

Taxonomic review of the tribe Sisyphini *sensu stricto* Mulsant, 1842 (Coleoptera: Scarabaeidae: Scarabaeinae) in southern Africa, including new species descriptions

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Abstract

The tribe Sisyphini *sensu stricto* Mulsant, 1842 comprises only three genera, the widespread *Sisyphus* Latreille, 1807 and *Neosisyphus* Müller, 1942, and the Mauritius endemic, *Nesosisyphus* Vinson, 1946. In southern Africa, *Sisyphus* and *Neosisyphus* are represented by five species groups in each genus. Together, they comprise a total of 33 valid species, of which six are new: *Sisyphus auricomus* **sp. n.**; *Sisyphus australis* **sp. n.**; *Sisyphus bicuariensis* **sp. n.**; *Sisyphus inconspicuus* **sp. n.**; *Sisyphus swazi* **sp. n.**; and *Neosisyphus tembyi* **sp. n.** A further Southern African species, *Sisyphus crispatus* Gory, 1833, is proposed as a *nomen dubium*. *Sisyphus natalensis* Balthasar, 1968 (**syn. n.**), and *Sisyphus bornemisszanus* Endrödi, 1983 (pars) (**syn. n.**) are made synonyms of *Sisyphus sordidus* Boheman, 1857. Lectotypes and paralectotypes are designated for *Sisyphus costatus* (Thunberg, 1818); *Sisyphus seminulum* Gerstaecker, 1871; *Sisyphus nanniscus* Péringuey, 1901; *Sisyphus transvaalensis* Péringuey 1901; *Neosisyphus spinipes* (Thunberg, 1818) and *Neosisyphus barbarossa* (Wiedemann, 1823). Diagnoses, photographs of habitus and male genitalia, lists of examined material and distribution maps are presented for all species. An identification key to the southern African sisyphine species is provided.

Keywords

Alpha taxonomy; Afrotropical; dung beetles; new species; species distribution

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Introduction

A recent, partial, tribal reclassification of the subfamily Scarabaeinae (Scarabaeidae: Coleoptera) has proposed to expand the tribe Sisyphini by incorporating the former

deltochiline genus *Epirinus* Reiche, 1841 (Tarasov & Dimitrov, 2016). Although molecular systematic analyses have shown that *Epirinus* is the closest relative of sisyphines (Monaghan et al. 2007; Mlambo et al. 2015), the proposed transfer was based on only 58% bootstrap support. Therefore, as relationships within Sisyphini *sensu lato* are weakly supported, this study will focus only on the Sisyphini *sensu stricto* Mulsant, 1842.

Members of the Sisyphini *sensu stricto* are easily recognized by eight antennomeres and a relatively short body that is laterally compressed and flattened, especially at the sides of the pronotum. The elytra are broad proximally and attenuate sharply to the posterior. The meso- and meta-thoracic legs are distinctly long (Mulsant 1842; Davis et al. 2008) with nearly half of the femoral length visible from above. Mesotibiae and metatibiae broaden towards the apex.

The tribe Sisyphini was proposed by Mulsant (1842) to accommodate a single genus, *Sisyphus* Latreille, 1807. A century later, Müller (1942) subdivided the genus into two subgenera: *Sisyphus sensu stricto* and *Neosisyphus*. Subsequently, these taxa have been cited as two genera in morphological and molecular phylogenies of the Scarabaeinae (Philips et al. 2004; Monaghan et al. 2007; Mlambo et al. 2015; Tarasov & Génier 2015). However, it was only recent that Montreuil (2015b) formally raised *Neosisyphus* to a generic level.

The tribe comprises a total of 103 valid species, belonging to three genera. *Nesosisyphus* is an endemic genus on the Indian Ocean island of Mauritius (four spp.). *Neosisyphus*, has been recorded from the Afrotropical (31 spp.) and Oriental (two spp.) regions. The most diverse and widespread genus, *Sisyphus* is represented in the Afrotropical (48 spp.), Oriental (15 spp.), Neotropical (two spp.) and Palaeartic (one sp.) regions. Three *Sisyphus* species are also subdivided into a total of nine subspecies (Daniel et al. 2016; Montreuil 2016, 2017; Schoolmeesters 2017).

Vinson (1946) described the endemic Mauritian genus under the name of *Nesosisyphus* to accommodate four species, namely: *N. vicinus* (Vinson, 1939); *N. regnardi* (Alluaud, 1898), *N. pygmaeus* Vinson, 1946, and *N. rotundatus* Vinson, 1946. *Nesosisyphus* differs from its sister genera (*Sisyphus* and *Neosisyphus*) by convex elytra with the lateral margins not reduced and slanting downwards. There are also nine markedly deep elytral striae (Vinson 1946). The other two genera bear somewhat flat elytra with 7 visible elytral striae and an 8th that is mostly vestigial.

Sisyphus is distinguished from *Neosisyphus* as follows. *Sisyphus* bears a complete lateral ridge that extends from the lateral to the posterior margin of the pronotal disc. A row of dense setae is present on the external edge of the first tarsal segment of the meso- and meta-thoracic legs. In *Neosisyphus*, the lateral ridge extends from the posterior margin without reaching the lateral margin of the pronotal disc, or, it may be absent in some cases. Strong setae are usually present on tarsal segments but not in straight lines and not on the external edge of the first tarsus as in *Sisyphus* (Paschalidis 1974, Davis et al. 2008, Montreuil 2015b, Daniel et al. 2016).

Identification of sisyphine species is based on subtle morphological differences. In *Neosisyphus*, it is based primarily on the presence or absence of spines and protuberances

on the legs, as well as the shape of the parameres. In *Sisyphus*, species delimitation is based on the shape of indentations, cephalic dentition, size of pronotal punctures, and the distribution and colour of setae. Overall for the tribe, a synergistic approach is advisable. Both morphological and biogeographic evidence is useful when identifying species.

Neosisyphus species show sexual dimorphism. Species separation is generally easier using male characters since females often closely resemble one another within species-groups. However, care should be taken even with males as characters vary in morphology with body size, i.e. between major and minor males. *Sisyphus* species mostly show little sexual dimorphism. If present, it is restricted to the shape of hind legs and abdominal sternites. Thus, species identifications can be accomplished using similar characters for both males and females.

To date, 33 valid species have been recorded in southern Africa comprising; Angola, Botswana, Lesotho, Mozambique, Malawi, Namibia, South Africa, Swaziland, Zambia and Zimbabwe. Of these, 22 belong to *Sisyphus* and 11 to *Neosisyphus*. However, the nomenclature of the majority of the species, currently, follows an unpublished revision of *Sisyphus* from southern Africa (Paschalidis 1974). Therefore, supported by ICZN articles 8, and 9.7, any taxonomic and nomenclatural corrections from Paschalidis (1974) are invalid, which warrants an urgent published taxonomic revision of southern African sisyphines.

Although a number of recent published papers have focused on revisions and new species descriptions of Afrotropical (Montreuil 2017, 2016; 2015a, b, c), and southern African sisyphines (Daniel et al. 2016), detailed taxonomic work on the group in southern Africa is incomplete. Therefore, in this paper we resolve some remaining nomenclatural issues, further revise the taxonomy, and provide identification keys and distribution maps for the species. In addition, we describe six new species, five of them belonging to *Sisyphus*, and the sixth to *Neosisyphus*. The current taxonomic revision is part of an integrated project on southern Africa Sisyphini, which includes molecular systematics, biogeography and evolutionary ecology of the tribe.

It might be added that, so far, eight species of southern African sisyphines have been assessed for the International Union for Conservation of Nature (IUCN) Red List of Threatened Species. Seven of the species were assessed as “Least Concern (LC)” and the eighth as “Data Deficient (DD)” (IUCN Red List, 2017). However, assessment of conservation status and extinction risk is dependent on accuracy of the alpha taxonomy (Bawa 2010; McNelly 2002; Mace 2004; Wheeler et al. 2004) that is addressed in this revision of southern African sisyphines.

