



The Afrotropical *Scopaeus paludicola* species group (Coleoptera: Staphylinidae: Paederinae), a primitive lineage of the genus

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Abstract

The Afrotropical *Scopaeus paludicola* species group (Staphylinidae: Paederinae: Lathrobiini) is defined and described. It comprises *S. jeanneli* Levasseur, 1981 from Kenya and the South African *S. insidiosus* Fagel, 1973, *S. ludificatus* Fagel, 1973, *S. nigerrimus* Cameron, 1945, *S. paludicola* Cameron, 1945, and *S. transvaalensis* Fagel, 1973, which are redescribed, and five new species from the Republic of South Africa: *S. bikoi* sp. nov., *S. capensis* sp. nov., *S. endrodyi* sp. nov., *S. rectiphallatus* sp. nov., *S. uhligorum* sp. nov..

Lectotypes are designated for *S. paludicola* Cameron, 1945 and *S. p. pallipes* Cameron, 1945. The doubtful synonymy of these taxa is discussed. An identification key for the *S. paludicola* species group is presented, and its distribution is mapped.

The *S. paludicola* species group differs from the current definition of *Scopaeus* in some characters, but it belongs to the genus according to the presence of the metathoracic/mesofemoral stridulum. The presence of a ventrolongitudinal, membranous split of the aedeagus is considered a derived character of the species group. A midlongitudinal groove of the mesobasisternum is apomorphic for the *S. paludicola* lineage from southern Africa, which comprises most species of the group. The *S. paludicola* species group is considered to be a basal lineage of *Scopaeus*, because it shares ancestral genital characters of the Scopaeina, such as a dorsally membranous aedeagus with a proximal median foramen and a simple sperm pump without the characteristic appendage of the chamber segment of most *Scopaeus*.

Based on the newly recognized characters of the *S. paludicola* species group and other *Scopaeus* species, a revised hypothesis on the basal phylogeny of the genus is presented.

Keywords new species | redescriptions | phylogeny | Scopaeina | southern Africa

1 Introduction

The speciose, globally distributed genus *Scopaeus* Erichson, 1839 (Coleoptera: Staphylinidae: Paederinae) has long been defined primarily by its dentate labrum

and the sclerotized, tripartite ligular lobe – characters that were already introduced in the original description, first in the form of a key (Erichson 1839: 29), only one year later as text description (Erichson 1840: 604, 605). *Scopaeus* is also known for its thin, stalk-like neck,



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which was also mentioned by Erichson (1840: 604) and later used by Mulsant & Rey (1878: 178, 179) to establish the “Scopéates”, the subtribe Scopaeina Mulsant & Rey, 1878, in which the authors had incorrectly classified *Scopaeus* and *Stilicus* Berthold, 1827, a synonym of *Rugilus* Leach, 1819.

Since then, almost 150 years later, the first comprehensive morphological study on the classification of the Scopaeina was published by Herman (2023), who thoroughly redefined the subtribe and its genera. I had also contributed to a better understanding of the Scopaeina since the mid-1990s (e.g. Frisch et al. 2002), but my work only dealt with taxa from the eastern hemisphere.

Herman (2023: 8) defined the Scopaeina based on a combination of homoplastic characters, including a cephalic trichobothrium and the tripartite ligular lobe. The latter is therefore no longer differentially diagnostic for *Scopaeus* alone. Similarly, a thin neck is widespread among the Paederinae (Herman 2023: 10), and a dentate labrum also occurs in other genera of the Scopaeina such as *Frischianus* Herman, 2025 (Herman in Frisch & Herman 2025: 223, 225), *Hyperscopaeus* Coiffait, 1984 (Herman 2023: 110, 111), or *Micranops* Cameron, 1913 (Herman 2023: 122). Thus, there was no apomorphic character left to define *Scopaeus*. Even though “Finding unique, derived characters to delimit *Scopaeus* proved a major challenge” (Herman 2023: 5), the author finally solved this puzzle by discovering a spectacular and convincing apomorphy for the genus, a metathoracic/mesofemoral stridulum (Herman 2023: 20–23, 67). He moreover distinguished *Scopaeus* from the other genera of the Scopaeina by long, apically acute metakatepisternal processes (Herman 2023: 67) and the sclerotized, fused dorsal surface of the aedeagus (Herman 2023: 68). I had already proposed *Scopaeus* as a monophyletic group based on a characteristic arrangement of the poststernal lobes of the aedeagus (Frisch et al. 2002: 31–35) and a typical extension of the proximal segment (chamber segment) of the sperm pump (Frisch et al. 2002: 30, 38). So far, so good.

For a long time I considered the so-called *S. paludicola* species group, which Fagel (1973: 13, 15, 167–176) had established for five species from South Africa, to be atypical for the genus due to the comparatively strong body punctation and the thin, small aedeagus, but only recently I examined it more closely. In contrast to the current definition of *Scopaeus* (Frisch et al. 2002: 38; Herman 2023: 67–70), the *S. paludicola* species group exhibits presumed primitive character states of the metakatepisternal processes, the aedeagus, and the sperm pump that are widespread in more basal genera of the Scopaeina. Nevertheless, the presence of the stridulum clearly assigns the *S. paludicola* species group to *Scopaeus*.

In this contribution, the *S. paludicola* species group is defined, the associated species are described or redescribed, and the definition of *Scopaeus* is revised in light of the characters of this clade.

2 Material and methods

Specimen depositories: The specimens this study is based on are stored in the following collections and were made available to me by the mentioned curators, collection managers, and private collectors: **DMNH** – Ditsong National Museum of Natural History, Pretoria (Ruth Müller, Werner Strümpfer); **JJCU** – Jiri Janák Private Collection, Ústí nad Labem; **MFNB** – Museum für Naturkunde Berlin; **MNHN** – Muséum National d’Histoire Naturelle, Paris (Azadeh Taghavian, Nicole Berti †); **NHML** – Natural History Museum, London (Max Barclay, Roger Booth, Martin Brendell, Dmitry Telnov); **NHMW** – Naturhistorisches Museum, Wien (Harald Schillhammer); **RMCA** – Royal Museum for Central Africa, Tervuren (Marc de Meyer).

Measurements: Specimens were measured magnified 140 x using a stereoscopic microscope with an eyepiece linear micrometer. Ten specimens per species were measured, if available. Total length of specimen – interval from apical denticles of labrum to posterior end of abdomen, depending on degree of contraction of abdomen; forebody length – interval from apical denticles of labrum to posterior margin of elytra at suture; head length – interval from anterior margin of clypeus to posterior margin in front of nuchal groove; head width – maximum distance between lateral margins including eyes; eye length – maximum distance from anterior most to posterior most point of ocular suture measured in lateral view; temporal length – distance from posterior most point of ocular suture to nuchal groove measured in lateral view; pronotal length – interval from anterior to posterior pronotal margin along midline; pronotal width – maximum distance between sinistral and dextral pronotal margin; elytral sutural length – interval from posterior end of scutellum to posterior end of suture; length of aedeagus measured longitudinally across aedeagus to tip of ventral process if this protrudes over aedeagus.

Photographs: The habitus photographs and their excerpts (Figs 30–40) are based on image stacks taken with an Olympus OM 1 camera and a 10 x Mitutoyo macro lens. The image stacks of bodyparts [Figs 1–4, 8–11, 12 (right image), 13–19, 21, 23] were made with the same camera and a 20 x Mitutoyo macro lens. These images were taken under diffuse lighting to clearly show the microstructure. The transmitted light microscopic images of the primary and secondary sexual characteristics are

based on image stacks taken with a Leica imaging system consisting of the DM6 B transmitted light microscope with the K3C camera and operated with the LasX software. The microscopic images were made with the following magnifications: 100 x [abdominal sternite VIII (Figs 41–46); 200 x [mouthparts (Figs 5–7), mesotibia (Fig. 12, left image), female genitals (Figs 24, 25), aedeagus (Figs 20, 22, 47–102, 106 ff.)]; 400 x [sperm pump (Figs 26–29, 107 ff.)]. The image stacks were processed into multifocus images with Helicon Focus.

Figs 77, 78 depicting the aedeagus of the holotype of *T. insidiosus* I took in the late 1990s with simple equipment under unfavorable conditions at RMCA.

Descriptions: In order to keep the descriptions brief and comprehensible, they are structured hierarchically. Thus, the species group characters are not repeated in the descriptions of the associated species. The identification key to the *S. paludicola* species group and their species replaces differential diagnoses in the species descriptions.

The descriptions of the microreticulation and punctuation of the species were created using the habitus images taken under diffuse light (Figs 30–40), which show these characters very precisely. Under the usual light source of a stereomicroscope, the specimens appear more shiny, and the punctuation of the forebody in particular appears coarser and denser.

Terminology: The terms used for the primary genital characters largely follow Frisch et al. (2002). The terminology for the ectoskeletal characters follows Herman (2023).

Material compilations: In the compilations of type material and additional records, the label data are not cited verbatim but standardized to make it easier for the reader to identify the localities. Old, nowadays uncommon locality names are replaced by the current names but added in rectangular brackets. In the case of old type specimens, the labels are also cited verbatim in quotation marks. To shorten the material paragraphs, names of superior administrative units such as states and provinces are only mentioned once per paragraph and the locality data compiled afterwards.

3 The *Scopaeus paludicola* species group

3.1 Description, distribution, and habitat

Diagnosis: The *Scopaeus paludicola* species group comprises both macropterous and micropterous, usually dark brown to black, notably punctured species. The presence of a metathoracic/mesofemoral stridulum

(Figs 8–12) supports placing the clade in *Scopaeus*. The following characters separate the *S. paludicola* group from all other previously defined species groups of *Scopaeus* and numerous examined, but undescribed species of the genus (many species groups still need to be established):

- The straight or slightly concave lateral margins of the pronotum (Figs 30–40) versus moderately to strongly convex pronotal margins (e.g. Frisch 2016: Figs 2–16; Frisch & Narakusumo 2023: Figs 1–26).
- The thin, stalk-like aedeagus that is membranous dorsally for entire length and width and has a ventrolongitudinal membranous split extending from the ostium to the median foramen (e.g. Figs 20, 21, 47, 74, 82) versus a convex, dorsally completely sclerotized aedeagus (Figs 22, 23; cf. Frisch et al. 2002: Figs 7–21), which may have a membranous dorsodistal window (Figs 106, 108, 110, 112, 114).
- The median foramen at the proximal end of the aedeagus (Fig. 20) versus the median foramen situated more anteriorly (e.g. Figs 106, 108, 124).
- Absence of a sclerotized dorsal lobe of the aedeagus (Figs 20–23; cf. Frisch et al. 2002: Figs 7–21).
- Absence of a sclerotized flagellum of the aedeagus (Figs 20–23; cf. Frisch et al. 2002: Figs 7–21).

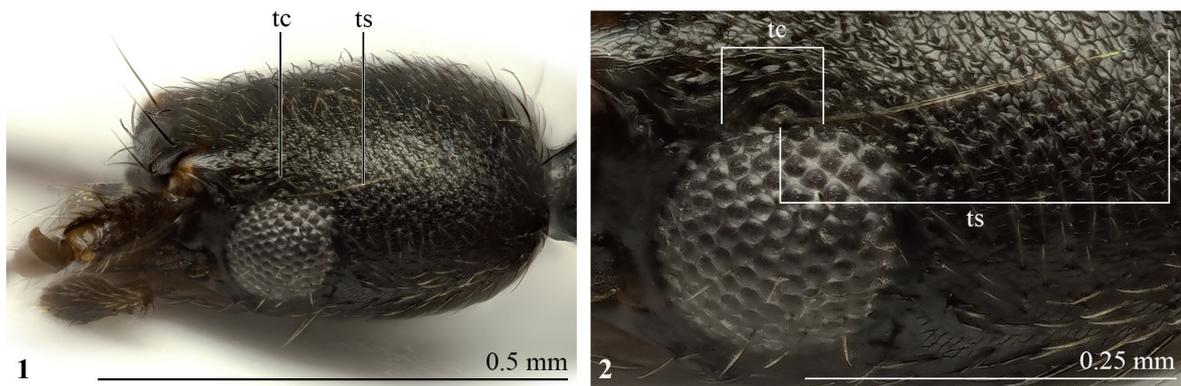
The *S. paludicola* species group is moreover distinguished from the vast majority of *Scopaeus* species by the pair of short metakatepisternal processes that are laterally about as wide as at their basis and shaped like an equilateral triangle (Figs 16, 17). In *Scopaeus*, the metakatepisternal processes are usually elongate and apically tapered to an acute point (Fig. 18; Herman 2023: 23, 25, e.g. Figs 125, 142). It is also distinguished from most *Scopaeus* species by the absence of the appendage of the proximal segment of the sperm pump (Figs 24–26).

Description: Total length 3.1–4.1 mm; forebody length 1.7–2.1 mm.

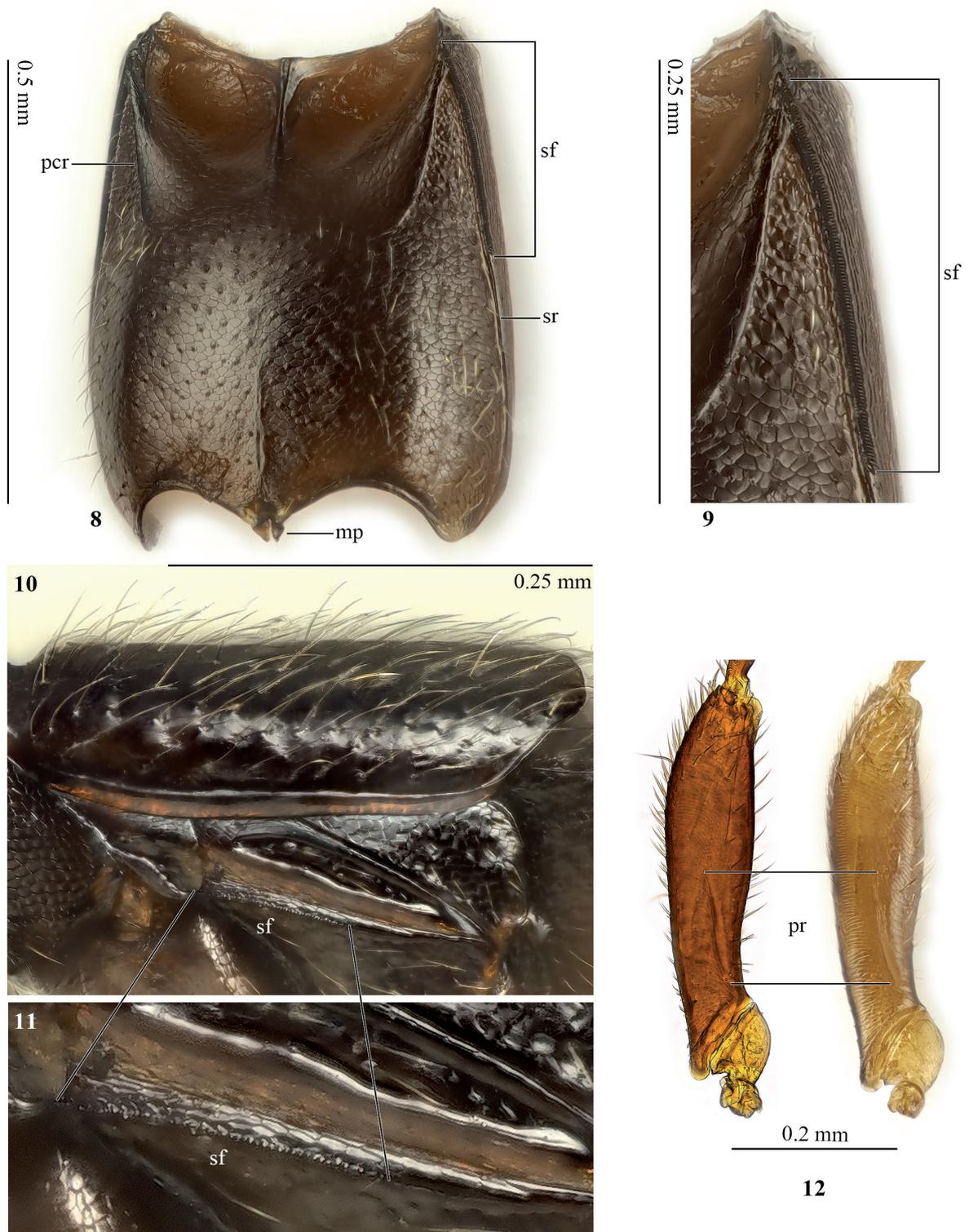
Body color usually dark brown to black with medium brown to black appendages (Figs 30–40); elytra sometimes gradually lighter brown posteriorly (Figs 31, 34).

Forebody surface shiny (Figs 33, 36, 40), or head and pronotum more or less matt due to fine, isodiametric microreticulation (Figs 30 a, b–32 a, b; 35 a, b; 37 a, b–39 a, b); abdomen with indistinct microreticulation (Figs 30 d–40 d); forebody surface with clear, setate punctuation; cephalic punctuation considerably denser than spacious pronotal and elytral punctuation; pronotal punctuation in some species increasingly coarser along impunctate midline (e.g. Figs 36 b–39 b); abdomen more finely punctate than pronotum and elytra (Figs 30 d–40 d).

Head 1.06–1.19 times as long as wide, parallel (Figs 30–32, 34–37) or somewhat trapezoidal (Figs 33, 38), with almost straight (e.g. Fig. 3, 33) to moderately rounded (Fig. 40) lateral margins; posterior angles



Figures 1–7. Head in lateral view (1), trichobothrial cavity with trichoid sensilla (2), head in ventral view (3, 4), labrum (5), labium and maxilla (6), and mandibles (7) of *Scopaeus paludicola*, Republic of South Africa, Western Cape: De Hoop NR (1–4); *S. uhligorum*, Republic of South Africa, Western Cape: Cederberg Wilderness Area (5–7). **Abbreviations:** **gs** – gular sutures; **ng** – nuchal groove; **tc** – trichobothrial cavity; **ts** – trichobothrial sensilla. **Arrow:** tripartite ligular lobe.



