; 703 – metatibia, dorsal view; 704 – ditto, ventral view.



Figs. 705–710. *Turanostyphrus ignoratus* Tishechkin, 2005, male terminalia: 705 – 8th sternite and tergite, ventral view; 706 – ditto, dorsal view; 707 – ditto, lateral view; 708 – 9th tergite, 10th tergite, dorsal view; 709 – aedeagus, dorsal view; 710 – ditto, lateral view.

taxon, supported by several 'strong' autapomorphies, e.g. explanate outer margin of protibia and metatibia, concealing denticles. Absent frontal and supraorbital striae can be regarded as putative synapomorphies, shared also with several other taxa, e.g. the '*Eremosaprinus* – *Myrmetes* – *Gnathoncus*' complex. Especially puzzling is the ciliate elytral epipleuron, which possibly represents an evolutionary reversal, or, alternatively a plesiomorphy.

***Turanostyphrus ignoratus* Tishechkin, 2005**

(Figs. 7, 138, 694–710)

Turanostyphrus ignoratus Tishechkin, 2005: 349, Figs. 1, 2, 5–8.

Type locality. Turkmenistan, Repetek.

Type material. HOLOTYPE: ♂, 'Turkm [= Turkmenistan], Repetek / *Haloxylon persicum* scrub, pitfall trap / 28.iv.[1]967, B. Kuznetsov [written] // *Hypocacculus eremobius* Rchdt. / Kryzhanovskij det. 1981 [printed-written] // HOLOTYPE / *Turanostyphrus ignoratus* sp. n. / A. Tishechkin des. 2004 [red label, printed-written] / D07-054 [pink label, written]' (ZIN).

Redescription. Body length: PEL: 1.625 mm; APW: 0.60 mm; PPW: 1.25 mm; EL: 1.075 mm; EW: 1.475 mm.

Body (Figs. 694–695) oval, dorsally rather flattened, moderately convex ventrally; cuticle light brown; antennal club and tarsi yellowish.

Antennal scape (Fig. 697) imbricate, slightly thickened, asetose; club (Figs. 7, 696) ovoid, without visible articulation, apical two-thirds (roughly) with rather sparse short sensilla; basal third of club (roughly) imbricate; sensory structures of antennal club not examined.

Mouthparts. Mandibles with rounded outer margin, mandibular apex acute; terminal labial palpomere truncate, elongate, its width about one-third its length; mentum sub-trapezoid, anterior margin medially with deep notch (Fig. 138), surrounded with several moderately long setae; lateral margins as well as disc of mentum with several similar setae; cardo of maxilla with several short setae; stipes triangular, with three short setae; terminal maxillary palpomere truncate, thickened, its width about half its length; remaining mouthparts not examined.

Clypeus (Fig. 697) rectangular, rounded laterally, imbricate-punctate; frontal and supraorbital striae absent; frontal disc (Fig. 697) imbricate-punctate, posterior third medially with shallow pit; eyes flattened, but visible from above.

Pronotal sides (Fig. 694) moderately narrowed anteriorly, apical angles obtuse; pronotal foveae absent; marginal pronotal stria complete, carinate laterally; pronotal disc medially regularly punctate, laterally punctures confluent, creating elongate wrinkles, interspaces imbricate; pronotal hypomeron setose; scutellum small, visible.

Elytral epipleura with short dense setae (Fig. 700); marginal epipleural and marginal elytral striae indistinct; humeral elytral stria weakly impressed on basal sixth; inner subhumeral stria well impressed, rather long, situated laterad to humeral elytral stria, almost reaching elytral apex, apically reaching as far as four-fifths of elytral length; elytra with four rather thin, impunctate dorsal elytral striae 1–4, apically reaching about elytral half; fourth dorsal elytral stria basally connected with complete sutural elytral stria; sutural elytral stria well impressed, complete, apically connected with vaguely impressed complete apical elytral stria. Elytral disc entirely covered with sparse, shallow punctures, punctures smaller and sparser apically, interspaces imbricate.

Propygidium partly covered by elytra, transverse, with punctation similar to that of elytral apex, interspaces imbricate; pygidium with similar, if somewhat sparser punctation, interspaces imbricate.

Anterior margin of median portion of prosternum (Fig. 699) almost straight, pre-apical foveae absent; marginal prosternal stria present laterally; prosternal process flattened; surface between carinal prosternal striae substrigulate; laterally strigulate-punctate; carinal prosternal striae distinctly divergent on prosternal apophysis, approximate, sub-parallel, slightly divergent apically, vaguely united anteriorly; surface between apices of carinal prosternal striae and anterior prosternal margin distinctly depressed; lateral prosternal striae well impressed, shortened, slightly carinate, convergent anteriorly, attaining carinal prosternal striae, but not united with them; anterior margin of mesoventrite deeply emarginate medially; discal marginal mesoventral stria laterally well impressed, widely obliterated anteriorly; disc of mesoventrite flattened, with shallow scattered punctation; meso-metaventral sutural stria

well impressed, sinuate, slightly distanced from meso-metaventral suture; intercoxal disc of metaventrite convex, with irregular sparse fine punctures, becoming larger and denser posteriorly; metaventrite with longitudinal suture. Lateral metaventral stria (Fig. 700) well impressed, carinate, slightly sinuate, almost reaching hind coxa; lateral disc of metaventrite (Fig. 700) flattened, with scattered shallow punctures, interspaces imbricate; metepisternum (Fig. 700) with larger and deeper punctures, interspaces imbricate; fused metepimeron with sparser punctation, several punctures with microscopic setae, interspaces not imbricate.

Intercoxal disc of the first abdominal sternite completely striate laterally; surface of disc with sparse fine scattered punctation, interspaces imbricate.

Protibia (Figs. 701–702) dilated, outer margin explanate, almost completely concealing dense row of short rounded denticles continuous along apical protibial margin and well observable only from ventral view (Fig. 702); anterior surface of protibia substrigulate; protarsal groove deep; setae of outer and median rows absent; two tiny tarsal denticles present near tarsal insertion; protibial spur tiny, growing out from apical margin of protibia; outer part of posterior surface of protibia (Fig. 702) strigulate, separated from glabrous median part of posterior surface by clear-cut boundary; posterior protibial stria absent, inner posterior denticles absent; inner row of setae lamelliform, strongly sclerotized, moderately long.

Mesotibia slender, outer margin slightly explanate, almost concealing two sparse rows of rather short denticles well observable only from ventral view; posterior surface with one row of regular, dense, rather long setae, their affiliation with either outer or median row difficult to determine; posterior mesotibial stria inconspicuous; anterior surface of mesotibia substrigulate-punctate; anterior mesotibial stria complete; inner anterior denticles absent; mesotibial spur inconspicuous, short; apical margin of mesotibia anteriorly without denticles; inner margin of mesotibia asetose; claws of apical tarsomere slightly bent, longer than half of apical-most tarsomere itself; metatibia (Figs. 703–704) dilated, posterior surface with single row of dense, long setae, their affiliation with either outer row or median row difficult to determine; posterior metatibial stria vaguely impressed on basal half; outer margin (Fig. 704) explanate, completely concealing two rows of morphologically different denticles observable only from ventral view, situated on anterior surface of metatibia: upper row sparse and denticles thin, acutely pointed and rather long, lower row of much denser, shorter rounded denticles; surface between these two rows imbricate; anterior metatibial stria absent; surface between lower row of denticles and inner metatibial margin substrigulate; inner margin of metatibia with single row of moderately dense and long setae; claws of apical-most metatarsomere slightly bent, longer than half its length.

Male genitalia. Eighth sternite (Figs. 705–706) weakly sclerotized, completely fused along its entire length, apically with small inflatable membrane (velum), without setae; eighth tergite and eighth sternite fused laterally (Fig. 707). Ninth tergite (Fig. 708) typical for the subfamily; spiculum gastrale lost during manipulation with genitalia. Aedeagus (Figs. 709–710) slender; basal piece of aedeagus rather short, ratio of its length : length of parameres 1 : 4.30; parameres fused along their basal two-thirds; aedeagus slightly curved ventrad (Fig. 710).

Xenonychus Wollaston, 1864

Xenonychus Wollaston, 1864: 179. Type species: *Xenonychus fossor* Wollaston, 1864 (= *Saprinus tridens* Jacquelin-Duval, 1852), by monotypy.

Xenonychus: Marseul (1864): 358; Schmidt (1887): 354; Ganglbauer (1899): 394; Reitter (1910): 13 (partim); Bickhardt (1913): 32; Bickhardt (1916–1917): 81, 102 (partim); Reichardt (1925): 137; Reichardt (1926): 14; Reichardt (1941): 156, 334; Peyerimhoff (1936): 227; Kryzhanovskij & Reichardt (1976): 112, 242; Vienna (1980): 115, 198; Mazur (1984): 108; Mazur (1997): 267; Yélamos (2002): 245, 340; Mazur (2004): 101.