Material and methods

Descriptive terminology largely employs the nomenclature established by Vaz-de-Mello et al. (2011), Montreuil (2015b) and Génier & Arnaud (2016). Species

delimitations are based on morphological boundaries established through comparisons between specimens and the original description. Furthermore, the biogeographical evidence is provided to support the species identity, mainly for those ones which we could not examine the type specimens.

Using an Olympus dissecting microscope, 8372 specimens were examined, including type material. Images of the habitus were taken with a Canon EOS 550D and 100 mm macro lens. Focus stacking was performed using the software Helicon Focus version 5.3 Male genitalia were photographed under a Leica M165 C microscope, using a Leica DMC 2900 digital camera.

Type label data are transcribed verbatim. Data from individual labels are separated by a slash “/” and followed by the media description. Additional information is in box brackets [()]. Data for examined non-type specimens are listed as Supplementary Information.

The main features of each species-group are provided in the identification key for the southern Africa sisyphine species. The names used for species-groups in *Sisyphus* refer to the oldest, included, described species. For *Neosisyphus* we follow the species group names proposed by Montreuil (2015b). However, it should be noted that species groups do not constitute valid taxonomic entities according to the International Commission on Zoological Nomenclature Code (ICZN 1999).

The designation of lectotypes proposed, herein, is in accordance with articles 74.1.1 and 74.7 (ICZN 1999). Thus, to provide nomenclatural stability, lectotype specimens were chosen from the original author’s collection of syntypes.

Institutions holding examined material are abbreviated as follows:

- CMN:** Canadian Museum of Nature, Ottawa, Canada.
HNHM: Hungarian Natural History Museum, Budapest, Hungary.
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A.
SMNH: Museum of Evolution–Zoology (Uppsala University), Uppsala, Sweden.
MNHUB: Museum für Naturkunde, Berlin, Germany.
MNHN: Muséum National d’Histoire Naturelle, Paris, France.
NHMD: Natural History Museum of Denmark, Copenhagen, Denmark.
NHML: Natural History Museum, London, England.
NHRS: Naturhistoriska Riksmuseet, Stockholm, Sweden.
NMBA: National Museum, Bloemfontein, South Africa.
SAM: Iziko South African Museum, Cape Town, South Africa.
SANC: National Collection of Insects, Plant Protection Research Institute, Pretoria, South Africa.
TMSA: Ditsong Museum of Natural History, Pretoria, South Africa (previously the Transvaal Museum).
UPSA: Department of Zoology & Entomology, University of Pretoria, Pretoria, South Africa.

Results and discussion

Identification key for males of southern African sisyphine species

1. Lateral ridge on the pronotal disc extends from the posterior margin without reaching the lateral margin (Fig. 1F); strong setae absent on the external margin of the first meso- and metatarsal segments (Fig. 1D).....*Neosisyphus* (2)
 - Lateral prothoracic ridge between pronotal disc and prothoracic episternum complete (Fig. 1E); first tarsal segments of the meso- and meta-thoracic legs with a row of dense setae in a straight line on the external edge (Fig. 1C).....*Sisyphus* (13)
2. Mesotibia strongly modified by indentations and protrusions; a large spine distally on the posterior margin of the mesofemur. Completely black, pygidium simple and lacking a pair of distinct tubercles. Eastern coastal forests of South Africa and South Mozambique (*tibialis* species-group; *Neosisyphus mirabilis* (Arrow, 1927) (Figs. 23, 24A)
 - Mesotibia simple, without any spine projected distally on the posterior margin of the mesofemur..... (3)
3. Femur and tibia of mesolegs without cuticular projections on the posterior margin..... *barbarossa* species-group (Figs. 17A–D) (4)
 - Femur and tibia of mesolegs with cuticular projections on the posterior margin... (7)
4. Metafemur with sharp pointed spine on the mid-posterior margin (Figs. 17A–B) (5)
 - Metafemur with angled-protuberance on the mid-posterior margin (Figs. 17C–D) (6)
5. Projecting metatrochanter longer than $\frac{3}{4}$ of the metafemur length in major males and $\frac{1}{2}$ of the metafemur length in minor males. In major males the metatrochanter is slightly inwardly-curved at the tip and straight in minor males; setae on the elytra black, recurved at the apex. Lowland dry savannas in southern Africa *Neosisyphus calcaratus* (Klug, 1855) (Figs. 17, 18B)
 - Projecting metatrochanter shorter in minor males ($<\frac{1}{4}$ the length of the metafemur) and longer in major males ($\frac{1}{2}$ the length of the metafemur), elytral setae yellow. Moist highveld and coastal upland grassland of South Africa *Neosisyphus barbarossa* (Wiedemann, 1823) (Figs. 17, 18A)
6. Projecting metatrochanter relatively short; four times shorter than total length of metafemur. Lowland and upland moist vegetation from northeast to southern Africa *Neosisyphus setiger* (Roth, 1851) (Figs. 17, 18D)
 - Metatrochanter slightly inwardly-projected at the apex, metatrochanter projection is $\frac{1}{2}$ the length of the metafemur. Upland woodland in southern Angola *Neosisyphus tembyi* Daniel & Davis sp. n (Figs. 17, 18C)
7. Posterior margin of the mesoleg with spine or projection distally on mesofemur and basally on mesotibia; first quarter of mesotibia from femoro-tibial joint abruptly narrowed *spinipes* species-group (Figs. 20A–C) (8)

- Mesotibial spine projecting posteriorly and gradually narrowing distally.....(10)
- 8. Spine present on the mid-posterior margin of the metafemur; metatrochanter relatively short, $\frac{1}{4}$ of the metafemur length.....(9)
 - Spine absent on posterior margin of the metafemur; metatrochanter is $\frac{1}{2}$ the length of the metafemur in major males. Shaded vegetation and thickets from east to southern Africa.....*Neosisyphus fortuitus* (Péringuey, 1901) (Figs. 20, 21A)
- 9. Distinct triangular shaped projection present on the basal posterior margin of the mesotibia. Parameres not curved at the apex (Fig. 21C). Moist upland and coastal grassland from east to southern Africa*Neosisyphus spinipes* (Thunberg, 1818) (Fig. 20C)
 - Lacking a triangular protuberance on the basal posterior margin of the mesotibia in minor males. There is a slight sinuosity in major males. Parameres curved downward apically (Fig. 21B). Lowland dry savanna from east to southern Africa*Neosisyphus infuscatus* (Klug, 1855) (Fig. 20B)
- 10. Basal posterior spine on mesotibia projecting perpendicularly; body uniformly brown; size of beetles 6.0–10 mm..... *rubrus* species-group (Figs. 29A–B) (11)
 - Basal posterior spine on mesotibia not projecting perpendicularly to the ventral apical margin of the femur; colour is not uniform overall, size of beetles 11.0–13.5 mm*quadricollis* species-group (Figs. 25A–B) (12)
- 11. Parameres with protrusion apical-laterally (Fig. 30B). Upland and coastal moist grassland and savanna in southern Africa.....*Neosisyphus rubrus* (Paschalidis, 1974) (Fig. 29B)
 - Parameres simple (Fig. 30A). Cool, dry savanna, karoo and grassland in South Africa (Northern Cape and Free State) and Namibia (Etosha Pan, Okaukuejo) ...
.....*Neosisyphus macrorubrus* (Paschalidis, 1974) (Fig. 29A)
- 12. Lateral margin of elytra emarginate; concavity of margin distinctly deep in the middle; short projecting metatrochanter in males ($\frac{1}{3}$ of metafemur length); metafemur lacking spines. Deep sands and shrubland of southwest coast, and karoo in the Eastern Cape (South Africa)*Neosisyphus quadricollis* (Gory, 1833) (Figs. 26, 27A)
 - Margin of elytra with regular shape; a protuberance distally on the posterior margin of the metafemur, the metatrochanter exceeds $\frac{1}{2}$ the length of the metafemur in males. Moist highland grassland in South Africa.....
.....*Neosisyphus kuehni* (Haaf, 1955) (Figs. 26, 27B)
- 13. Setae on the elytral interstriae arranged in tufts
.....*muricatus* species-group (Figs. 2A–F) (14)
 - Setae on the elytral interstriae evenly distributed, not grouped in tufts(20)
- 14. Setae arranged in tufts on the pronotum, which alternate with depressed bare patches(15)
 - Setae on the pronotum not arranged in tufts(17)
- 15. Concave and upwardly curved margin between the anterior medial teeth of the clypeus; macropterous (Fig. 2I). Woodland thickets and forest in north South Africa and Swaziland*Sisyphus fasciculatus* Boheman, 1857 (Figs. 2, 3C)

