Rove beetles of the subtribe Scopaeina Mulsant & Rey (Coleoptera: Staphylinidae) in the West Palaearctic: Phylogeny, biogeography and species catalogue

Johannes Frisch¹, *, Daniel Burckhardt², Volkmar Wolters¹

¹ Institut für Systematische Zoologie, Museum für Naturkunde, Humboldt-Universität zu Berlin, Germany
² Naturhistorisches Museum, Basel, Switzerland

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Abstract

A cladistic analysis of the West Palaearctic Scopaeina Mulsant & Rey, 1878 (Coleoptera, Staphylinidae: Paederinae) is presented along with biogeographic and biogeographic information. A total of 76 morphological characters were coded for the 88 currently known West Palaearctic species, except for S. bifossicapitata (Outerelo & Oromi, 1987). Results show that Scopaeina comprises two well-supported monophyletic groups in the West Palaearctic, Micranops Cameron, 1913 and Scopaeus Erichson, 1840, which are considered to represent distinct genera. Phylogenetic relationships to Orus Casey, 1884, distributed in North and South America, are briefly discussed. Whereas Micranops is only represented by M. pilicornis (Baudi, 1869) in the region under study, 87 species of Scopaeus are currently known from the West Palaearctic. Within Scopaeus, the cladistic analysis yielded many well-supported monophyletic species groups, most of which are restricted to the West Palaearctic. However, except for Hyperscopaeus Coiffait, 1984, they are not in agreement with the widely used subgeneric concept sensu Coiffait (1952–1984). The following polyphyletic subgenera are consequently synonymized: Alloscopaeus Coiffait, 1968, Anomoscopaeus Coiffait, 1968, Geoscopaeus Coiffait, 1960, and Hyposcopaeus Coiffait, 1960 synn. n. = Micranops Cameron, 1913. The monotypical genus Coecoscopaeus Coiffait, 1984, established for C. coecus (Peyerimhoff, 1906), is excluded from Scopaeina. Scopaeus mitratus perroti Ochs, 1953 is raised to species rank, and S. nigellus Wollaston, 1864, formerly a synonym of S. didymus Erichson, 1840, is revalidated. The following polyphyletic subgenera are consequently synonymized: Alloscopaeus Coiffait, 1968, Anomoscopaeus Coiffait, 1968, Geoscopaeus Coiffait, 1960, and Hyposcopaeus Coiffait, 1960 synn. n. = Micranops Cameron, 1913. The monotypical genus Coecoscopaeus Coiffait, 1984, established for C. coecus (Peyerimhoff, 1906), is excluded from Scopaeina. Scopaeus mitratus perroti Ochs, 1953 is raised to species rank, and S. nigellus Wollaston, 1864, formerly a synonym of S. didymus Erichson, 1840, is revalidated. Finally, we present a catalogue of species and synonyms of West Palaearctic Scopaeina along with distributional data and five new synonyms of species group names: S. bordei Peyerimhoff, 1914 syn. n. = S. portal Luze, 1910; S. tassiliensis Jarrige, 1958, S. mauretanicus Coiffait, 1960 syn. n. = S. crassipes Wollaston, 1867; S. saoudiensis Coiffait, 1981 = S. sinaicus Coiffait, 1970; S. mateui Coiffait, 1953 syn. n. = S. didymus Erichson, 1840. A lectotype is designated for S. didymus Erichson, 1840.

Key words: Staphylinidae, Scopaeus, Coecoscopaeus, Micranops, Orus, West Palaearctic, cladistics, biogeography, catalogue

See also Electronic Supplement (Parts 1–3) at http://www.senckenberg.de/odes/02-02.htm

Introduction

With over 45,700 nominal species rove beetles or staphylinids probably constitute the most species-rich group of Coleoptera (Smetana & Herman 2001). The family includes some very large genera with externally similar species. These genera often have a confused taxonomic history and are in need of critical revision. One of these groups is the subtribe Scopaeina Mulsant & Rey, 1878 of the paederine group, tribe Paederini, which is traditionally defined by the four-toothed labrum (e.g. Coiffait 1982, 1984). Scopaeus, with about 400 described species world-wide (Frisch 1997c), is the largest genus in the subtribe. The predominantly riparian beetles are small and range from 2–4 mm in length. The taxonomy of the West Palaearctic Scopaeus has been treated recently by Frisch (1994–2001). The present paper examines the phylogenetic relationships of the West Palaearctic members of the subtribe, testing in particular the validity of subgenera and informal species groups

*Corresponding author: Dr. Johannes Frisch, Humboldt-Universität zu Berlin, Museum für Naturkunde, Institut für Systematische Zoologie, Invalidenstraße 43, D-10115 Berlin, Germany; Tel.: +49 (0) 30-20 93-88 36; Fax: +49 (0) 30-20 93-85 28; e-mail: johannes.frisch@museum.hu-berlin.de
proposed by various authors, discusses biogeographic aspects, and summarises taxonomic and distributional data in a catalogue.

**Taxonomic history**

Erichson (1840) erected *Scopaeus* for several species which were originally described in other staphylinid genera, mainly based on mouthpart characters: dentate labrum, acute ultimate segment of maxillary palpi, and strongly sclerotised and tridentate ligula. The oldest species now referred to *Scopaeus* is *Paederus laevigatus* Gyllenhall, 1827. The first monograph of European *Scopaeus* was provided by Mulsant & Rey (1854) who described some widespread European species. Binaghi (1935), describing some South European taxa, first used the aedeagus for species definition. Coiffait (1952, 1953, 1960, 1968, 1969, 1970, 1971, 1973, 1976, 1981, 1984), who extensively published on the genus, caused much taxonomic confusion in misjudging variability and significance of external morphological characters and, hence, producing numerous synonyms at the species level. In addition, Coiffait (1952, 1960, 1968, 1981, 1984) and others introduced a series of subgenera which do not represent monophyletic groups (Frisch 1997c). Exceptions are *Micranops* Cameron and *Hyperscopaeus* Coiffait. Frisch (1994–1999c) introduced informal species groups whose monophyly will be tested here.

*Micranops*, also a member of Scopaeina, resembles *Scopaeus* in the four-dentate labrum and the narrow neck. It differs in the (probably plesiomorphic) structure of the aedeagus (Figs. 4–6) and in the distinct setiferous neck. It differs in the (probably plesiomorphic) structure of the aedeagus (Figs. 4–6) and in the distinct setiferous neck.

**Biology and ecology**

Little is known about ecology, habitat requirements and phenology of *Scopaeus* species. Available information relates mostly to Central European (e.g. Bohac 1985; Frisch 1997c, 1998; Horion 1965; Koch 1989) or East Mediterranean species (e.g. Frisch 1997c, 1998, 1999–1999d). Most *Scopaeus* species are found under stones or in gravel on damp, sandy soil of banks of both large rivers and streams, which are more or less exposed to sun and covered with organic litter and sparse pioneer vegetation. They are, however, absent from sterile, coarse gravel near the waterline. *Scopaeus* populations frequently colonise very narrow banks not wider than 10 cm, or small, suitable zones within large banks. In general, the genus can be termed ripicolous and hygro-thermophilous. *Scopaeus* species are collected from sea level up to over 2000 m. The occurrence of *Scopaeus* species depends more on the availability of suitable habitat structures near flowing waters than on altitude. Like most stenotopic riparian animals, *Scopaeus* species are increasingly endangered through habitat destruction.

Some Central European species differ in their habitat requirements from other congeners. *Scopaeus minimus* is a paludicolous humicolous species, known from marshy grounds such as wet meadows, swamps, bogs and even woods (Bohac 1985, Horion 1965, Koch 1989). *Scopaeus sulcicollis* and *S. minutus* are less hygrophilous, occurring also in barrens, grassland and forest steppes (Bohac 1985, Horion 1965, Koch 1989). In Hesse (Germany), *S. sulcicollis* was frequently found in relatively dry grassland such as Brometalia erecti or Arrhenatheretum elatioris (J. Frisch, pers. observation).

Nothing is known about feeding habits, and neither larval instars nor larval habitat requirements have been described (Coiffait 1984). Frank (1982) and Santamaria (1997) reported Neotropic, Oriental and Palaearctic *Scopaeus* species as hosts of parasitic ascomycetes.

**Material and methods**

**Abbreviations, conventions and definitions**

Over 10,000 specimens of West Palaearctic *Scopaeus* were examined, including available types. Depositories are cited as follows:

- BMNH = Natural History Museum, London; DEIC = Deutsches Entomologisches Institut, Eberswalde; FMNH = Field Museum of Natural History, Chicago; HECO = Hope Entomological Collections, Oxford; HKCB = Horst Korge Private Collection, Berlin; HNHM = Hungarian Natural History Museum, Budapest; ISNB = Institut Royal des Sciences Naturelles de Belgique, Brussels; JFCG = Johannes Frisch Private Collection, Gießen; MCSN = Museo Civico di Storia Naturale
The analysis is restricted to West Palaearctic taxa and includes 86 (82 described + 4 undescribed) of the 87 presently known Scopaeus species, and one species each of Micranops and Luzea Blackwelder, 1952. The latter, another member of the tribe Paederini but subtribe Medonina Casey, 1905, served as outgroup. It was chosen for its relatively primitive aedeagal condition in which it resembles the basal Micranops.

The anophthalmous, endogean species Scopaeus bifossicaptata (Outerelo & Oromi, 1987) from the Canaries was not included in this study, because males are unknown and no specimens were available. Scopaeus bifossicaptata was first described as a species of Domene, but later transferred to Scopaeus by Outerelo & Gamarra (1989). Coecoscopaeus coecus (Peyerimhoff, 1906) from Tunisia, originally described in Scopaeus, is also excluded from the present study. Coecoscopaeus was placed by Coiffait (1984) in the subtribe Scopaeina, but differs considerably in external and aedeagal characters from the definition of Scopaeina by Coiffait (1982) which is adopted here.