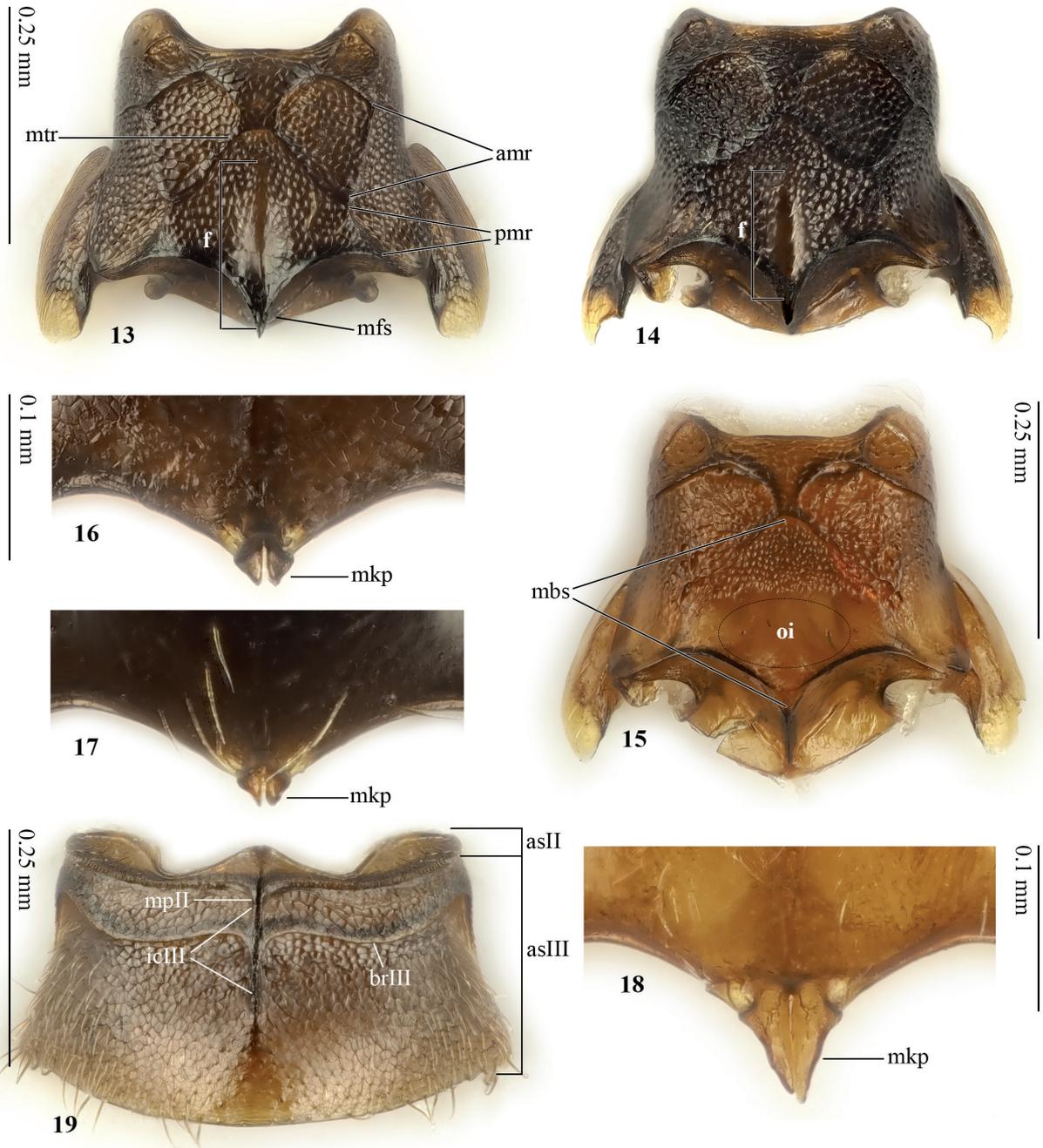
Figures 8–12. Metaventrite with stridular file in ventrolateral (8, 9) and lateral view (10, 11), and mesotibia (12) of *Scopaeus paludicola*, Republic of South Africa, Western Cape: De Hoop NR (8, 9, 12) and *S. jeanneli*, Kenya: Mt Elgon (10, 11). **Abbreviations:** mp – metakatepisternal processes; pcr – pericoxal ridges; pr – plectral ridges; sf – stridular file; sr – submarginal ridge.

strongly rounded (Figs 30–40); posterior margin somewhat convex (Figs 30, 31), straight (Figs 32–39), or moderately concave (Fig. 40).

Neck moderately deeply constricted with nuchal groove 0.19–0.28 times as wide as greatest head width (Figs 3, 4, 30–40).

Eyes present, in macropterous species 0.47–0.58 times as long as temples (Figs 30–39), in only known micropterous species 0.38 times as long as temples (Fig. 40).

Trichobothrial cavity semicircular with trichoid sensilla in medial position, connected to middorsal margin of eye (Figs 1, 2).



Figures 13–19. Mesoventrite (13–15), medioposterior portion of metaventrite (16–18), and abdominal sternites II and III (19) of *Scopaeus paludicola*, Republic of South Africa, Western Cape: De Hoop NR (13, 16, 19); *S. ludificatus*, Republic of South Africa, Western Cape: Table Mountain (14, 17); *S. testaceus* Motschulsky, Vietnam, Cuc Phuong (15, 18). **Abbreviations:** amr – anterior mesanapleural ridge; asII – abdominal sternite II; asIII – abdominal sternite III; brIII – basal ridge of abdominal sternite III; f – midlongitudinal groove of mesobasisternum; icIII – intercoxal carina of abdominal sternite III; mbs – mesobasisternum; mfs – mesofurcasternum; mkp – metakatepisternal processes; mpII – medioposterior point of abdominal sternite II; mtr – mesotransventral ridge; oi – oval impression; pmr – posterior mesanapleural ridge.

Gular sutures moderately widely separated, subparallel for most of length, somewhat diverging posteriad (Figs 3, 4).

Labrum quadridentate with denticles tapered to acute apex; submedial denticles notably broader and longer than sublateral denticles (Fig. 5).

Mandibles with three large denticles on left and four on right (Fig. 7).

Labium with tripartite ligular lobe (Fig. 6).

Antenna with subparallel scapus about 2.5–3.0 times as long as wide, from moderately elongate pedicellus and median segments increasingly shorter towards quadrate or slightly transverse segment 10; antennal segment 11 about 1.5 times longer than wide (Figs 30–40).

Pronotum 1.13–1.31 times longer than wide, 0.93–1.08 times as long as head, and 0.81–1.0 times as wide as head, without marginal ridge, with medially straight or slightly concave lateral margins, and widest at pronounced anterior angles (Figs 30–40).

Prothoracic leg with tarsal segments in both sexes dilated, twice as wide as long or somewhat wider, in males slightly wider than in females (Figs 30–40).

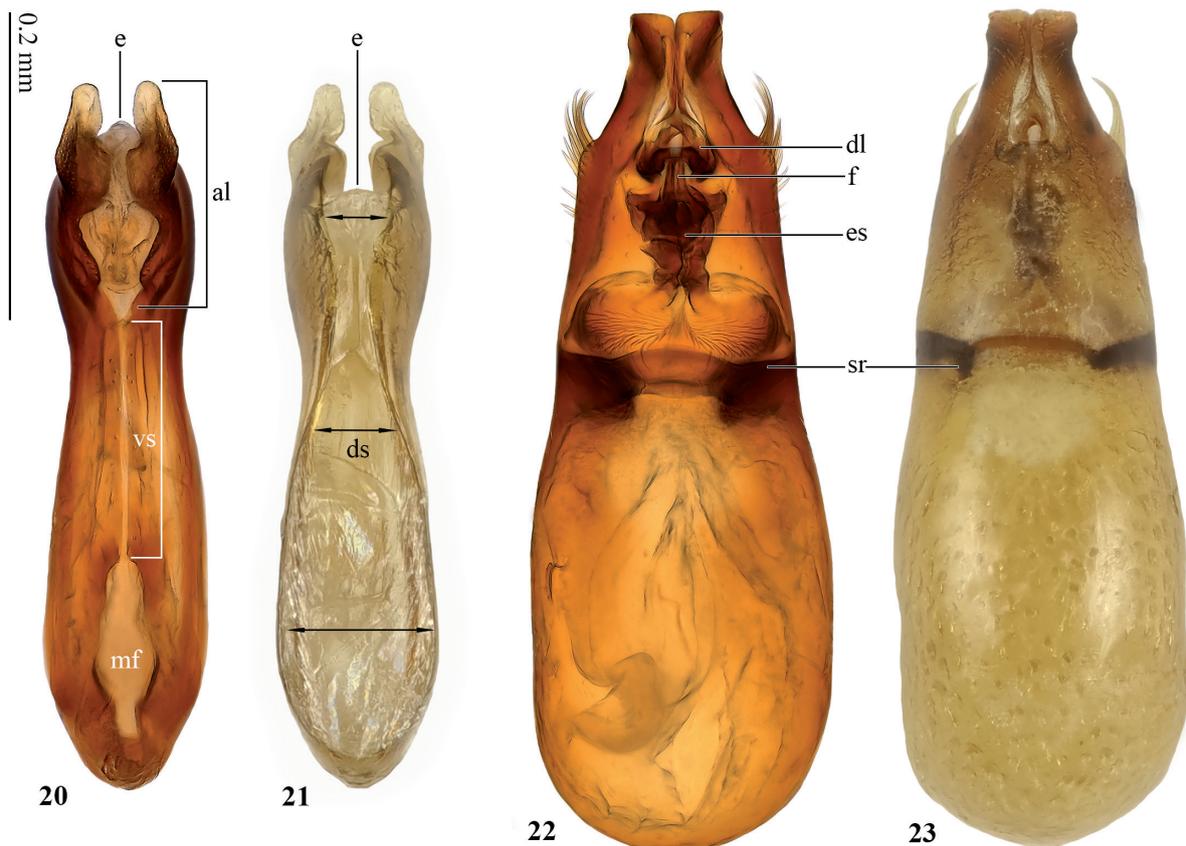
Mesoventrite (Figs 13, 14) with mesobasisternum with oval, medial depression or deep, midlongitudinal groove opening posteriorly, anterior mesanapleural ridge well developed, posterior mesanapleural ridge indistinct, and mesofurcasternal apophysis absent.

Elytra in macropterous species along suture 0.8–1.05 times as long as wide, 0.84–1.21 times as long as pronotum, 0.84–1.14 times as long as head, and 1.0–1.39 times as wide as head (Figs 30–39); elytra in only known micropterous species along suture 0.72–0.74 times as long as wide, 0.63 times as long as pronotum, 0.66–0.68 times as long as head, and 0.94–1.0 times as wide as head (Fig. 40).

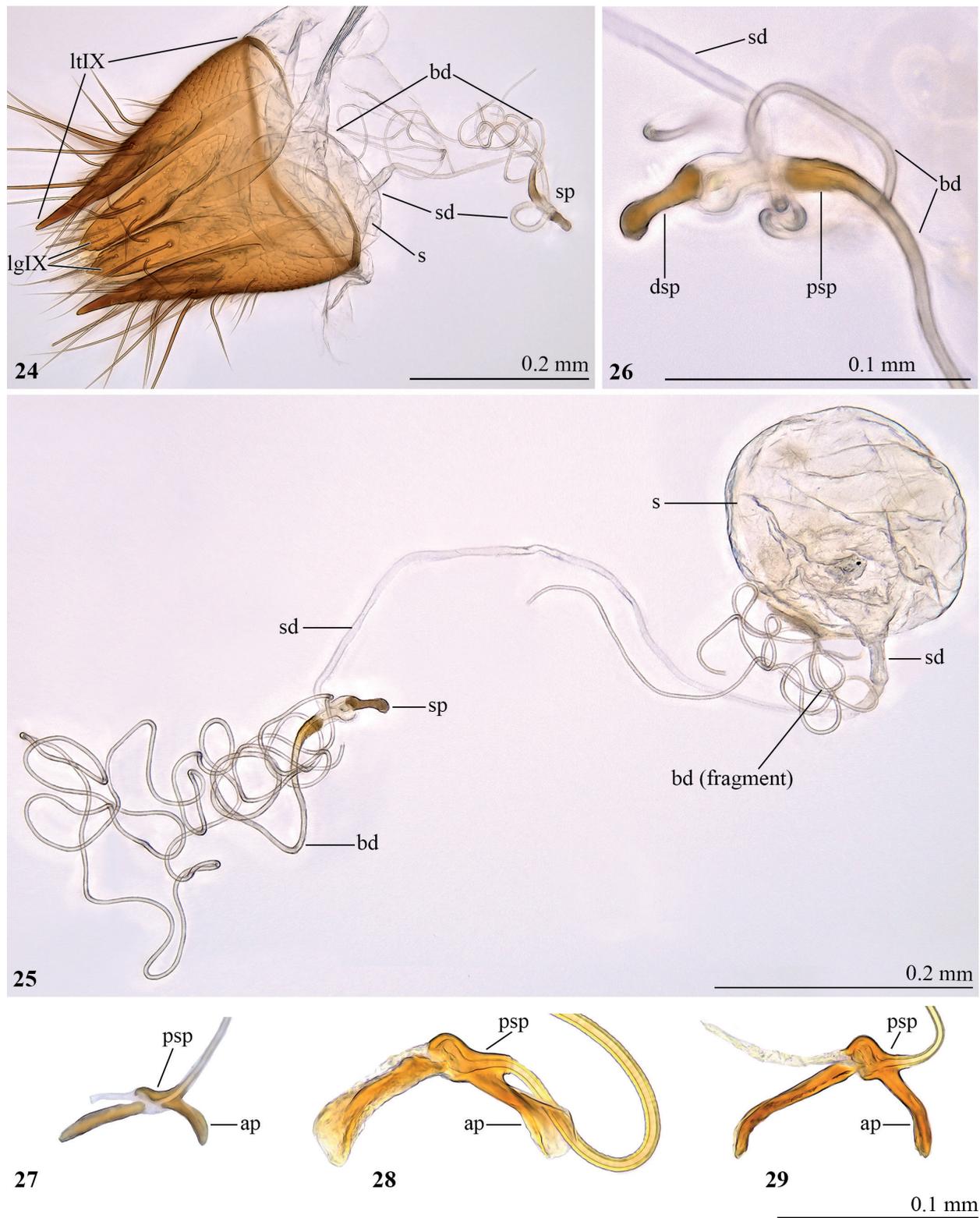
Metaventrite with pericoxal ridge longer than mesocoxal cavity (Fig. 8), stridular file adjacent to submarginal ridge (Figs 8–11), and pair of short, triangular metakatepisternal processes about as long as wide at bases (Figs 16, 17).

Metathoracic wings well developed in macropterous species, vestigial in only known micropterous species.

Metatibia with inner apical comb of long tines; outer apical comb absent.



Figures 20–23. Aedeagus in ventral (20) and dorsal view (21–23) of *Scopaeus ludificatus*, Republic of South Africa, Western Cape: Cape Town (20); *S. ludificatus*, Republic of South Africa, Western Cape: Ceder Mountain (21); *S. complex* Sharp, Vietnam, Cuc Phuong: Ninh Binh (22); *S. complex*, Japan: Kyoto (23). **Abbreviations:** al – apical lobe; dl – dorsal lobe; ds – dorsal split of aedeagus; e – apical end of endophallus; es – endophallic sclerites; f – flagellum; mf – median foramen; sr – sclerotized ring; vs – ventral split of aedeagus.



Figures 24–29. Female genital characters of *S. uhligorum*, paratype, Republic of South Africa, Western Cape: De Hoop NR (24); *S. jeanneli*, Kenya: Mt Elgon (25, 26); *S. kritschi* Frisch, Cambodia: Angkor (27); *S. cuspidobatus* Frisch, Indonesia, Jawa Barat, Sukabumi: Sirnarasa (28); *S. diversilobatus* Frisch, Indonesia, Jawa Barat, Sukabumi: Djampang Kulong (29). **Abbreviations:** ap – appendage of proximal segment of sperm pump; bd – bursal duct; dsp – distal portion of sperm pump; lgIX – lateral gonocoxal plate IX; ltIX – laterotergite IX; psp – proximal portion of sperm pump; s – spermatheca; sd – spermathecal duct; sp – sperm pump.

Abdominal sternite II with trilobed anterior margin and posterior margin with median point (Fig. 19).

Abdominal sternite III with subbasal ridge extended to long intercoxal carina (Fig. 19).

Male: Abdominal sternite VII without species diagnostic modifications.

Abdominal sternite VIII with triangular incision of posterior margin occupying about posterior third of sternite length (Figs 41–46).

Aedeagus narrow, stalk-like, dorsally membranous for entire length and width, and with ventrolongitudinal, membranous split extending from ostium to median foramen; aedeagus thus divided into two sclerotized, ventrolateral halves extended into paired ventral extensions at either side of ventrolongitudinal split (e.g. Figs 20, 21, 47, 65) and paired apical lobes with proximal portion lengthened into proximoventral extension and distal portion set-off from each other by ventral or ventrodorsal constriction (e.g. Figs 47, 65, 79); distal portion of apical lobes with dorsal, mediad pointing dilatation in about middle of length (e.g. Figs 52, 70, 87); median foramen located close to posterior end of aedeagus; vestigial parameres present; endophallus membranous without sclerotized structures, in variable extent projecting from ostium (Figs 20, 21, 47–102).

Female: Abdominal sternites VII and VIII without species specific modifications, with convex posterior margins.

Abdominal segment IX with two separated gonocoxal plates (Fig. 24).

Female primary sexual organs consisting of hyaline, versicular spermatheca, sperm pump made up of simple chamber segment and terminal segment of about same length, very long, winding bursal duct, and membranous bursa (Figs 24–26).

Bionomics: According to the detailed label information of Jiří Janák, Sebastian Endrödy-Younga, and Manfred Uhlig, species of the South African lineage of the *Scopaeus paludicola* species group were collected in riparian habitats by sifting phytodebris, treading humid ground, shore washing, and turning stones. The South African species therefore inhabit riparian habitats such as the banks of streams, rivers, and lakes, which is typical for the genus. Frisch et al. (2002: 28) described the species of *Scopaeus* as hygrophilic inhabitants of sparsely vegetated, moist, sandy, or gravelly soils, preferably in riparian areas. Some species of the macropterous *S. paludicola* subgroup were collected with light traps.

The micropterous *S. jeanneli* of Mt Elgon was collected at altitudes of 3,000–3,500 m. The habitat of the type series was not specified by Levasseur (1981). According to their labels, subsequently collected specimens were found in the humus of a moist gorge.

Distribution: The *Scopaeus paludicola* species group is an Afrotropical faunal element and known from two widely separate areas, Mount Elgon in Kenya (the micropterous *S. jeanneli*) and southern Africa (ten closely related, macropterous species), but it is certainly more widespread (Figs 103–105). The species richness in the Republic of South Africa, especially in the Cape region, is certainly an artifact of higher collection activities due to the tourist infrastructure there.

3.2 Species of the *Scopaeus paludicola* species group

The *Scopaeus paludicola* species group currently comprises eleven species distributed in Sub-Saharan Africa, five of which are new to science. They are described below. The following identification key provides page references to the species descriptions or redescrptions below.