- Anterior margin between medial clypeal teeth not upcurved; hind wings reduced or completely brachypterous (Figs. 2H–J)(16)
- 16. Anterior margin between medial clypeal teeth concave; pronotum wider anteriorly than posteriorly. Parameres (Fig. 3F). Only known from Swaziland.....
.....*Sisyphus swazi* Daniel & Davis sp. n (Fig. 2F)
- Straight edge between medial teeth of clypeus; width of pronotum uniform from anterior to posterior margins. Parameres (Fig. 3G). Popa Falls forest (Namibia), Central Mozambique and East Africa
..... *Sisyphus alveatus* Boucomont, 1935 (Fig. 2G)
- 17. Very strong lateral emargination and distinct shiny punctation on pronotum. Cooler southern forest and montane grassland in South Africa
..... *Sisyphus muricatus* (Olivier, 1789) (Figs. 2, 3A)
- No distinct lateral emargination on the pronotum.....(18)
- 18. Punctation on the pronotum unclear; interstriae 1, 3, 5, and 7 with rows of black setae arranged in tufts, interstriae 2, 4, and 6 with sparsely arranged single setae. Coastal sand forest of northeast South Africa and southeast Mozambique
..... *Sisyphus neobornemisszanus* Daniel & Davis, 2016 (Figs. 2, 3B)
- Punctation on the pronotum conspicuous; setae on pronotal disc arise from the centre of ocellate punctures (Fig. 5H).....(19)
- 19. Proximal elytral setae evenly arranged; mid-basal elytral setae arranged in tufts of scattered individual setae. Pronotal disc with three prominent round depressions. Parameres (Fig. 3E). Primarily upland and highland grassland in Gauteng, Kwa-Zulu Natal, Limpopo, Mpumalanga and Northwest Province
..... *Sisyphus manni* Montreuil, 2015 (Fig. 2E)
- Elytra entirely covered in tufts of setae, each tuft dense and compact; depressions on the pronotal disc absent; body larger than *S. manni* and oval. Parameres (Fig. 3D). Unshaded vegetation in the Eastern Cape
..... *Sisyphus perissinottoi* Montreuil, 2015 (Fig. 2D)
- 20. Well-developed tufts of epipleural setae (Fig. 5H); edge between medial teeth almost straight; setae on the pronotum evenly distributed
..... *goryi* species-group (Figs. 5A–E) (22)
- Weak tufts of epipleural setae; margin between medial teeth V-shaped)
..... *umbraphilus* species-group
- 21. Pronotal disc with setae interspersed with bald patches. Dense woodland and thicket in KwaZulu Natal, Gauteng and North West Provinces (South Africa)
..... *Sisyphus umbraphilus* Daniel & Davis, 2016 (Fig. 8A)
- Pronotal disc without clear setae interspersed with bald patches(26)
- 22. Setae on the pronotum inserted between or on the posterior margin of ocellate punctures (Fig. 5F).....(23)
- Setae on the pronotum inserted centrally on ocellate punctures
..... (Fig. 5G) (25)
- 23. Fine setae on elytra arranged in single rows, epipleural tufts containing few setae (<10); larger-bodied species. Highland grassland under cooler conditions in

- South Africa, Botswana, and Namibia
 *Sisyphus caffer* **Boheman, 1857** (Figs. 5, 6B)
- Much finer setae on elytra, distributed in single rows; epipleural tufts containing many setae (>10); elongate body shape (24)
24. Setae on the pronotum and elytra of uniform colour and regularly arranged. Parameres (Fig. 6D). Widespread woodland species in sub-Saharan Africa
 *Sisyphus goryi* **Harold, 1859** (Fig. 5D)
- Setae on pronotum and elytra bicoloured (black and gray). Parameres (Fig. 6A). Open woodland in southern Angola
 *Sisyphus bicuariensis* **Daniel & Davis, sp. n** (Fig. 5A)
25. Elytral setae thick, arranged in non-single rows and forming bunches; body size: 6.6–4.4 mm. Open lowland vegetation in South Africa, Mozambique, and Zimbabwe
 *Sisyphus sordidus* **Boheman, 1857** (Figs. 5, 6E)
- Elytral setae fine, regularly arranged on interstriae; body size: 10–8.0 mm. East African miombo woodland; known only from Quirimbas National Park (Northern Mozambique)
 *Sisyphus genierorum* **Montreuil, 2015** (Figs. 5, 6C)
26. Setae on outer margin of elytra not arranged in tufts; margin between medial teeth concave or straight; very large ocellate punctures on dorsal surface of pronotal disc
 *costatus* species-group (Figs. 11A–E) (27)
- Setae on outer margin of elytra not arranged in tufts; margin between medial teeth narrowed (almost V-shaped); very fine ocellate punctures on dorsal surface of pronotal disc
 *seminulum* species-group (Figs. 6A–C) (30)
27. Dorsal surface of the clypeus and frons with inconspicuous ocellate punctation, but more visible on the vertex (Figs. 11G–I) (28)
- Dorsal surface of the head (clypeus, frons and vertex) with distinct ocellate punctation (Figure 11J) (30)
28. Vertex with dense ocellate punctation, margin between medial teeth straight; genae convex anteriorly (Fig. 11I); elytral setae fine and uniformly arranged. Moist savanna or dense woodland and riverine vegetation in the interior of South Africa. Shaded vegetation on coastline from Sofala Bay (Mozambique) to Eastern Cape (South Africa)
 *Sisyphus inconspicuus* **Daniel & Davis, sp. n** (Fig. 5B)
- Vertex with scattered ocellate punctation (Fig. 11G–H), elytral setae thicker, alternating on the interstriae between rows of well-developed and less developed setae (Fig. 11F) (29)
29. Margin between medial teeth distinctly concave and upcurved; lacking carinae on the frons; genae virtually straight laterally (Fig. 11G). Parameres (Fig. 12B). Highland grassland in South Africa
 *Sisyphus costatus* (**Thunberg, 1818**) (Fig. 11B)
- Edge between medial teeth straight; well-defined clypeo-frontal carina; genal margin virtually convex (Fig. 11H). Parameres (Fig. 12E). Shaded vegetation from Western and Eastern Cape Provinces, South Africa
 *Sisyphus australis* **Daniel & Davis sp. n** (Fig. 11E)
30. Small-bodied; genae with shallow depression dorsally; pronotal disc showing distinct pattern of bare patches amongst sparse short setae; metafemur simple.