Diagnosis. Cuticle dark brown with bronze to greenish hue; frontal disc smooth or laterally with vaguely impressed rugae, frontal stria straight or slightly curved outwardly (occasionally interrupted); eyes flattened, invisible from above. Pronotal foveae absent, disc shallowly punctate; pronotal hypomeron setose; dorsal elytral striae 1–4 almost reaching elytral apex; elytral epipleuron setose. Pre-apical foveae large and deep, both sets of prosternal striae present; lateral discs of ventrites and all visible abdominal sternites setose. Outer margin of protibia with three large distal triangular teeth topped with large triangular rounded denticle, followed by 5 short proximal denticles; claws of meso- and metatarsomeres long, almost straight.

Differential diagnosis. *Xenonychus* is the only genus of the Palaearctic Saprininae that has almost complete dorsal elytral striae 1–4, stopping short of elytral apex. Judging from its general appearance it could be confused with the genera *Chivaenius* or *Exaesiopus*, but differs from them by the almost complete dorsal elytral striae; furthermore it differs from *Chivaenius* by the present, well developed pre-apical foveae (absent in *Chivaenius*), setose elytral epipleuron (glabrous in *Chivaenius*) as well as the differently shaped prosternum (knife-like, strongly compressed in *Chivaenius*) and the differently shaped protibia. From *Exaesiopus* it likewise differs by the length of dorsal elytral striae, as well as by the shape of protibia, frontal disc (with elongate rugae in *Exaesiopus* and almost glabrous in *Xenonychus*) and the glabrous elytral epipleuron.

Biology. Both species of the genus *Xenonychus* are typical inhabitants of the desert areas and shifting sands, often found on carrion, usually together with the other psammophilous Saprininae (Lackner, pers. observ.).

Distribution. This genus has two Palaearctic representatives: *Xenonychus tridens* (Jacquelin-Duval, 1852) distributed from the Cape Verde Archipelago and Canary Islands through the Sahara Belt along the Mediterranean coasts as far as the Arabian Peninsula; and *X. aralocaspius* Kryzhanovskij, 1976 in Kryzhanovskij & Reichardt (1976), occurring around the Caspian and Aral Seas (Kryzhanovskij & Reichardt 1976, Mazur 1997).

Species examined. *Xenonychus aralocaspius* Kryzhanovskij, 1976; *Xenonychus tridens* (Jacquelin-Duval, 1852).

Discussion. This taxon is probably sister to the most derived 'grade' of Palaearctic Saprininae: genera *Philothis* and *Ctenophilothis* as indicated by the results of the preliminary cladistic analysis (Lackner, in prep.). It is probably a monophyletic taxon supported by several putative synapomorphies: almost complete dorsal elytral striae, large, well-developed pre-apical foveae, but these characters might be also plesiomorphies. Setose underside of the body, shape of protibia and flattened eyes are possible homoplasies that have little informativness for the phylogeny of Saprininae in general.

Xenonychus tridens (Jacquelin-Duval, 1852)

(Figs. 28, 72, 106, 139, 711–729)

Saprinus tridens Jacquelin-Duval, 1852: 703.
Saprinus tridens: Marseul (1855): 501, t. XIX, Fig. 118; Schmidt (1885a): 309.
Saprinus ciliaris Mulsant & Rey, 1853: 99. Synonymized by Kraatz (1858): 131.
Saprinus serripes Marseul, 1855: 677. Synonymized by Marseul (1862): 482.
Xenonychus fossor Wollaston, 1864: 181. Synonymized by Schmidt (1887): 354.
Saprinus (*Hypocaccus*) *tridens*: Schmidt (1885a): 309.
Styphrus tridens: Bickhardt (1910): 107; G. Müller (1931): 102.
Xenonychus tridens: Ganglbauer (1899): 394; Reitter (1910): 13; Reichardt (1941): 334; Thérond (1963): 69; Kryzhanovskij & Reichardt (1976): 112, 242, Fig. 471; Vienna (1980): 115, 198, Fig. 70; Mazur (1984): 108; Mazur (1997): 267; Yélamos (2002): 245, 340, Figs. 12A, 161H, 170B, 171; Mazur (2004): 101.
Note. Sensory structures of antennal club and spermatheca were studied by De Marzo & Vienna (1982a,b).

Type locality. France, Le Grau de Roi.
Type material. *Xenonychus tridens*. Neotype (here designated): ♂, 'FRANCE / Le Grau de Roi / (13) 8.viii.1962 [written] // tamissage au / pied des / Graminées [written] // Y. Gomy [printed] // Collection Y. Gomy [printed] // NEOTYPUS / *Xenonychus* / *tridens* / (Jacquelin-Duval, 1852) / Des. T. Lackner 2009 [red label, written]' (MNHN).
Comment. The type specimen of this species was not found in the collection of Jacquelin-Duval housed in MNHN. According to Mrs. Azadeh Taghavian, the type specimen of this species is probably lost, since there is an empty mounting card with the label '*Saprinus tridens*'. Although the author has inspected the fragments of various histerids on the bottom of the box, none of them contained pieces of *Xenonychus tridens*. The neotype is designated here to fix the identity of the type species of *Xenonychus*.
Additional material examined. ALGERIA: Ghardaia, 1.v.1987, 1 ♂, A. Olexa lgt.; Sahara, Béni Abbès, 20.x.1980, 1 ♀, A. Olexa lgt.; 1 ♂, ditto, but 27.iv.1987; Ain Sefra, 26.iv.1987, 1 ♂, A. Olexa lgt. **MOROCCO**: Mogador [= Essaouira], 2 ♀♀, Quedenfeldt lgt. (TLAN).

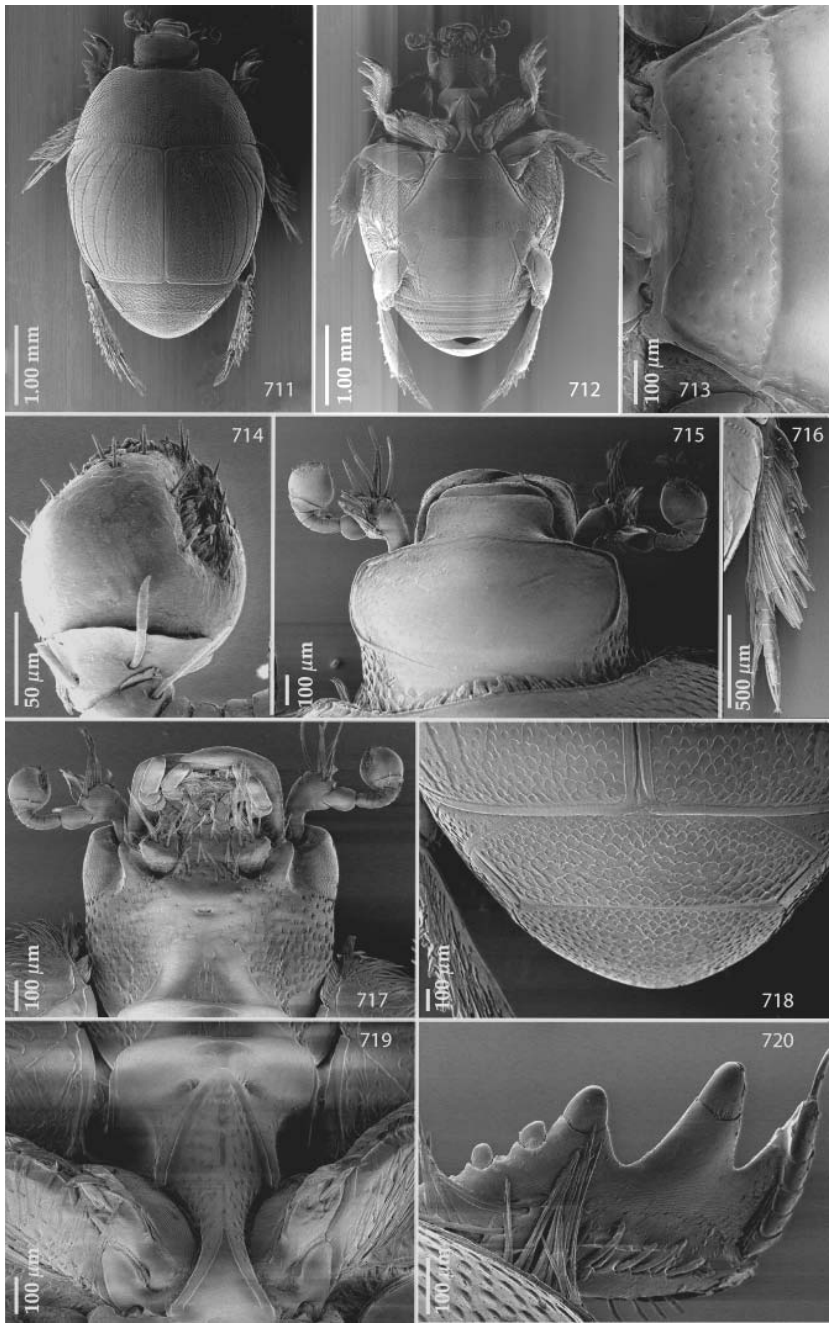
Redescription. Body length: PEL: 2.175–2.80 mm; APW: 0.825–1.075 mm; PPW: 1.775–2.125 mm; EL: 1.425–1.70 mm; EW: 1.975–2.475 mm.