3.2.1 Key to the subgroups and species of the *Scopaeus paludicola* species group

- 1 Microphthalmous, micropterous species without palisade fringe of abdominal sternite VII (Fig. 40). Eyes 0.38 times as long as temples. Mesobasisternum with oval, medial depression (cf. Fig. 15). Elytra along suture 0.72–0.74 times as long as wide and 0.63 times as long as pronotum. Aedeagus as in Figs 100–102. Kenya (Mt Elgon)..... *jeanneli* (p. 116)
- Macrophthalmous, macropterous species with palisade fringe of abdominal sternite VII (Figs 30–39). Eyes 0.47–0.58 times as long as temples. Mesobasisternum with midlongitudinal groove (Figs 13, 14). Elytra along suture 0.8–1.05 times as long as wide and 0.84–1.21 times as long as pronotum. Southern Africa (*S. paludicola* lineage) 2
- 2 Apical lobes of aedeagus with distal portion narrow, ending in small, more or less membranous, apicoventral lobe or in several ventral microlobes (Figs 47–78) 3
- Apical lobes of aedeagus with distal portion compact, strongly sclerotized, without membranous lobes (Figs 79–99)..... 5
- 3 Head and pronotum without microreticulation. Apical lobes of aedeagus with small apicoventral lobe and huge, strongly projecting proximoventral extension (Figs 77, 78) *insidiosus* (p. 109)
- Head and pronotum matt, fine-meshed microreticulate (Figs 30–32). Apical lobes of aedeagus with microlobes, usually appearing frayed; proximoventral extension notably smaller (Figs 47–76) 4

4 Apical lobes of aedeagus with proximoventral extension of proximal portion dentiform and proximoventral extension of distal portion shorter, less strongly curved distad (Figs 47–64) *paludicola* (p. 106)
 - Apical lobes of aedeagus with proximoventral extension of proximal portion wider, not dentiform, and proximoventral extension of distal portion longer, strongly curved distad (Figs 65–76).....
 *transvaalensis* (p. 109)
 5 Pronotum evenly finely punctured, without coarser punctures along impunctate midline (Figs 33–35) 6
 - Pronotum with coarser punctures along impunctate midline (Figs 36–39) 8
 6 Aedeagus with ventral extension, only dorsal margin of apical lobes curved ventrad (Figs 88–90). Head and pronotum with microreticulation, weakly shiny (Figs 35 a, b) *uhligorum* (p. 112)
 - Aedeagus without ventral extension; apical lobes strongly curved ventrad (Figs 79, 82, 85). Head and pronotum without clear microreticulation, strongly shiny (Figs 33 a, b; 34 a, b) 7
 7 Apical lobes of aedeagus extended into widely triangular apex not extended dorsally (Figs 79, 82); proximal extensions of proximal portion of apical lobes weakly convex (Figs 79, 82) with ventral margins strongly concave, together forming “window” (Figs 80, 83)
 *ludificatus* (p. 110)
 - Apical lobes of aedeagus with truncate apex projecting over dorsal margin of apical lobes (Fig. 85); proximal extensions of proximal portion of apical lobes strongly convex (Fig. 85) with ventral margins close to each other, subparallel (Fig. 86) *endrodyi* (p. 112)
 8 Head superficially microreticulate; pronotum smooth and shiny (Fig. 36 a, b). Male characters unknown
 *nigerrimus* (p. 113)
 - Head and pronotum microreticulate, weakly shiny (Figs 37–39 a, b) 9
 9 Aedeagus with parallel lateral margins (Figs 92, 93); apical lobes hardly curved ventrally (Fig. 91), with ventral dilation of distal portion not widened mediad, but extend into distad curved tip (Figs 92, 93)
 *rectiphallatus* (p. 115)
 - Aedeagus moderately convex laterally (Figs 95, 96, 98, 99); apical lobes strongly curved ventrally (Figs 94, 97), with ventral dilation of distal portion triangularly widened mediad without distad curved tip (Figs 95, 96, 98, 99) 10
 10 Apical lobes of aedeagus in lateral view with distal portion about as wide as proximal portion across weakly projecting proximoventral extension bearing short, proximal tooth (Fig. 94) *capensis* (p. 115)
 - Apical lobes of aedeagus in lateral view with distal portion notably narrower than proximal portion across strongly projecting, subtriangular proximoventral extension without proximal tooth (Fig. 97)..... *bikoi* (p. 116)

3.2.2. Species descriptions and redescrptions

Scopaeus paludicola Cameron

(Figs 1–4, 8, 9, 12, 13, 16, 19, 30, 41, 47–64)

Scopaeus paludicola Cameron, 1945: 711.

Scopaeus paludicola Cameron, 1944; Fagel 1973: 169.

Scopaeus paludicola var. *pallipes* Cameron, 1945: 711; synonymized with *S. paludicola* by Fagel, 1973: 169.

Type specimens examined: *Scopaeus paludicola*: Lectotype ♀, Republic of South Africa, Western Cape, Cape Town: Simon’s Town, IV.–VI.1915, Cameron leg.; here designated (NHML); labelled “type” (printed, round, red border), “Marsh” (printed), “Simon’s Town / IV–VI–15. M.C.” (printed), “Sc. / paludicola / TYPE Cam.” (handwritten, “TYPE” in red), “M. Cameron / Bequest / B.M.1955-147.” (printed), “NHMUK016510542” (printed), “LECTOTYPE / *Scopaeus* ERICHSON / *paludicola* / CAMERON, 1945 / des. J. FRISCH, 2026” (red, printed).

Scopaeus paludicola var. *pallipes*: Lectotype ♀, Republic of South Africa, Western Cape, Cape Town: Simon’s Town, IV.–VI.1915, Cameron leg.; here designated (NHML); labeled “type” (printed, round, red border), “Bank of Stream” (printed), “Simon’s Town / IV–VI–15. M.C.” (printed), “v. / pallipes / TYPE Cam.” (handwritten, “TYPE” in red), “M. Cameron / Bequest / B.M.1955-147.” (printed), “G. Fagel det., 1968 / *Scopaeus* / *paludicola* / Cam.” (printed, “68” and species name handwritten), “LECTOTYPE / *Scopaeus* ERICHSON / *paludicola pallipes* / CAMERON, 1945 / des. J. FRISCH, 2026” (red, printed).

Cameron (1945: 711) named *Scopaeus paludicola* and *S. paludicola* var. *pallipes* in the same description. He wrote “Type in my collection,” but did not specify the number of syntypes or the name to which this type refers. Therefore lectotype designations to stabilize the names *S. paludicola* and *S. paludicola* var. *pallipes* are required (ICZN 1999: Article 74.1). The NHML, where Cameron’s collection is kept (Horn et al. 1990: 65), has one syntype each of *S. paludicola* (Fig. 30) and *S. paludicola* var. *pallipes* (Fig. 31). Both specimens bear the round, subsequent type label from the London collection, a locality label that matches the type locality Simon’s Town, and a handwritten identification label by Cameron (cf. handwritten label example in Horn et al. 1990: 447) with the indication “Type.” These syntypes are here designated as lectotypes.

Fagel (1973: 169), who had examined the syntypes of *S. paludicola* and *S. paludicola* var. *pallipes*, considered the latter (Fig. 20) to be a teneral specimen of *S. paludicola* and consequently synonymized it. According to Article 45.6.4. (ICZN 1999), the name *pallipes* is an available

species group name with the rank of a subspecies. Since var. *pallipes* was published before 1961, Cameron did not declare this “variety” to be infrasubspecific, and it is not clear from the context of its introduction that he intended the name to be infrasubspecific.

New records: Republic of South Africa: Gauteng: 5 miles S Johannesburg, 5.X.1970, coll. Hammond (B.M. 1970-603) (MFNB, NHML). Western Cape: Bot River near R 43 bridge (34°18.7'S, 19°8.8'E), 17.+18.X.2013, Janák leg. (JJC); De Hoop NR (34°27'S, 20°24'E),



Figures 30–32. Habitus and microsculpture of head (a), pronotum (b), elytra (c), and abdomen (d) of *Scopaeus paludicola*, lectotype ♀, Republic of South Africa, Western Cape, Cape Town: Simon's Town (30); *S. p. pallipes*, lectotype ♀, Republic of South Africa, Western Cape, Cape Town: Simon's Town (31); *S. transvaalensis*, ♂, Republic of South Africa, Western Cape, Citrusdal: Boschklouf (32, abdominal segments VIII–X removed for genital dissection).

17.XI.1993, 9.+10.XI.1997, Uhlig leg. (MFNB); De Hoop NR: Potberg Dam (34°24.45'S, 20°34.25'E), 26.XI.2022, Janák leg. (JJC); Garden Route NP [Wilderness NP]: Eilandvlei (33°59'S, 22°38'E), 13.XI.1996, 13.+14.XI.1997, Uhlig leg. (MFNB); Garden Route NP [Wilderness NP]: Langvlei (33°59'S, 22°40'E), 6.II.2012, Janák leg. (JJC), 14.XI.1997, Uhlig leg. (MFNB).

Redescription: Habitus as in Fig. 30. Macrophthalmous, macropterous species with palisade fringe of abdominal tergite VII; body blackish brown to black; appendages medium brown to blackish brown; basis of tibiae, tarsi, and mouthparts except for segment 3 of maxillary palpi lighter brown; head and pronotum matt; elytra shiny.

Head with straight, parallel lateral margins, straight to somewhat convex posterior margin, distinct, fine-meshed microreticulation and fine, setose punctation with punctures separated from each other by about twice their diameter or on average by two meshes of microreticulation; head without unreticulate, impunctate midline (Fig. 30 a).

Pronotum with parallel or slightly concave lateral margins and dense, distinct microreticulation slightly less impressed than microreticulation of head; setose punctation fine, somewhat irregular, with average puncture interstices notably wider than on head and punctures usually separated from each other by more than twice their diameter or on average by two to four meshes of microreticulation; pronotum without coarse punctures close to midline; pronotum with unreticulate, impunctate midline linearly narrow, often indistinct, at most as long as posterior third of pronotal length (Fig. 30 b).

Mesobasisternum with midlongitudinal groove (Fig. 13).

Elytra without clear microreticulation; setose punctation slightly coarser than cephalic and pronotal punctation, slightly granular with puncture interstices about two to three-times as wide as puncture diameters (Fig. 30 c).

Abdomen with coarse-meshed microsculpture and fine, slightly granular, setose punctation (Fig. 30 d).

Total body length 3.3–3.9 mm; forebody length 1.8–2.1 mm.

Abdominal sternite VIII (Fig. 41) with subbasal ridge slightly pointed medially; triangular incision with slightly convex lateral margins; sternite in approximately median third of width asetate.

Aedeagus moderately convex laterally in dorsal and ventral view (e.g. Figs 48, 49); ventral extension strongly projecting with broadly convex distal end and distal margin sloping proximad (e.g. Fig. 47); apical lobes comprising about third of aedeagal length, notably curved ventrad (e.g. Fig. 47), widely separate at base, strongly convex laterally and more or less evenly curved towards each other at apex (e.g. Figs 48, 49); apical lobes separated from ventral extension by narrow incision, with distal portion separated by widely triangular, ventral

incision (e.g. Fig. 47); proximoventral extension in lateral view dentiform, in ventral view broadly convex with slight lateroproximal angle (e.g. Fig. 48); distal portion of apical lobes with proximoventral lobe irregularly triangular, somewhat curved distad (e.g. Fig. 47) with acute, medially directed tip (e.g. Fig. 48), and with variable, lobiform apical portion appearing irregularly frayed due to varying number of variable, ventral microlobes (e.g. Fig. 47); dorsomedial dilatation of apical lobes elongate subsemicircular to subrectangular (e.g. Fig. 52); dorsal membrane of aedeagus entirely hyaline (cf. Figs 49, 56); length of aedeagus 0.4–0.43 mm.

Distribution: *Scopaeus paludicola* has been recorded in Gauteng and Western Cape, and is therefore widespread in South Africa (Figs 104, 105). According to current knowledge, it is the most widespread species of the *S. paludicola* species group.

Remarks: The original description of *Scopaeus paludicola* appeared in volume 11 (11) of *The Annals and Magazine of Natural History* for the year 1944, which was not published until January 1945 according to a note on the cover page (Herman 2003: 3875). Thus, the year of description of *S. paludicola* and *S. paludicola* var. *pallipes* is 1945.

Fagel (1973: 169, 170) synonymized *S. paludicola* var. *pallipes* with *S. paludicola*, as he considered the lighter colored specimen (Fig. 31) as teneral. However, this specimen is actually mature. He incorrectly wrote that it was a male whose aedeagus he had dissected, but it is an undissected female. I am not convinced of the conspecificity of the lectotypes of *S. paludicola* and *S. paludicola* var. *pallipes*, because the latter specimen has a lighter coloration, a slightly broader head [1.14 versus about 1.15–1.19 ($\mu = 1.17$) times as long as wide] and a slightly more granular punctation of the elytra (Fig. 31). Nevertheless, and as it is a female, I defer to Fagel's assessment and refrain from raising *S. paludicola pallipes* to species rank.

My interpretation of *S. paludicola* is based on a topotypic male from the Cameron collection, which is conspecific with the female lectotype and has the same locality label in terms of both layout and data. Thus, it could originate from the same sample as the lectotype. However, there is no indication that it has a type status, as it bears neither Cameron's identification label nor a subsequent type label of the NHML. It was genital-dissected by Fagel and bears Fagel's identification label, but is not listed in "Matériel examiné" in Fagel (1973: 170). It is possible that Fagel (1973: 170) confused the sex of this specimen with the female syntype of *S. paludicola* var. *pallipes* (Fig. 20), as he mistakenly wrote that the latter was a male that he had dissected.

***Scopaeus transvaalensis* Fagel**

(Figs 32, 42, 65–76)

Scopaeus transvaalensis Fagel, 1973: 175, 176.

Type specimen examined: Holotype ♂, Republic of South Africa, Limpopo [Transvaal], Polokwane [Pietersburg]: Helpmekaar River, IX.1960, Leleup leg. (RMCA).

According to Fagel (1973: 175), the holotype of *Scopaeus transvaalensis* was to be deposited at the DMNH in Pretoria, South Africa, but was not returned there (W. Strümpfer, pers. comm.). I examined it at the RMCA in Tervuren, Belgium, in the 1990s.

New records: Namibia: Karas, 15 km SE Rosh Pinah: Dreigratdrif (Orange River) (28°06'27"S, 15°52'59"E), 1.IX.2002, Uhlig leg. (MFNB). Republic of South Africa: Eastern Cape, Little Karoo: Baviaanskloof (33°37'S, 24°15'E), 28.X.1993, Endrödy-Younga leg. (DMNH); Western Cape: Assegaaibosch NR (33°58.0'S, 18°55.4'E), 11.II.2012, Janák leg. (JCU); Western Cape: Eland's Bay (32°18.9'S, 18°21.5'E), 6.X.2017, Janák leg. (JCU); Western Cape: Groot Toren Farm (31°20'S, 19°44'E), 15.IX.1994, Endrödy-Younga leg. (DMNH, MFNB); Western Cape, 8 km NE Citrusdal: Boschkloof (32°33'42"S, 19°03'28"E), 16.+7.XII.2002, Uhlig leg. (MFNB); Western Cape: Matjiesrivier NR (32°30.0'S, 19°19.9'E), 750 m, 13.XI.2022, Janák leg. (JCU, MFNB).

Redescription: Habitus as in Fig. 32. Almost identical to *Scopaeus paludicola* in terms of body proportions, microreticulation, and punctation, but somewhat smaller with total body length 3.4–3.7 mm and forebody length 1.8–1.9 mm.

Abdominal sternite VIII as in *S. paludicola* (Fig. 42).

Aedeagus similar to that of *S. paludicola*, but different as follows: ventral extension of aedeagus somewhat aligned distad with distal margin less sloping proximad (Figs 68, 71, 74) or horizontal with concave curve (Fig. 65); proximoventral tooth of proximal portion of apical lobes notably blunter, more strongly directed proximad (e.g. Fig. 65); incision between ventral extension of aedeagus and proximoventral tooth of apical lobes usually notably wider (e.g. Fig. 65); proximoventral tooth of distal portion of apical lobes much longer, more strongly curved distad (e.g. Fig. 65) with mediad pointing tip longer and thinner (e.g. Figs 66, 67); distal portion of apical lobes usually shorter and/or more strongly curved ventrad (Figs 65, 68, 71, 74), somewhat concave laterally with narrower, more or less pointed apex (e.g. Fig. 72, 73); dorsomedial dilatation of apical lobes somewhat larger (e.g. Fig. 70); length of aedeagus 0.39–0.41 mm.

Distribution: *Scopaeus transvaalensis* is widespread in southern Africa. The species has been recorded from

the very south of Namibia (Orange River) and the South African provinces of Limpopo, Western Cape, and Eastern Cape (Figs 104, 105).

***Scopaeus insidiosus* Fagel**

(Figs 77, 78)

Scopaeus insidiosus Fagel, 1973: 174, 175.

Type specimens examined: Holotype ♂, Republic of South Africa, Western Cape, Caledon: Sonder End River, I.1961, Leleup leg. (RMCA).

The holotype of *Scopaeus insidiosus* was to be deposited at the DMNH in Pretoria, South Africa (Fagel 1973: 175), but was not returned there (W. Strümpfer, pers. comm.). I took images of the aedeagus at the RMCA in Tervuren, Belgium, in the 1990s.

Description: Since no specimens of *Scopaeus insidiosus* were available for this manuscript, I cannot redescribe the species, but can only illustrate and describe the aedeagus of the holotype. However, I cite some excerpts of the original description that appear relevant to me. Fagel (1973: 174, 175) compared *S. insidiosus* with *S. ludificatus* as follows (translated from French).

“Very similar to *S. ludificatus* n. sp., but significantly smaller in size and much more slender in stature.

Overall coloration similar, posterior margin of elytra tends to be lighter in color, posterior sutural angles sometimes orange; legs and appendages distinctly reddish.

Head significantly less elongated (1.08), eyes roughly same size (0.28–0.50), temples subparallel, base broadly concave at neck, posterior angles more rounded; glossy, upper surface without reticulation [...], punctation not very different from that of previous species, except for being slightly denser. [...]

Pronotum more elongated (1.30), much narrower (0.84) but same length as head, maximum width located less towards front, anterior angles less pronounced, then subparallel sides, base less wide; strongly convex median band barely visibly protuberant, median line imperceptibly canaliculate towards posterior margin; shiny, without any trace of microsculpture, punctation of same strength as on head, slightly less dense but still much denser than in *S. ludificatus* [...].

Elytra more elongated (1.23), much wider (1.33) and longer (1.23) than pronotum; shiny, microsculpture, punctation, and pubescence not very different from those of *S. ludificatus*. [...]