- Highland forest under cooler conditions in Zimbabwe and Malawi.....
 *Sisyphus gazanus* Arrow, 1907 (Figs. 11, 12C)
- Large-bodied; genal depression absent; setae arranged regularly on pronotal disc; anvil-shaped projection on mid-posterior margin of metafemur. Lowland shaded Savanna from east to southern Africa.....
 *Sisyphus impressipennis* Lansberge, 1886 (Figs. 11, 12A)
31. Relatively large-bodied; pronotal disc with conspicuous metallic sheen; open woodland in north of Namibia and south of Angola.....
 *Sisyphus splendidus* Montreuil, 2015 (Fig. 14A)
- Relatively small to medium-bodied.....(32)
32. Very small-sized body (3.0–3.8 mm); pronotal disc dull bearing some depressions. Shaded vegetation in eastern and southern Africa.....
 *Sisyphus nanniscus* Péringuey, 1901 (Figs. 14C, 15B)
- Medium-sized body (3.9–5.0 mm).....(33)
33. Pronotal disc bears sparse, long and fine yellow setae, separated by linear bare patches (Fig. 14E); parameres notched dorsally (Fig. 15A). Dense coastal woodlands and forest from northeast South Africa to southern Mozambique.....
 *Sisyphus oralensis* Daniel & Davis, 2016 (Fig. 14B)
- Pronotum bears thick and short golden setae; directional projection of the setae well-defined (Fig. 14F); parameres without excavation dorsally, attenuating sharply at the apex (Fig. 15C). Forest and dense woodland species in central Mozambique.....
 *Sisyphus auricomus* Daniel & Davis sp. n (Fig. 14D)

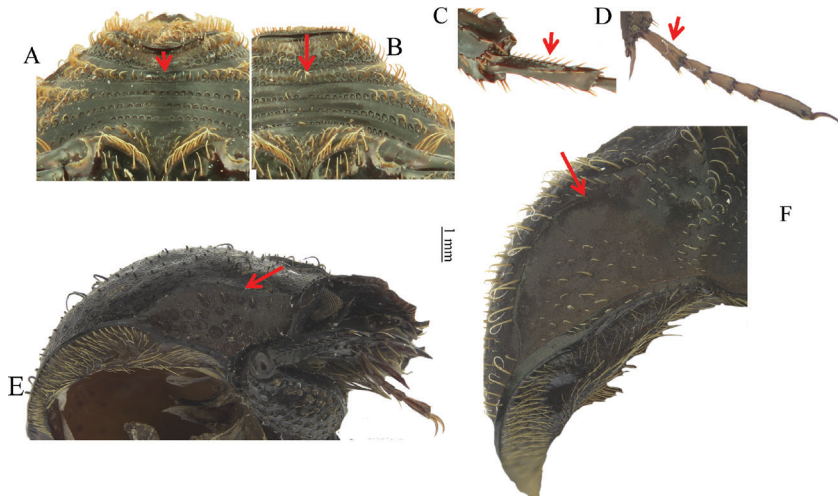


Fig. 1. A- medially narrow sternite, typical for males in *Sisyphus*. B- Abdominal sternite in females of *Sisyphus* species; C- *Sisyphus*; bears strong setae on the external edge of the first metatarsus; D- *Neosisyphus*, lacking strong setae on the external margin of the first metatarsus. E- Complete lateral ridge, which divides propisternum from pronotal disc in *Sisyphus*. F- Lateral ridge does not reach antero-lateral edge of the pronotum in *Neosisyphus*.

Species groups of Sisyphini in southern Africa

In southern Africa, five species-groups are proposed for the genus *Sisyphus* according to their morphological affinities. Due to the limited amount of sexual dimorphism in *Sisyphus*; characterization largely applies equally to males and females.

(1) *S. muricatus* group: Seven southern African species, comprising: *S. muricatus*; *S. neobornemisszanus*; *S. fasciculatus*; *S. perissinottoi*; *S. manni*; *S. swazi* **sp. n** and *S. alveatus*. The external morphology (Figs. 2A–G) and the genitalia (Figs. 3A–G) differ among the members of the group.

(2) *S. goryi* group: Five species, comprising: *S. bicuariensis* **sp. n**; *S. caffer*; *S. genierorum*; *S. goryi* and *S. sordidus*. Although external morphological differences are subtle (Figs. 5A–E), the shapes of parameres are relatively different between species (Figs. 6A–E).

(3) *S. umbraphilus* group: Comprises a single southern African species, *S. umbraphilus* (Fig. 8A); genitalia (Fig. 9A)

(4) *S. costatus* group: Five species, comprising: *S. impressipennis*; *S. costatus*; *S. gazanus*; *S. inconspicuus* **sp. n**; and *S. australis* **sp. n** (Figs. 11A–E). The shape of the parameres differs between species (Figs. 12A–E).

(5) *S. seminulum* group: Four southern African species: *S. splendidus*; *S. oralensis*; *S. nanniscus*; and *S. auricomus* **sp. n** (Figs. 14A–D). The genitalia of *S. splendidus* were not studied because no male specimens were available. The parameres of other species members of the group are clearly different (Figs. 15A–C).

In *Neosisyphus*, identification is complicated by sexually dimorphic characters that vary in morphology with body size. Females are often difficult to separate into species. Species-groups defined for *Neosisyphus* follow Montreuil (2015b). In southern Africa five species-groups have been recorded.

(1) *N. barbarossa* group: Four species: *N. barbarossa*; *N. calcaratus*; *N. tembyi* **sp. n** and *N. setiger* (Figs. 17A–D). Morphological differences are clear in major males, but, less so in minor males and females. However, species members are easily separable through the differences between the phallobase and shapes of the parameres (Figs. 18A–D).

(2) *N. spinipes* group: Three species: *N. fortuitus*; *N. infuscatus* and *N. spinipes* (Figs. 20A–C). All species bear distinctly different parameres (Figs. 20A–C). Although there are clear differences between major males, in the latter two species, there are often close morphological similarities.

(3) *N. tibialis* group: One southern African species: *N. mirabilis* (Fig. 23A). The species shows distinctive spinose sculpturing of the legs. The aedeagus is shown in Fig. 24A.

(4) *N. quadricollis* group: Two southern African species: *N. quadricollis* and *N. kuehni* (Figs. 26A–B). Both species show differences in the phallobase and the shape of parameres (Figs. 27A–B).

(5) *N. rubrus* group: Composed of two similar southern African species: *N. macrorubrus* and *N. rubrus* (Figs. 29A–B). Parameres differ in shape between the species (Figs. 30A–B).

Taxonomy

Sisyphus Latreille 1807

Latreille 1807: 79; Gory 1833: 1–15; Kolbe 1914: 317; Harold 1869: 984–5; Péringuey 1901: 98–108; Gillet 1911: 22–25; Arrow 1909: 517–519; Arrow 1927: 456–465; Haaf 1955: 341–381; Balthasar 1968: 954, Ferreira 1972: 789–844; Paschalidis 1974b: 299–303; Endrödi 1983: 207–210; Schäfer & Fischer 1992: 119–137; Schäfer & Fischer 2001: 1–93; Montreuil 2014: 177–180; Montreuil 2015a: 91–100; Montreuil 2015b: 1–2; Montreuil 2015c: 1–13; Montreuil 2016: 167–174; Daniel et al. 2016: 67–74; Montreuil 2017: 1–22

Type species: *Sisyphus schaefferi* Linnaeus, 1758

muricatus species-groups (Figs. 2, 3A–F; 4)

Sisyphus muricatus (Olivier, 1789) (Figs. 2, 3A)

Scarabaeus muricatus Olivier, 1789

Olivier 1789: 188–9, Gory 1833: 7–8; Harold 1869: 985; Péringuey 1902: 105–6; Arrow, 1927: 458; Haaf 1955: 367–8; Ferreira 1972: 801; Paschalidis 1974: 7–9, Montreuil 2015c: 3, 11; Daniel et al. 2016: 71.

Type locality: Cape of Good Hope (South Africa).

Size: Male: length: 12.5–11.0 mm, width: 8.0–6.5 mm; Female: length: 12–9.6 mm, width 6.5–5.0 mm.

Diagnosis: *S. muricatus* is similar to *S. neobornemisszanus*. However, it differs by bearing, mostly, more strongly developed clypeo-frontal carinae; also, very strong, deep, lateral emargination and distinct shiny punctuation on the pronotum.

Examined non-type material: See Supplementary information.

Distribution: *S. muricatus* shows an Afrotropical forest and montane grassland distribution in South Africa (Davis et al., 2008, 2002a, 1999) (Fig. 4). It has been recorded from grassland in the Golden Gate Highlands National Park and the foothills of the Drakensberg. It has also been collected in grassland at Mount Sheba. There are records of this species in coastal afrotropical forest (Davis et al. 1999) in the Cape (Knysna Forest, Garden of Eden, and George). However, these qualitative data are insufficient to support a significant association with shaded vegetation on the south coast of South Africa.