Character assessment

The exoskeleton of Scopaeus provides few distinguishing characters except for male sternite 8. The spermathecae and particularly the aedeagi, in contrast, provide many meaningful apomorphic features of high value for phylogenetic examinations on the species-group level. The mouthparts appear to be informative at the genus-group or higher level, but not for defining species or species groups. Derived characters of single species (autapomorphies) are not discussed in the present study. Characters and their character states are compiled in Appendix 1.

Exoskeleton

Descriptions of Scopaeus species usually contain extensive information on punctuation and microsculpture of the body surface, which are similar in related species and even species groups. They are of little use for this analysis. Two fundamental groups exist: most species share rather shiny, sparsely punctate and weakly reticulate surfaces (char. 5:0). In contrast, some groups of related species, including Luzea and Micranops, have dull, very finely and densely punctate, microsculptured bodies (char. 5:1).

Scopaeus is characterized by a very narrow neck which is only from one fifth (char. 1:1) to about one eighth (char. 1:2) as wide as the head (Figs. 2, 3). In Micranops, the neck measures about one quarter of the head width (char. 1:1; Fig. 1a). Luzea has a notably broader neck (char. 1:0).

Within Paederinae, the shape of the labrum is a distinguishing character at the genus level (Coiffait 1982). Although there are some exceptions (Herman, pers.
sent cladistic analysis, hence, these taxa are compared with the remaining species (char. 7:0).

The protarsomeres of staphylinids are frequently dilated (Uhlig 1990). This convergence is without use for this phylogenetic study. In *Scopaeus*, the protarsomeres are also dilated (chars 8:2, 8:3) but somewhat elongate (char. 8:0) or slightly transverse (char. 8:1) in few species groups. The protarsomeres of *S. portal* are transverse in the male and slender in the female, and thus even sexually dimorphic. The slender states of the protarsomeres (chars 8:0, 8:1) are considered to be pleisiomorphic.

Even though the mesotibiae of *Scopaeus* species are frequently dilated, the members of the *S. sulcicollis* group (Frisch 1999b) agree in possessing remarkably dilated mesotibiae which are at least five times as wide as long (char. 9:1). These species are coded separately. The distal antennomeres of most *Scopaeus* are more or less transverse (char. 11:2), but in some species groups they are slightly elongate (char. 11:1), and even very slender in *Hyperscopaeus* (char. 11:0). Transverse antennomeres are most likely apomorphic.

Whereas both the legs and antennae of *Scopaeus* are studded with few longer setae only, the appendages of *Micranops* and *Hyperscopaeus* bear many long, black setae (chars 10:1, 12:0). However, it remains doubtful which character state is derived, because these setae occur in many paederines.

Spermatheca

Whereas the outgroup taxa *Luzea* and *Micranops pilicornis* share the primitive one-piece spermatheca of Coleoptera (char. 13:0; Fig. 22), which was described by many authors (e.g. Heberdey 1931, de Marzo 1982), the spermathecae of all hitherto examined *Scopaeus* and the *Micranops* species illustrated by Herman (1965a) have the additional portion (char. 13:1; Figs. 23–29) described by Frisch (1996, 1997c). Because the chamber and the additional portion are connected by muscles, we interpret the two-piece spermatheca as a sperm-pump. Furthermore, except for *Hyperscopaeus* (char. 16:0; Fig. 23), the chamber of the spermatheca bears a typical process (char. 16:1; Figs. 24–29). Even though the spermathecae of *Scopaeus* species are similar and of little use for distinguishing species (Frisch 1998), the spermathecal duct and the chamber provide some characters typical for species groups. Moreover, the spermathecal duct in some species groups ends in a strongly sclerotized, bursiform structure of characteristic shape. Considering its position within the genital segments (Fig. 30), it is assumed to be the bursa copulatrix (Frisch, in press). Various character states of the spermathecal duct (char. 14), the “bursa” (char. 15) and the chamber of the spermatheca (chars 16, 17) were used for this analysis.
Abdominal terminal sclerites

In staphylinids, the abdominal terminal sternites of males usually provide various, frequently species-specific, secondary sexual modifications such as planations, groups of setae or distal emarginations (Blackwelder 1936, Naomi 1990). In particular, sternite 8 is strongly emarginate terminally, because the aedeagus comes out ventrally. These emarginations are rather small in Luzea and Micranops (char. 21:1), whereas it is convex in the remaining taxa included in this study (char. 21:0; Fig. 31), but large and frequently strongly derived (Figs. 32–36) in Scopaeus and, hence, of high phylogenetic value. Most species, however, have a simple, triangular emargination (char. 32:0; Fig. 34), most likely the plesiomorphic character state for Scopaeus. Further characters are provided by the male abdominal sternite 7, which bears some thick setae in Micranops (char. 21:1) and has a deep, quadrilateral emargination in the Scopaeus group (char. 21:2), and by the hind margin of the female sternite 8, which is somewhat emarginate in Hyper-scopaeus (char. 18:0), whereas it is convex in the remaining taxa included in this study (char. 18:2).

The apex of laterotergite 9 (Figs. 37–39) provides useful characters regarding the phylogenetic relationships between Scopaeina and allied groups. In Luzea, it is deeply incised and extended into two teeth of equal length (char. 19:0), whereas the dorsal tooth is strongly reduced or even lacking and the sclerite thus unidentate in the examined Scopaeina (char. 19:1).

Aedeagus

Most characters used in this phylogenetic study are taken from the aedeagus. Bearing in mind the primitive type of the aedeagus of staphylinids and the Paederinae as described by Blackwelder (1936) and Naomi (1990), the aedeagi of Scopaeus (Figs. 7–21) appear highly derived due to the reduced median lobe, which became divided into a large, distinct dorsal lobe and two large, lateral apical lobes (Frisch 1994). Luzea and Micranops (Figs. 4–6), however, agree in rather plesiomorphic aedeagi with short such lobes (char. 26:0) but with an additional, remarkable ventral lobe (char. 33:1) which is found in many paederines. This ventral lobe is part of the median lobe and was erroneously considered to represent ventro-medially fused parameres (Herman, pers. comm.). Unlike this, the large aedeagi of Hyperscopaeus (Figs. 7–9) are quite different, because the feebly sclerotized distal portion of the long median lobe (char. 26:1) bears distinct lobes only at the very end (char. 57:0). Character states for parts of the aedeagi are compiled in Appendix 1, but major characters are described below.

Following Blackwelder (1936), the sclerotized end of the ejaculatory duct is termed the flagellum. Whereas the flagellum is long and surrounded by various tooth-like structures in Hyperscopaeus (char. 28:0; Figs. 7–9), it is stout in Micranops (char. 28:2; Figs. 4–6) and Luzea (char. 28:1), though surrounded by teeth in the latter. Unlike this, the flagellum of Scopaeus s. str. is more or less lengthened and of variable shape (char. 28:3; Figs. 7–21). Frequently specific for species groups.

According to Coiffait (1982), the subtribe Scopaeina lacks distinct parameres. However, the parameres are represented in Scopaeus and the New World genus Orus and in many other paederines by strongly reduced lobes of varying lengths and widths appressed to the median lobe near the median foramen (Figs. 7–21) (Herman, pers. comm.). The so-called lateral lobes (e.g. Coiffait 1982, Frisch 1994) of Scopaeus (chars 39:1–9; Figs. 7–21) are not parameres but lobes of the median lobe (Herman, pers. comm.). These variable lobes are reduced in many groupings or even lacking and provide valuable characters for this study.

The aedeagus of Scopaeus bears a variable ventral process of the endophallic structures (char. 35:1), which provides derived characters specific for species groups. For example, the S. elegans group (Frisch 1994) has a flagellate process (char. 36:5; Figs. 19, 20), and in the species allied to S. didymus it is short and hook-shaped (char. 36:4). This endophallic process, however, is absent in the outgroup and some basal groups of Scopaeus (char. 35:0).

Except for the outgroup, Micranops and Hyperscopaeus, Scopaeus species agree in the presence of testaceous, ventrally more or less enlarged apical lobes (char. 58:2; Figs. 10–21) which provide striking apomorphic characters for both species and species groups. These apical lobes, however, are rather simple in the S. debilis (Frisch 1999), the S. longicollis (Frisch 1999c), and the S. signifer (Frisch 1997c) groups (Figs. 10–12).
Figs. 7–9. Scopaeus (Hyperscopaeus) spathiferus, holotype, aedeagus in 7) lateral, 8) ventral, 9) dorsal view. Abbreviations: a = apical lobe, d = dorsal lobe, f = flagellum, s = sclerotized ring of phallobase, v = ventral process of phallobase. Scale = 0.1 mm.

Figs. 10–12. Scopaeus debilis (S. debilis group), Tunisia, Kasserine, aedeagus in 10) lateral, 11) ventral, 12) dorsal view. Abbreviations: a = apical lobe, d = dorsal lobe, e = ventral endophallic process, f = flagellum, l = lateral lobe, m = median foramen, p = paramere, s = sclerotized ring of phallobase. Scale = 0.1 mm.
Figs. 13–15. *Scopaeus siculus* (*S. gracilis* group), lectotype, aedeagus in 13) lateral, 14) ventral, 15) dorsal view. Abbreviations: a = apical lobe, d = dorsal lobe, e = ventral endophallic process, f = flagellum, l = lateral lobe, m = median foramen, p = paramere, s = sclerotized ring of phallobase. Scale = 0.1 mm.