Male: 5th sternite unmodified, incision much smaller, almost equilateral.

Total body length 3.2–3.5 mm”

Aedeagus in ventral view very narrow, straight

laterally, proximally of broad, subquadrate apical lobes first strongly tapered, then moderately tapered towards proximal end (Fig. 78; Fagel 1973: Fig. 204); ventral extension of aedeagus very shallow (Fig. 77); apical lobes comprising about third of aedeagal length, with distal portion separated by wide, deep, concave emargination (Fig. 77); proximoventral extension of apical lobes long lobiform with widely convex end (Fig. 77), in ventral view with convex medial margin (Fig. 78); distal portion of apical lobes very short, strongly curved ventrad with small, lobiform, distoventrad pointing, membranous apical extension (Figs 77, 78), in ventral view with short, proximad pointing tooth (Fig. 78); dorsal membrane of aedeagus seemingly entirely hyaline (Fig. 77); length of aedeagus 0.4 mm.

Distribution: *Scopaeus insidiosus* is only known from the type locality Sonder End River in the Western Cape province, Republic of South Africa (Figs 104, 105).

Scopaeus ludificatus Fagel

(Figs 14, 17, 20, 21, 33, 43, 79–84)

Scopaeus ludificatus Fagel, 1973: 172–174.

Type specimen examined: Holotype ♂, Republic of South Africa, Western Cape, Cape Town (ISNB); labelled “Capetown” (handwritten), “R.I.Sc.N. B. 17479 / Coll. et det. [sic] Fauvel (printed), “G. Fagel det. 1969 / *Scopaeus / ludificatus / n. sp.*” (printed, “69” and species name handwritten), “TYPE” (red, printed label), “HOLOTYPE / *Scopaeus* ERICHSON / *ludificatus* FAGEL, 1973 / label by J. FRISCH, 2025” (red, printed), “*Scopaeus* ERICHSON, 1839 / *ludificatus / (FAGEL, 1973) / det. J. Frisch*” (printed).

Fagel (1973: 174) designated this specimen as the holotype of *Scopaeus ludificatus* and labeled it “TYPE”. Therefore I have added a holotype label.

New records: Republic of South Africa, Western Cape: Cederberg (32°28'S, 19°14'E), 1130 m, 7.XI.1983, Endrödy-Younga leg. (DMNH); Grootswartberg: Meulrivier Gorge (33°24.25'S, 22°23.25'E), 23.XI.2022, Janák leg. (JJCU, MFNB); W Suurbrack: Buffeljags Rivier (34°0.05'S, 20°34.9'E), 27.XI.2022, Janák leg. (JJCU); Table Mountain, 18.X.1983, Peez leg. (MFNB, NHMW).

Redescription: Habitus as in Fig. 33. Macrophthalmous, macropterous species with palisade fringe of abdominal tergite VII; body blackish brown to black; appendages medium brown with femora darker brown and segment 4 of maxillary palpi blackish; elytra occasionally gradually lighter brown posteriorly; forebody shiny.

Head shape somewhat variable, subtrapezoidal with straight, slightly posteriorly diverging temples and

pronounced posterior angles (Fig. 33) or with moderately convex temples and more strongly rounded posterior angles; posterior margin straight; cephalic surface without microreticulation and with comparatively coarse, dense, setose punctation with average puncture interstices about as wide as puncture diameters (Fig. 33 a); impunctate midline about as wide as pedicellus, tapered posteriorly, extending over about anterior two-thirds of head length.

Pronotum with parallel or slightly concave lateral margins; pronotal surface without microreticulation, with setose punctation finer and distinctly more spacious than cephalic punctation with uneven puncture interstices twice as wide as puncture diameters or notably wider (Fig. 33 b); pronotal punctation notably finer and more spacious dorsolaterally, but coarser and denser close to impunctate midline about as wide as scapus; impunctate midline somewhat tapered anteriorly and posteriorly and hardly perceptibly keeled in about posterior third.

Mesobasisternum with midlongitudinal groove (Fig. 14).

Elytra without microreticulation; setose punctation as coarse as cephalic punctation, about as spacious as pronotal punctation laterad of impunctate midline, not granular (Fig. 33 c).

Abdomen with superficial, coarse-meshed microsculpture and fine, slightly granular, setose punctation (Fig. 33 d).

Total body length 3.5–4.1 mm; forebody length 1.9–2.1 mm.

Abdominal sternite VIII (Fig. 43) with subbasal ridge moderately convex; triangular incision with straight lateral margins; sternite lighter and asetose in about posterior half of length and third of width.

Aedeagus widely concave laterally towards apical lobes (e.g. Figs 80, 81), ventrally straight without ventral extension (Figs 79, 82); apical lobes long, comprising about third of aedeagal length, strongly bent ventrad, with distal portion separated by slight, dorsoventral and lateral constriction (Figs 79–84); proximal portion of apical lobes with moderately convex dorsal margin and wide, shallow, moderately convex proximoventral extension (Figs 79, 82), in ventral view widely concave medially and with proximomedial dilatation moderately convex (Figs 80, 83); distal portion of apical lobes in lateral view widely truncate, convex ventrally, and extended into triangular, distally directed apex (Figs 79, 82), in dorsal view with straight, medially projected proximal portion (Fig. 84), and distally of short, medially tapered section ending in long, subtriangular apex (Figs 81, 84); dorsomedial dilatation of apical lobes indistinct (Fig. 84); dorsal surface of aedeagus entirely membranous, hyaline (Fig. 82); length of aedeagus 0.44–0.49 mm.

Distribution: *Scopaeus ludificatus* is known from from the Cederberg in the north southeastward to the the southwestern Western Cape province, Republic of Meulrivier Gorge (Figs 104, 105). South Africa, where it was recorded southwest of a line



Figures 33–35. Habitus and microsculpture of head (a), pronotum (b), elytra (c), and abdomen (d) of *Scopaeus ludificatus*, holotype ♂, Republic of South Africa, Western Cape: Cape Town (33); *S. endrodyi*, paratype ♀, Republic of South Africa, Western Cape: Groot Toren Farm (34); *S. uhligorum*, paratype ♂, Republic of South Africa, Western Cape: Harkerville Forest (35, abdominal segments VIII–X removed for genital dissection).

***Scopaeus endrodyi*, sp. nov.**

(Figs 34, 85–87)

Type specimens: Holotype ♂, Republic of South Africa, Western Cape: Groot Toren Farm (31°20'S, 19°44'E), 15.IX.1994, Endrödy-Younga leg. (DMNH). Paratype: 1 ♀, same data as holotype (DMNH).

Description: Habitus as in Fig. 34. Macrophthalmous, macropterous species with palisade fringe of abdominal tergite VII; body blackish brown; appendages medium brown except for blackish segment 4 of maxillary palpi; elytra gradually lighter brown posteriorly; forebody shiny.

Head with slightly convex, almost parallel temples and slightly to moderately concave posterior margin; cephalic surface without microreticulation and with comparatively coarse, dense, setose punctation with average puncture interstices about as wide as puncture diameters (Fig. 34 a); impunctate midline about as wide as pedicellus, tapered posteriorly, extending over about anterior two-thirds of head length.

Pronotum with parallel or slightly concave lateral margins; pronotal surface without microreticulation, with setose punctation finer and distinctly more spacious than cephalic punctation and with uneven puncture interstices approximately twice as wide as puncture diameters or somewhat wider (Fig. 34 b); pronotum without coarse punctures close to midline; impunctate pronotal midline about as wide as scapus, somewhat tapered anteriorly and posteriorly; midline hardly perceptibly keeled in about posterior third.

Mesobasisternum with midlongitudinal groove (cf. Figs 13, 14).

Elytra without microreticulation; setose punctation as coarse as cephalic punctation, about as spacious as pronotal punctation, not granular (Fig. 34 c).

Abdomen with coarse-meshed microsculpture and fine, slightly granular, setose punctation (Fig. 34 d).

Total body length 3.9 mm; forebody length 2.0–2.1 mm.

Abdominal sternite VIII with subbasal ridge moderately convex; triangular incision with straight lateral margins; sternite lighter and asetose in about posterior half of length and third of width (cf. Fig. 43).

Aedeagus in dorsal view moderately concave in about median third of length (Fig. 87), without ventral extension (Fig. 85); apical lobes long, comprising about third of aedeagal length, strongly curved ventrad, with moderate, dorsal convexity, and distal portion separated by sharp, triangular, ventral incision (Fig. 85); proximoventral extension of apical lobes in lateral view convexly projecting (Fig. 85); both proximoventral extensions in ventral view with weakly convex inner margins close to each other forming long, ventral opening (Fig. 86); distal portion of apical lobes in lateral view with truncate apex extended in dorsally projecting, blunt

end and short, ventral tooth (Fig. 85), in ventral view moderately concave laterally, with triangular, ventral dilatation, and tapered, slightly laterad curved apex (Fig. 86); dorsomedial dilatation of apical lobes elongate, moderately projecting medially; dorsal membrane of aedeagus probably not hyaline for entire length (c.f. Fig. 88); length of aedeagus 0.49 mm.

Distribution: *Scopaeus endrodyi* is only known from the type locality Groot Toren Farm in the northwest of the Western Cape province, Republic of South Africa (Figs 104, 105).

Etymology: By choosing the epithet *endrodyi* (Latinized noun, derived from the Hungarian family name Endrödy, genitive), I honor the great achievements of Sebastian Endrödy-Younga, a well-known coleopterologist at the former Transvaal Museum in Pretoria and collector of this new species, in researching the beetles of South Africa (cf. Bellamy & Jäch 1999).

***Scopaeus uhligorum*, sp. nov.**

(Figs 5–7, 24, 35, 44, 88–90)

Type specimens: Republic of South Africa, Western Cape: Holotype ♂, Harkerville Forest (34°04'S, 23°10'E), 14.XII.1975, Endrödy-Younga leg. (DMNH). Paratypes (25 specimens): 5 ♂, 8 ♀, same data as holotype (DMNH, MFNB); 3 ♂, 3 ♀, Garden of Eden (34°02'S, 23°12'E), 13.XII.1976, Endrödy-Younga leg. (DMNH); 1 ♂, Western Cape, Cape Peninsula: Silvermine 2.+3.I.1972, Southern African Expedition B. M. 1972-I leg. (NHML); 1 ♂, Swellendam, 17.XII.1931, Turner leg. (NHML); 1 ♂, Cederberg Wilderness Area, Mt Ceder: Groot River (32°38'56"S, 19°24'33"E), 23.X.2006, M. & B. Uhlig leg. (MFNB); 2 ♂, 1 ♀, Western Cape: Matjiesrivier NR (32°30.0'S, 19°19.9'E), 750 m, 13.XI.2022, Janák leg. (JJCU).

Description: Habitus as in Fig. 35. Macrophthalmous, macropterous species with palisade fringe of abdominal tergite VII; body blackish brown; appendages medium brown except for blackish segment 4 of maxillary palpi; elytra occasionally gradually lighter brown posteriorly; head and pronotum matt; elytra shiny.

Head with temples straight and parallel in median third of length or slightly convex, straight to slightly concave posterior margin, distinct, fine-meshed microreticulation and fine, setose punctation with punctures separated from each other by twice their diameter or approximately one mesh of microreticulation (Fig. 35 a); impunctate midline of head as strongly reticulate as remainder of head, about as wide as pedicellus, extending over anterior two-thirds of head length.

Pronotum with parallel or slightly concave lateral margins, distinct microreticulation less impressed and

more finely meshed than microreticulation of head, and fine, setose, very spacious punctation with punctures separated from each other by approximately three or four meshes of microreticulation; pronotum without coarse punctures close to midline; impunctate pronotal midline microreticulate, about as wide as scapus, somewhat tapered anteriorly and posteriorly, hardly perceptibly keeled in about posterior third (Fig. 35 b).

Mesobasisternum with midlongitudinal groove (cf. Figs 13, 14).

Elytra without clear microreticulation; setose punctation coarser than cephalic and pronotal punctation, about as spacious as pronotal punctation, notably granular (Fig. 35 c).

Abdomen with coarse-meshed microsculpture and fine, granular, setose punctation (Fig. 35 d).

Total body length 3.3–3.6 mm; forebody length 1.8–2.0 mm.

Abdominal sternite VIII (Fig. 44) with subbasal ridge moderately curved medially; triangular incision with straight lateral margins; posterior incision followed by lighter, narrow, asetose depression extending over posterior half of sternite length.

Aedeagus with ventral extension narrow and evenly tapered posteriorly (Fig. 88); apical lobes comprising about fourth of length of aedeagus, laterally convexly widened (Figs 89, 90), dorsally evenly curved ventrad (Fig. 88); distal portion of apical lobes separated by deep, triangular, ventral incision with concave distal margin and proximad curved end, and by shallow, dorsal constriction (Fig. 88); proximoventral extension of apical lobes strongly projecting, subrectangular with somewhat variable ventral margin (Fig. 88), in ventral view with small, proximolaterally pointing tooth (Fig. 89); distal portion of apical lobes in lateral view with convex apex and triangular, proximad pointing ventral tooth, in ventral view with large, medially convex ventral dilatation, and short, slightly tapered, moderately distolaterad curved apex (Fig. 89); dorsomedial dilatation of apical lobes subrectangular (Fig. 90); dorsal membrane of aedeagus moderately sclerotized, hyaline only distally (Fig. 88); length of aedeagus 0.37–0.39 mm.

Distribution: *Scopaeus uhligorum* has been recorded in the southwestern Western Cape province, Republic of South Africa, southwest of a line from the Cederberg in the north southeastward to the Garden of Eden NP (Figs 104, 105).

Etymology: By choosing the epithet *uhligorum* (Latinized noun, derived from the surname Uhlig, genitive plural) I dedicate this new species to Manfred Uhlig, specialist of *Erichsonius* (Staphylinidae) at the Naturkundemuseum Berlin, Germany, and his wife Barbara Uhlig, who collected it at Mount Ceder.

Scopaeus nigerrimus Cameron

(Figs 36)

Scopaeus nigerrimus Cameron, 1945: 711, 712.

Type specimen examined: Holotype ♀, Republic of South Africa, Western Cape, Cape Town: Simon's Town, IV.–VI.1915, Cameron leg. (NHML); labelled “type” (printed, round, red border), “Marsh” (printed), “Simon's Town / IV–VI–15. M.C.” (printed), “Sc. / nigerrimus / TYPE Cam.” (handwritten, “TYPE” in red), “M. Cameron / Bequest / B.M.1955-147.” (printed), “NHMUK014532749” (printed), “HOLOTYPE / *Scopaeus* ERICHSON / *nigerrimus* / CAMERON, 1945 / label by J. FRISCH, 2025” (red, printed).

Cameron (1945: 712) described *Scopaeus nigerrimus* according to a “unique” specimen from his own collection, which is therefore a holotype by monotypy (ICZN 1999, Article 73.1.2). The NHML collection, where Cameron's collection is kept (Horn et al. 1990: 65), contains a specimen (Fig. 36) that bears the round, subsequent type label of that collection. Based on its locality label which matches the type locality Simon's Town and the identification label handwritten by Cameron (cf. handwritten label example in Horn et al. 1990: 447) with the notification “type”, this specimen is the holotype of *S. nigerrimus*. I have labeled it accordingly.

Fagel identified two historical specimens (1 ♂, 1 ♀ from Cape Town) from the Fauvel collection at the ISNB as *S. nigerrimus* by comparing them with the female holotype. However, the holotype and the two specimens from the Fauvel collection do not match in terms of their external characters, which is why I disagree with Fagel's interpretation of *S. nigerrimus*. While the forebody of the holotype of *S. nigerrimus* is more finely punctured and lacks clear microreticulation (Fig. 36), the other specimens have a distinctly microreticulated head and coarser pronotal punctation (Fig. 39). They are described below as *S. biko* sp. nov.. The holotype of *S. nigerrimus* differs from the other species of the *S. paludicola* species group in terms of its ectoskeletal characters. The male characters of *S. nigerrimus* are unknown.

Redescription: Habitus as in Fig. 36. Macrophthalmous, macropterous species with palisade fringe of abdominal tergite VII; body black except for dark brown antennae, femora, and segment 3 of maxillary palpi, and medium brown tibiae, tarsi, and basal segments of maxillary palpi; forebody shiny.

Head with straight, parallel temples, straight posterior margin, superficial microreticulation, and relatively fine, dense, setose punctation with puncture interstices approximately 1.0–1.5 times as wide as puncture diameters (Fig. 36 a); impunctate midline of head about as wide as pedicellus, extending over anterior two-thirds

of head length.

Pronotum with parallel lateral margins, without microreticulation; setose punctation dorsolaterally fine, remarkably spacious with irregular puncture interstices, but along impunctate midline forming two irregular rows of relatively coarse punctures; impunctate pronotal midline broad, along entire length about as wide as end of protibia, and without median, posterior keel (Fig. 36 b).

Mesobasisternum with midlongitudinal groove (cf. Figs 13, 14).

Elytra without microreticulation; setose punctation coarser than cephalic and dorsolateral pronotal punctation,

with puncture interstices about twice as wide as puncture diameters, slightly granular (Fig. 36 c).

Abdomen with coarse-meshed microsculpture and fine, slightly granular, setose punctation (Fig. 36 d).

Total body length 3.1–3.4 mm; forebody length 1.7–1.9 mm.

Male unknown.

Distribution: The holotype of *Scopaeus nigerrimus*, the only known specimen, was collected in Simon's Town on the Cape Peninsula in the far southwest of the Republic of South Africa (Figs 104, 105).



Figures 36–38. Habitus and microsculpture of head (a), pronotum (b), elytra (c), and abdomen (d) of *Scopaeus nigerrimus*, holotype ♀, Republic of South Africa, Western Cape, Cape Town: Simon's Town (36); *S. rectiphallatus*, paratype ♀, Republic of South Africa, Western Cape: Ruitersbos (37); *S. capensis*, holotype ♂, Republic of South Africa, Western Cape, Table Mts NP: Olifantbos (38, abdominal segments IX and X removed for genital dissection).

***Scopaeus rectiphallatus*, sp. nov.**

(Figs 37, 45, 91–93)

Type specimens: Holotype ♂, Republic of South Africa, Western Cape: Ruitersbos (33°54'S, 22°02'E), Endrödy-Younga leg. (DMNH). Paratypes: 4 ♂, 3 ♀, same data as holotype (DMNH, MFNB).

Description: Habitus as in Fig. 37. Macrophthalmous, macropterous species with palisade fringe of abdominal tergite VII; body black except for medium brown to dark brown antennae, femora, and segment 3 of maxillary palpi, and light brown or medium brown tibiae, tarsi, and basal segments of maxillary palpi; forebody with relatively matt head and shiny pronotum and elytra.