Body (Figs. 711–712) ovoid, moderately convex from above, underside strongly convex, cuticle light to dark brown with feeble bronze metallic tinge; legs, mouthparts and antennal scape rufopiceous, antennal flagellum yellow.

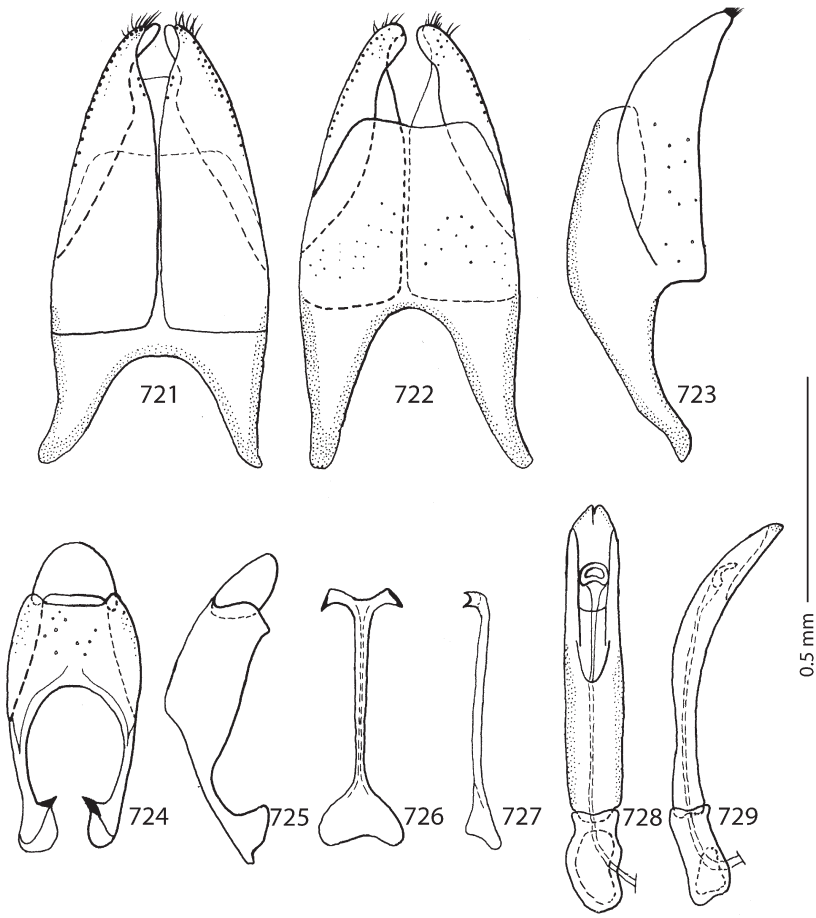
Antennal scape (Fig. 715) with long numerous setae; club (Fig. 714) rather small, without visible articulation, surface (apart from two sensory areas on apical part of club furnished with thick short sensilla, intermingled with thicker sparse erect sensilla) glabrous; sensory structures of antennal club (Fig. 28) in form of stipe-shaped vesicle situated under circular sensory area on internal distal margin of the ventral side of antennal club.

Mouthparts. Mandibles (Fig. 106) with straight carinate outer margin strongly curved inwardly; mandibular apex acutely pointed; sub-apical tooth on left mandible prominent, acute; labrum (Fig. 72) almost smooth, slightly convex; labral pits with single weakly sclerotized seta; epipharynx almost completely hidden under labral fold; terminal labial palpomere elongated, its width about one-third its length; mentum sub-trapezoid, anterior margin (Fig. 139) with shallow median notch, surrounded with several moderately long ramose setae, disc of mentum with few similar setae, lateral margins with single row of shorter ramose setae; cardo of maxilla on lateral margin with several long setae; stipes triangular, with numerous much longer setae; terminal maxillary palpomere elongated, its width about one-third its length, approximately twice as long as penultimate.

Clypeus (Fig. 715) rectangular, broader than long, slightly depressed laterally, with scattered microscopic punctation, almost smooth; frontal stria well impressed, thin, almost



Figs. 711–720. *Xenonychus tridens* (Jacquelin-Duval, 1852), SEM micrographs: 711 – habitus, dorsal view; 712 – ditto, ventral view; 713 – mesoventrite; 714 – antennal club, ventral view; 715 – head, dorsal view; 716 – mesotibia, dorsal view; 717 – head, ventral view; 718 – propygidium and pygidium; 719 – prosternum; 720 – protibia, dorsal view.



Figs. 721–729. *Xenonychus tridens* (Jacquelin-Duval, 1852), male terminalia: 721 – 8th sternite and tergite, ventral view; 722 – ditto, dorsal view; 723 – ditto, lateral view; 724 – 9th tergite and 10th tergite, dorsal view; 725 – ditto, lateral view; 726 – spiculum gastrale, ventral view; 727 – ditto, lateral view; 728 – aedeagus, dorsal view; 729 – ditto, lateral view.

straight (occasionally weakened medially or interrupted), continued as well impressed carinate supraorbital stria; frontal disc (Fig. 715) flat, almost smooth, broader than long, laterally exceptionally with vague interrupted rugae; eyes very flattened, invisible from above.

Pronotal sides (Fig. 711) moderately convergent forwardly; apical angles prominent; anterior incision for head shallow; marginal pronotal stria well impressed, complete; disc entirely covered with shallow round regular punctation, becoming denser laterally; pronotal base with a row of oval dense punctures; pronotal hypomeron with long yellow setae; scutellum small, conspicuous.

Elytral epipleuron with round, rather deep punctures fringed with long setae; marginal epipleural stria complete; marginal elytral stria deeply impressed, continued as weakly impressed (at times intermittent) apical elytral stria. Humeral elytral stria distinctly impressed on basal third; inner subhumeral stria present medially, deep, rather long, rarely joining marginal elytral stria; elytra with four dorsal elytral striae 1–4, almost reaching elytral apex (seldom fourth dorsal elytral stria slightly shortened apically), fourth dorsal elytral stria basally connected with sutural elytral stria; sutural elytral stria well impressed, apically usually connected with apical elytral stria. Elytral punctation confined to interspace between fourth dorsal and sutural elytral striae, basally along elytral suture almost reaching elytral base, punctation irregular and shallow, becoming confluent apically.

Propygidium (Fig. 718) completely exposed, with shallow confluent punctures of various sizes; pygidium (Fig. 718) long, with similar punctation, punctures becoming finer and sparser apically.

Anterior margin of median portion of prosternum (Fig. 719) almost straight; marginal prosternal stria present laterally and as short anterior fragment; pre-apical foveae deep; prosternal process slightly concave, compressed, surface between lateral prosternal striae substrigulate-punctate, punctures shallow, surface laterad to lateral prosternal striae substrigulate, impunctate; carinal prosternal striae divergent on prosternal apophysis, thence strongly convergent, intermittent, vaguely attaining united lateral prosternal striae; lateral prosternal striae well impressed, carinate, convergent anteriorly, united in front.

Anterior margin of mesoventrite (Fig. 713) shallowly emarginate medially; discal marginal mesoventral stria well impressed, carinate, weakened anteriorly; disc with scattered deep punctures separated by about 2–3 times their diameter; meso-metaventral sutural stria (Fig. 713) well impressed, almost straight, undulate, exposing meso-metaventral suture; intercoxal disc of metaventrite almost smooth, only with microscopic punctation, along base with a band of irregular deep punctation; lateral metaventral stria well impressed, carinate, obliquely arcuate, shortened apically; lateral disc of metaventrite concave, with deep setiferous punctures of various sizes; metepisternum + fused metepimeron with very dense setae, punctation unrecognizable beneath them.

Intercoxal disc of the first abdominal sternite almost completely striate laterally; basal half of disc with punctures of varied sizes, separated by about their own to twice their own diameter, apically replaced by very fine scattered microscopic punctation; along apical margin a row of larger punctures appears; lateral disc of all visible abdominal sternites setose laterally.