Remarks: The species was originally described as *Scarabaeus muricatus* by Olivier (1789) from an unspecified type locality in “la Amérique méridionale”. Gory (1833) transferred the species to the genus *Sisyphus* citing the Cape of Good Hope (South Africa) as the type locality.

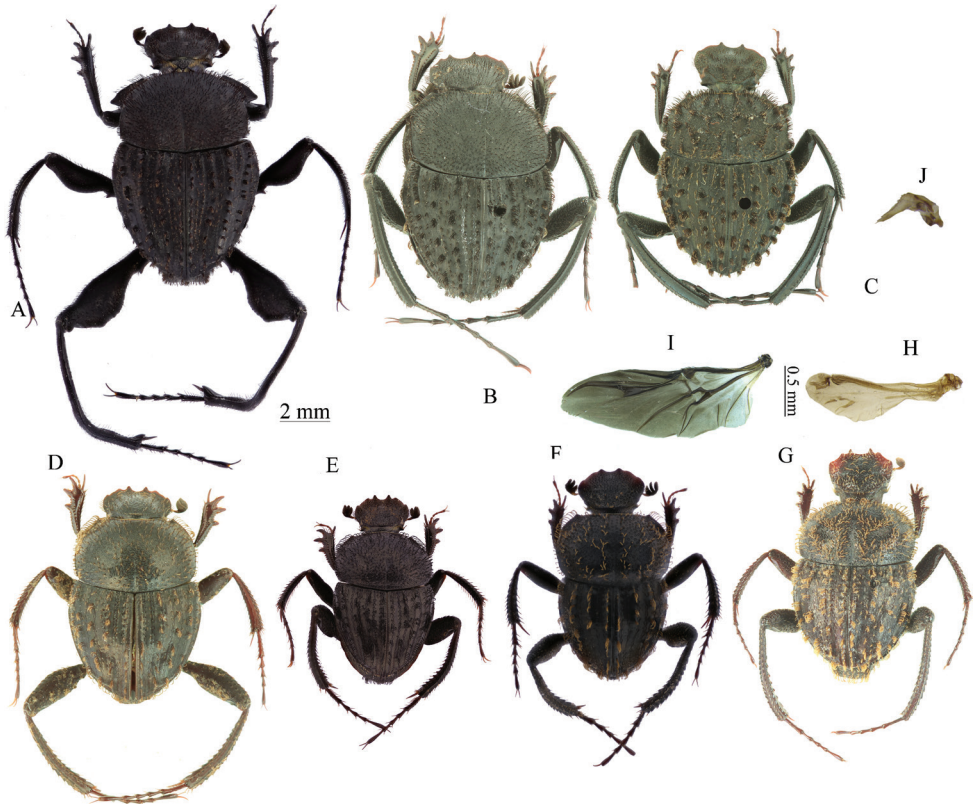


Fig. 2. Images of the habitus of the *muricatus* species-group: **A.** *S. muricatus*; **B.** *S. neobornemisszanus*; **C.** *S. fasciculatus*; **D.** *S. perissinottoi*; **E.** *S. manni*; **F.** *S. swazi* sp. n. **G.** *S. alveatus*. **I.** Fully developed hind wing, which is typical to most of *Sisyphus* species in southern Africa **H.** Brachypterous hind wing of *S. alveatus*. **J.** Sclerite represents a reduced hind wing of *S. swazi* sp. n.

***Sisyphus neobornemisszanus* Daniel & Davis, 2016** (Fig. 2, 3B).

Daniel et. al. 2016: 67, 71, 73

Type locality: Zululand, St. Lucia (South Africa).

Size: Male: length: 9.7–7.6 mm, width: 5.6–4.6 mm. Female: length: 10.0–8.0 mm, width 5.62–4.4 mm.

Diagnosis: *S. neobornemisszanus* resembles *S. muricatus*. However, it may be distinguished by the following combination of features: inconspicuous punctation on the pronotum; interstriae 1, 3, 5, and 7 with rows of black setae arranged in tufts; interstriae 2, 4, and 6 with sparsely arranged single setae.

Examined type material

(♂ TMSA) Holotype: SOUTH AFRICA, Zululand, St. Lucia 28°13'12"S 32°15'00"E, 7.xii.1975, leg: Endrödy-Younga. Paratypes: (1♀ TMSA) SOUTH AFRICA, Zululand, Mission Rock, 28°15'36"S 32°17'24"E, 7.xii.1975, legs: Endrödy-Younga. (2♂ TMSA) SOUTH AFRICA, Zululand, St. Lucia 28°13'12"S 32°15'00"E, 28.viii.1971.

leg. GF. Bornemissza. (2♂ TMSA) SOUTH AFRICA, Zululand, St. Lucia, Estuary. 28.viii.1971, leg: GF. Bornemissza. (15♂, 13♀ TMSA) SOUTH AFRICA, Zululand, Sodwana Bay, 5 km, 27°21'0"S 32°23'24"E, 2.xi.1992, leg. Endrödy-Younga. (1♀ UPSA) SOUTH AFRICA, KZN. Richard's Bay, 28°37'39"S 32°17'24"E, 27.i.2000, leg: Davis & Delpont. (2♀, 6♂ UPSA) SOUTH AFRICA, KZN, Richard's Bay, 28°43'28"S 32°10'52"E, 27.i.2000, leg: Davis & Delpont. (5♀, 2♂ UPSA) SOUTH AFRICA, KZN. Sileza Nature Reserve 27°06'S 32°36'E, 03.iv.1996, leg: Van Rensburg. (1♀ UPSA) SOUTH AFRICA, KZN, Sodwana, 27°32'S 32°41'E, 07.iv.1989, leg: Mansfield. (2♀, 5♂ UPSA) MOZAMBIQUE, Maputo, Elephant Maputo Reserve, 26°22'30"S 33°47'50"E, 14–16.i.2003, leg: Scholtz & Holter. (2♀ UPSA) MOZAMBIQUE, Maputo, Elephant Maputo Reserve, 26°39'S 32°43'E, 10–16.xi.2007, pitfall trap, leg: Strümpher & Deschodt. (2♂ TMSA) MOZAMBIQUE, Inhambane, Inharrime, 24°28'37"S 35°01'49"E, 1974, leg: Moor.

Examined non-type material: See Supplementary information.

Distribution: *S. neobornemisszanus* is an endemic, east coastal, dune forest species (Davis et al. 2002b). It has been recorded in the Maputaland Coastal Forest Mosaic (Olson et al. 2001) from KwaZulu Natal to southern Mozambique (Endrödi, 1983, Davis et al. 2002; Daniel et al. 2016) (Fig. 4).

***Sisypus fasciculatus* Boheman 1857** (Figs. 2, 3C)

Boheman 1857: 192; Harold 1869: 984; Péringuey 1902: 101–106, Arrow 1927: 465; Haaf 1955: 376; Ferreira 1972: 799; Davis et al, 2008: 154; Montreuil 2015c: 3, 11.

Type locality: Caffraria

Size: Male: length: 9.4–7 mm, width: 5.7–3.5 mm. Female: length: 9.0–7.0 mm, width 5.6–3.5 mm.



Fig. 3. Images of the aedeagi of the *muricatus* species-group: **A.** *S. muricatus*; **B.** *S. neobornemisszanus*; **C.** *S. fasciculatus*; **D.** *S. perissinottoi*; **E.** *S. manni*; **F.** *S. swazi* **sp. n.**; **G.** *S. alveatus*.

Diagnosis: *S. fasciculatus* is similar to *S. muricatus* and *S. neobornemisszanus*, but differs from these two species by bearing tufts of dense setae on the pronotum, which alternate with bare patches of short setae.

Examined type material

Holotype (photograph): (♀ NHRS): /Caffraria/, /J. Wahlb/, /type/, brown label, handwritten /*fasciculatus* Bohem/; red label /Typus: *Sisyphus fasciculatus*, det. Dr. E. Haaf, 1954/, /311:72/, /247:73/; /9415 E92 +/, brown label, handwritten /*fasciculatus* Boh/, /NHRS-SRAH 000000228/.