Head subtrapezoidal with slightly convex, slightly to moderately diverging temples, moderately concave posterior margin, clear microreticulation, and relatively fine, setose punctation with puncture interstices approximately as wide or twice as wide as puncture diameters (Fig. 37 a); impunctate midline of head microreticulated, about as wide as pedicellus, extending over anterior two-thirds of head length.

Pronotum with straight lateral margins, superficially microreticulate; setose punctation dorsolaterally relatively fine and spacious with irregular puncture interstices, but along impunctate midline forming two irregular rows of relatively coarse punctures; impunctate pronotal midline broad, along entire length about as wide as scapus, microsculptured except for smooth, slightly convex or indistinctly keeled posterior fourth (Fig. 37 b).

Elytra without microreticulation; setose punctation coarser than cephalic and dorsolateral pronotal punctation, with puncture interstices about twice as wide as puncture diameters, slightly granular (Fig. 37 c).

Mesobasisternum with midlongitudinal groove (cf. Figs 13, 14).

Abdomen with coarse-meshed microsculpture and fine, slightly granular, setose punctation (Fig. 37 d).

Total body length 3.1–3.6 mm; forebody length 1.7–1.8 mm.

Abdominal sternite VIII (Fig. 45) with subbasal ridge nearly straight; triangular incision with somewhat convex lateral margins; sternite lighter and asetose in about posterior half of length and third of width.

Aedeagus straight, parallel laterally (Figs 92, 93), with ventral extension long, convex, and evenly tapered proximad (Fig. 91); apical lobes short, comprising about fifth of aedeagal length, slightly curved ventrad, with distal portion separated by small, triangular, ventral incision (Fig. 91); proximoventral extension of apical lobes large, in lateral view convexly dilated ventrad and triangularly extended distad (Fig. 91), in ventral view widely convex and extended into acute, distolaterad pointing tooth (Fig. 92); distal portion of apical lobes in lateral view with broad, convex end extended into short, proximodorsad pointing

tooth and small, blunt, ventral tooth (Fig. 91), in dorsal view with transverse, subrectangular, dorsal dilatation almost right-angled bent mediad (Fig. 93), in ventral view with narrow, ventral dilatation extended into short, thin, distad curved point (Figs 92, 93); dorsomedial dilatation of apical lobes large, triangular with round inner end (Fig. 93); dorsal membrane of aedeagus with long, shallowly convex, more strongly sclerotized portion extending from bases of apical lobes to approximately middle of aedeagal length (Fig. 91); length of aedeagus 0.44–0.46 mm.

Distribution: *Scopaeus rectiphallatus* is only known from the type locality Ruitersbos in the Outeniqua Mts in the south of the Western Cape province, Republic of South Africa (Figs 104, 105).

Etymology: The epithet *rectiphallatus* [adjective, Latin, composed of the adjectives *rectus* (straight) and *phallatus* (derived from the noun *phallus* with suffix *-atus*, expressing a quality/attribute of the species related to the phallus)] refers to the straight, parallel aedeagus of this new species in ventral and dorsal view (Figs 92, 93).

***Scopaeus capensis*, sp. nov.**

(Figs 38, 94–96)

Type specimens: Republic of South Africa, Western Cape, Table Mts NP: Holotype ♂: Olifantbos (34°15.0'S, 18°23.1'E), 8.IX.2022, Janák leg. (DMNH). Paratypes (4 specimens): 1 ♂, 2 ♀, same data as holotype (JJCU, MFNB); 1 ♂, NW of Cape Point (34°20.2'S, 18°27.8'E), 11.IX.2022, Janák leg. (JJCU).

Description: Habitus as in Fig. 38. Very similar to *Scopaeus rectiphallatus* (Fig. 28) in ectoskeletal characters, but distinguished according to aedeagal features; differences in elytral length and strength of microreticulation in Figs 37 and 38 within range of infraspecific variation.

Total body length 3.1–3.4 mm; forebody length 1.7–1.9 mm.

Abdominal sternite VIII as in Fig. 45.

Aedeagus straight, parallel laterally except for slightly convex median third of length (Figs 95, 96); ventral extension long, with almost angled distal end, and evenly tapered proximad (Fig. 94); apical lobes comprising about fourth of aedeagal length, strongly curved ventrad, and with distal portion separated by short, narrow, ventral incision (Fig. 94); proximoventral extension of apical lobes in lateral view elongate, not much projecting ventrad, from convex distal end evenly tapered proximally and with small, proximal tooth (Fig. 94), in ventral view narrow, curved mediad (Fig. 94); distal portion of apical lobes in lateral view with broad, strongly convex apex extended into short, blunt, proximodorsad pointing end (Fig. 94), in dorsal view

with truncate dorsodistal dilatation (Fig. 96), in ventral view with ventrodistal dilatation extended into acute, proximally directed tip (Fig. 95); dorsomedial dilatation of apical lobes subquadrate (Fig. 96); dorsal membrane of aedeagus with long, shallowly convex, more strongly sclerotized portion extending from bases of apical lobes to approximately middle of aedeagal length (Fig. 94); length of aedeagus 0.36–0.37 mm.

Distribution: *Scopaeus capensis* is only known from the type locality in the Table Mts NP on the Cape Peninsula in the far southwest of the Republic of South Africa (Figs 104, 105).

Etymology: The epithet *capensis* [Latinized adjective (“from the Cape”) with the Latin suffix *-ensis*, which expresses geographical origin] is a toponym which refers to the distribution of this new species in the Cape Peninsula, South Africa.

***Scopaeus bikoi*, sp. nov.**
(Figs 39, 97–99)

Type specimens: Holotype ♂, Republic of South Africa, Western Cape, Cape Town, ex coll. Fauvel (ISNB). Paratype ♀, same data as holotype (ISNB).

Description: Habitus as in Fig. 39. Very similar to *Scopaeus rectiphallatus* (Fig. 37) and *S. capensis* (Fig. 38) in ectoskeletal characters, but distinguished according to aedeagal features.

Total body length 3.3 mm; forebody length 1.7 mm.

Abdominal sternite VIII as in Fig. 45.

Aedeagus straight, somewhat convex laterally in about median third of length (Figs 98, 99); ventral extension shallow, evenly tapered proximad (Fig. 97); apical lobes comprising about fourth of aedeagal length, strongly curved ventrad, with distal portion separated by short, narrow, proximally directed ventral incision and slight dorsal emargination (Fig. 97); proximoventral extension of apical lobes in lateral view strongly projecting ventrad, with convex proximoventral end, slightly convex, longitudinally aligned ventral margin, and triangular distal end (Fig. 97), in ventral view subrectangular with short, acute proximomedial point and somewhat longer proximolateral end (Fig. 98); distal portion of apical lobes in lateral view with broad, strongly convex, almost semicircular apex ending in minute, obtuse, ventral angle (Fig. 97), in dorsal view with convex dorsodistal dilatation (Fig. 99), in ventral view with large, triangular, medially directed ventrodistal dilatation (Fig. 98); dorsomedial dilatation of apical lobes subrectangular, somewhat extended mediad and slightly curved proximad (Fig. 99); dorsal membrane of aedeagus with long, shallowly convex, more strongly sclerotized portion extending from bases of apical lobes to approximately middle of

aedeagal length (Fig. 97); length of aedeagus 0.4 mm.

Distribution: *Scopaeus bikoi* is only known from Cape Town in the far southwest of the Republic of South Africa (Figs 104, 105).

Etymology: I dedicate this new species to the South African anti-apartheid activist Bantu Stephen Biko, who was tortured to death by regime security officers in 1977 (epithet *bikoi*: Latinized noun, derived from the family name Biko, genitive).

***Scopaeus jeanneli* Levasseur**

(Figs 10, 11, 25, 26, 40, 46, 100–102)

Scopaeus jeanneli Levasseur, 1981: 19–21.

Type specimens examined: Holotype ♂, Kenya, Mt Elgon (camp 3), 3500 m, 1932, 1933, Arambourg, Chappuis & Jeannel leg. (MNHN). 18 paratypes, same data as holotype (MNHN).

New record: Kenya, Mt Elgon (eastern slope), 3000 m, 8.XII.1953, Leleup leg. (MFNB, RMCA).

Redescription: Habitus as in Fig. 40. Microphthalmous, micropterous species without palisade fringe of abdominal tergite VII. Body black; antenna, femora, and segment 3 of maxillari palpi medium brown to dark brown; tibiae, tarsi, and basal segments of maxillary palpi medium brown; forebody shiny.

Head broad, 1.06 times as long as wide, subtrapezoidal with moderately convex temples and moderately concave posterior margin; eyes small, 0.38 times as long as temples; microreticulation absent; setose punctation with average puncture interstices twice as wide as puncture diameters (Fig. 40 a); impunctate midline of head indistinct.

Pronotum compact, 1.17 times longer than wide, 1.05–1.08 times longer than head, and 0.94–0.97 times as wide as head, with straight lateral margins notably widened towards anterior angles; microreticulation absent; setose punctation somewhat coarser than cephalic punctation, spacious with irregular puncture interstices on average twice to four times as wide as puncture diameters (Fig. 40 b); impunctate midline narrow, indistinct, disturbed by punctures, not reaching anterior pronotal margin by far.

Mesobasisternum with oval, median depression (cf. Figs 13, 14).

Elytra reduced without humeral calli, along suture 0.72–0.74 times as long as wide, 0.63 times as long as pronotum, 0.66–0.68 times as long as head, and 0.94–1.0 times as wide as head; microreticulation absent; elytral surface somewhat uneven with unclear microsculpture and setose punctation much coarser than cephalic and pronotal punctation; puncture interstices about once to twice as wide as puncture diameters, not granular (Fig. 40 c).

Metathoracic wings vestigial, dysfunctional.

Abdomen with coarse-meshed microsculpture and fine, slightly granular, setose punctation (Fig. 40 d).

Total body length 3.1–3.7 mm; forebody length 1.7–1.9 mm.

Abdominal sternite VIII (Fig. 46) with subbasal ridge sinuate medially; triangular incision with lateral margins slightly convex; sternite setose throughout.

Aedeagus subparallel laterally, somewhat tapered distally (Figs 101, 102); ventral extension absent (Fig. 100); apical lobes long, comprising about third of aedeagal length, strongly curved ventrad with moderately concave dorsal margin (Fig. 100); distal portion of apical lobes short and narrow, separated by deep, narrow, proximally curved,

ventral incision (Fig. 100); proximoventral extension of apical lobes in lateral view triangularly enlarged, forming right-angle with aedeagus, and extended into short, distal tooth (Fig. 100); both proximoventral extensions in ventral view concave towards each other, forming long-oval window (Fig. 101); distal portion of apical lobes in lateral view narrow, slightly curved ventrad, with convex apex and extended into short, ventral tooth (Fig. 100), in dorsal view gradually tapered towards moderately dilated, subtriangular apex (Fig. 102); dorsomedial dilatation of apical lobes triangular (Fig. 102); dorsal membrane of aedeagus with long, shallowly convex, more strongly sclerotized portion in about middle of aedeagal length (Fig. 100); length of aedeagus 0.46–0.5 mm.



Figures 39–40. Habitus and microsculpture of head (a), pronotum (b), elytra (c), and abdomen (d) of *Scopaeus bikoï*, holotype ♂, Republic of South Africa, Western Cape: Cape Town (39); *S. jeanneli*, ♂, Kenya: Mt Elgon (40); abdominal segments VIII–X removed for genital dissection.

Distribution: *Scopaeus jeanneli* is probably endemic to Mt Elgon, Kenya (Fig. 103).

4 Discussion

4.1 Relationships within the *Scopaeus paludicola* species group

The *Scopaeus paludicola* species group consists of the flightless *S. jeanneli* from Kenya (Fig. 40) and the macropterous South African *S. paludicola* lineage (Figs 30–39). However, I see no derived characters that would suggest that *S. jeanneli* represents a separate phylogenetic lineage. In contrast, the South African species apparently constitute a monophyletic group due to their longitudinal groove of the mesobasisternum – a derived character that was previously unknown in *Scopaeus*.

Within this South African lineage, *S. paludicola* (Fig. 30) and *S. transvaalensis* (Fig. 32) are closely related due to the dense microreticulation of the head (Figs 30 a, 32 a) and the similar aedeagus with a weakly sclerotized, ventrally frayed distal portion of the apical lobes (Figs

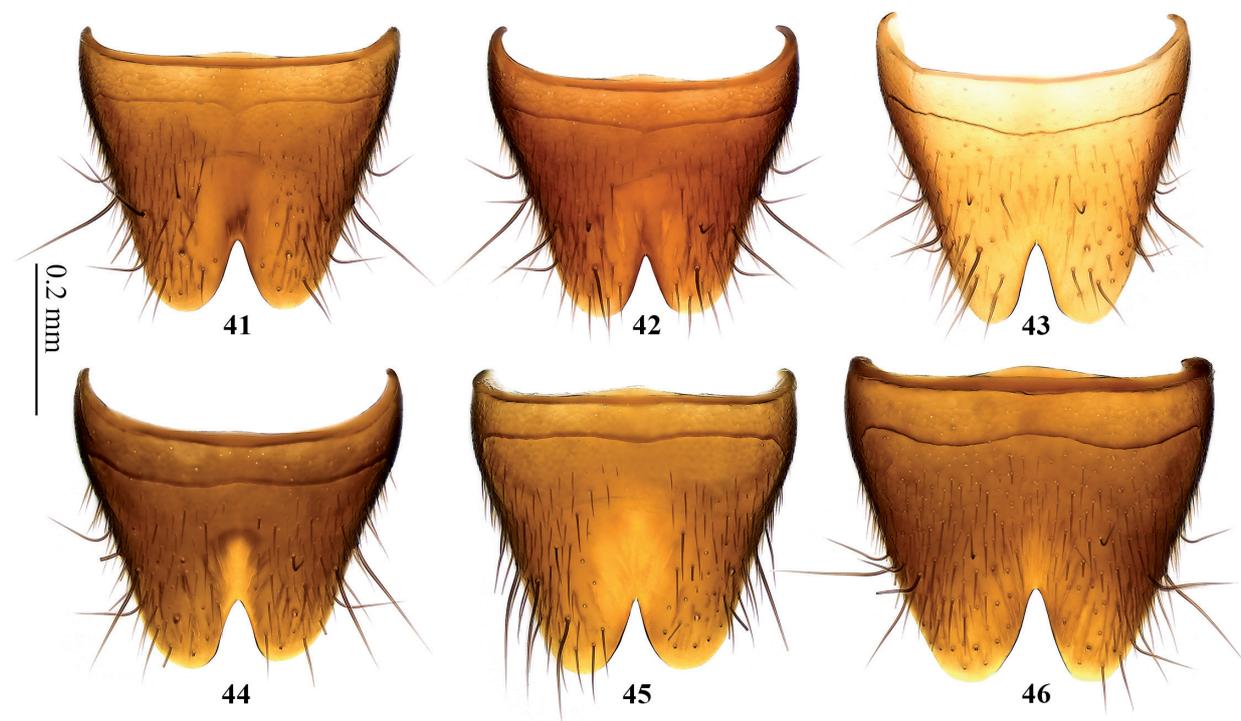
47–76). *Scopaeus insidiosus*, which I have seen only once about 30 years ago, seems to be closely related to these species based on the narrow, membranous lobe of the apical lobes (Figs 77, 78), but according to Fagel (1973: 174, 175) it has a shiny forebody surface.

Scopaeus ludificatus (Fig. 33) and *S. endrodyi* (Fig. 34) appear to be close relatives due to their strongly ventrally curved apical lobes and the absence of the ventral aedeagal extension (Figs 79–87). They moreover have in common a shiny forebody surface.

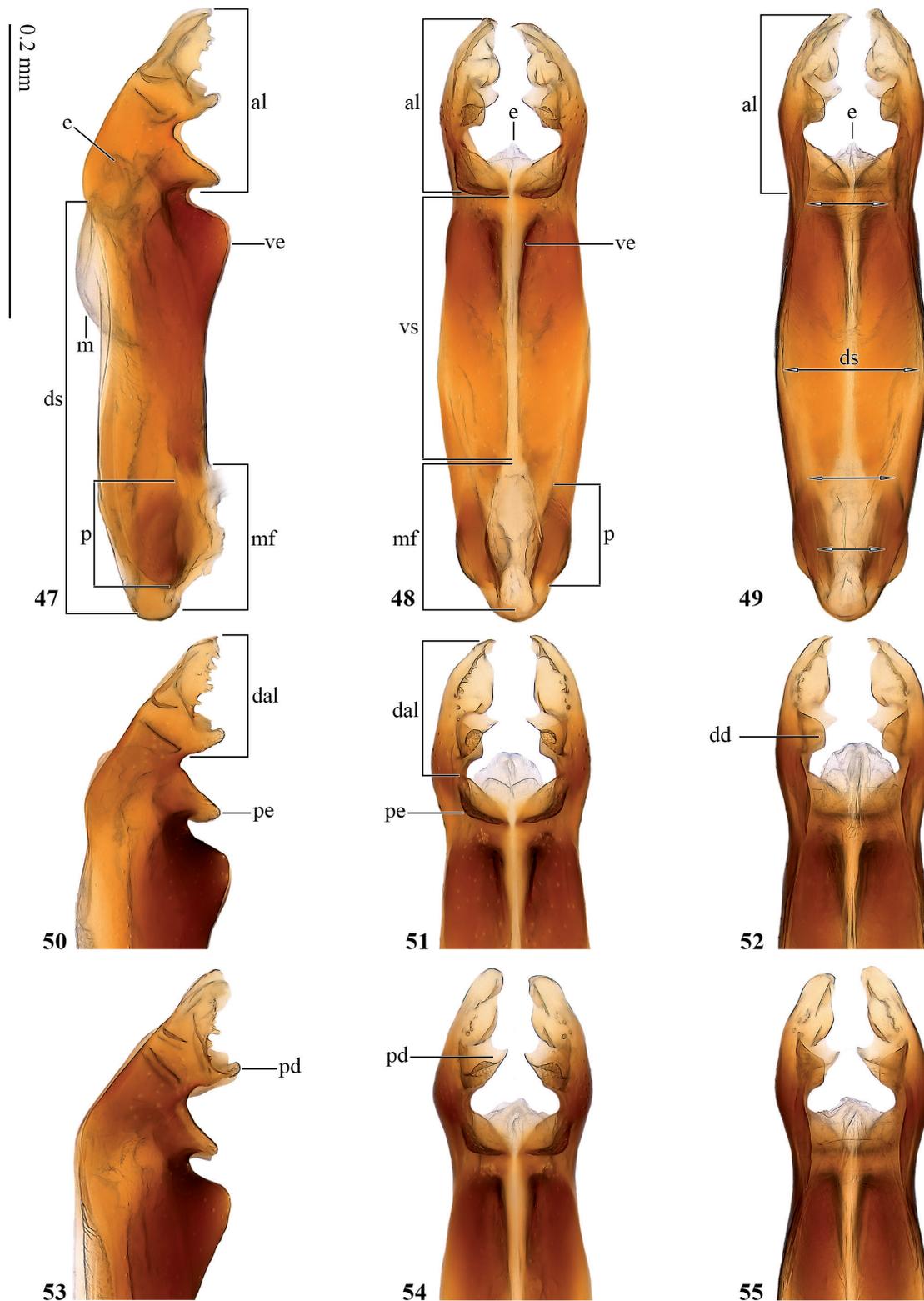
Scopaeus uhligorum (Fig. 35) appears isolated within the lineage from southern Africa. Its aedeagus (Figs 88–90) is similar to those of the following group of related species (Figs 91–99), but it lacks the coarse punctures of the pronotum (Fig. 35 b).