Protibia (Fig. 720) flattened and dilated, outer margin with three large triangular teeth topped with moderately large triangular denticle, followed by five short rounded denticles diminishing in size in proximal direction; setae of outer row long, confined to basal third of protibia; setae of median row much shorter than those of outer row, but strongly sclerotized and present almost along entire length of protibia; protarsal groove rather deep; anterior protibial stria inconspicuous; single, short tarsal denticle present apically; protibial spur tiny, bent, growing out from apical protibial margin; apical margin of protibia posteriorly with two tiny apical denticles; outer part of posterior surface of protibia areolate-rugose; distinctly separated from glabrous median part of posterior surface; posterior protibial stria complete; inner-ventral denticles absent; inner margin with row of strongly sclerotized lamelliform long setae.

Mesotibia (Fig. 716) slightly thickened, outer margin with two dense rows of thin denticles growing in size apically, abutting each other; posterior mesotibial surface with dense, strongly sclerotized long setae growing out near inner mesotibial margin and covering almost entire posterior surface of mesotibia, their affiliation with either dorsal or median row dubious; posterior mesotibial stria inconspicuous; anterior surface of mesotibia glabrous; anterior mesotibial stria almost complete, shortened apically; mesotibial spur long and thin; apical margin with several short denticles; claws of apical tarsomere almost straight, almost as long as apical-most mesotarsomeres itself; each tarsomere with single long strongly sclerotized seta posteriorly and anteriorly; metatibia basically similar to mesotibia, but more thickened and dilated and denticles on outer margin much longer, three rows of denticles present (as opposed to two in mesotibia).

Male genitalia. Eighth sternite (Figs. 721–722) segment longitudinally separated medially, apically with tiny inflatable membrane (velum); apex laterally fringed with short brush of setae; eighth tergite and eighth sternite fused laterally (Fig. 723). Morphology of 9th tergite (Figs. 724–725) typical for the subfamily; spiculum gastrale (Fig. 726) expanded on both ends. Basal piece of aedeagus (Figs. 728–729) rather short, ratio of its length : length of parameres 1 : 4; parameres fused along their basal half; aedeagus slightly curved ventrad (Fig. 729).

Remarks. *Xenonychus tridens* is a widely distributed species and as such exhibits a large degree of variation, especially regarding punctation of dorsal surface, frontal stria and other characters.

Xenophilothis Kryzhanovskij, 1987

Xenophilothis Kryzhanovskij, 1987: 25. Type species: *Philothis choumovitchi* Thérond, 1965 in Thérond & Hollande (1965), original designation.

Xenophilothis: Olexa (1990): 142; Mazur (1997): 267, Mazur (2004): 101.

Diagnosis. Cuticle not metallic; head comparatively small, narrow; eyes convex, visible from above, clypeus very large, semicircular; labrum larger than clypeus, expanding anteriorly; mentum widening anteriorly, anterior margin fringed with a dense row of long lamelliform setae; antennal scape thickened, with deep large punctures with long lamelliform setae; frontal stria vaguely impressed, frontal disc with confluent elongate prominent punctures. Pronotal sides strongly convergent anteriorly, anterior angles very acute and prominent, marginal pronotal stria complete; pronotal foveae absent; disc with irregular confluent punctures and wrinkles; pronotal hypomeron with long dense setae. Inner subhumeral stria complete, originating near elytral base, parallel to marginal elytral stria; dorsal elytral striae 3–5 strongly reduced basally; elytral epipleura setose; apical elytral stria obliterated; sutural elytral stria abbreviated on basal third. Pre-apical foveae absent, prosternal process compressed, punctate and setose, both sets of prosternal striae present, reduced. Protibia with two large triangular distal teeth topped by tiny rounded denticle, second tooth conspicuously larger than first, followed by a much shorter tooth topped by conspicuous denticle and followed by two microscopic denticles; all tarsal claws thin, straight, several times as long as apical-most tarsomere itself.

Differential diagnosis. *Xenophilothis* is doubtless the most curious and peculiar genus of the Palaearctic Saprininae, differing from the all known taxa by its peculiar shape of mentum (in all studied taxa it is rectangular, sub-rectangular or sub-trapezoid) that is widening ante-

riorly, fringed with a dense row of long lamelliform setae, by the extraordinary labrum that is larger than clypeus (labrum is never larger than clypeus in all studied taxa) as well as by the almost complete inner subhumeral stria, originating from the elytral base and resembling a true dorsal elytral stria and by the basally strongly reduced dorsal elytral striae. Likewise, the shape of outer margin of protibia is very peculiar: second tooth is much larger than the first (usually teeth or denticles diminish in size in proximal direction). By the combination of these characters it cannot be confused with any currently known Palaearctic taxon.

Biology. *Xenophilothis* is a psammophilous genus, collected in pitfall traps in Saudi Arabia (Kryzhanovskij 1987); it has also been collected at light (Kanaar 2008).

Distribution. *Xenophilothis* contains a single species so far recorded from Algerian Sahara and deserts of Saudi Arabia, Oman and the United Arab Emirates (Mazur 1997, Kanaar 2008).

Discussion. This taxon is characterised by many autapomorphies: mentum widening anteriorly, anterior margin of mentum fringed with dense row of long lamelliform setae, large, semi-circular clypeus, labrum larger than clypeus and peculiarly shaped protibia with second tooth comparatively larger than first. Among possible plesiomorphic characters could be listed the complete inner subhumeral stria, non-dilated meso- and metatibiae, present protarsi. In the preliminary cladistic analysis of the Palaearctic genera of Saprininae (Lackner, in prep.) this genus comes near the most-derived genera like *Philothis* or *Ctenophilothis*.

Species examined. *Xenophilothis choumovitchi* (Thérond, 1965).

Xenophilothis choumovitchi (Thérond, 1965)

(Figs. 29, 73, 107, 140, 143, 145, 730–746)

Philothis choumovitchi Thérond, 1965 in Thérond & Hollande (1965): 858, Fig. 1.
Philothis choumovitchi: Mazur (1984): 109.
Xenophilothis choumovitchi: Kryzhanovskij (1987): 26; Olexa (1990): 142, figs. 1, 7, 14, 23, 28, 29; Mazur (1997): 267; Mazur (2004): 101.

Type locality. Algeria, Béni Abbès.
Type material. Paratype: ♂, 'Béni-Abbès / Saouza / iv.1960 / J. Thérond [written] // *Philothis* / *choumovitchi* / nov. sp. [written] // Paratype (red label, written) // 06-040 (blue label, written) // D07-034 [pink label, written]' (TLAN).
Additional material examined. UNITED ARAB EMIRATES: SSW of Ad Dhaid, 25º09'N 55º48'E, at light, 23.iv.2005, 1 spec., A. van Harten & K. Szpila lgt. (TLAN).

Redescription. Body length: PEL: 2.25–2.65 mm; APW: 0.60–0.65 mm; PPW: 1.70–1.825 mm; EL: 1.375–1.625 mm; EW: 1.825–2.125 mm.

Body (Figs. 730–731) ovoid, dorsally convex, ventrally somewhat flattened, cuticle brown; legs and mouthparts rufopiceous, antennal scape yellow.

Antennal scape (Fig. 733) strongly thickened, with numerous long lamelliform setae inserted in deep round punctures; club (Fig. 734) comparatively small, flattened dorso-ventraly, without visible articulation, almost entirely glabrous apart from apical elongate sensory area densely covered with short sensilla intermingled with much sparser, erect sensilla; sensory structures of antennal club (Fig. 29) in form of stipe-shaped vesicle situated under large apical sensory area.

Mouthparts. Mandibles (Fig. 107) with rounded lateral margins, short and stout; mandibular apex obtuse, concealing a tiny acute tooth situated between dorsal and ventral mandibular

surface; sub-apical tooth inconspicuous; labrum (Fig. 73) conspicuously large, larger than clypeus, microscopically punctate, almost smooth; setae of lateral fringe growing out from ventral side of labrum; labral pits and setae absent; terminal labial palpomere strongly thickened, its width approximately equals its length; mentum (Figs. 143, 732) large, broadening anteriorly, anterior margin (Fig. 143) with numerous long lamelliform setae, lateral margins and disc of mentum glabrous; cardo of maxilla with single rather long lamelliform seta; stipes (Fig. 145) triangular, with three long lamelliform setae; terminal maxillary palpomere (Fig. 145) gradually narrowing anteriorly, its width approximately half its length, several times as long as penultimate; remaining mouthparts not examined.