Figs. 16–18. *Scopaeus alaschiacus* (*S. minutus* group), holotype, aedeagus in 16) lateral, 17) ventral, 18) dorsal view. Abbreviations: a = apical lobe, d = dorsal lobe, e = ventral endophallic process, f = flagellum, l = lateral lobe, p = paramere, r = lateral ridges of median foramen, s = sclerotized ring of phallobase. Scale = 0.1 mm.
The dorsal lobe of the aedeagus of Scopaeus also provides phylogenetically informative features for both species and species groups. The aedeagus in Luzea and Micranops still has a short, lobiform dorsal lobe (char. 43:0) which is, however, derived in the former genus due to the remarkable inner setae (char. 44:1; Figs. 5, 6). Contrary to the aedeagus of Hyperscopaeus, which lacks a distinct dorsal lobe (char. 42:0; Figs. 7–9), those of the remaining Scopaeus are more or less elongate and strongly sclerotized (char. 43:2; Figs. 12, 15, 18, 21). Except for the simple ones of the S. sericans group or the S. signifer group (char. 45:1), other groupings within Scopaeus are characterized by a highly apomorphic dorsal lobe.

The phallobase of Scopaeus is divided by a strongly sclerotized, median ring (char. 72:1; Figs. 7–21) into a proximal and a more strongly sclerotized distal portion bearing lobes. Additional characters are provided by the structures beside the median foramen (chars 74, 75; Figs. 11, 17, 20).

**Results**

The cladistic analysis of the data matrix (Appendix 3; Electr. Suppl. 02–02, Pt 2) with NONA including 73 informative characters coded for West Palaearctic species of Micranops and Scopaeus resulted in a total of 1,195 most parsimonious cladograms (length 249 steps, CI = 82, RI = 95). The resulting bootstrap consensus tree (Fig. 40) shows that West Palaearctic taxa form several well-supported monophyletic clades, whereas their phylogenetic relationships remain unclarified. In most cases, the resulting clades agree with the informal species groups introduced by Frisch (1997–1999c), but are highly different from the subgenera described by Coiffait (1952, 1960, 1968, 1981, 1984).

Taking into account the geographical restriction of this analysis, the monophyly of the Scopaeina remains doubtful, because the New World genus Orus was not considered. However, all West Palaearctic taxa agree in...
Figs. 22–29. Spermatheca (lateral and dorsal views) and spermathecal duct (not illustrated in full length) of 22) Micranops pilicornis; 23) Hyperscopaeus (Scopaeus andrewesi, India); 24) S. laevigatus group (S. laevigatus); 25) S. minimus group (S. minimus); 26) S. longicollis group (S. kovaci); 27) S. elegans group (S. trifurcatus); 28) S. gracilis group (S. siculus); 29) S. debilis group (S. debilis). Abbreviations: b = bursa copulatrix, c = chamber, p = process, pc = process of chamber, s = spermathecal duct. Scale = 0.1 mm.

Fig. 30. Scopaeus laevigatus group: position of spermatheca and bursa copulatrix within genital segments of S. laevigatus, ventral view. Abbreviations: b = bursa copulatrix, sp = spermatheca. Scale = 0.1 mm.

possessing a slender neck (char. 1:1), an oblong pronotum which is strongly tapering towards the narrow anterior margin (char. 2:2), a quadridentate labrum (char. 3:1), and an unidentate laterotergite 9 (char. 19:1). These characters are probably synapomorphies of Scopaeina.

The basal taxon of the Scopaeina is *Micranops*. The group is distinguished by a setiferous furrow behind the eyes (char. 4:1; Fig. 1b), thick median setae at the hind margin of the male abdominal sternite 7 (char. 21:1), and by the aedeagus (Figs. 4–6) with a stout flagellum without surrounding teeth (char. 28:2), a large, lobiform ventral endophilic process (char. 36:1) and a dorsal lobe bearing long inner setae (char. 44:1).

The next grouping represents *Scopaeus*. All species included share a two-piece spermatheca (char. 13:1; Figs. 23–29) and the sclerotized aedeagal ring between the phallobase and the remarkable distal lobes (char. 72:1; Figs. 7–21). Even though two-piece spermathecae occur in the scopaeine genera *Orus* and *Micranops* as well (Herman 1965a), *Scopaeus* is most likely monophyletic according to the aedeagal characters. Within *Scopaeus*, two highly different clades can be distinguished.
Figs. 31–36. Abdominal tergite 8 of male of 31) Micranops (M. pilicornis); 32) Scopaeus debilis group (S. debilis); 33) S. gracilis group (S. gracilis); 34) S. elegans group (S. kurdistanicoides); 35) S. laevigatus group (S. biskrensis); 36) S. sulcicollis group (S. ponticus). Scale = 0.1 mm. Abbreviations: i = inner border, o = outer border.

Figs. 37–39. Abdominal laterotergite 9 of 37) Scopaeus laevigatus group (S. ebneri); S. minimus group (S. minimus); S. sulcicollis group (S. ponticus). Scale = 0.1 mm. Abbreviations: e = dorsal emargination, t = dorsal tooth.
Fig. 40. NONA bootstrap consensus tree of 1,195 most parsimonious cladograms (length = 249 steps, CI = 82, RI = 95). Numbers below nodes represent bootstrap support values. A species of the subtribe Medonina, Luzea infirma, served as the outgroup, and the 88 known West Palaearctic taxa of the Scopaeina were included in the analysis with 76 morphological characters, mainly features of the male and female primary genitalia. The resulting species groups are shown on the right.
The first grouping, *Hyperscopaeus*, is distinguished by the following most likely derived characters: the extraordinarily slender neck is only one eighth of the width of the elongate, parallel head the hind margin of which is notably concave (chars 1:2, 6:0; Fig. 2). The lateral margins of the pronotum are parallel as well (char. 2:1). The extraordinarily wide protarsomeres are about three times as wide as long (char. 8:3). The females differ by the emarginate abdominal sternite 7 (char. 18:1), and sternite 8 of the males is more deeply emarginate than those of the remaining *Scopaeus*. *Hyperscopaeus* also differs in the notably larger aedeagus (Figs. 7–9) with a long, rather membranous, unipartite apical portion of the median lobe (chars 42:1, 57:1) with distinct lobes only at the very apex. This long, unipartite median lobe, however, corresponds to the primitive type of aedeagus of staphylinids (Blackwelder 1936, Naomi 1990) and is perhaps not an apomorphy. *Hyperscopaeus* is furthermore assumed as monophyletic due to the remarkably broad sclerotized ring of the phallobase (char. 73:9) and the derived position of the median foramen at the proximal end of the phallobase (char. 75:1). Despite the obviously apomorphic shapes of both the body and the aedeagus, *Hyperscopaeus* is linked with the outgroup according to the denticles or teeth (char. 27:0) along the flagellum (Figs. 7–9). Hence, this character has to be taken as plesiomorphic for Scopaeina. Judging from this large number of derived characters, *Hyperscopaeus* is considered to be a basal clade of *Scopaeus* and probably the sister group of the remaining *Scopaeus*.

The latter clade, here termed *Scopaeus* s. str., is proved as monophyletic according to the following synapomorphies: the chamber of the spermatheca is extended into a terminal process (char. 16:1; Figs. 24–29); the aedeagus (Figs. 10–21) bears well-developed distal lobes (char. 26:3) of which the dorsal lobe is strongly sclerotized and elongate (char. 43:2), and the remarkable apical lobes are testaceous and more or less enlarged ventrally (char. 58:2); the lengthened flagellum lacks the surrounding tooth-like structures (char. 28:3) of *Hyperscopaeus* (Figs. 7–9) and *Luzea*, and the phallobase bears lateral lobes (char. 76:2) with apical setae. However, both the lateral lobes and the apical setae are frequently strongly reduced (Figs. 13–15) or even lacking (Figs. 19–21).

Within *Scopaeus* s. str., the terminal species groups are predominantly well founded both by characters (Fig. 40) and geographically and therefore considered as monophyletic, whereas the results regarding the relationships among those species groups remain preliminary, bearing in mind the geographical restriction of this analysis.

The basal branch of *Scopaeus* s. str. comprises three well-founded groupings. The *S. mutatus* group is considered as monophyletic according to following features: the spermatheca is comparatively small with little-flexed portions, the process is dentate terminally (char. 17:7); the emargination of male sternite 8 is short, wide and almost semicircular (char. 25:1); the ventral process of the phallobase is very short and obtusely rounded (char. 46:2); the apical lobes have a distinct apical portion as well, are dorsally fused either completely (*S. talyschensis*) or except for the very apex (char. 61:1), and have parallel inner margins (char. 62:1); finally, the sclerotized ring of the phallobase is comparatively broad with rather slender lateral portions (char. 73:3). Judging from the characteristic shape of the flagellum (char. 29:5) and the distal portions of the apical lobes (chars 63:1, 64:1), the allopatriate *S. alaniensis*, *S. mutatus* and an undescribed species from Central Turkey form a distinct clade, with *S. talyschensis* as the sister.

The *S. laevigatus* group (Frisch, in press) is postulated as monophyletic according to the following synapo-
The S. debilis group is considered to be monophyletic according to the short, strongly tapering flagellum of the aedeagus (char. 29:9; Fig. 10) and the small, additional canal of the chamber of the spermatheca (char. 17:5; Fig. 29). Two subgroups are distinguished, of which only the S. debilis subgroup (= S. tenuis group sensu Fagel 1973) is known from the West Palaearctic (Frisch 1999). Derived characters of the latter are the very narrow emargination of the male sternite 8 (char. 23:7; Fig. 32), the hook-shaped ventral endophalic processes (char. 36:9; Fig. 10), the strongly reduced lateral lobes with few ventrally pointing setae (char. 39:6; Figs. 10, 11), and the vestigial dorsal lobes (45:8; Fig. 12).