Scopaeus bikoi, *S. capensis*, *S. nigerrimus*, and *S. rectiphallatus* (Figs 36–39) are close relatives, all of which have coarse punctures along the midline of the pronotum (Figs 36 b–39 b). In addition, they have a narrow, parallel aedeagus with a broad, convex apex and a convex, more strongly sclerotized portion within the dorsal membrane (Figs 91–99). The aedeagus of *S. nigerrimus* is unknown.

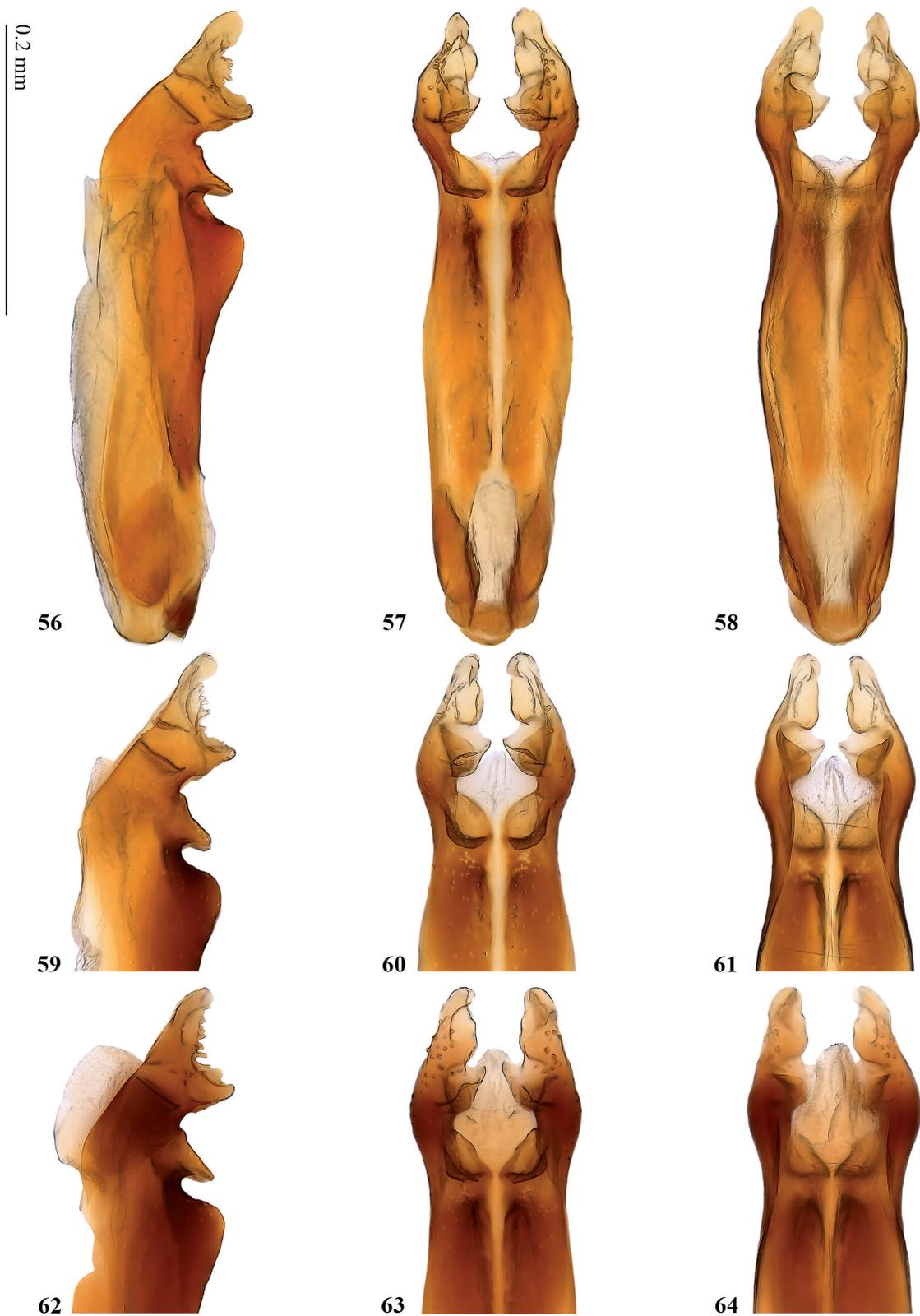
From a biogeographical perspective, the high number of predominantly sympatric species of the *S. paludicola*



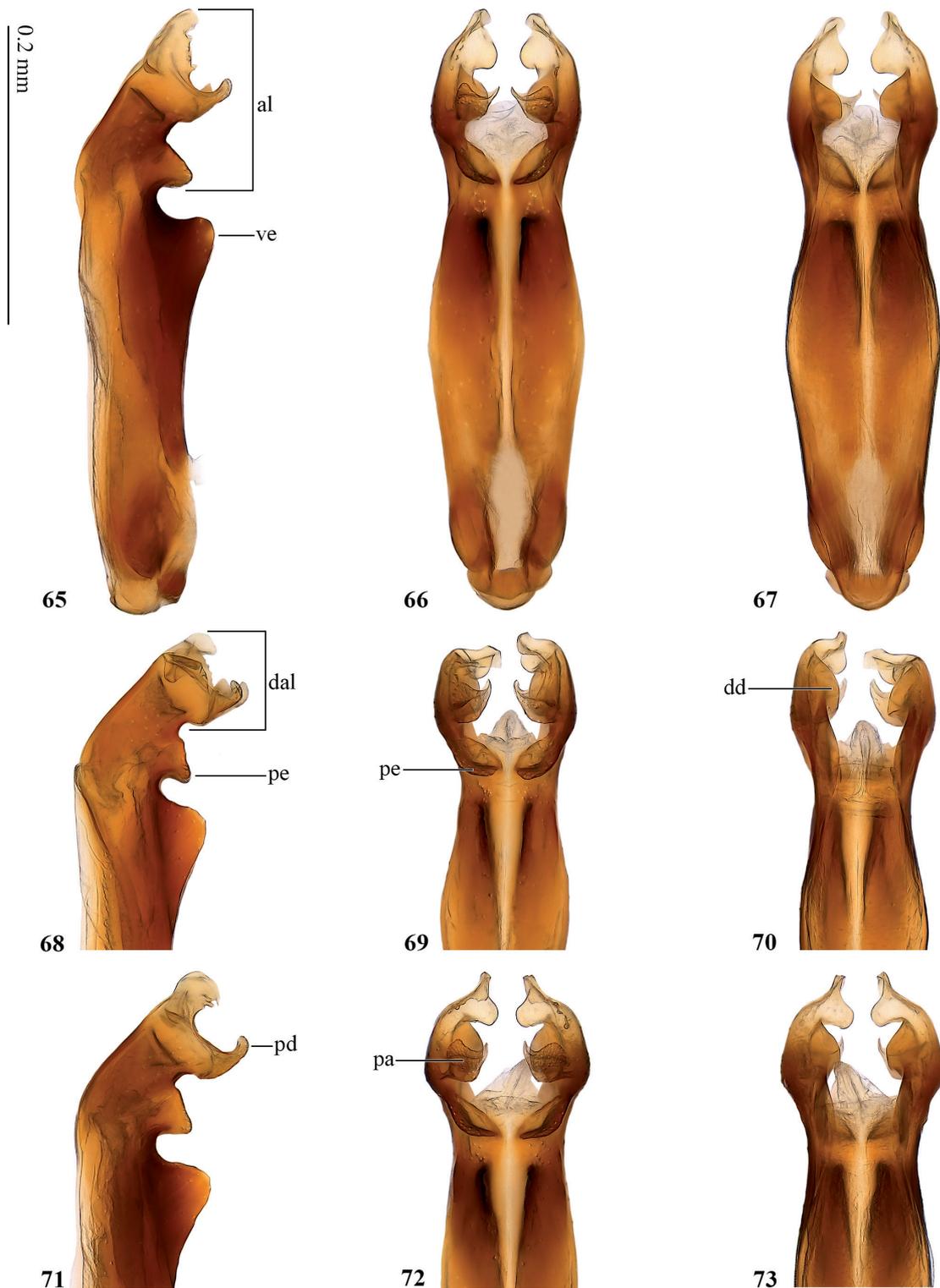
Figures 41–46. Abdominal sternite VIII of ♂ of *Scopaeus paludicola*, Republic of South Africa, Western Cape: De Hoop NR (41); *S. transvaalensis*, Republic of South Africa, Western Cape: Citrusdal (42); *S. ludificatus*, Republic of South Africa, Western Cape: Table Mts NP (43); *S. uhligorum*, holotype, Republic of South Africa, Western Cape: Harkerville Forest (44); *S. rectiphallatus*, holotype, Republic of South Africa, Western Cape: Ruitersbos (45); *S. jeanneli*, Kenya: Mt Elgon (46).



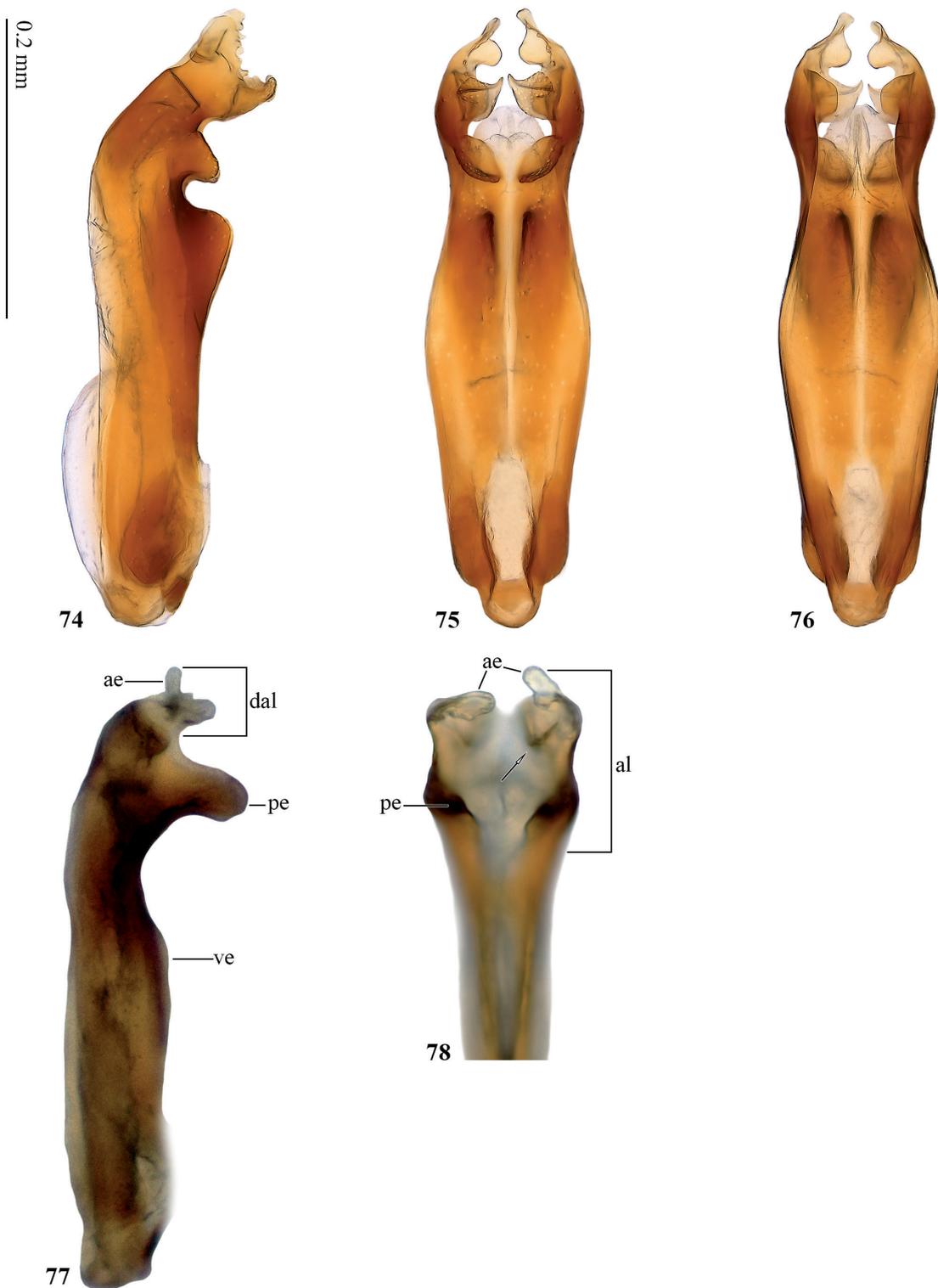
Figures 47–55. Aedeagus in lateral (47, 50, 53), ventral (48, 51, 54), and dorsal view (49, 52, 55) of *Scopaeus paludicola*, Republic of South Africa, Western Cape: Cape Town: Simon’s Town (47–49); De Hoop NR (50–52); Garden Route NP (53–55). **Abbreviations:** al – apical lobes; dal – distal portion of apical lobes; dd – dorsomedial dilatation of apical lobes; ds – dorsal split of aedeagus; e – endophallus; m – membrane of dorsal split of aedeagus, dorsally protruding; mf – median foramen; p – vestigial paramere; pd – proximoventral lobe of distal portion of apical lobes; pe – proximoventral extension of apical lobes; ve – ventral extension of aedeagus; vs – ventral split of aedeagus.



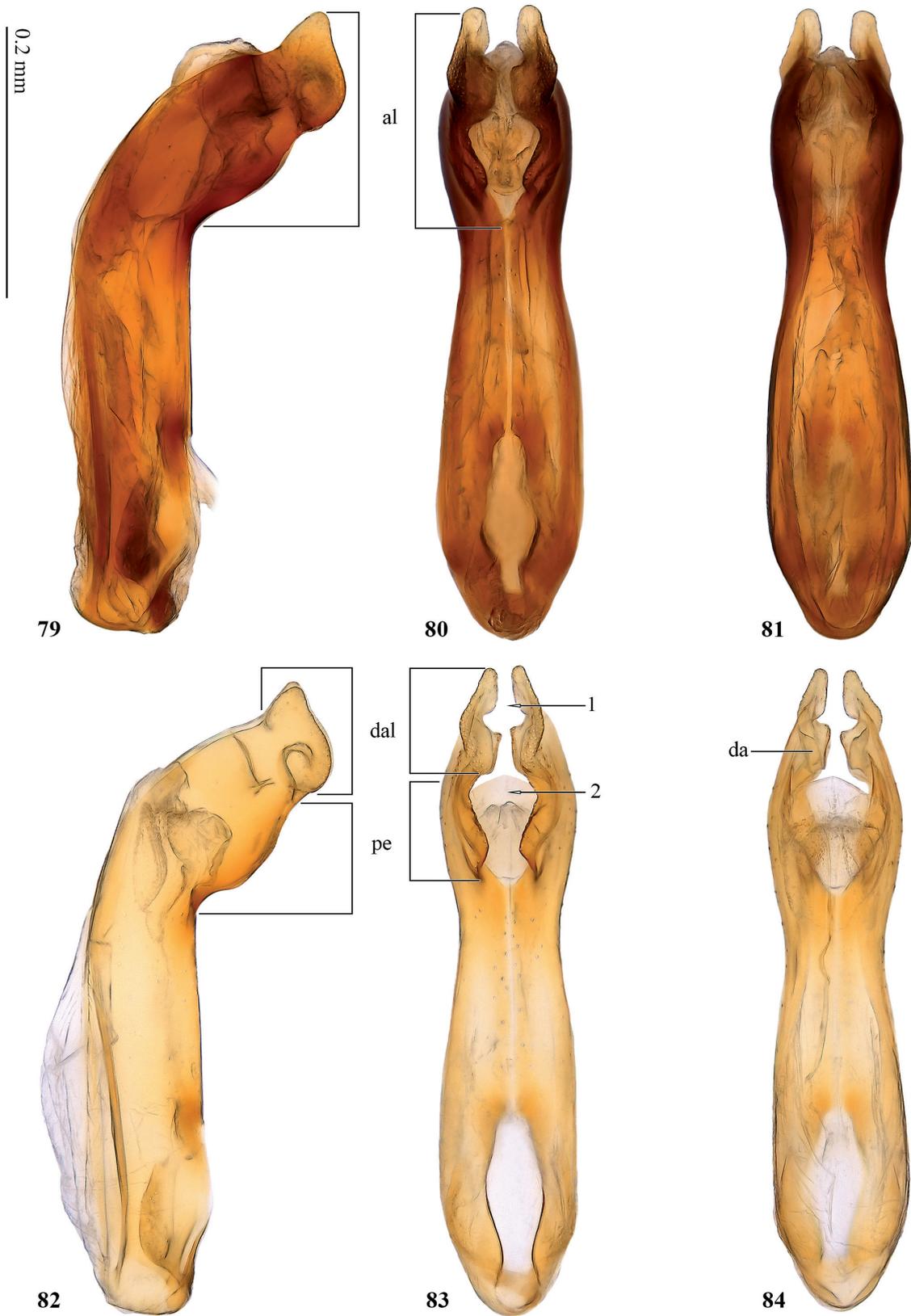
Figures 56–64. Aedeagus in lateral (56, 59, 62), ventral (57, 60, 63), and dorsal view (58, 61, 64) of *Scopaeus paludicola*, Republic of South Africa, Gauteng: Johannesburg.