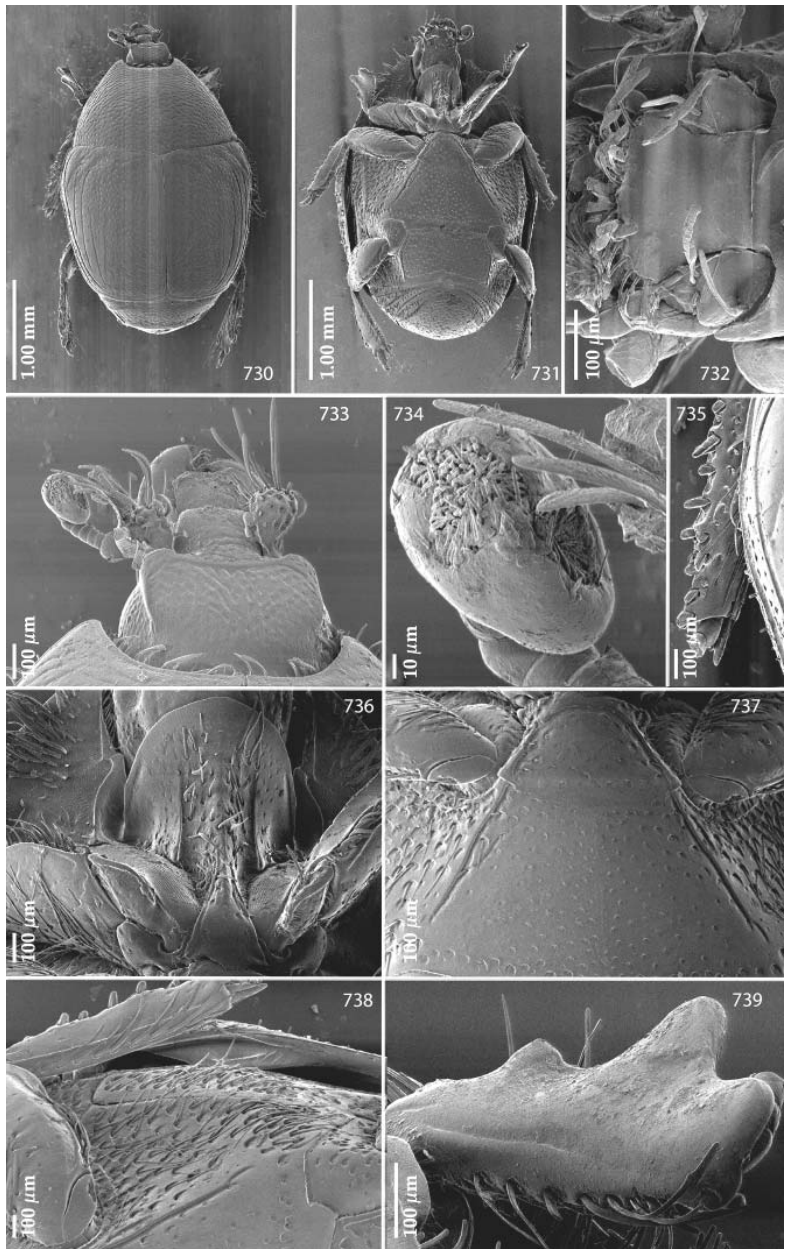
Clypeus (Fig. 733) comparatively large, broadening anteriorly, anterior half smooth, posterior half with fine granularity; frontal stria well-impressed, carinate, acutely angularly elevated behind eyes; supraorbital stria vague; frontal disc (Fig. 733) shallowly rugulose-lacunose; eyes convex, visible from above.

Pronotal sides (Fig. 730) strongly convergent anteriorly; apical angles very acute, anterior pronotal margin with a deep semicircular incision for head; marginal pronotal stria well impressed, carinate on lateral margins, weakened behind head; pronotal disc moderately convex, with deep irregular dense confluent punctures, laterally and anteriorly turning into coarse longitudinal wrinkles; pronotal hypomeron with long yellow setae; scutellum small, well-visible.

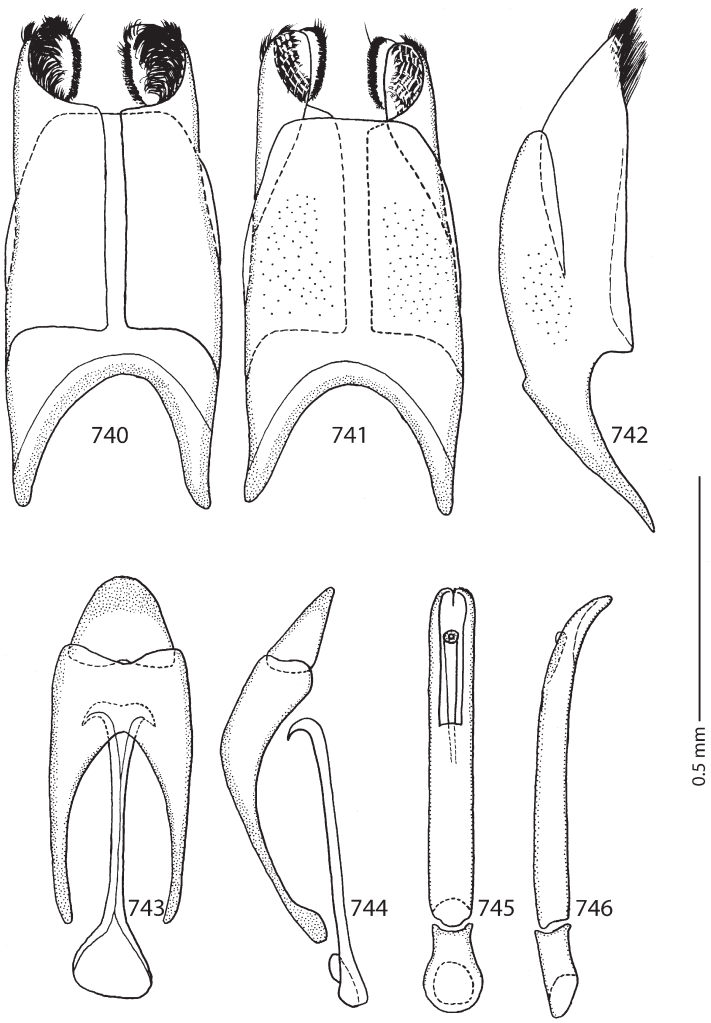
Elytral humeri prominent, epipleura setose, densely and coarsely punctate; marginal epipleural stria thin, complete, shortly continued along elytral apex; marginal elytral stria well impressed, carinate and bisinuate, almost reaching elytral apex; apical elytral stria obliterated; surface between marginal elytral and inner subhumeral striae with sparse setae. Humeral elytral stria vaguely impressed on basal fifth; inner subhumeral stria complete, carinate, originating almost from elytral base, parallel to marginal elytral stria; first dorsal elytral stria present on basal half, next evanescent; second dorsal elytral stria reaching about three-fourths of elytral length apically; third dorsal elytral stria obliterated on basal half, reaching nine-tenths of elytral length apically; fourth dorsal elytral stria basally slightly shorter than third; fifth dorsal elytral stria absent; sutural elytral stria well impressed, on basal half slightly distanced from elytral suture, on apical tenth obliterated; interspace between sutural elytral stria and elytral suture on basal third with additional thin short stria, sutural stria shortly continuous along elytral base as basal elytral stria, in several deep punctures; elytral base somewhat elevated, without bulge. Elytral disc with dense round and deep punctation, punctures becoming sparser laterally, elytral humeri and flanks almost smooth; medio-apical area of elytral disc finely rugulose, matt.

Propygidium completely exposed, transverse, about half as long as broad, with dense large shallow punctures of various shapes and sizes, space inside punctures with micro-punctures; pygidium about as long as broad, convex, with dense confluent punctation, similar to that of propygidium, but sparser.

Anterior margin of median portion of prosternum (Fig. 736) evenly rounded; marginal prosternal stria present as vague lateral fragment; pre-apical foveae absent; prosternal process compressed, surface between and anterad of lateral prosternal striae substrigulate, with deep large punctures fringed with short setae; surface laterad to lateral prosternal striae substrigu-



Figs. 730–739. *Xenophilothis choumovitchi* (Thérond, 1965), SEM micrographs: 730 – habitus, dorsal view; 731 – ditto, ventral view; 732 – mentum, cardines and stipites of maxilla, ventral view; 733 – head, dorsal view; 734 – antennal club, dorsal view; 735 – mesotibia, dorsal view; 736 – prosternum; 737 – mesoventrite and metaventrite; 738 – lateral disc of metaventrite, metepisternum + fused metepimeron; 739 – protibia, ventral view.



Figs. 740–746. *Xenophilothis choumovitchi* (Thérond, 1965), male terminalia: 740 – 8th sternite and tergite, ventral view; 741 – ditto, dorsal view; 742 – ditto, lateral view; 743 – 9th tergite, 10th tergite (dorsal view) and spiculum gastrale (ventral view); 744 – 9th tergite, 10th tergite and spiculum gastrale, lateral view; 745 – aedeagus, dorsal view; 746 – ditto, lateral view.

late, finely punctate but punctures without setae; carinal prosternal striae vaguely impressed on prosternal apophysis, next erased; lateral prosternal striae straight, carinate, parallel, on apical third of prosternum evanescent.