The S. signifer group (Frisch 1997c) is characterized by the following synapomorphies: the spermatheca is stout with strongly flexed portions and a right-angled, upflexed spermathecal duct (char. 17:2); the hind margin of male sternite 7 has a deep, rectangular emargination (char. 21:2), and the terminal sclerites are sparsely setose (char. 22:1). Sternites 8 of the males agree in short, distal emarginations with wave-like, convex lateral margins (char. 23:8); the strong flagellum of the aedeagus shortly tapers at the apex and reaches the apices of the apical lobes (char. 29:8), and the obtuse lateral lobes bear a line of setae which are flexed ventrally and therefore invisible in dorsal view (char. 39:9).

Whereas the preceding taxa within Scopaeus share more or less elongate distal antennomeres, the next clade...
comprises species groups with square or somewhat transverse distal portions (char. 11:2). This character, however, occurs in many staphylinids, as well as in Lueza and Micranops. The following species of Sco-paues agree also in a simple, triangular emargination of the male sternite 8 (char. 24:1; as in Fig. 34), but lack definite synapomorphies.

The S. sericans group is probably monophyletic according to the ventrally curved flagellum (char. 29:4), the remarkable, hook-shaped ventral endophallic process (char. 36:6), and the broad sclerotized ring of the phallobase, the lateral portions of which are very close (chars 45:4, 59:6). Within this grouping, S. cylindricus and S. sericans are linked by the apical lobes of the aedeagus being studded with long setae (char. 40:5), the deeply emarginate dorsal lobe with apical teeth strongly recurved towards the phallobase (char. 45:9), and the characteristic shaping of the apical lobes (char. 59:8).

The S. ryei group (Frisch 1998) is considered as monophyletic based on the following diagnostic features: the ventral endophallic process of the aedeagus is curved and emarginate at the apex (char. 36:7), the long setae of the apical lobes are pointing ventrally (char. 40:4), and the apical lobes are strongly reduced and much shorter than the strongly enlarged, bilobed dorsal lobe (chars 45:4, 59:6).

The S. longicollis group comprises S. anxius, the S. longicollis group sensu Frisch (1999c), and the S. hispanicus group (Frisch 1997c), which all agree in the shape of the head (char. 6:3) and particularly in large, strongly projecting lateral lobes which are ventrally studded with numerous setules (char. 39:4). The S. hispanicus and S. longicollis subgroups agree in the following synapomorphies: the spermathecal duct is rather short, its sclerotized section shows a distinct terminal thickening (char. 14:3; Fig. 26), and sternite 8 of the females carries a densely setose median ridge with neighbouring, little-setose planations (char. 24:5; similar to Fig. 36). Hence, these two taxa are taken as sister groups. The S. hispanicus subgroup is monophyletic according to the long, hook-shaped, apically emarginate ventral endophallic process of the aedeagus (char. 36:8), the prominent lateral lobes, which became membranous and lost the setules (char. 39:5), and apical lobes with distinct, membranous apical portions (char. 59:9). The S. longicollis subgroup is considered as monophyletic according to the dorsal lobe, which bears two distal and two ventral teeth (char. 47:1). The distal teeth are widely separated (char. 48:1) in S. bertiae, S. kovaci and S. longicollis, which probably represent a monophyletic group with S. proculus as its sister. Moreover, S. bertiae and S. kovaci are taken as sister species according to the moderately developed lateral lobes.

The S. minutus group is considered to be monophyletic according to the ventral denticles of the flagellum (char. 29:0) and the knife-shaped apical lobes (Figs. 16–18) which, in most species, are emarginate ventrally (char. 59:2). It comprises two monophyletic sister groups, the S. minutus and S. micropterus subgroups. The former, which includes the S. minutus and the S. pusillus groups sensu Frisch (1997c), is different according to the short, triangular dorsal lobe (char. 50:1, 50:2), whereas the S. micropterus subgroup is characterized by short lateral lobes with long apical setae (char. 40:7; Figs. 16–18) and a very long and slender, deeply emarginate dorsal lobe (char. 49:2; Fig. 18). Within the S. minutus subgroup, S. leobli, S. minutus and S. subopacus form a monophyletic group according to the short setae of the apical lobes (char. 40:6), the stout apical teeth of the dorsal lobe (char. 59:8).
50:2), and the deeply emarginate apical lobes with straight, slender distal halves (chars 65:4, 66:3). Moreover, S. loebli and S. minutus are probably sister species according to the widely separate distal teeth of the short, triangular dorsal lobe (char. 51:2). Even though shown as a polytomy in the bootstrap consensus tree (Fig. 40), S. chalcodactylus, S. pusillus and S. pusilloides form a monophyletic group as well according to the characteristic apical lobes, the apices of which are strongly flexed dorsally (char. 65:3). Scopaeus binaghi and S. fageli are obviously close to this grouping. The S. micropterus subgroup first comprises S. minutoides and S. gladifer, which agree in the long, deeply emarginate dorsal lobes with adjacent apical teeth (char. 52:2). In S. alaschiacus, S. championi and S. micropterus, those teeth are strongly diverging (char. 52:3; Fig. 18) and bearing apical teeth or denticles (char. 53:1). The species allied to S. didymus are characterized by the male sternite 8 with a distinct median ridge and lateral, asetose planations (char. 15:3) and by features of the aedeagus such as the hook-shaped ventral endophallic process (char. 36:4), long, slender lateral lobes (char. 40:2), and apical lobes with a shallow, ventral emargination and a dorsally curved apex (65:1). Judging from the slender dorsal lobe, which is emarginate at the distal half only (char. 52:1), and from the deep emarginations of the apical lobes (char. 65:2), S. didymus, S. mitratus and S. perroti constitute a monophyletic subgroup.

The next clade is made up of the S. sulcicollis group, which was defined and revised by Frisch (1997c, 1999b), and the S. elegans group (e.g. Frisch 1994, Frisch & Wolters 1999). Both taxa form a monophyletic group according to the lack of lateral lobes, which are, however, indicated by few setules (char. 76:1; Figs. 19, 20); the dorsal lobe with various ventral teeth (char. 45:3); but in particular according to an inner row of setae of the apical lobes (char. 59:4), which, within the S. elegans group, occurs in the basal S. cypris subgroup only.

The S. sulcicollis group is well founded according to the small and feebly sclerotized bursa of the spermathecal duct (char. 15:3) and the asymmetric apical lobes of the aedeagus, which bear an inner row of setae (chars 68:1, 68:2). Within this monophyletic group, the male sternites 8 of S. rubidus, S. argonauta and S. sulcicollis agree in having a median ridge (as in Fig. 36) which is strongly setose at the distal margin and laterally marked by setose planations (char. 24:6). Scopaeus argonauta and S. sulcicollis are probably sister species according to the short dorsal lobe which bears two short, ventrally curved apical teeth (char. 54:1).

The S. elegans group is considered as monophyletic according to the extremely lengthened, strongly winding...
spermathecal duct which ends in a large, strongly sclerotized, species-specific bursa (char. 14:1; Fig. 27); the deep emargination in at least the hind third of the male sternite 8 (char. 24:2; Fig. 34); and the flagelliform ventral endophallic process of the aedeagus (char. 36:5; Figs. 19, 20). The most basal grouping within the *S. elegans* group, the *S. cyprius* subgroup, comprises *S. cyprius* and *S. bituberculatus*, which share the inner row of setae of the apical lobes (char. 59:4) and a strongly lengthened, acute dorsal lobe (char. 54:4). The other species are characterized by a comparatively large spermatheca with little-flexed portions (char. 17:3; Fig. 27), and by a flagellum with apical teeth (char. 29:6; Fig. 20). Within the polytomy of *S. elegans* group, the *S. armeniacus* subgroup as defined by Frisch (1994) and Frisch & Wolters (1999) is well founded, even though *S. elegans* has to be excluded. Unlike this, the *S. bilaminulatus* subgroup (Frisch 1994) was not supported by this analysis, because its diagnostic character, the little emarginate, various ventral teeth bearing dorsal lobes (char. 54:2), proved to be a symplesiomorphy. However, *Scopaeus bilaminulatus* and *S. haemusensis* are sister species according to the bidentate dorsal lobe (char. 55:2), and *S. graeus*, *S. trifurcatus* and *S. schillhammeri* agree in dorsal lobes with three remarkable ventral teeth (char. 55:1).

Apart from the deeply emarginate dorsal lobe, which is extended into two ventrally curved teeth of unequal length (char. 54:3; Figs. 19–21), the *S. armeniacus* subgroup is characterized by a comparably large spermatheca with little-flexed portions (char. 17:3; Fig. 27), and by a flagellum with apical teeth (char. 29:6; Fig. 20). Within the polytomy of *S. elegans* group, the *S. armeniacus* subgroup as defined by Frisch (1994) and Frisch & Wolters (1999) is well founded, even though *S. elegans* has to be excluded. Unlike this, the *S. bilaminulatus* subgroup (Frisch 1994) was not supported by this analysis, because its diagnostic character, the little emarginate, various ventral teeth bearing dorsal lobes (char. 54:2), proved to be a symplesiomorphy. However, *Scopaeus bilaminulatus* and *S. haemusensis* are sister species according to the bidentate dorsal lobe (char. 55:2), and *S. graeus*, *S. trifurcatus* and *S. schillhammeri* agree in dorsal lobes with three remarkable ventral teeth (char. 55:1).

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A proper biogeographical analysis with West Palaearctic *Scopaeus* is premature at the present state of knowledge. Despite the relatively restricted geographical distributions of most species, the taxon cladogram is not sufficiently resolved from a biogeographical point of view. On a much coarser level, e.g., that of widely distributed species groups, the cladogram lacks the non-Palaearctic members. Much information on distribution patterns of West Palaearctic *Scopaeus* and *Micranops* has been published by Frisch (1994–2001) and Frisch & Wolters (1999), and basic distributional information is compiled in the species catalogue (Appendix 2; Electr. Suppl. 02–02, Pt 1). The biogeography of the species groups confirmed by the present cladistic analysis is briefly discussed below.