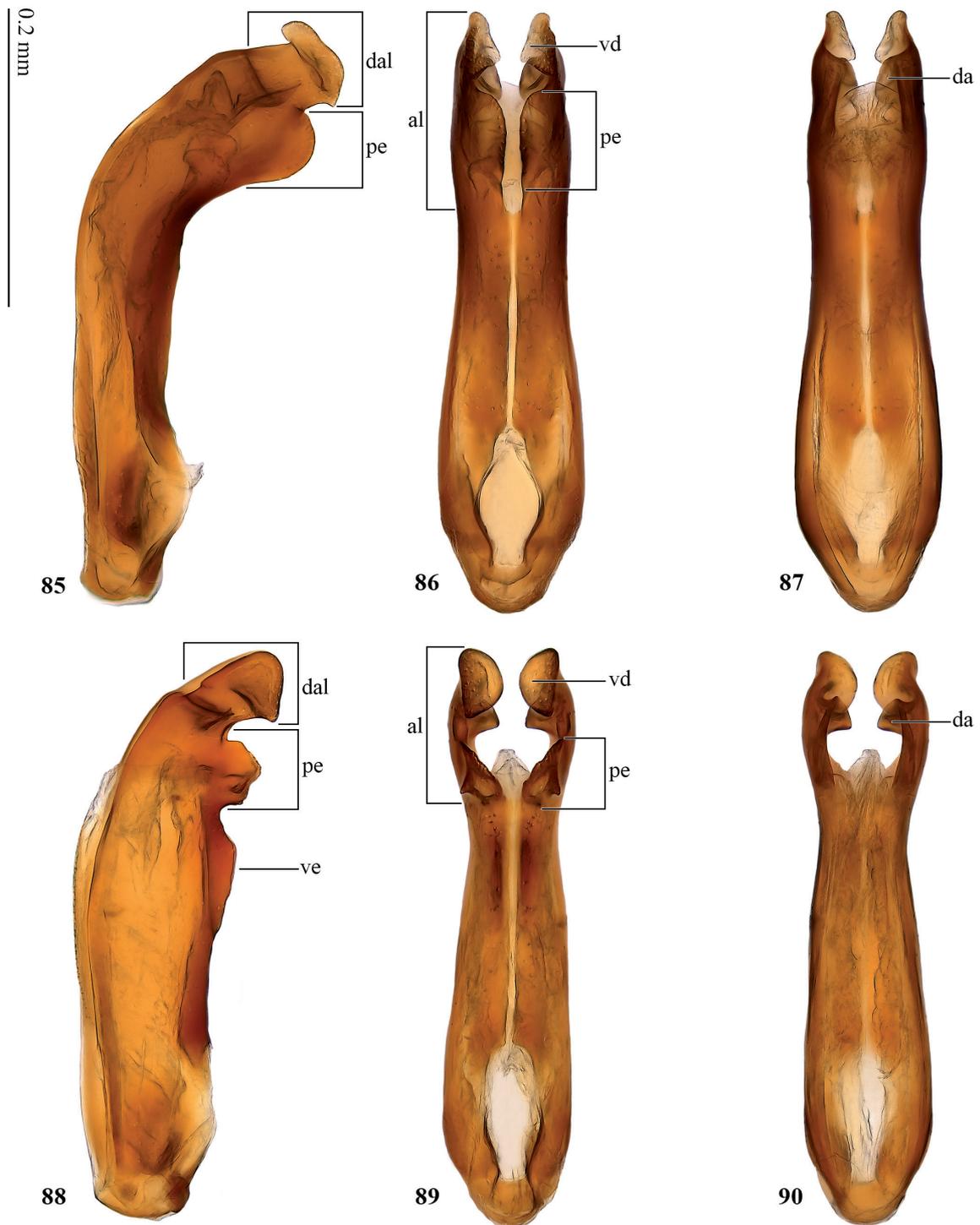
Figures 65–73. Aedeagus in lateral (65, 68, 71), ventral (66, 69, 72), and dorsal view (67, 70, 73) of *Scopaeus transvaalensis*, Republic of South Africa: Western Cape, Citrusdal: Boschklouf (65–67); Eastern Cape, Little Karoo: Baviaanskloof (68–70); Western Cape: Groot Toren Farm (71–73). **Abbreviations:** **al** – apical lobes; **dal** – distal portion of apical lobes; **dd** – dorsomedial dilatation of apical lobes; **pd** – proximoventral lobe of distal portion of apical lobes; **pe** – proximoventral extension of apical lobes; **ve** – ventral extension of aedeagus.



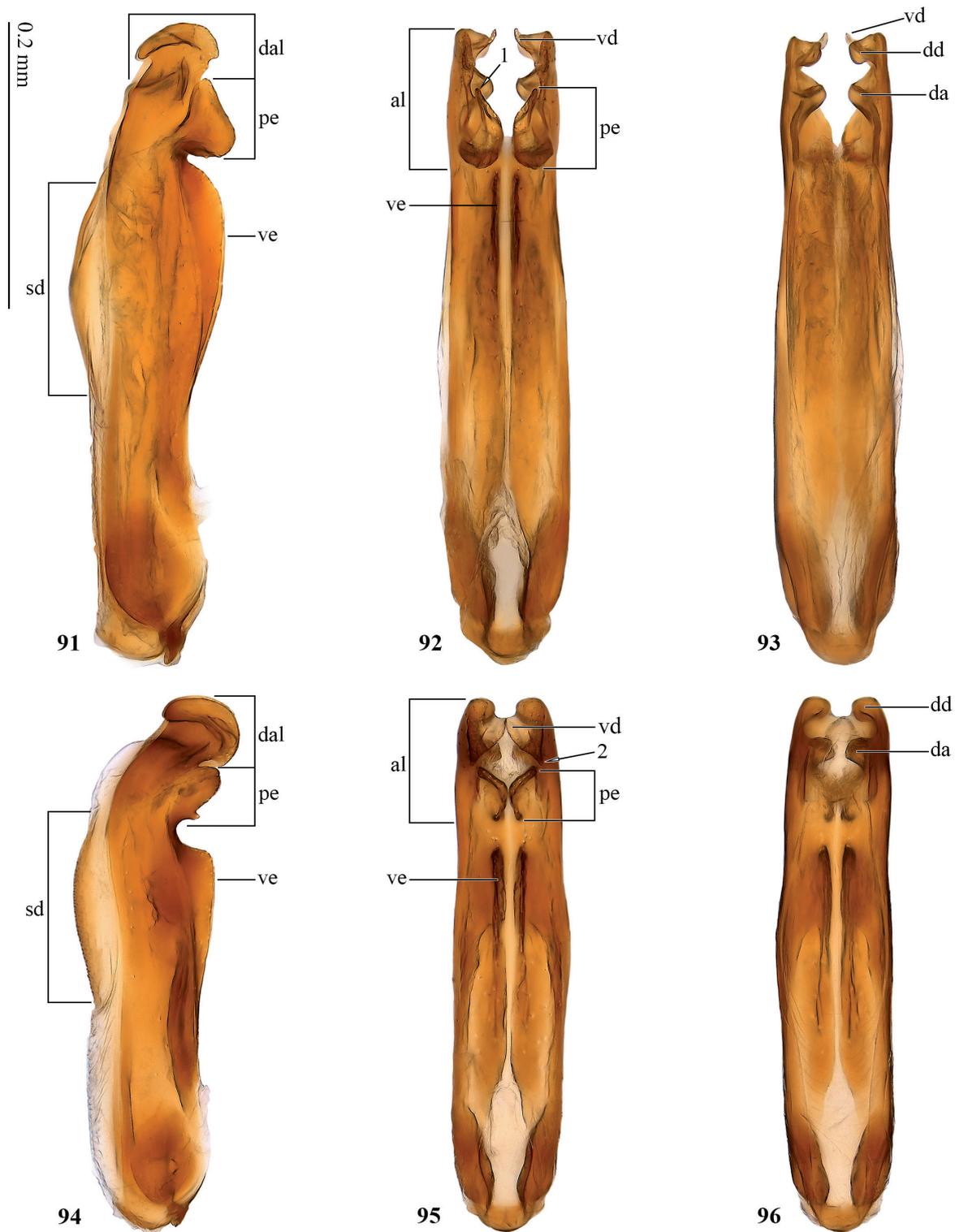
Figures 74–78. Aedeagus in lateral (74, 77), ventral (75, 78), and dorsal view (76) of *Scopaeus transvaalensis*, Namibia, Karas, SE Rosh Pinah: Dreigratdrif (Orange River) (74–76); *S. insidiosus*, holotype, Republic of South Africa, Western Cape, Caledon: Sonder End River (77, 78). **Abbreviations:** **ae** – apical extension of apical lobes; **al** – apical lobes; **dal** – distal portion of apical lobes; **pe** – proximoventral extension of apical lobes; **ve** – ventral extension of aedeagus.



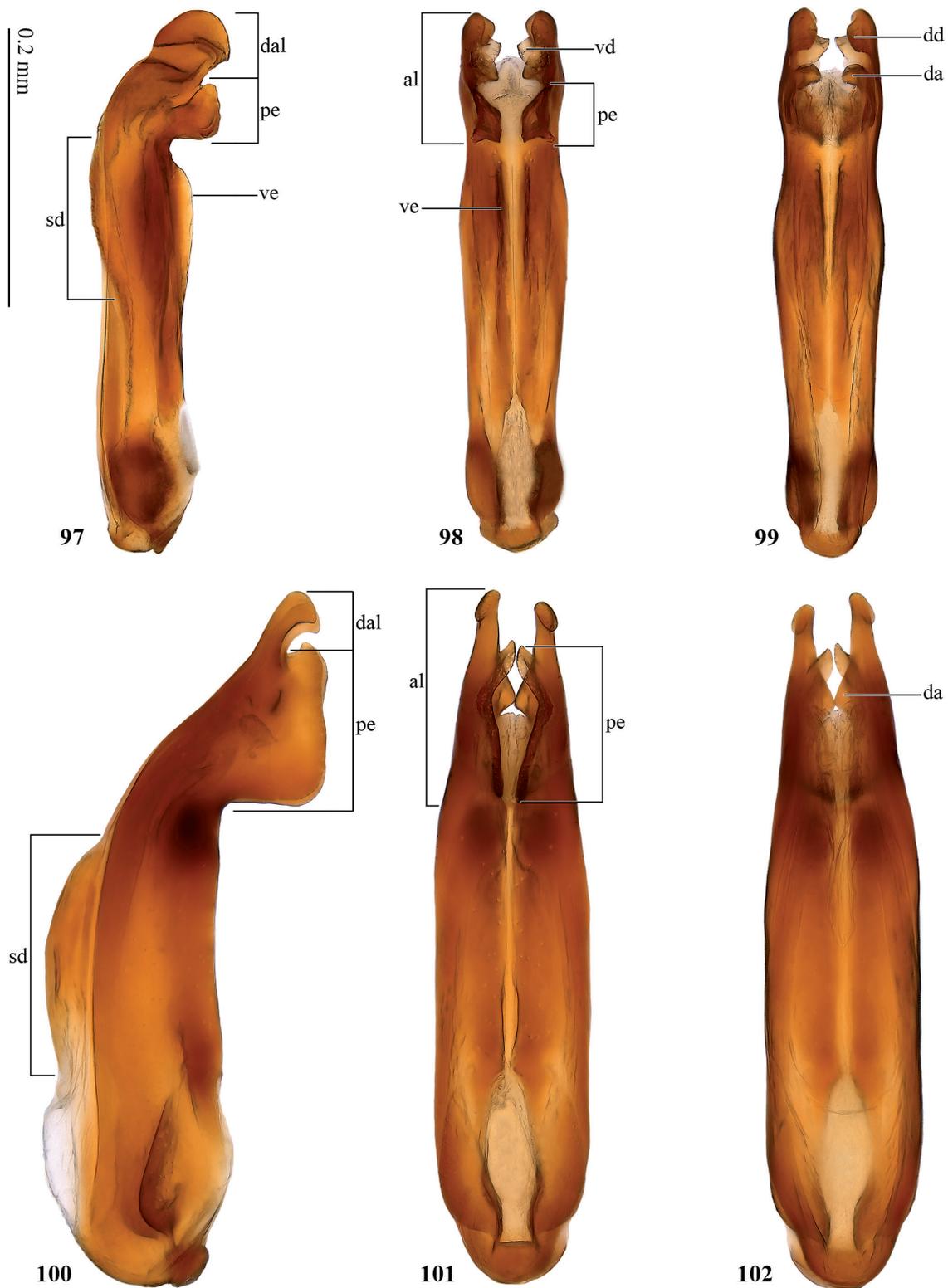
Figures 79–84. Aedeagus in lateral (79, 82), ventral (80, 83), and dorsal view (81, 84) of *Scopaeus ludificatus*, Republic of South Africa, Western Cape: holotype, Cape Town (79–81); Table Mountain (82–84). **Abbreviations:** **al** – apical lobes; **da** – dorsomedial dilatation of apical lobes; **dal** – distal portion of apical lobes; **pe** – proximoventral extension of apical lobes.



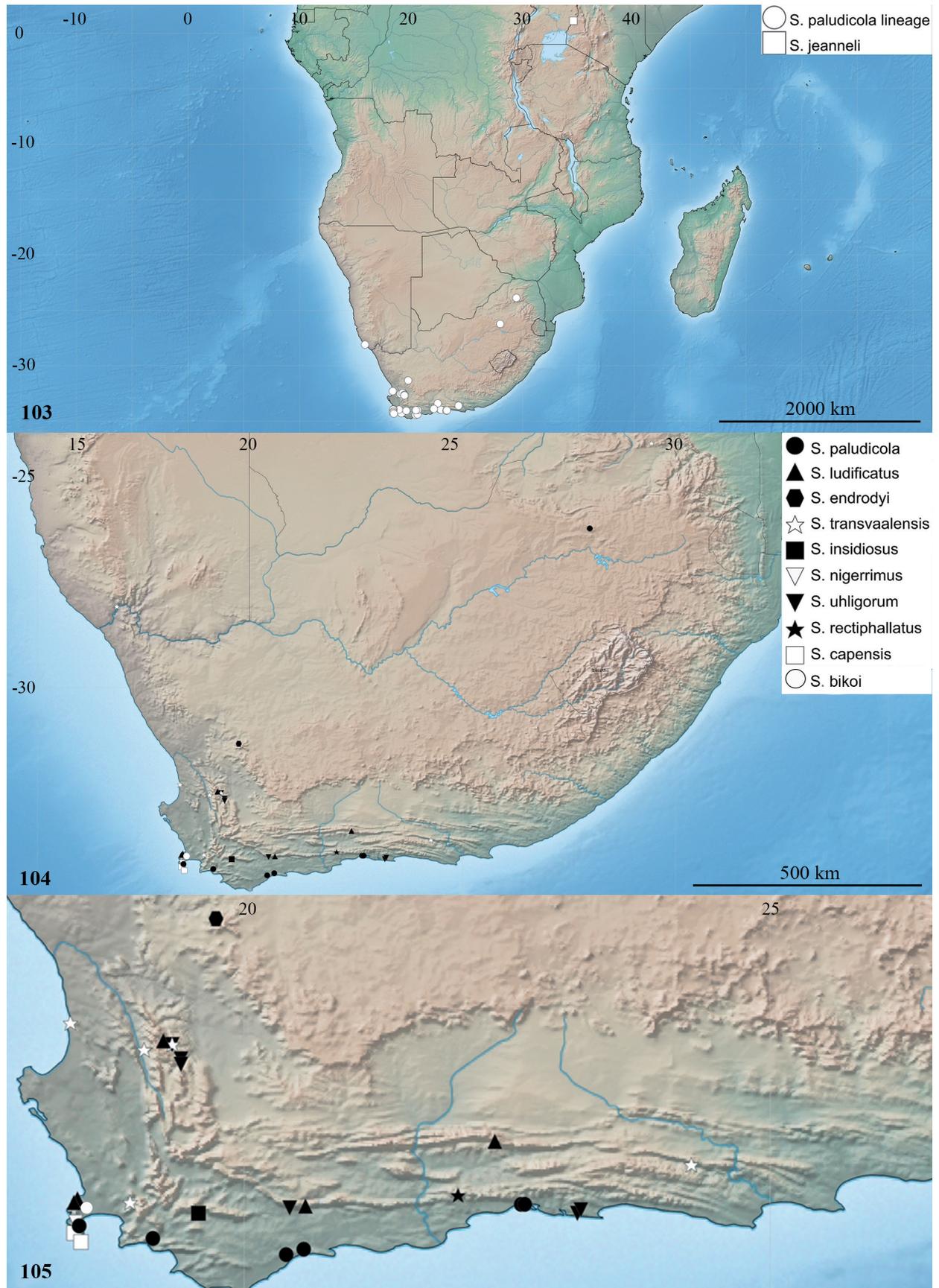
Figures 85–90. Aedeagus in lateral (85, 88), ventral (86, 89), and dorsal view (87, 90) of *Scopaeus endrodyi*, holotype, Republic of South Africa, Western Cape: Groot Toren Farm (85–87); *S. uhligorum*, holotype, Republic of South Africa, Western Cape: Harkerville Forest (88–90). **Abbreviations:** al – apical lobes; da – dorsomedial dilatation of apical lobes; dal – distal portion of apical lobes; pe – proximoventral extension of apical lobes; vd – ventrodistal dilatation of apical lobes; ve – ventral extension of aedeagus.