Anterior margin of mesoventrite (Fig. 737) almost straight; discal marginal mesoventral stria well impressed, laterally carinate, slightly weakened anteriorly; disc of mesoventrite with deep round punctures of various sizes, some of the punctures with microscopic setae; meso-metaventral sutural stria absent; meso-metaventral suture well visible, almost straight;

intercoxal disc of metaventrite (Fig. 737) flattened, with scattered deep irregular-sized punctures finer than those of mesoventrite, with longitudinal suture in male; lateral metaventral stria (Fig. 738) well impressed, straight, carinate on outer margin, stopping short of hind coxa. Lateral disc of metaventrite (Fig. 738) concave, with irregular shallow punctures, fringed with long setae; metepisternum (Fig. 738) with similar punctures and setae, punctation almost unrecognizable; on fused metepimeron punctures slightly weaker.

Intercoxal disc of the first abdominal sternite with carinate striae laterally, with scattered deep punctation, similar to that of metaventrite; lateral discs of all visible abdominal sternites setose.

Protibia (Fig. 739) slightly dilated, with two large triangular distal teeth topped by tiny rounded denticle, second tooth conspicuously larger than first, followed by a much shorter tooth topped by conspicuous denticle, followed by two microscopic denticles; setae of outer row long, confined to basal half of protibia; setae of median row regular, shorter than those of outer row, but present along entire protibial length; protarsal groove shallow; anterior protibial stria complete; tarsal denticles absent; protibial spur large, stout, bent, growing out from near tarsal insertion (as in *Alienocacculus*); apical margin of protibia ventrally without denticles; outer part of posterior surface of protibia (Fig. 739) smooth, distinction between median part of posterior surface inconspicuous; posterior protibial stria vaguely impressed on basal two-thirds, next obliterated; inner margin with single row of dense long strongly sclerotized setae.

Mesotibia (Fig. 735) slender, outer margin with two dense rows of thin long denticles abutting each other; setae of outer row moderately dense, strongly sclerotized, rather long, longer than denticles themselves; setae of median row inconspicuous; posterior mesotibial stria inconspicuous; anterior surface of mesotibia glabrous; anterior mesotibial stria complete; mesotibial spur double, thin, rather long; apical margin with single short denticle; mesotarsomeres telescope-like, their diameter diminishes apically; each mesotarsomeres with one long sclerotized seta dorsally and one ventrally; claws of apical tarsomere thin, straight, twice as long as apical tarsomere itself; metatibia somewhat more dilated than mesotibia, outer margin with three teeth: basal-most tooth low, situated at approximately basal third of outer margin of metatibia, topped with moderately long stout denticle, median tooth large, triangular, supporting two close-set long stout denticles, third tooth shorter than second, situated near tarsal insertion, topped with single stout denticle; apart from these three teeth outer margin with another dense row of much shorter denticles, similar to that of mesotibia; metatibia otherwise similar to mesotibia, but setae of posterior metatibial surface dense, entirely covering it.

Male genitalia. Eighth sternite (Figs. 740–741) longitudinally separated medially, apically with large inflatable membrane (velum) fringed with dense brush of close-set moderately long setae; apex of eighth sternite laterally with short setae; eighth tergite and eighth sternite fused laterally (Fig. 742). Morphology of 9th tergite (Figs. 743–744) typical for the subfamily; spiculum gastrale expanded (Fig. 743) on both ends. Basal piece of aedeagus (Figs. 745–746) rather short, ratio of its length : length of parameres 1 : 4.75; parameres fused along their basal half; aedeagus only slightly curved ventrad apically (Fig. 746)

Remarks. This redescription is based on a paratype, a male from Algeria. The second available specimen of this species, originating from United Arab Emirates differs from the paratype in several aspects: inner subhumeral stria present only on basal half, next obliterated; first and second dorsal elytral striae reaching nine-tenths of the elytral length apically; fifth dorsal elytral

stria present as a short fragment on the apical fifth. Furthermore, the teeth on outer protibial margin are more articulated in this specimen (more obtuse with the paratype); the outer part of the ventral surface of protibia is transversely carinate (glabrous with the paratype), clearly separated from the median part of median surface by a clear-cut carinate stria; ventral tibial stria is complete and the teeth of metatibia are more articulated than those of the paratype. However, the structure of prosternum and the male genitalia are almost identical between the two specimens. The identity of the two specimens must be confirmed by study of larger series of specimens, preferably originating from the regions between the two very distant (more than 5000 km) localities.

Zorius Reichardt, 1932

Zorius Reichardt, 1932: 16, 25. Type species: *Saprinus funereus* Schmidt, 1890, original designation.
Zorius: Reichardt (1941): 154, 274; Dahlgren (1969c): 230; Kryzhanovskij & Reichardt (1976): 196; Mazur (1984): 78; Mazur (1997): 245; Mazur (2004): 101; Lackner (2009b): 120.

Diagnosis. Cuticle dark brown to pitch black, in *Zorius funereus* almost entirely imbricate, without metallic luster; anterior margin of clypeus elevated; frontal stria well impressed, slightly curved outwardly; pronotal foveae absent; pronotal hypomeron setose; both sets of prosternal striae present; pre-apical foveae absent. Protibia on outer margin with up to 10 low teeth topped with short denticle.

This genus has been recently revised by Lackner (2009b). For the sake of consistency its diagnosis, biology and distribution are repeated here, if slightly altered to fit the style used in this publication. Likewise, since this paper introduces some new terminology, this has also been taken into the account and the relevant parts are altered.

Differential diagnosis. Genus *Zorius* superficially most resembles the members of the genus *Saprinus* especially by the absence of pre-apical foveae, general body form and elytral striae. It differs from them by the presence of a complete frontal stria (usually widely interrupted in *Saprinus*), flattened eyes (usually convex and well-visible from above in *Saprinus*) and the anteriorly elevated clypeus (not elevated in *Saprinus*). The sensory structures of the antennal club likewise differ from those of the species of the genus *Saprinus*: antennal club of *Zorius* possesses one sensory area on internal distal side with a corresponding single vesicle beneath it, whereas species of *Saprinus* usually have multiple sensory areas on the ventral as well as dorsal sides of antennal club, sometimes supplemented by slit-like pits, with a single vesicle situated under one of them (for more details see Lackner (2009b)). Members of *Zorius* could further be confused with several species of the genus *Hypocacculus* or *Chalcionellus* but can be easily separated from them by a larger body size and absent pre-apical foveae (almost universally present in *Hypocacculus* and *Chalcionellus*). Further, *Zorius* lacks any metallic luster that is often present in the species of *Hypocacculus* or *Chalcionellus*.

Biology. *Zorius* is a very rare taxon, its biology is unknown.

Distribution. *Zorius funereus* (Schmidt, 1890) and *Z. exilis* Reichardt, 1932 are known from Palestine, Israel and Syria. *Zorius exilis* Reichardt, 1932 is known only from the holotype.

Mazur (1997) erroneously mentions *Zorius exilis* Reichardt, 1932 from Syria. The original description mentions Nablus, which is in Palestine. Also, the same author (Mazur 1997) mentions *Z. funereus* from Palestine and Syria, giving Palestine as the type locality. The correct

type locality is Haifa, which is not in Palestine, but in Israel (see also LACKNER 2009b).
Species examined. *Zorius exilis* Reichardt, 1932, *Z. funereus* (Schmidt, 1890).
Discussion. Taxonomic position of this rare genus is somewhat unclear; in the preliminary cladistic analysis of the Palaearctic Saprininae (LACKNER, in prep.) it came out near the *Hypocaccus – Eopachylopus – Exaesiopus* complex, but at that time the sensory structures of the antennal club have not been studied. It is probably a monophyletic taxon, supported by several putative synapomorphies: absent pre-apical foveae, complete frontal stria, elevated anterior margin of clypeus; on the other hand the ciliate pronotal hypomeron or protibia with numerous teeth on outer margin are possible homoplasies.

Zorius funereus (Schmidt, 1890)

(Figs. 30, 141, 747–766)

Saprinus funereus Schmidt, 1890: 82.
Saprinus sublaevis Sahlberg, 1913b: 17. Synonymized by REICHARDT (1941): 275.
Hypocacculus funereus: BICKHARDT (1916): 97.
Hypocacculus sublaevis: BICKHARDT (1916): 98.
Zorius funereus: REICHARDT (1932): 25, 94, 142; REICHARDT (1941): 275; DAHLGREN (1969): 230; KRYZHANOVSKIJ & REICHARDT (1976): 111, 196; MAZUR (1984): 78; MAZUR (1997): 245; MAZUR (2004): 101; LACKNER (2009b): 121, Figs. 1–10, 18–28.