A large number of species and most species groups of West Palaearctic *Scopaeus* without doubt originate in the Mediterranean region. Except for the Afroeremial regions of North Africa, Saudi Arabia or Iraq, the species richness of *Scopaeus* remarkably increases towards the south, and only eleven species occur north of the Alps. Besides Mediterranean and Near Eastern faunal elements, some West Palaearctic Scopaeina such as *Micranops* and *Hyperscopaeus*, which are species-rich in the Palaetropical realms (sensu Müller 1981), originate in different zoogeographical regions. Likewise, the *S. debilis* and *S. laevigatus* groups are very widespread and occur in the West Palaearctic with few species only.

**Biogeography**

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Micranops is distributed world-wide and rather speciose in the Old World. Twelve species are described from the Afrotropical region (Fagel 1973), and several unnamed ones occur in the Oriental region. Micranops pilicornis, the only species in the West Palaearctic, shows a Pontomediterranean and Caspian (Gusarov 1992b) type of distribution. It was recently found in southern Italy (Abruzzese Mts., Campania) and hence has a trans-Adriatic distribution as described for many organisms (e.g. Gridelli 1950, Witte 1965).

Hyperscopaeus is very speciose in the Palaeotropical realm. Both West Palaearctic members are restricted to the Nile Valley and obviously Afrotropical faunal elements.

The S. mutatus group, distributed in the Near East, comprises S. talschenensis from the southern Caspian region and the Anatolian species S. alaniensis and S. mutatus as well as an undescribed one, which constitute a monophyletic group of allopatric species.

The S. laevigatus group comprises 20 known species in the Palaearctic and Oriental regions, of which one also occurs in the Afrotropical region (Frisch, in press). Five species of the Palaearctic S. laevigatus subgroup are known from the West Palaearctic. Whereas S. laevigatus is widely distributed from West Europe to the far east of Siberia and China, the remaining species have not only smaller ranges in the Mediterranean and Caspian regions (Frisch, in press).

The S. gracilis group is distributed throughout the Old World. Scopaeus crassipes, S. sinaicus and an undescribed species from the Canaries, which reach the eremial regions in the very south of the West Palaearctic, belong to the species-rich Palaeotropical S. crassipes subgroup. The S. gracilis subgroup is distributed in the Palaeotropics as well. In the West Palaearctic, it comprises the allopatric species S. gracilis, widespread in mountainous regions of the southern and temperate West Palaearctic, S. flavofasciatus from Cyprus, S. siculus from South Italy, and an undescribed Sardinian species.

The S. debilis group comprises five species in the tropics and warm-temperate regions of the Old World. Whereas the S. mendosus subgroup is Afrotropical only, two species of the S. debilis subgroup (= S. tenuis group sensu Fagel 1973) are known from the West Palaearctic (Frisch 1999): Scopaeus debilis is Holomediterranean, whereas S. filiformis, widely distributed in the Palaeotropical realm, reaches the Palaearctic only in the very south (Algeria, Egypt, Iran, Morocco, Saudi Arabia, Turkey).

The S. signifer group (Frisch 1997c) comprises three allopatric species which are distributed thoughout the southern West Palaearctic to Tadzhikistan in the east.

The S. sericans group is known from the West Palaearctic only. It comprises S. cylindricus from South France, S. sericans, distributed in mountainous regions of southern Central Europe (Alps, Carpathians), and S. sareptanus from South Russia.

The S. minutus group (Frisch 1998) only comprises S. minutus, widespread in Central and South-East Europe and Anatolia, and the Near Eastern S. palaestinus.

The S. ryei group (Frisch 1998) comprises four species in the West Mediterranean, of which only S. ryei is distributed thoughout large parts of Central Europe and the northern Balkans.

The West Mediterranean S. longicollis group is made up of S. anxius from South France and the Iberian Peninsula, the S. longicollis group sensu Frisch (1999c) from South-West Europe and North Africa, and the S. hispanicus group sensu Frisch (1997a). Whereas the latter grouping consists of two allopatric Iberian species, the former comprises the North African S. bertiae and S. proculus, the distribution of which is poorly known, S. kovaci from Morocco and South Spain, and the widespread S. longicollis which occurs northwards to Central France and western Germany (Frisch 1996).

The S. minutus group, species-rich in the West Palaearctic region, is widespread in the Holartic. Scopaeus pusillus is known to range east to Central Asia (Altai Mts.), and S. minutus was recorded from Canada (Montréal). The terminal monophyla of the S. minutus group are made up of allopatric taxa. Scopaeus loebli (Anatolia), S. minutus (Canada, Europe) and S. subopacus (Madeira), for instance, constitute a monophyletic group of allopatric species just as do S. chalcodactylus from the Caucasus and East Anatolia, the widespread Palaearctic S. pusillus and the Iberian S. pusilloides. The North African S. binaghi and S. fageli are closely related to the latter grouping. The S. micropterus subgroup comprises allopatric species, too, such as S. minutoides from West Anatolia and S. gladifer, distributed around the Black Sea and in South Russia (Samara), or S. alaschiacus from Cyprus, S. championi from the Alps, Carpathians and the Balkans, and S. micropterus from northern Italy. Likewise, S. didymus (Iberian Peninsula, South France, Tyrrhenian Islands), S. mitratus (Italy, Corfu) and S. perroti (North Africa) constitute a monophyletic group of allopatric taxa as well.

The S. sulcicollis group is distributed in the West Palaearctic but unknown from North Africa (Frisch 1999b). It comprises five species, amongst which S. sulcicollis, widespread in South and Central Europe, and the Caucasian S. argonausta are obviously allopatric sister species.

The species-rich S. elegans group is widespread in the Pontomediterranean region and the Near East (Frisch, in press). It also consists mainly of groups of allopatric species. The basal S. cyprius subgroup comprises the allopatric species S. cyprius from Cyprus and S. bituberculatus from southern Anatolia. Scopaeus bilaminulatus from eastern Anatolia and S. haemusensis from Bulgaria.
and Northwest Anatolia are allopatric sister species, as are *S. graecus* from the South Balkans, *S. trifurcatus* from South Anatolia and *S. schilhammeri* from eastern Anatolia and Iran. Likewise, the monophyletic *S. armeniacus* subgroup comprises ten allopatric species from Albania eastward to Armenia and North Iran (Frisch, in press).

**Conclusions**

**Character evolution**

This phylogenetic study, even though restricted to the West Palaearctic, makes some assumptions concerning general tendencies in the evolutionary process both towards and within *Scopaeus*. As most underlying structures, predominantly features of the aedeagus and the spermatheca, occur in groupings of *Scopaeus* from the remaining zoogeographic realms as well, the following evolutionary hypotheses are probably representative for the whole group.

In *Scopaeus*, characters of the body depend rather more on habits and niche choice than on relations. Nevertheless, whereas most basal *Scopaeus* (*S. mutatus - *S. longicollis* groups) share large eyes, long elytra and functional hind wings and have comparatively large geographical ranges, more strongly derived species agree in smaller eyes, and many of them are wing-dimorphous or flightless and, hence, distributed in small ranges. Therefore we assume an evolutionary tendency within *Scopaeus* towards the loss of ability to fly and endemism.

Bear in mind the wide neck of most staphylinids and paederines, the comparatively slender neck of the Scopaeina (Figs. 1–3) has to be regarded as derived. This character, however, is found both in many staphylinids and paederines and most likely evolved several times.

During evolution, the genital segments of staphylinids became variously modified (Blackwelder 1936, Uhlig 1989). The unidentate laterotergite 9 of the Scopaeina (Figs. 37–39) is here regarded as apomorphic because in many staphylinids, just as in the outgroup *Luzea*, these sclerites have two apical teeth of the same length. Unlike this, the simple, triangular emargination of the distal margin of male sternite 8 of many *Scopaeus* (Fig. 34) is found in most staphylinids, and thus primitive. However, this emargination is highly derived and apomorphic for various groupings of *Scopaeus* such as the *S. laevigatus-* (Fig. 35) or the *S. mutatus* group.

The two-piece spermatheca (Figs. 23–29), probably a sperm-pump, is an important synapomorphy connecting *Scopaeus, Micranops* and the New World genus *Orus*. However, the additional joint of the spermatheca is absent in the West Palaearctic *Micranops pilicornis* (Fig. 22) as well as in both the outgroup and the remaining staphylinids. Perhaps it was reduced secondarily in *M. pilicornis*. Within *Scopaeus*, however, the spermatheca of *Hyperscopaeus* (Fig. 23) lacks the typical process of the chamber, an important apomorphy of *Scopaeus* s.str. (Figs. 24–29). This process is an apophysis for muscles as well (sperm-pump). The characteristic bursa (Figs. 24, 27, 30) at the end of the spermathecal duct of some species groups is considered to be an apomorphy of *Scopaeus*, too. Because it occurs in some unrelated groupings (e.g. the *S. laevigatus* and *S. elegans* groups) only, it might have been reduced several times. Even though variously sclerotized bursal sacs are known in Coleoptera (e.g. Heberdey 1931), they have not been described from other staphylinids yet.

Regarding the various derived character states of the aedeagus of both Paederinae and Scopaeina, it is difficult to recognize evolutionary tendencies. According to Naomi (1990), the apical part of the median lobe is reduced or even lost in many paederines. Thus, bearing in mind the short aedeagal lobes of *Luzea* and the basal scopaeine taxa *Micranops* (Figs. 4–6) and *Orus*, the distal lobes of the aedeagus of *Scopaeus* (Figs. 7–21) probably became enlarged, more prominent and specific to species and species groups. However, it remains doubtful whether the long, membranous apical portion of the median lobe in *Hyperscopaeus* (Figs. 7–9) corresponds to the unipartite median lobe as described by, e.g., Blackwelder (1936) for the primitive aedeagus of staphylinids, or whether it must be taken as a secondary fusion of distinct distal lobes. The presence of short, distinct apical lobes near the apex of the median lobe, however, indicates a secondary fusion of distinct lobes.