Examined non-type material: See Supplementary information.

Distribution: *S. fasciculatus* occurs in South Africa and Swaziland where it is a shade specialist (Davis et al. 1999). It is associated with riverine and lower hillside forest to dense partially shaded woodland thickets, particularly, on the eastern escarpment of Limpopo, Mpumalanga, west KwaZulu Natal and Swaziland. However, it also occurs in the warmer inland parts of the Maputaland Coastal Forest Mosaic ecoregion of Olson et al. (2001) southwards to the northernmost extent of the KwaZulu-Pondoland Coastal Forest Mosaic (Fig. 4).

Conservation status: Although currently assessed as Least Concern (LC), *S. fasciculatus* is a potentially threatened species, due to the loss of forest and shaded woodland

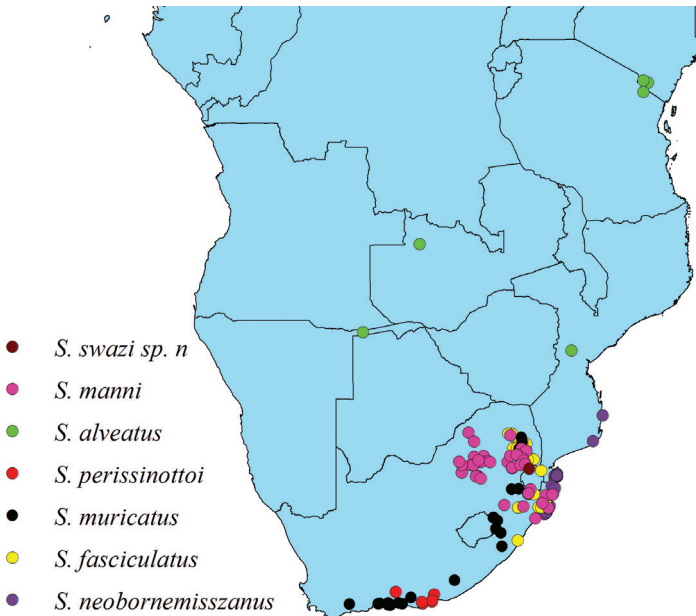


Fig. 4. Distribution map for the *muricatus* species-groups.

across its fairly restricted range (Davis 2013a). However, the species has been recorded in reserves where shaded vegetation is protected, such as in Hluhluwe, Umfolozi and Ithala Game Reserves (KwaZulu Natal) as well as Mlawula Nature Reserve (Swaziland). Because of this protection, it can be locally abundant in both coastal reserves and along the lower part of the northern escarpment of the Drakensberg.

***Sisyphus perissinottoi* Montreuil, 2015** (Fig. 2, 3D).

Montreuil 2015:10

Type locality: Amsterdamhoek (South Africa, Eastern Cape)

Size: Male: length: 7.0–5.0 mm; width: 3.0–2.5 mm. Female: length: 7.3–5.0 mm, width 3.0–2.5 mm.

Diagnosis: *S. perissinottoi* resembles *S. manni*. Setae on the pronotal discs of both species arise from the centre of ocellate punctures (Fig. 5H). However, *S. perissinottoi* differs by bearing tufts of dense and compact setae on the elytra and, lacking depressions on the latero-posterior edge of the pronotal disc. *S. perissinottoi* is also larger than *S. manni*.

Examined type material

Holotype: (MHNH, through photograph without locality data).

Examined non-type material: See Supplementary information.

Distribution: *S. perissinottoi* is only known from the Eastern Cape (South Africa) (Montreuil 2015c). It has been recorded from unshaded vegetation. (Fig. 4).

***Sisyphus manni* Montreuil, 2015** (Fig. 2E).

Montreuil 2015c: 2–3

Type locality: Limpopo, Kruger National Park.

Size: Male: length: 5.5–4.0 mm; width: 2.5–2.0 mm. Female: length: 5.5–4.0 mm, width 2.5–2.0 mm.

Diagnosis: In *S. manni*, proximal elytral setae are primarily distributed uniformly becoming arranged in sparse tufts mid-basally and posteriorly, unlike in *S. perissinottoi* where dense tufts of setae occur across the entire elytra. *S. manni* bears three depressions on the pronotal disc, which are lacking in *S. perissinottoi*.

Examined type material

Holotype: (MHNH, through photograph without locality data).

Examined non-type material: See Supplementary information.

Distribution: *S. manni* is only known from South Africa. The species is associated with upland to highland grassland and open woodland in Gauteng (cited as *S. alveatus* by Davis et al. 2005), KwaZulu Natal, Mpumalanga and Northwest Provinces. It has also been collected in unshaded riverine vegetation in Limpopo (Fig. 4).

***Sisyphus swazi* Daniel & Davis sp. n.** (Fig. 2F)

ZooBank: <http://zoobank.org/C42533D7-5760-4187-8415-45608ED98DD0>

Diagnosis: *Sisyphus swazi* sp. n is similar to *S. alveatus* in that both bear tufts of setae on the elytra. However, it differs by having a concave anterior margin between the medial clypeal teeth whereas in *S. alveatus* the margin is straight. In *S. swazi* sp. n the anterior margin of the pronotum is wider than the posterior margin, unlike in *S. alveatus* where the width is almost uniform. Pronotal setae arise from the centre of ocellate punctures in the new species, while in *S. alveatus* they are inserted between ocellate points. The interior edges of the metatibiae are weakly serrated in *S. swazi* sp. n whereas in *S. alveatus* they bear strong dentition.

Examined type material

Holotype: (♂ SANC): SWAZILAND (Mbabane) Ekuvinjelweni, 26.09353°S 31.30082°E, baited pitfalls, leg: Cebisile N. Magagula.

Description: Male holotype: **Size.** 5.0 mm, width: 2.7 mm. **Colour.** body and setae brown; meso- and metasternum black. **Head.** Margin between clypeal medial teeth concave; dorsal surface of the clypeus setose and punctate; clypeo-frontal suture visible; vertex setigerous with ocellate points. **Pronotum.** Complete lateral prothoracic margin between the prothoracic disc and prothoracic episternum. Strong antero-lateral emargination; anterior edge wider than posterior margin. Setae arise from the centre of ocellate punctures on the pronotal disc. Setae not uniform, but randomly arranged in patches; forming distinct bald spots on pronotal disc. **Elytra.** Short; narrow posteriorly; elytral striae minutely punctate and crenulate; double line of striae non-continuous, interrupted by fine ocellate strial punctures. Interstitial setae arranged in tufts. Hind wing and venation reduced to small sclerites (Fig. 2J). **Pygidium.** U-shaped and setigerous with ocellate punctures. **Sternites.** Abdominal sternites finely crenulate, setigerous with ocellate punctation; setae arranged in rows laterally; meso-metasternal suture visible; punctate depression on the postero-medial surface of the metasternum. **Legs.** In ventral view, antero-lateral carina of profemur punctate, with a lateral row of fine and well developed setae; meso- and metafemur very small anteriorly, enlarged mid-posteriorly, densely punctate and setose; protibia with three teeth and a single terminal spine; mesotibia punctate and setose with two terminal spines; metatibia setose with weak indentation anteriorly, serrated laterally with two spurs; pro- meso- and metatarsi five segmented with two claws, setose laterally; first tarsal

segment of the meso- and meta-thoracic legs with a row of strong setae on the external edge. **Aedeagus.** Parameres symmetrical, somewhat truncated towards the apex. In ventral view, a knob-like structure present basally (Fig. 2F)

Female: unknown.

Distribution: The new species has only been recorded in shaded vegetation along the escarpment of the Lebombo Mountains in Swaziland (Fig. 4).