Type locality. Israel, Haifa.
Type material. *Saprinus funereus*. SYNTYPES: ♀, 'KAIFA 1 [written] // Syrien / Kaifa / Reitter [black-framed label, printed] // *funereus* / Schm. typ [written] // *funereus* / Schmidt [double-framed, black and yellow label, written] // Type [brick-red label, printed] // coll. J. Schmidt [printed] // SYNTYPUS / *Saprinus funereus* / Schmidt, 1890 / labeled by ZMHB 2008 [red label, printed] // D08–083 [yellow label, written]'. ♀, 'Haifa / Simon [written] // Type [brick-red label, printed] // SYNTYPUS / *Saprinus funereus* / Schmidt, 1890 / labeled by ZMHB 2008 [red label, printed] // D08–081 [yellow label, written]' (ZMHB).
Additional material examined. ISRAEL: Zekharya, 17.v.[20]02, 1 ♂, Y. Mandelik & V. Chikatunov lgt.; Ramat Gan, 15.v.1944, 1 spec., collector unknown (TLAN).

Redescription. Body length: PEL: 3.45–3.50 mm; APW: 1.20–1.25 mm; PPW: 2.50–2.60 mm; EL: 2.00–2.10 mm; EW: 2.85–3.00 mm.

Body (Figs. 747–748) rectangular oval, convex; cuticle matt, pitch-black, large part of surface microscopically imbricate; legs and mouthparts dark-brown. Antennal scape dark brown, moderately thickened, with three setae; funicle and club lighter, rufopiceous; basal half of club glabrous, apical half with short sensilla intermingled with sparse longer erect sensilla; sensory structures of antennal club (Fig. 30) in form of stipe-shaped vesicle situated under circular sensory area on internal distal margin of the ventral side of antennal club.

Mouthparts. Mandibles with rounded outer margin curved inwardly, mandibular apex bluntly pointed; labrum coarsely punctate with two well impressed labral pits; two setae arising from each; terminal labial palpomere elongated, its width about one-fourth its length; mentum sub-trapezoid; anterior margin (Fig. 141) medially with a shallow notch; anterior margin with a row moderately long ramose setae; lateral margins with one row of shorter ramose setae; disc of mentum imbricate, with sparse short setae; cardo of maxilla on outer margin with few short setae; stipes triangular, with three longer setae; terminal maxillary palpomere elongated, its width about one-fourth its length.

Clypeus (Fig. 749) regularly and densely punctate, rounded laterally; anterior margin elevated; frontal stria well impressed, complete, slightly curved outwardly, interrupted behind eyes; supraorbital stria vaguely impressed (absent?); frontal disc (Fig. 750) evenly punctate, punctures separated by their own to twice their own diameter, interspaces imbricate; anterolaterally with two shallow depressions and one rather deep depression in mid-posterior area; eyes flattened, visible from above.

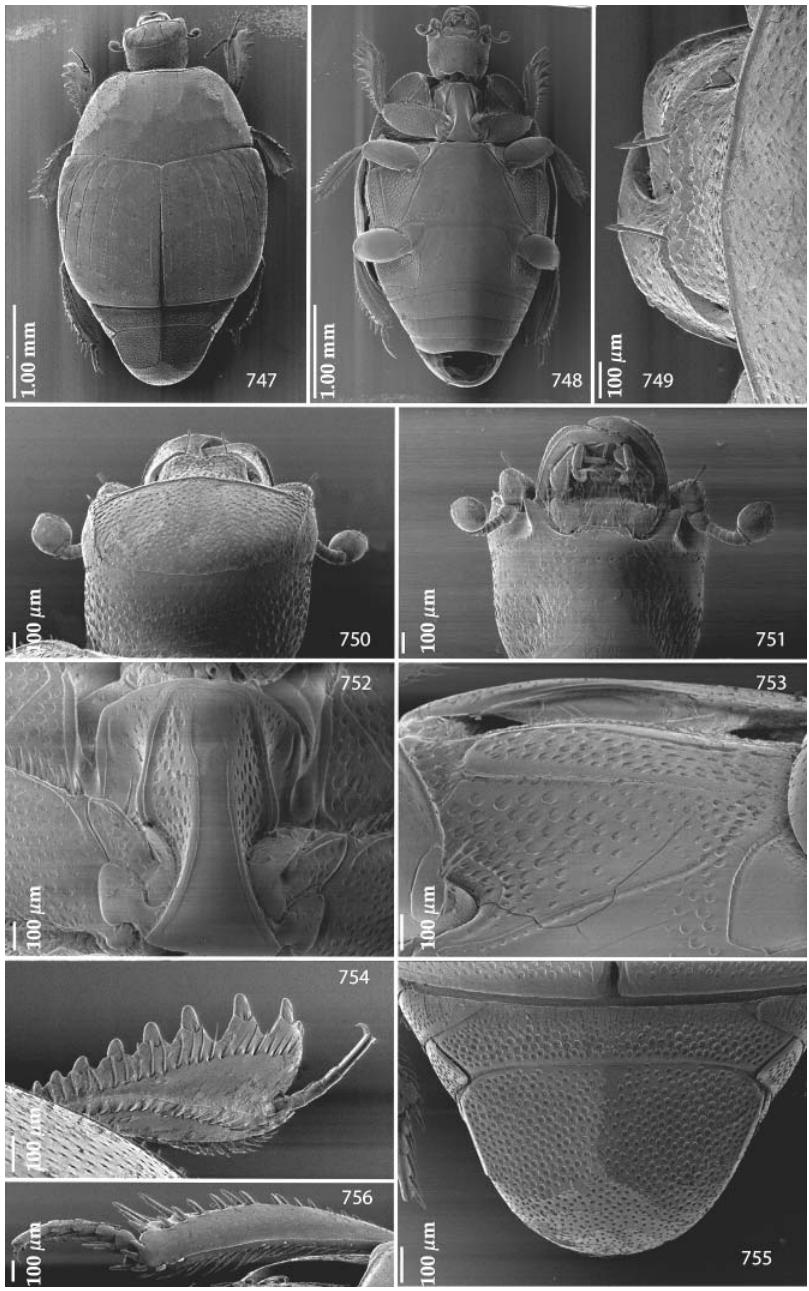
Pronotal sides (Fig. 747) evenly arcuate, slightly convergent forward on basal two-thirds, thence moderately convergent apically; apical angles blunt; pronotal foveae absent; marginal pronotal stria well impressed, carinate, on apical tenth slightly distanced from pronotal margin; pronotal disc flattened; laterally coarsely and densely punctate, punctures become fine and sparse medially; pronotal base with a row of deep round punctures; pronotal hypomeron with short amber setae.

Elytral epipleura almost smooth, finely imbricate; marginal epipleural stria complete, well impressed; marginal elytral stria well impressed, in deep round punctures, apically continued as complete (rarely vaguely impressed) apical elytral stria; humeral elytral stria vaguely impressed on basal third; inner subhumeral stria present as medial fragment, occasionally joining humeral elytral stria apically; elytra with four dorsal elytral striae 1–4, about the same length, surpassing three-fourths of elytral length apically, fourth dorsal elytral stria basally connected with complete sutural elytral stria; entire elytral disc with punctation, punctures becoming finer and sparser on basal two-thirds; on apical third punctation becomes denser and larger, interspaces imbricate; extreme apical band of elytra just before the apical stria translucent, reddish.

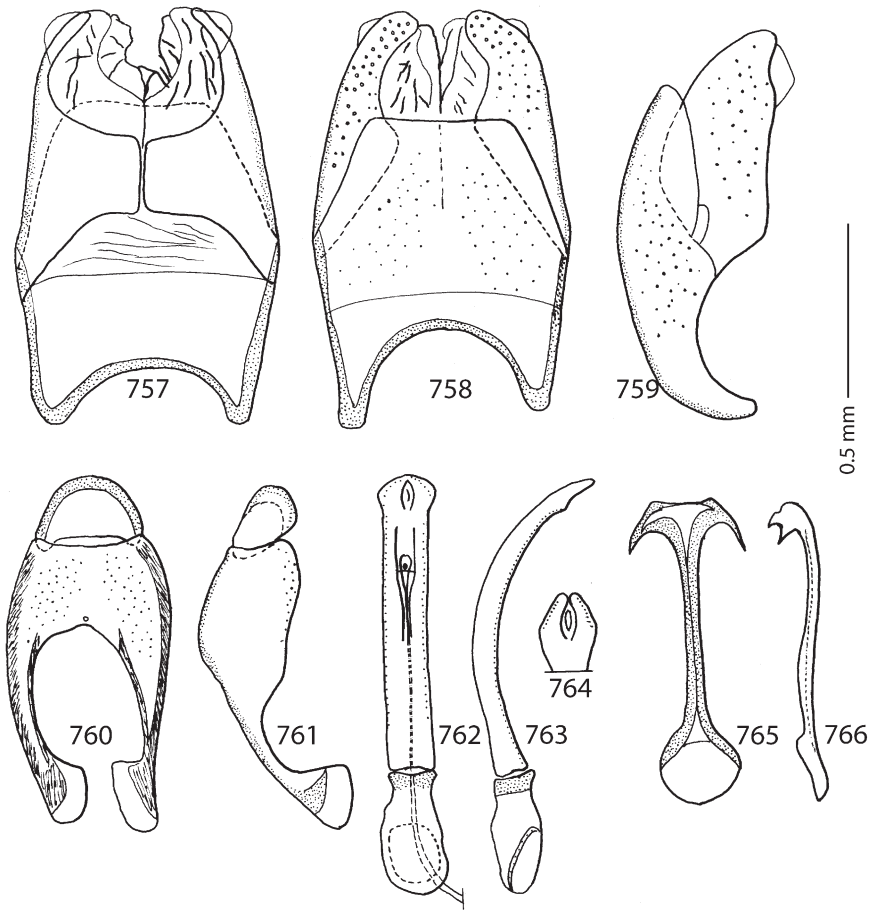
Propygidium (Fig. 755) completely exposed, apical half with coarse and dense punctures, basal half covered with much finer and sparser punctation; punctation of pygidium (Fig. 755) sparser than that of the propygidium, punctures round, regular, separated by their own to twice their own diameter; becoming sparser and finer apically; interspaces in both cases imbricate.