*Hyperscopaeus, Micranops* and the outgroup *Luzea* lack the setiferous, so-called lateral lobes of *Scopaeus* s. str. (e.g. Figs. 16–18), which are thus considered to be an apomorphy of *Scopaeus* s. str. These lateral lobes, which are not parameres but part of the median lobe (Herman, pers. comm), reveal an obvious tendency of reduction (e.g. Figs. 13–15), and strongly derived clades such as the *S. sulphicolis* and *S. elegans* groups even share completely reduced lateral lobes which are indicated by very few setules only (Figs. 19–21).

The aedeagus of *Scopaeus* reveals a tendency to lengthening of the flagellum. Whereas it is rather short and stout in *Luzea* and *Micranops* (Figs. 4–6), it is slender in *Scopaeus* and frequently strongly extended in groupings – which are, however, little related – like the *S. gracilis* (Figs. 13–15) and the *S. minimus* groups or the *S. armeniacus* subgroup (Figs. 19–21) within the *S. elegans* group.

Within *Scopaeus*, the phallobase of basal groups such as *Hyperscopaeus*, the *S. mutatus* and *S. laevigatus*
groups or the S. crassipes subgroup of the S. gracilis group have a ventral process (char. 34; Figs. 7, 8). It is absent in both the outgroup and Micranops and probably an apomorphy of Scopaeus, which, however, became lost in more derived taxa. Unlike this, except for the basal S. mutatus and S. laevigatus groups, West Palaearctic species of Scopaeus s. str. share a ventral process of the endophallic structures (char. 35:1; Figs. 10–21), which is lacking in both the outgroup and Hyperscopaeus. The large, ventral lobe of the aedeagus of Micranops and Scopaeus, which, however, was reduced in Hyperscopaeus and the S. mutatus and S. laevigatus groups.

Generalizing evolutionary tendencies within West Palaearctic Scopaeina, it turned out that the aedeagus developed various highly derived structures of the distal lobes and the endophallus, which are specific to both species groups and species, whereas size and body shape behaved conservatively and changed very little. However, some plesiomorphic character states of the aedeagus are still found in the basal group Micranops, such as the remarkable ventro-median lobe (Figs. 4, 5) which was considered as representing the parameres by Herman (1965a, b), and the short distal lobes of the median lobe.

**Classification**

In the West Palaearctic, Scopaeina sensu Coiffait (1982) comprises the genera Micranops and Scopaeus only. The monotypic genus Coecoscopaeus, established for Scopaeus coecus Peyerimhoff, 1906 from Tunisia, is here excluded from Scopaeina. Even though Coiffait (1984) placed this genus near Scopaeina, however, he doubted its own classification. In adding Coecoscopaeus coecus to Scopaeina, Coiffait (1984) formed an obvious polyphyletic grouping. Coecoscopaeus coecus is a rather large (5 mm), light brown, depressed, flightless and anophthalmous species with bilobed labrum, yet very sparsely and coarsely punctate, with a shining surface and a very simple, primitive aedeagus.

The present phylogenetic analysis gives specific reasons for Scopaeus and Micranops to be distinct groups. Besides the convincing apomorphies (see chapter “Results”), Micranops lacks the remarkable distal lobes of the aedeagus of Scopaeus. Micranops was erected by Cameron (1913) for the Jamaican species M. brunneus Cameron. Later, Coiffait (1981) established Microscopaeus, a junior synonym of Micranops (Herman, pers. comm.), as a subgenus of Scopaeus and designated S. microphthalmus Eppelsheim (= Micranops pilicornis (Baudi)) as the type species. Nivorus Herman, 1965, established as a subgenus of Orgus Casey (genotype: O. cameroni Blackwelder), is also a junior synonym of Micranops (Herman, pers. comm.). Micranops was not noticed by recent authors. Fagel (1973), however, had already picked up the group as a distinct genus for the Afrotropical members according to the setigerous furrow behind the eyes (Fig. 1b), but he erroneously used the name Geoscopaeus, which was introduced by Coiffait (1960) as replacement name for the preoccupied name Stilpon Coiffait, 1952, established as a subgenus of Scopaeus with S. baudrimonti (= S. ryei) as the genotype (see also Coiffait 1984). Geoscopaeus is a junior synonym of Scopaeus.

The various subgenera which Coiffait (1952, 1960, 1968, 1981, 1984) described for West Palaearctic Scopaeus proved to be polyphyletic, except for Hyperscopaeus. Coiffait’s subgeneric concept is quite absurd and mostly based on unsuitable features. He combined unrelated species in a subgenus or even placed the same species in different subgenera. For instance, Amnoscopaeus, established for West Palaearctic species of the S. gracilis group (Coiffait 1968), includes also S. rubidus which in fact belongs to the S. sulcicollis group. Likewise, Coiffait (1968) combined species of the S. minutus group with members of the S. longicollis group as subgenus Alloscopaeus.

Hyperscopaeus, described as a subgenus of Scopaeus by Coiffait (1984), differs strongly from Scopaeus s. str. and might be considered a distinct genus according to many external and sexual apomorphies (see chapter “Results”). A final classification of Hyperscopaeus within Scopaeina, however, should be left to an overdue generic revision of paederines.

Subgenus Polyodontus Solier, 1849 was established for the Chilean S. angustatus Solier. This preoccupied name (Coiffait 1968) was widely used for Scopaeus species with trapezoidal heads (e.g. Coiffait 1952, Mulan & Rey 1878). As the genotype, S. angustatus, was described only from one female specimen (Coiffait 1960, 1968), the position of this subgenus, which with little doubt does not occur in the West Palaearctic, is doubtful. A phylogenetically founded subgeneric structuring of Scopaeus is not possible at the present state of taxonomic knowledge and requires a worldwide study.

Scopaeus bifossicapitata, an anophthalmous, endo-geal Canarian species, differs considerably from Scopaeus according to the lack of the two-piece spermatheca and the presence of a strong, setiferous postocular furrow. The latter character refers rather to Micranops, but S. bifossicapitata is remarkably larger (3.5 mm), and the spermatheca is completely different. A final classification is impossible without knowledge of male characters.
Judging from the results of the present cladistic analysis, we propose the following supraspecific classification for the Scopaeina of the West Palaearctic, including new synonymies of supraspecific names (see also Appendix 2; Electr. Suppl. 02–02, Pt 1):

1. Genus Micranops Cameron, 1913
Nivorus Herman, 1965: 119, described as subgenus of Orus Case; type species: Orus camerounensis Blackwelder, 1943 (= Micranops cameroni (Blackwelder, 1943)); syn. n.
Microscopaeus Coiffait, 1981: 19, described as subgenus of Scopaeus; type species: S. microphthalmus Eppelsheim, 1888 (= Micranops pilicornis (Baudi, 1869)); syn. n.

2. Genus Scopaeus Erichson, 1840
Geoscopaeus Coiffait, 1960: 284; replacement name for Stilpon Coiffait, 1952: 6 (nec Stilpon Loew, 1859); type species: S. baudrimonti Coiffait, 1952 (= S. ryei Wollaston, 1872); syn. n.
Hyposcopaeus Coiffait, 1960: 285; type species: S. scitulus Baudi, 1857 (= S. debilis Hochhuth, 1851); syn. n.
Anomoscopaeus Coiffait, 1968: 426; type species: S. gracilis (Sperk, 1835); syn. n.

The New World genus Orus Casey, 1884 was not examined for this study. However, judging from the revision by Herman (1965a, b), Orus appears closely related to Micranops according to the characteristic shape of the emargination of the male abdominal sternite 8 (Fig. 31), and to the general shape of the aedeagi (Figs. 4–6), which agree in the hook-shaped postforamen and the remarkable, ventro-medial lobe (parameres sensu Herman 1965a, b) and the short distal lobes. Orus is also linked with both Scopaeus and Micranops according to the two-piece spermatheca which, however, lacks the additional process of the chamber, here considered an apomorphy of Scopaeus s. str. According to Herman (1965a, b), Orus is distinguished from Scopaeus by the wider neck, which is at least as wide as one quarter of the head, but not from Micranops the neck of which is just as wide (Fig. 1a). This character, however, seems to be of little value for distinguishing these genera (Herman, pers. comm.). The phylogenetic relationships between Micranops, Orus and Scopaeus remain unclear pending a future generic revision of Paederinae.

Besides the supraspecific classification of the Scopaeina, the revision of species group names of Scopaeus resulted in further nomenclatorial changes and synonymies, as presented below. For full synonymies of the respective species and for biogeographical information see the species catalogue (Appendix 2; Electr. Suppl. 02–02, Pt 1).

Scopaeus crassipes Wollaston, 1867: 242; syntypes: 2 males, 5 females, Cape Verde Islands (BMNH); 1 male, Cape Verde Islands, Brava (HECO).
S. tassilienus Jarrige, 1958; holotype male, Algeria, Tassili n’Ajer (MNHN); syn. n.
S. mauretanicus Coiffait, 1960: 289; holotype male, Mauritania, Rgueibat Temba (MNHN); syn. n.
Comments: The syntypes of S. crassipes from the BMNH and the HECO collections were examined as well as the holotypes of S. mauretanicus and S. tassilienus. The latter are conspecific to S. crassipes according to the matching aedeagi, and here synonymized.