Remarks: By showing a concave edge between the medial teeth of the clypeus and setae on the pronotum arising from the centres of ocellate points, *Sisyphus swazi* **sp. n.** is superficially similar to two other southern African species of the *muricatus* species-group: namely, *S. manni* and *S. perissinottoi*. However, both species differ from *S. swazi* **sp. n.** by having uniformly arranged setae on the pronotum, which lacks bald patches. Furthermore, both species bear a pronotum of uniform width, in contrast to *S. swazi* **sp. n.** in which the latero-anterior margins of the pronotum are expanded.

Etymology: Patronym is a noun in apposition, which reflects the name of the country (Swaziland) in which the holotype specimen was collected.

***Sisyphus alveatus* Boucomont 1935** (Figs. 2, 3G).

Boucomont 1935: 280; Haaf 1955: 344; Ferreira 1972: 792; Schaefer & Fischer 2001: 49; Montreuil 2015c: 2.

Type locality: Kenya, Uasin Gishu,

Size: Male: length: 5.0–2.7 mm, width: 2.5–2.1 mm. Female: length: 5.1–2.7 mm, width: 2.5–2.0 mm.

Diagnosis: *S. alveatus* is similar to *S. perissinottoi* and *S. manni*. However, it is distinguished by the straight edge between the medial clypeal teeth, unlike in *S. perissinottoi* and *S. manni* where this feature is concave. *S. alveatus* also bears bare patches of setae on the pronotum, whereas in *S. perissinottoi* and *S. manni* the setae are uniformly distributed.

Examined type material

Holotype: (MHNH, through photograph without locality data).

Examined non-type material: See Supplementary information.

Distribution: In southern Africa, *S. alveatus* is known from forest at Popa Falls in Namibia and from open woodland in Central Mozambique (Fig. 4). It has also been recorded from miombo woodland and moist highland forest in East Africa

(Montreuil 2015c). It is unlikely to occur in South Africa where records for *S. alveatus* (Paschalidis 1974, Montreuil 2015c) probably relate to other species, presumably, *S. manni*.

goryi species-group (Figs. 5, 6A–E).

Sisyphus bicuariensis Daniel & Davis sp. n. (Fig. 3A).

ZooBank: <http://zoobank.org/E02CDE50-8BB1-45D9-87A9-610A7C3713A0>

Diagnosis: *S. bicuariensis* sp. n. resembles *S. trichodichromaticus* Montreuil, 2015. Both bear bicoloured setae. However, *S. trichodichromaticus* bears a shallow notch separating the medial teeth from the blunt lateral teeth; the clypeo-genal suture shows an obtusely angled cleft; and the genae are simple and arcuate. This differs to *S. bicuariensis* sp. n., where a markedly deep notch separates the medial teeth from the sharp lateral teeth; the clypeo-genal suture shows a rectangular cleft; and the genae are long and virtually parallel. Additionally, the shapes of the parameres are different in both species.

Description: Male holotype: **Size.** Length: 4.2 mm; width: 2.2 mm. **Colour.** Black body with grey and black setae (Fig. 5G); clypeus shiny brown antero-laterally; meso- and metasternum black with brown and white setae; antennal club brown. **Head.** Clypeus upcurved antero-laterally; margin between medial teeth straight; a deep notch between medial and lateral teeth. Clypeo-genal suture with a rectangular cleft; genae long and virtually straight. Frons and vertex with dorsal ocellate punctation and setation. Frons declivous dorso-medially; epicranial suture visible; vertex with a few granules antero-medially. **Pronotum.** Convex with maximum width longer than maximum length; disc bearing three depressions and ocellate punctation; setae black and grey medially on the central disc, grey laterally; setae on pro-episternum grey, well-developed antero-laterally. A complete lateral prothoracic ridge between the pronotal disc and pro-episternum. **Elytra.** Narrow posteriorly bearing thicker black setae alternating with thin and thick grey setae either in equal proportion (1:1) or with less grey setae; weakly developed tufts of setae protrude from the epipleurae below the edge of the elytra (<5) (Fig. 5H); elytral surface crenulate with distinct double crenulate line, which is interrupted by fine, ocellate strial punctures; elytral striae with minute punctation; granulation and depressions basally on elytral striae 1–4. **Hind wing.** Wing and venation fully developed. **Pygidium.** Bearing scattered setae and ocellate punctation; narrow basally. **Sternites.** Margin between abdominal sternites finely crenulate; setation well-developed laterally, less so medially; punctation dense laterally and sparse medially; meso-metasternal suture visible; meso- and metasternum densely punctate with matted setae antero-laterally; metasternum with a punctate depression postero-medially. Mesepimerum and metepisternum finely punctate and setose. **Legs.** In ventral view, profemur punctate and pubescent, carinate antero-laterally with a lateral row of fine and well-developed setae; in lateral

view, meso- and metafemur with granulation, also densely punctate and setose; meso- and metatrochanter contiguous with femur, metatrochanter larger and slightly projected backwards; metacoxa punctate and shagreened ventro-anteriorly; protibia with three teeth and a single terminal spine; mesotibia punctate and setose with two terminal spines; metatibia densely setose, serrated laterally with two spurs; pro-, meso- and metatarsus five-segmented, with two claws, setose laterally; first tarsal segment of meso- and metathoracic legs with a row of dense setae on the external margin. **Aedeagus.** Phallobase slightly curved. Median lobe clearly visible. Parameres (Fig. 6A).

Morphological variation

Size: Male: length: 5.0–4.0 mm; width: 2.6–2.0 mm; Female: length: 4.9–4.1 mm, width 2.7–2.0 mm.

Male. Meta- and mesotibia curved; with a carina on the dorso-posterior edge of the meta- and mesofemur; last abdominal sternite narrowed medially (Fig. 1A). **Female.** Meta- and mesotibia almost straight; lacking a carina on the dorso-posterior margin of the meta- and mesofemur; last visible abdominal sternite two times wider than in males (Fig. 1B).

Examined type material

Holotype: (♂ SANC) ANGOLA, Bicuari NP (15.375173°S 14.752320°E) (2 km N Camp); 18.xii.1974; leg: Davis & Temby/1671/, /Ex coll. CSIRO, Div. Entomology, South Africa Station/. Paratypes: (20♂, 16♀ SANC) with the same data as the holotype. (10♂, 6♀ SANC) ANGOLA, Caconda (37 & 30 km SW); 21.xii.1974; leg: Davis & Temby; /1678/, /Ex coll. CSIRO, Div. Entomology, South Africa Station/. (2♂, 3♀ SANC) ANGOLA, Sá da Bandeira (11 & 3 km W), 29.xii.1974; leg: Davis & Temby/1691/, /Ex coll. CSIRO, Div. Entomology, South Africa Station/. (2♂, 2♀ SANC) ANGOLA, Paiva Coucero (50 & 45 km E); 18.xii.1974; leg: Davis & Temby, /1671/, /Ex coll. CSIRO, Div. Entomology, South Africa Station/. (1♂, 1♀ SANC) ANGOLA, Huila; 22.xii.1974, leg: Davis & Temby/1683/, /Ex coll. CSIRO, Div. Entomology, South Africa Station/.

Additional examined type and non-type material: *S. trichodichromaticus* (Holotype: MHNH, through photograph without locality data); (3♂, 4♀ TMSA) ZAMBIA, Li-uwa Plains; 14.643259°S 22.626423°E, 29–30.xi.2003, 1050 m, leg: Deschodt & Groenewald. (2♂, 4♀ SANC) ZAMBIA, idem; (2♂, 2♀ UPSA) ZAMBIA, with the same data.

Etymology: Patronym is a noun in apposition, which reflects the name of the area in which the majority of type specimens were collected: Bicuari National Park, South Angola.

Distribution: The new species may be associated with unshaded vegetation and open woodland in southern Angola (Fig. 7).

***Sisypbus caffer* Boheman, 1857** (Figs. 5, 6B).

Boheman 1857: 195–6; Harold 1869: 984; Péringuey 1902: 106–7; Haaf 1955: 362–4; Ferreira 1972: 82, Schäfer & Fischer 1992:121; Schäfer & Fischer 2001:53

Size: Male: length: 7.8–6.9 mm, width: 4.4–3.5 mm. Female: length: 7.6–7.1 mm, width: 4.5–3.0 mm.