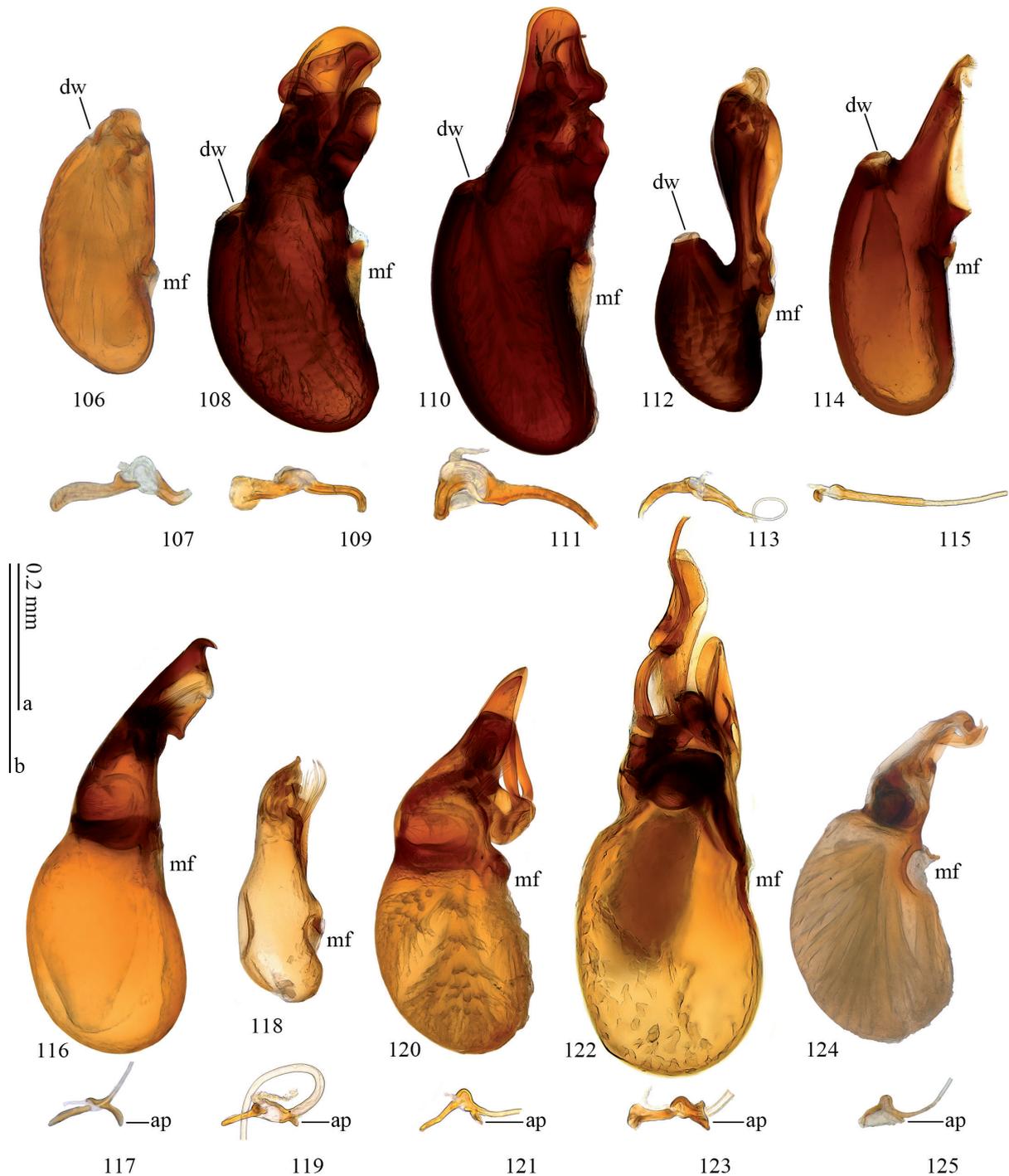
Figures 91–96. Aedeagus in lateral (91, 94), ventral (92, 95), and dorsal view (93, 96) of *Scopaeus rectiphallatus*, holotype, Republic of South Africa, Western Cape: Ruitersbos (91–93); *S. capensis*, holotype, Republic of South Africa, Western Cape, Table Mts NP: Olifantbos (94–96). **Abbreviations:** al – apical lobes; da – dorsomedial dilatation of apical lobes; dal – distal portion of apical lobes; dd – dorsodistal dilatation of apical lobes; pe – proximoventral extension of apical lobes; sd – sclerotization of dorsal membrane of aedeagus; vd – ventrodistal dilatation of apical lobes; ve – ventral extension of aedeagus. **Arrows:** 1 – distal tooth of proximoventral extension of apical lobes; 2 – proximal tooth of ventrodistal dilatation of apical lobes.



Figures 97–102. Aedeagus in lateral (97, 100), ventral (98, 101), and dorsal view (99, 102) of *Scopaeus bikoï*, holotype, Republic of South Africa, Western Cape: Cape Town (97–99); *S. jeanneli*, Kenya: Mt Elgon (100–102). **Abbreviations:** *al* – apical lobes; *da* – dorsomedial dilatation of apical lobes; *dal* – distal portion of apical lobes; *dd* – dorsodistal dilatation of apical lobes; *pe* – proximoventral extension of apical lobes; *sd* – sclerotization of dorsal membrane of aedeagus; *vd* – ventrodistal dilatation of apical lobes; *ve* – ventral extension of aedeagus.



Figures 103–105. Distribution of the *Scopaeus paludicola* species group in the Afrotropical Region (103), the southern Afrotropics (104), and the south of the Republic of South Africa (105).



species group in the southwestern part of the Republic of South Africa is unusual and surprising (Figs 104, 105). Five closely related species occur on the Cape Peninsula alone. Although our good knowledge of the diversity of the *S. paludicola* species group in southwestern South Africa is due to the touristic infrastructure there, it is nevertheless surprising that no specimens have been collected in northern regions of the Afrotropics to date, except for *S. jeanneli* on Mt Elgon (Fig. 103).

4.2. Relationships of the *Scopaeus paludicola* species group within the Scopaeina

I would like to introduce this chapter with a statement, as I feel uncomfortable revising the solid research of a friend and colleague. For me, Lee Herman's (2023) generic revision is an important inspiration and a catalyst for a more in-depth understanding of this subtribe. Without Herman's thorough morphological description of the genera of the Scopaeina, I would not have recognized the significance of the characters discussed below. I had the opportunity to read the manuscript of the generic revision and had no criticism at the time, but the more species we examine, the more seemingly clear diagnoses become blurred. The continuous advancement of scientific knowledge about the Scopaeina can only grow on a solid foundation – Herman's generic revision of the Scopaeina.

The *Scopaeus paludicola* species group deviates from the current definition of *Scopaeus* according to Frisch et al. (2002: 29–35) and Herman (2023: 67–70) in a few characters, some of which indicate an ancestral position of this lineage within the genus. The diagnostic and phylogenetic significance of these features is discussed below in the context of their distribution in *Scopaeus* and among the genera of the Scopaeina.

In the *S. paludicola* species group, the pronotum appears quite slender and parallel with pronounced lateroanterior angles due to its straight or slightly concave lateral margins (Figs 30–40). Conversely, the pronotum of the many *Scopaeus* species I have seen so far has moderately to notably convex lateral margins and therefore a more oval shape with less pronounced lateroanterior angles (e.g. Frisch 2016: Figs 2–16; Frisch & Narakusumo 2023: Figs 1–26). *Frischianus* Herman, 2025 (Frisch & Herman 2025: Figs 1–4, 43–60) and *Hyperscopaeus* Coiffait, 1984 (e.g. Frisch 2016: Fig. 6; Frisch & Narakusumo 2023: Fig. 26) have convex lateral margins of the pronotum, while nearly straight pronotal lateral margins are widespread in *Trisunius* Assing, 2011 (e.g. Assing 2011: Figs 2, 11, 18) and also found in *Micranops* Cameron, 1913 (Frisch 2025: Fig. 1) and *Orus* Casey, 1885 (Herman 2023: Fig. 257).

A midlongitudinal groove of the mesobasisternum that opens posteriorly, as found in the *S. paludicola* lineage of the *S. paludicola* species group (Figs 13, 14), has not been described for the Scopaeina. According to Herman (2023: 19), the Scopaeina exhibit a round or oval, median depression of the mesobasisternum that varies in depth, shape, and size (Fig. 15). Tokareva & Żyła (2025: 6, 17) also describe a „ventral median oval invagination of the mesoventral plate“ for this subtribe.

The *S. paludicola* species group has a pair of short, triangular metakatepisternal processes (Figs 16, 17). Herman (2023: 69) distinguished *Scopaeus* from the other genera of the Scopaeina by elongate metakatepisternal processes that taper to an acute end (Fig. 18; Herman 2023: 23, 25, e.g. Figs 97, 125, 142), but he pointed to *S. filiformis* Wollaston, 1867 as an exception (Herman 2023: Figs 89, 94), whose metakatepisternal processes correspond in shape to those of the *S. paludicola* species group. Herman (2023: 25) wondered whether he depicted an aberrant specimen of *S. filiformis*, but I have examined a number of specimens and can confirm the short processes of this species. It is true that the vast majority of *Scopaeus* exhibit long, pointed metakatepisternal processes, but images in Herman (2023) show that these structures can be shorter in some lineages [e.g. *S. limbatus* group (Fig. 131); *S. minimus* group (Fig. 137)] and can be seen as transition into the short, triangular processes of *S. filiformis* and the *S. paludicola* species group, which are, however, not closely related to each other. Since the metakatepisternal processes are also short-triangular in *Micranops* (Herman 2023: 122, Fig. 270) and even shorter and apically rounded in the other genera of the Scopaeina [*Frischianus* (Frisch & Herman 2025: 228, Fig. 26); *Hyperscopaeus* (Herman 2023: 111, Figs 241, 251); *Orus* (Herman 2023: 136, e.g. Fig. 300); *Trisunius* (Herman 2023: 147, Fig. 335)], I assume that short processes are the ancestral character state.

In the *S. paludicola* species group, the aedeagus differs drastically from that of the remaining *Scopaeus* and the other genera of the Scopaeina. First of all, it is divided into two sclerotized ventrolateral halves by a thin, midlongitudinal, membranous ventral split between the ostium and the medium foramen (e.g. Fig. 20) and by the broadly membranous dorsal surface, which is clearly separated from the sclerotized lateral parts of the aedeagus and apparently opens into the ostium (e.g. Fig. 21). In contrast to this and in contrast to the widespread midlongitudinal split of the aedeagus of the presumably basal genera of the Scopaeina (Frisch 2025: 59; Frisch & Herman 2025: 286), the dorsal surface of the aedeagus of the other *Scopaeus* species I examined to date is neither membranous nor midlongitudinally split (Figs 22, 23). Therefore, Herman (2023: 70) considered a completely sclerotized dorsal surface of the aedeagus

to be a diagnostic feature of the genus. A ventral split of the aedeagus is unknown in the other Scopaeina, which is why I consider it as apomorphic for the *S. paludicola* species group.

The location of the median foramen at the proximal end of the aedeagus (Fig. 20) is another ancestral character of the Scopaeina and suggests a basal position of the *Scopaeus paludicola* species group within the subtribe. In *Scopaeus*, the median foramen is usually in a more distal position (Figs 106–124). The location of the median foramen in the scopaeine genera was discussed in Frisch & Herman (2025: 286).

The *S. paludicola* species group lacks the so-called sclerotized ring of the aedeagus of *Hyperscopaeus* and most *Scopaeus*, a presumably stabilizing, strongly sclerotized and therefore dark-colored structure that separates the proximal phallobase and the distal portion of the aedeagus, which contains the endophallic sclerites and from which the postostial lobes extend (Figs 22, 23; Frisch *et al.* 2002: 34, Figs 7–21). The presumably ancestral absence of this aedeagal sclerotization connects the *S. paludicola* species group with the basal scopaeine genera *Micranops*, *Orus*, and *Trisunius* (cf. discussion in Frisch & Herman 2025: 286).

Similarly, the absence of the characteristic, sclerotized dorsal lobe of *Scopaeus* (Fig. 22; Frisch *et al.* 2002: 34, Figs 10–21) is another presumed ancestral character that the *S. paludicola* species group shares with the remaining genera of the Scopaeina.

Another striking feature of the aedeagus of the *S. paludicola* species group is the complete absence of sclerotized endophallic structures (Figs 47–102). All other genera of the Scopaeina exhibit specific sclerotized endophallic sclerites [*Frischianus* (Frisch & Herman 2025: 286, Figs 61–198); *Hyperscopaeus* (Frisch *et al.* 2002: 31, Figs 7–9); *Micranops* (Frisch 2025: Figs 11–142); *Orus* (Herman 2023: Fig. 325); *Trisunius* (Assing 2011: e.g. Figs 15, 25, 33)]. Consequently, the aedeagus of the *S. paludicola* species group lacks the sclerotized flagellum found in all other species of *Scopaeus* that I have examined to date (e.g. Frisch *et al.* 2002: 31, Figs 10–21).

In the *S. paludicola* species group, the females possess the typical two-piece sperm pump of the Scopaeina (Figs 24–26; cf. Frisch *et al.* 2002: 24–30), but it lacks the appendage of the proximal (chamber) segment (Figs 27–29, 117, 119, 121, 123, 125), which is present in the majority of *Scopaeus* species I have examined, but absent in some (Figs 107, 109, 111, 113, 115) and in the presumed ancestral genera of the Scopaeina (cf. Frisch & Herman 2025: 286, 287). Thus, the absence of the appendage of the chamber segment of the sperm pump is another plesiomorphic feature of this species group.

Therefore, if we take the complex, highly derived stridulum as the genus-defining apomorphic character

of *Scopaeus*, the following features can no longer be considered diagnostic for the genus according to the characters of the *S. paludicola* species group. These are an oval, median depression of the mesobasisternum, long, pointed metakatepisternal processes, a completely sclerotized dorsal surface of the aedeagus, and an appendage of the chamber segment of the sperm pump.

4.3 Reconsideration of the basal phylogeny of *Scopaeus*

The characters of the *Scopaeus paludicola* species group and of some other *Scopaeus* species I have studied in recent years have implications for my hypothesis on the basal phylogeny of the genus (Frisch *et al.* 2002). Based on a large, but nevertheless limited number of species, most of them Palearctic, I proposed the so-called sclerotized ring of the aedeagus (Fig. 22, 23) to be apomorphic for *Scopaeus* (Frisch *et al.* 2002: 38). Since then, *Hyperscopaeus* has been elevated to genus rank by Herman (2023: 110). I moreover considered the appendage or process of the chamber segment of the sperm pump (e.g. Figs 27–29) to be apomorphic for *Scopaeus* s. str. [= *Scopaeus* *sensu* Herman (2023)] (Frisch *et al.* 2002: 38). In the meantime, however, I came across a good number of *Scopaeus* including the *S. paludicola* species group, which lack both the sclerotized ring of the aedeagus and the appendage of the sperm pump (Figs 106–115). Interestingly, these species exhibit a membranous dorsal surface of the aedeagus in varying degrees. The dorsal aedeagal surface is completely membranous (*S. paludicola* species group) or has a dorsodistal opening or „window“ of unknown function (e.g. Figs 108, 110, 114), which may be indistinct (Fig. 106) or strongly pronounced (Fig. 112). Furthermore, these species usually have a more strongly sclerotized and narrower aedeagus (Figs 106–115) than the lineage that has the sclerotized ring, the dorsally sclerotized aedeagus, and the appendage of the sperm pump (Figs 22, 23, 27–29, 116–125). Given the completely membranous dorsal surface of the aedeagus in the *S. paludicola* species group, the much smaller dorsodistal window in the other species, and other aedeagal differences, I see no synapomorphic feature in these species and therefore consider them to represent different phylogenetic lineages. In contrast, the lineage that has the sclerotized ring, a completely sclerotized dorsal surface of the aedeagus, and the appendix of the sperm pump should represent a monophyletic group, as these characters are absent in the remaining Scopaeina. I am familiar with the first lineages from the southern hemisphere, but also from the Nearctic region. The latter lineage is distributed worldwide in temperate to tropical climates and appears to be more species-rich.

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References

- Assing, V. (2011): *Trisunius* gen. nov. from the southern East Palaearctic and the Oriental regions (Coleoptera: Staphylinidae: Paederinae: Medonina). *Linzer biologische Beiträge* 43(1), 195–220.
- Bellamy, C.L. & M.A. Jäch (1999): In memoriam Sebastian Endrödy-Younga (1934–1999). *Koleopterologische Rundschau* 69, 209–214.
- Cameron, M. (1945): New species of South African Staphylinidae (Col.). *The Annals and Magazine of Natural History* 11(11), 705–730. [Published January 1945 according to note on bottom of cover page.]
- Erichson, W.F. (1839): *Genera et species Staphylinorum insectorum coleopterorum familiae* (Vol. 1 400 pp.). F.H. Morin, Berlin.
- Erichson, W.F. (1840): *Genera et species Staphylinorum insectorum coleopterorum familiae* (Vol. 2, pp. 401–954). F.H. Morin, Berlin.
- Fagel, G. (1973): Revision des *Scopaeus* (Coleoptera - Staphylinidae - Paederinae) de l'Afrique noir. *Études du Continent Africain* 1: 1-247.
- Frisch, J. (2016): On the Scopaeina Mulsant & Rey of Australasia (Staphylinidae, Paederinae): type revisions and new biogeographic data. *Soil Organisms* 88(1), 55–88.
- Frisch, J. (2025): *Micranops* Cameron, 1913 in the Old World. New species, redescriptions, and new records (Coleoptera: Staphylinidae: Paederinae). *Megatataxa* 017(2), 500–562.
- Frisch, J., D. Burckhardt & V. Wolters (2002): Rove beetles of the subtribe Scopaeina Mulsant & Rey (Coleoptera: Staphylinidae) in the West Palaearctic: Phylogeny, biogeography and species catalogue. *Organisms, Diversity & Evolution* 2, 27–53.
- Frisch, J. & H. Herman (2025): *Frischianus* gen. nov., a new genus of the Scopaeina Mulsant & Rey, 1878 from the Oriental Region (Coleoptera: Staphylinidae: Paederinae: Lathrobiini). *Megatataxa* 017(2): 217–290.
- Frisch, J. & R.P. Narakusumo (2023): Revision of *Scopaeus* Erichson, 1839 (Coleoptera, Staphylinidae, Paederinae) of Indonesia, with description of 19 new species. *Soil Organisms* 95(1), 23–73.
- Herman, L. (2023): Generic Revisions of the Scopaeina and the Sphaeronina (Coleoptera: Staphylinidae: Paederinae: Lathrobiini). *Bulletin of the American Museum of Natural History* 460, 1–193.
- Herman, L. (2025): *Frischianus* Herman, new genus. – pp. 220–229 in: Frisch, J. & Herman, L. (2025): *Frischianus* gen. nov., a new genus of the Scopaeina Mulsant & Rey, 1878 from the Oriental Region (Coleoptera: Staphylinidae: Paederinae: Lathrobiini). *Megatataxa* 017(2), 217–290.
- Horn, W., I. Kahle, G. Friese & R. Gaedike (1990): *Collectiones entomologicae. Ein Kompendium über den Verbleib entomologischer Sammlungen der Welt bis 1960 (Teil I. A bis K, Teil II: L bis Z, 573 pp.)*. Berlin: Akademie der Landwirtschaftswissenschaften der Deutschen Demokratischen Republik.
- International Commission on Zoological Nomenclature (ICZN) (1999) *International Code of Zoological Nomenclature. (4th ed., xxix + 306 pp)*. London: The International Trust for Zoological Nomenclature.
- Levasseur, L. (1981): Contribution a la connaissance des Coléoptères Staphyliniidae [sic] d'Afrique noire (19^e note). Deux *Scopaeus* nouveaux du Mont Elgon (Kenya). – *Revue Française d'Entomologie (N.S.)*, 3, 19–22.
- Tokareva, A. & D. Żyła (2025): Insights for the subtribal-level phylogenetic reconstructions in Paederinae (Coleoptera: Staphylinidae: a study on mesoventral plate with elements of comparative morphology. *Arthropod Structure & Development* 88(101473), 1–22.