Scopaeus didymus Erichson, 1840: 606; lectotype male, Italy, Sardinia (ZMHB); here designated.
S. mateui Coiffait, 1953: 268; holotype male, Spain, Almeria, Albanchez (MNHN); syn. n.
Comments: The lectotype of Scopaeus didymus is designated because the original type series was mixed; the other of the two former syntypes from Sardinia (ZMHB) is a male of S. lanceolatus. The lectotype is labeled as follows: “Sardinien Gena T. (handwritten) / 6353 / didymus Er (handwritten) / Zool. Mus. Berlin / Type / Lectotypus Scopaeus Erichson 1840 didymus Erichson 1840 / des. J. Frisch 2002”.

The description of S. mateui Coiffait is based on specimens of S. didymus from southern Spain, the aedeagi of which have somewhat wider apical lobes than those of specimens from northern parts of the range, but in Spain both forms of the aedeagus are linked by transitional forms.

Scopaeus nigellus Wollaston, 1864: 585; holotype female, Canary Islands, Gomera (BMNH); synonymized with S. minimus by Fauvel (1902: 86), here revalidated (stat. n.).
Comments: Scopaeus nigellus is not a synonym of S. minimus, because the spermatheca of the female holotype differs distinctly from that of S. minimus, which was illustrated by Frisch (1998). Moreover, because
S. minimus is unknown from South-West Europe and North Africa (Frisch 1998), occurrence on the Canary Islands is very unlikely.

**Scopaeus perroti** Ochs, 1955: 65; holotype male, Algeria, El Djazair (MHNG); stat. n.

Comments: *Scopaeus perroti* was described as a subspecies of *S. mitratus*. It is here elevated to species rank according to the different shape of the aedeagus.

**Scopaeus portai** Luze, 1910: 393; lectotype male, Italy, Umbria, Porta (NHMW), designated by Frisch (1997c: 534).

*S. bordei* Peyerimhoff, 1914: 249; holotype female, Algeria, Biskra, Hamam-Salahin (MNHN); syn. n.

Comments: According to the shape of the spermatheca and the slender protarsomeres (see Frisch 1997c), the female holotype of *S. bordei* Peyerimhoff belongs to the yellowish-brown form of *S. portai* Luze from southern North Africa, from where Coiffait (1970) described *S. portai marocanus*. Frisch (1997c) synonymized *S. portai marocanus* because there is no difference regarding the shape of the aedeagus.

Acknowledgements

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References


Coiffait, H. (1960): Démembrement du genre *Scopaeus* et de-


Appendices®

Appendix 1: List of characters used for the cladistic analysis of West Palaearctic Scopaeina

Appendix 2: Synonymic catalogue of West Palaearctic Scopaeina, including biogeographic information

Appendix 3: Data matrix of characters used for the cladistic analysis

Appendix 4: NONA file for phylogenetic analysis

® For Appendices 2 to 4 see Parts 1 to 3 of the Electronic Supplement at http://www.senckenberg.de/odes/02-02.htm
Appendix 1

List of the 76 external morphological and primary sexual characters used for the phylogenetic analysis of West Palaearctic species of Scopaeina.

1 – Width of neck (measured at hind margin of head) – 0: about one third of head width; 1: from one fourth to one fifth (Figs. 1a, 3); 2: about one eighth of head width (Fig. 2).

2 – Pronotum – 0: trapezoid, foreangles distinct; 1: parallel, foreangles rounded (Fig. 2); 2: tapering towards fore and hind margins, foreangles indistinct (Figs. 1a, 3).

3 – Labrum – 0: bidentate, laterally rounded; 1: quadridentate (Figs. 1a, 2, 3).

4 – Setigerous postocular furrow – 0: absent (Figs. 2, 3); 1: present (Figs. 1a, b).

5 – Surface – 0: dull, finely and densely punctate, microsculpture distinct; 1: shining, sparsely punctate, microsculpture indistinct.

6 – Head – 0: elongate, tempora parallel, hind margin distinctly concave (Fig. 2); 1: tempora parallel or slightly tapering, hind margin straight or somewhat convex (Fig. 1a); 2: more or less trapezoid, hind margin straight or somewhat concave, slightly vaulted; 3: parallel or somewhat trapezoid, hind margin straight, notably vaulted (Fig. 3).

7 – Eye length – 0: less than 0.7 of temporal length (Figs. 1a, 2, 3); 1: at least 0.7 of temporal length.

8 – Protarsomeres – 0: slightly elongate; 1: slightly transverse (Fig. 1a); 2: about twice as wide as long (Fig. 3); 3: three times as wide as long (Fig. 2).

9 – Mesotibiae – 0: slender, at least five times as long as wide (Figs. 1a, 2, 3); 1: dilated, not more than five times as long as wide.

10 – Tibiae – 0: without; 1: with long, black setae.

11 – Distal antennomeres – 0: distinctly elongate; 1: slightly elongate; 2: square or transverse (Figs. 1a, 2, 3).

12 – Distal antennomeres – 0: with; 1: without long setae.

13 – Spermatheca – 0: in one piece (Fig. 22); 1: composed of two pieces (Figs. 23–29).

14 – Spermathecal duct – 0: very long, winding; 1: very long, winding, ending in bursa (Fig. 27); 2: short, ending in bursa (Fig. 24); 3: rather short, sclerotized section with terminal thickening (Fig. 26); 4: very short, sclerotized section with terminal thickening (Fig. 28); 5: very short, without thickening at transition to hyaline section.

15 – Bursa of spermathecal duct – 0: absent; 1: large (Figs. 24, 27, 30); 2: small, strongly sclerotized; 3: small, weakly sclerotized.

16 – Chamber of spermatheca – 0: without process (Fig. 22), evenly tapering towards spermathecal duct (Fig. 23); 1: with process (Figs. 24–29).

17 – Two-piece spermatheca – 0: absent (Fig. 22); 1: different; 2: stout, portions strongly flexed, chamber small, spermathecal duct strong and flexed up at right angle; 3: large, portions weakly flexed (Fig. 27); 4: with chamber notably lengthened (Fig. 25); 5: with chamber having a short, additional canal (Fig. 29); 6: with portions strikingly short; 7: small, portions little flexed, process dentate terminally.

18 – Sternite 8 of female – 0: not emarginate; 1: emarginate terminally.

19 – Laterotergite 9, apex – 0: bidentate; 1: unidentate, with dorsal emargination marked by a tooth or angle (Figs. 37–39).

20 – Laterotergite 9, dorsal emargination – 0: absent; 1: large, marked by a strong tooth (Fig. 37); 2: small, marked by a strong tooth (Fig. 38); 3: small, marked by a small tooth; 4: small, without tooth (Fig. 39); 5: large, without tooth.

21 – Male sternite 7, hind margin – 0: straight or slightly concave; 1: with some short, thick median setae; 2: with deep, rectangular emargination.

22 – Male abdominal sclerites – 0: regularly setose; 1: sparsely setose.

23 – Male sternite 8, hind emargination – 0: triangular (Fig. 34, 36); 1: short, semicircular; 2: small, narrow, triangular (Fig. 31); 3: narrow, deep, proximally round, surrounded by an outer margin extended into two distal teeth (Fig. 35); 4: short, wide, with a median, triangular emargination; 5: wide, very deep, proximally round; 6: short, wide (Fig. 33); 7: very deep but narrow (Fig. 32); 8: short, lateral margins wave-like convex.

24 – Male sternite 8, triangular emargination – 0: absent; 1: up to one fourth of sternite 8 length; 2: acute proximally, at least one third of sternite 8 length (Fig. 34); 3: up to one fourth of sternite 8 length, sternite with distinct median ridge and asetose, lateral planations; 4: one third of sternite 8 length, sternite with distinct median ridge and lateral, asetose planations (Fig. 36); 5: up to one fourth of sternite 8 length, sternite with densely setose median ridge and lateral, little-setose planations; 6: up to one fourth of sternite 8 length, sternite with median ridge setose terminally and with lateral, setose planations; 7: with convex lateral margins and a very acute apex.

25 – Male sternite 8, short, wide emargination – 0: absent; 1: almost semicircular; 2: with slightly convex middle, without median setae (Fig. 33).

26 – Aedeagus – 0: with short, distinct apical lobes and dorsal lobe (Figs. 4–6); 1: with unipartite, rather membranous apical portion of median lobe (Figs. 7–9); 2: with well-developed, large apical lobes and dorsal lobe (Figs. 10–21).