Anterior margin of median portion of prosternum (Fig. 752) evenly rounded; pre-apical foveae absent; prosternal process slightly concave, almost flat, surface between carinal prosternal striae with scattered microscopic punctures, laterally with large deep round punctures, interspaces substrigulate; carinal prosternal striae well impressed, slightly divergent between on prosternal apophysis, subparallel, not united in front; lateral prosternal striae well impressed, carinate, convergent anteriorly and united in front of apices of carinal striae by marginal prosternal stria.

Mesoventrite slightly emarginate medially, discal marginal mesoventral stria well impressed, somewhat weakened medially; disc of mesoventrite with scattered microscopic punctation, interspaces imbricate; meso-metaventral sutural stria vaguely impressed in several deep punctures, inconspicuous; intercoxal disc of metaventrite with fine scattered punctures; area around hind coxa with coarse round punctures; lateral metaventral stria (Fig. 753) well impressed, straight, in tiny punctures, stopping short of hind coxa. Lateral disc of metaventrite (Fig. 753) with shallow round setiferous punctures; metepisternum with much coarser and denser punctation, on apical third and fused metepimeron punctures sparser and finer; interspaces in both cases finely imbricate, metepisternal stria present along entire metepisternum + fused metepimeron, intermittent.



Figs. 747–756. *Zorius funereus* (Schmidt, 1890), SEM micrographs: 747 – habitus, dorsal view; 748 – ditto, ventral view; 749 – clypeus; 750 – head, dorsal view; 751 – ditto, ventral view; 752 – prosternum; 753 – lateral disc of metaventrite, metepisternum and fused metepimeron; 754 – protibia, dorsal view; 755 – propygidium and pygidium; 756 – metatibia, ventral view.



Figs. 757–765. *Zorius funereus* (Schmidt, 1890), male terminalia: 757 – 8th sternite and tergite, ventral view; 758 – ditto, dorsal view; 759 – ditto, lateral view; 760 – 9th tergite and 10th tergite, dorsal view; 761 – ditto, lateral view; 762 – aedeagus, dorsal view; 763 – ditto, lateral view; 764 – apex of aedeagus, frontal view; 765 – spiculum gastrale, ventral view; 766 – ditto, lateral view.

Intercoxal disc of the first abdominal sternite completely striate laterally; disc with scattered fine punctation, interspaces imbricate; along apical margin row of fine punctures present.

Protibia (Fig. 754) flattened and slightly dilated, outer margin with a row of nine moderately large teeth topped with short denticle diminishing in size in proximal direction; setae of outer row rather dense, regular and moderately long; setae of median row similarly dense and regular, shorter than those of outer row; protarsal groove rather deep; anterior protibial stria complete; single, rather long tarsal denticle present apically; protibial spur tiny, bent, growing out from apical protibial margin; apical margin of protibia posteriorly with single tiny apical denticle; outer part of posterior surface of protibia areolate-rugose; distinctly separated from glabrous median part of posterior surface, basally with row of about five minuscule denticles;

posterior protibial stria complete, in minuscule sparse setae turning into dense row of about five well sclerotized inner-posterior denticles apically; inner margin with double row of dense short setae, progressively becoming longer apically.

Mesotibia slightly thickened, outer margin with two sparse rows of thin denticles growing in size apically; setae of outer row moderately dense, strongly sclerotized, growing in size in apical direction; setae of median row regular, shorter than those of outer row; posterior mesotibial stria complete; anterior surface of mesotibia imbricate with rather dense minuscule punctures with microscopic setae; anterior mesotibial stria complete, terminating in two tiny denticles; mesotibial spur stout, rather short; apical margin with several short denticles; claws of apical tarsomere shorter than half its length; metatibia (Fig. 756) basically similar to mesotibia, but slenderer and longer and denticles of outer margin much sparser than those of mesotibia.

Male genitalia. Eighth sternite (Figs. 757–758) longitudinally separated medially, apically with large asetose inflatable membrane (velum); apex of eighth sternite without setae; eighth tergite and eighth sternite not fused laterally (Fig. 759). Morphology of 9th tergite (Figs. 760–761) typical for the subfamily; spiculum gastrale (Fig. 765) expanded on both ends. Basal piece of aedeagus (Figs. 762–763) rather short, ratio of its length : length of parameres 1 : 3; parameres fused along their basal half; aedeagus curved ventrad (Fig. 763).

Discussion

The aim of this study is to describe in detail the morphology and outline the genera and subgenera of the Palaearctic Saprininae with additional views on their phylogeny. It is hoped that this paper will be the first step towards a fully resolved higher phylogeny of the Saprininae of the world. The inclusion of cladistic analyses would be premature at this time given the absence of other than Palaearctic taxa, although the current knowledge of the group permits a partial discussion of the monophyly, paraphyly and polyphyly of the genera in question. Future studies should focus on the most phylogenetically informative characters, which include the sensory organs of the antennal club (formerly known as the Reichardt's organ), mouthparts (with special focus on the lacinia and labrum), the structure of the prosternum and the male genitalia. It would also be beneficial to include the study of the female genitalia, with special focus on the coxites, styli and spermatheca. Due to time contraints, the female genitalia could not have been included in this study.

The Palaearctic Region harbors an unusually high number of genera and subgenera of the Saprininae, 33 out of 59; 19 of them are endemic. In comparison, the Afrotropical Region has only seven, the Nearctic Region eight, the Neotropical Region five, the Australo-Pacific Region four and the Oriental Region no endemic genera or subgenera (Mazur 1997; Penati & Vienna 1996; Kanaar 1996, 2008; Tishechkin 2005). This suggests that the Palaearctic Region is the centre of origin of the Saprininae, since it harbors the greatest number of extant genera, is probably the most ecologically suitable region and circumscribes the greatest morphological diversity for the group, together with the greatest number of 'advanced' forms (e.g., the genera *Philothis*, *Xenonychus*, *Xenophilothis* and *Ctenophilothis*).

However, a preliminary cladistic analysis places the genera *Gnathoncus*, *Eremosaprinus* and *Myrmetes* together with *Euspilotus* (*N.*) *perrisi* as the most basal taxa (Lackner, unpublished

data). *Gnathoncus* has the highest diversity in the Holarctic Region, with only a handful of species known from the Afrotropical and Oriental Region. No *Gnathoncus* are believed to be native to the Australo-Pacific and Neotropical Regions. *Myrmetes*, with the single species *M. paykulli*, is another Palaearctic endemic, and the genus *Eremosaprinus* contains five species, four of which are North American endemics and only one is restricted to the Palaearctic Region. It is believed that this Palaearctic representative belongs to a different genus (see the diagnosis of *Eremosaprinus* for details).

The future focus should thus be directed towards the species-rich genus *Euspilotus* that is native to the Nearctic and Neotropical Regions, since it may represent an old Gondwanan clade that currently survives only in the Neotropics. The genus *Tomogenius*, endemic to the Australo-Pacific Region, is presumably also a member of this group (Lackner, unpublished results). This genus might likewise be one of the basal Gondwanan elements that dispersed via the ancient connection between South America, Antarctica, Australia and New Zealand. This would mean that the centre of origin of the Saprininae is, on the other hand, the ancient continent of Gondwana, in lines with Hennig's progression rule: plesiomorphy in the centre of origin, with increasing apomorphy peripherally. The presence of only one species, *Euspilotus* (*N.*) *perrisi*, in the Palaearctic Region and one species, *E.* (*N.*) *loebli*, in the Oriental Region could be attributed to extinctions of the members of this genus elsewhere. However, in the same way that the distribution of these two taxa can be interpreted by a dispersal scenario, a sound cladistic analysis must be used to test such hypotheses.

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