27 – Flagellum of aedeagus – 0: surrounded by denticles or teeth (Figs. 7–9); 1: without additional structures (Figs. 4–6, 10–21).
<table>
<thead>
<tr>
<th>Flagellum of aedeagus</th>
<th>0: flagellate, surrounded by denticles and teeth (Figs. 7–9); 1: stout, with denticles; 2: stout, without denticles (Figs. 4–6); 3: flagellate, without additional structures (Figs. 10–21).</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flagellum of aedeagus</td>
<td>0: bearing some ventral denticles (Fig. 16); 1: filiform terminally, strongly projecting from apical lobes; 2: asymmetrical, at least as long as apical lobes (Figs. 13–15); 3: strikingly short; 4: with ventrally curved apex; 5: somewhat thickened but at about its half length tapering and flexed ventrally; 6: bearing apical teeth (Figs. 19, 20); 7: strong, knife-shaped, reaching; 8: strong, shortly tapering at apex, reaching apices of apical lobes; 9: strong, strongly tapering at apex, not reaching apices of apical lobes (Figs. 10, 11).</td>
</tr>
<tr>
<td>Flagellum of aedeagus</td>
<td>0: absent; 1: S-shaped, orientated longitudinally (Fig. 19); 2: evenly curve ventrally.</td>
</tr>
<tr>
<td>S-shaped flagellum of aedeagus</td>
<td>0: absent or different; 1: as long as dorsal lobe (Fig. 19).</td>
</tr>
<tr>
<td>Asymmetric flagellum of aedeagus</td>
<td>0: absent; 1: without basal tooth; 2: with, in ventral view, right basal tooth (Fig. 14).</td>
</tr>
<tr>
<td>Ventrino-median process of median lobe</td>
<td>0: absent (Figs. 7–21); 1: present (Figs. 4–6).</td>
</tr>
<tr>
<td>Ventroneal process of phallobase</td>
<td>0: absent (Figs. 4–6, 10–21); 1: long, rod-shaped (Figs. 7–9); 2: very short, obtusely rounded; 3: lamelliform; 4: short, rod-shaped.</td>
</tr>
<tr>
<td>Ventroneal process of phallobase</td>
<td>0: absent (Figs. 7, 8); 1: present (Figs. 4, 5, 10–21).</td>
</tr>
<tr>
<td>Ventroneal process of phallobase</td>
<td>0: absent (Figs. 7, 8); 1: lobiform, as long as apical lobes (Figs. 4, 5); 2: small, stout (Fig. 14); 3: disc-shaped or almost triangular (Figs. 16, 17); 4: short, acute, semicircularly curved; 5: flagelliform (Figs. 19, 20); 6: long, hook-shaped; 7: curved with emarginate apex; 8: long, hook-shaped with emarginate apex; 9: short, hook-shaped (Fig. 10).</td>
</tr>
<tr>
<td>Ventroneal process of phallobase</td>
<td>0: absent; 1: extremely small, invisible in lateral view (Fig. 14); 2: visible in lateral view; 3: acute, triangular.</td>
</tr>
<tr>
<td>Ventroneal process of phallobase</td>
<td>0: absent or different; 1: hook-like, flexed to the right in ventral view (Fig. 20); 2: slender, more or less hook-shaped, little curved in ventral view.</td>
</tr>
<tr>
<td>Lateral lobes</td>
<td>0: absent (Figs. 19–21); 1: reduced, each marked by two groups of setae; 2: each bearing an apical group of long setae (Figs. 16–18); 3: large, each with two groups of setae; 4: large, strongly projecting, with numerous ventral setae; 5: weakly sclerotized, without setae; 6: reduced, obtuse, each bearing a group of about five ventrally pointing setae (Figs. 10–12); 7: absent, each indicated by a ventral group of long setae (Figs. 13–15); 8: of unequal length, bearing long apical setae; 9: obtuse, each bearing a line of setae invisible in dorsal view.</td>
</tr>
<tr>
<td>Lateral lobes</td>
<td>0: absent or different; 1: reduced, obtuse, each bearing a group of about five ventrally pointing setae; 2: elongate, apex acute; 3: short, very wide, bearing some short additional ventral setae; 4: pointing ventrally; 5: curved laterally, with groups of long setae; 6: with setae half as long as apical lobes; 7: short, setae long (Figs. 16–18).</td>
</tr>
<tr>
<td>Lateral lobes</td>
<td>0: absent or different; 1: moderately developed.</td>
</tr>
<tr>
<td>Dorsal lobe</td>
<td>0: indistinct (Figs. 7–9); 1: distinct (Figs. 4–6, 10–21).</td>
</tr>
<tr>
<td>Dorsal lobe</td>
<td>0: different; 1: large, weakly sclerotized (Figs. 4–6); 2: more or less elongate, strongly sclerotized (Figs. 7–21).</td>
</tr>
<tr>
<td>Dorsal lobe</td>
<td>0: different; 1: bearing long inner setae (Figs. 5, 6).</td>
</tr>
<tr>
<td>Dorsal lobe</td>
<td>0: different; 1: without distal emargination or ventral teeth; 2: emarginate or bilobed at apex, without distinct ventral teeth (Figs. 16, 18); 3: emarginate or not, with various ventral teeth (Figs. 19–21); 4: strongly enlarged, bilobed; 5: asymmetrical (Figs. 13–15); 6: stout, bearing two apical teeth; 7: with distinct apical portion; 8: vestigial (Figs. 10, 12); 9: deeply emarginate, apical teeth strongly curved towards phallobase.</td>
</tr>
<tr>
<td>Dorsal lobe</td>
<td>0: absent; 1: emarginate at apex, bearing two pairs of ventral teeth and two ventral lamellae; 2: convex at apex, without ventral teeth.</td>
</tr>
<tr>
<td>Bidentate dorsal lobe</td>
<td>0: absent or different; 1: with two ventral teeth.</td>
</tr>
<tr>
<td>Bidentate apical portion of dorsal lobe</td>
<td>0: absent or different; 1: with widely separate apical teeth.</td>
</tr>
<tr>
<td>Emarginate dorsal lobe</td>
<td>0: absent; 1: short, triangular; 2: slender (Figs. 16, 18).</td>
</tr>
<tr>
<td>Triangular dorsal lobe</td>
<td>0: absent; 1: with, in lateral view, wide, convex apical teeth; 2: with, in lateral view, slender, stout apical teeth.</td>
</tr>
<tr>
<td>Short triangular dorsal lobe</td>
<td>0: absent; 1: deeply emarginate, with separate apical teeth; 2: slightly emarginate.</td>
</tr>
<tr>
<td>Long triangular dorsal lobe</td>
<td>0: absent or different; 1: emarginate in distal half, distal teeth separate; 2: emarginate in distal half, distal teeth adjacent; 3: with diverging distal teeth (Figs. 16, 18).</td>
</tr>
<tr>
<td>Diverging teeth of triangular dorsal lobe</td>
<td>0: different; 1: with (Figs. 16, 18); 2: without apical teeth or denticles.</td>
</tr>
<tr>
<td>Dorsal lobe</td>
<td>0: different; 1: half as long as apical lobes, bearing two short, ventrally curved apical teeth; 2: little emarginate at apex, bearing different teeth; 3: deeply emarginate, extended into two ventrally curved teeth of unequal length (Figs. 19–21); 4: extended into a long tooth; 5: claviform in lateral view.</td>
</tr>
<tr>
<td>Dorsal lobe</td>
<td>0: different; 1: with three ventral teeth; 2: with two ventral teeth.</td>
</tr>
<tr>
<td>Dorsal lobe</td>
<td>0: different; 1: with lobiform apical teeth (Fig. 19).</td>
</tr>
<tr>
<td>Apical lobes</td>
<td>0: distinct from median lobe at very apex (Figs. 7, 8); 1: distinct (Figs. 4–6, 10–21).</td>
</tr>
<tr>
<td>Distinct apical lobes</td>
<td>0: absent; 1: short, lobiform, about parallel, not enlarged apically (Figs. 4–6); 2: of different shape, but apically enlarged (Figs. 10–21).</td>
</tr>
</tbody>
</table>
59 – Distinct apical lobes – 0: different or absent; 1: each with distinct, triangular distal portion; 2: knife-shaped (Figs. 16–18); 3: very short, angled, flexed ventrally (Figs. 10–12); 4: with inner row of setae; 5: asymmetrical (Figs. 13–15); 6: conspicuously shorter than dorsal lobe; 7: simple, convex ventrally, widening laterally; 8: ventrally curved with longitudinally curved, round apex; 9: convexly enlarged ventrally, each with distinct, membranous apical portion.


63 – Distinct distal portions of apical lobes – 0: absent; 1: with widening outer ventral margins.

64 – Distinct distal portions of apical lobes – 0: absent; 1: with inner ventral margins each forming a right angle.

65 – Knife-shaped apical lobes – 0: absent; 1: very slender, each with shallow emargination; 2: slender, widened distally, each with deep emargination and dorsally upturned apex; 3: with deep, narrow or semicircular emargination, apex dorsally upturned; 4: with very wide emargination, distal halves straight; 5: without emargination (Figs. 16–18).

66 – Apex of knife-shaped apical lobes – 0: apical lobes different; 1: evenly tapering (Figs. 16–18); 2: upturned; 3: knife-shaped.

67 – Apical lobes – 0: without long setae; 1: with long, lateral or ventral setae.

68 – Apical lobes with inner row of setae – 0: absent; 1: short, almost symmetrical; 2: different, slightly asymmetrical.

69 – Asymmetrical apical lobes – 0: absent; 1: long and slender (Figs. 13–15); 2: shorter, strongly asymmetrical.

70 – Apical lobes – 0: different; 1: with laterally enlarged, ventrally emarginate apical portion (Figs. 19–21).

71 – Apical lobes with enlarged apical portion – 0: absent; 1: slender, emargination shallow (Fig. 19); 2: hook-shaped distally.

72 – Sclerotized ring of phallobase – 0: absent (Figs. 4–6); 1: present (Figs. 7–21).

73 – Sclerotized ring of phallobase – 0: absent (Figs. 4–6); 1: rather broad; 2: broad, ventrally enlarged, lateral portions rather slender; 3: slender, lateral portions transverse and widely separate in dorsal view; 4: broad, lateral portions strong, separate in dorsal view; 5: broad, lateral portions widely separate in dorsal view (Figs. 13–15); 6: broad, with two close lateral portions in dorsal view; 7: broad, with longitudinal lateral portions separate from lateral margins of aedeagus (Figs. 10–12); 8: very narrow and widening ventrally, lateral portions slender (Figs. 16–18, 19–21); 9: striking, broad (Figs. 7–9).

74 – Lateral ridges of median foramen – 0: absent (Figs. 4, 5); 1: short, little sclerotized; 2: about half as long as phallobase, strongly sclerotized.

75 – Median foramen – 0: at distal end of phallobase; 1: near round end of phallobase; 2: different.

76 – Lateral lobes – 0: absent (Figs. 4–9); 1: absent, indicated by not more than a few setules (Figs. 19–21); 2: present (Figs. 10–18).