Type locality: Caffraria (South Africa).

Diagnosis: *S. caffer* is close in appearance to *S. sordidus* Boheman, 1857. However, they can be separated morphologically by the following features: *S. caffer* bears much finer elytral setae, which are distributed in single rows; *S. sordidus* bears thicker elytral setae, which are distributed in non-single rows forming bunches. In *S. caffer*, pronotal setae are inserted between ocellate punctures (Fig. 5F), whereas in *S. sordidus*, the setae originate from the centre of ocellate punctures (Fig. 5H). Furthermore, *S. sordidus* occurs in unshaded lowland vegetation associated with warm temperatures whereas *S. caffer* is associated with highland grassland under cooler conditions.

Examined type material

Holotype (photograph): (1♂ NHRS): /type/; /Caffraria/; /leg: J.Wahlb/; /309; 72/; /244; 73/; /*S. caffer* Bohm/; red label: /typus/; white label (handwritten): /TYPE *Sisypbus caffer* BOHEMAN, det. J. Ferrer/; /Naturhistoriska, Riksmuseet Stockholm; loan 37/90/; /9385 E92+/; /NHRS-SRAH 000000221/.

Examined non-type material: See Supplementary information.

Distribution: *S. caffer* occurs in South Africa, Namibia, Lesotho and Botswana. The species has been recorded in upland and highland grasslands under cooler conditions (Davis et. al. 2005) in both South Africa and Lesotho (29.7°S 27.4°E). In South Africa, the localities extend northwards from the Eastern Cape and eastern Free State to the latitude of Pretoria (28.19°E 25.80°S) and also along the eastern escarpment of KwaZulu Natal and Mpumalanga. The lowlands beyond the northern Gauteng Mountains of the Witwatersrand (24.54°S 27.08°E) may act as barriers, although the species is also found in isolated uplands further to the northwest, such as the Blouberg. *S. caffer* has also been recorded in unshaded vegetation at the margins of its range in Kneneng (Botswana) (23.78°S 25.27°E) and in a dry upland outlier in the north of Namibia (Kaoko Otavi) (Fig. 7). Kaoko Otavi represents a disjunction in the distribution of *S. caffer* from its main range on the Highveld of South Africa. It is noteworthy that *N. macrorubrus* and *Proagoderus lanista* (Castelnau, 1840) also show similar disjunct occurrences on the South African Highveld and as rarities in north Namibia (Davis 1997).

Remarks: We cannot confirm or refute the validity of *S. crispatus* because the type specimen has been lost. Furthermore, the original description and image presented by Gory (1833) are imprecise and insufficient to determine the identity of the species. *S. crispatus* was described from the same imprecise type locality (Caffraria) as two other species (*S. caffer* and *S. sordidus*). Under these circumstances, we are not confident to state which of the two species might be a junior synonym of *S. crispatus*. According to the ICZN, article 75.5 “when an author considers that the taxonomic identity of a nominal species-group taxon cannot be determined from its existing name-bearing type, its name is a *nomen dubium*”. Therefore, we propose *S. crispatus* as a *nomen dubium*.

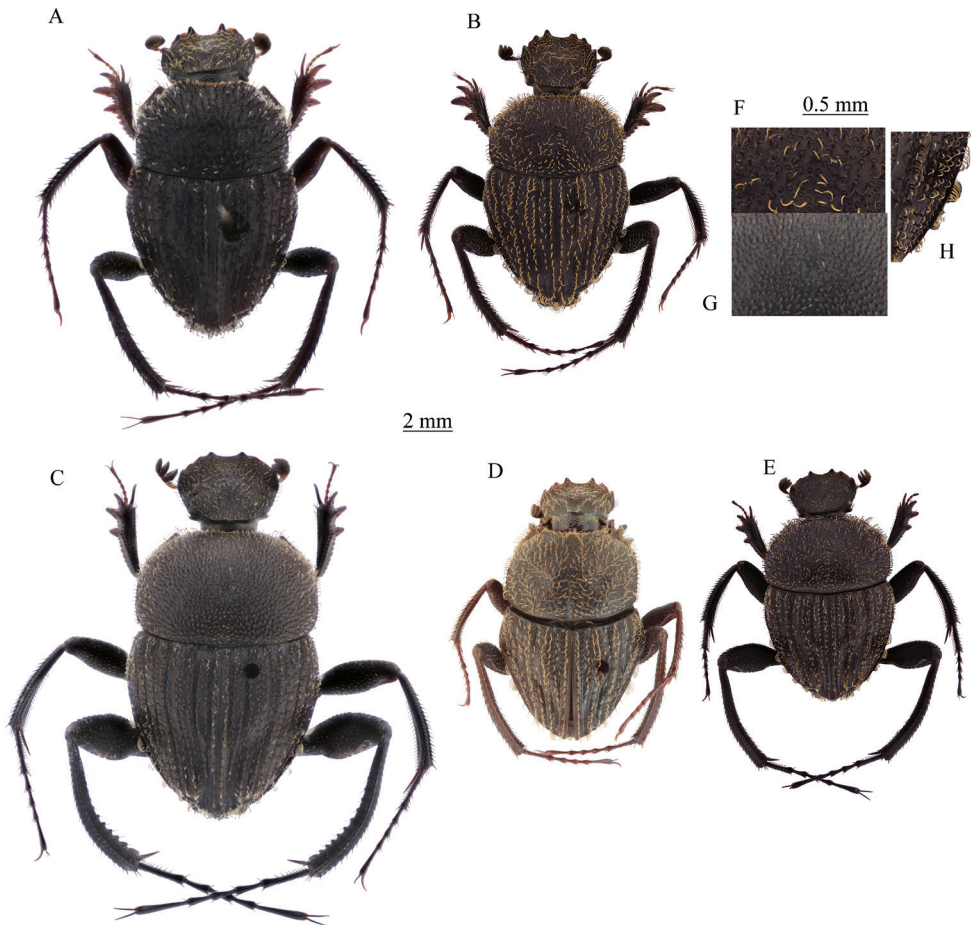


Fig. 5. Images of the habitus of the *goryi* species-group: **A.** *S. bicuariensis* sp. n; with emphasis of the black and gray setae on pronotum and elytra; **B.** *S. caffer*; **C.** *S. genierorum*; **D.** *S. goryi*; **E.** *S. sordidus*. **F.** Pronotal setae originate from the posterior edge or between ocellate points. **G.** Pronotal setae arise from the centre of ocellate punctures, commonly seen in *S. genierorum*, *S. sordidus*; *S. perissinottoi*; *S. manni* and *S. swazi* sp. n. **H.** Tufts of setae on the epipleurae visible from above.

***Sisyphus genierorum* Montreuil, 2015** (Figs. 5, 6C).

Montreuil 2015a: 91, 93, 99–100

Type locality: Quirimbas National Park, Mareja (Cabo Delgado, Moçambique)

Size: Male: length: 10–8.0 mm, width: 5.5–5 mm. Female: length: 9.5–8.5 mm, width: 5.0–4.7 mm.

Diagnosis: *S. genierorum* resembles *S. sordidus*. In both species, tufts of epipleural setae are visible from above at the outer margin of the elytra (Fig. 5H); also, pronotal setae arise from the centre of ocellate punctures. However, *S. genierorum* differs by the much finer and uniformly arranged setae on the elytral interstriae. It is also much larger than *S. sordidus*.

Examined type material

Paratypes: (2♀ CMN) MOZAMBIQUE: /Cabo Delgado, Taratibu (site 3), P.N. Quirimbas, 340 m; 12°48'02"S 39°41'49"E, 8.i.2013, eastern Miombo woodlands, dung trap 24 h. F & S. Génier.2013-47/; /World Scarab database WSD00024494/, *Sisyphus genierorum* n. sp.; O. Montreuil dét. 2014. (1♀, 3♂ CMN) MOZAMBIQUE: /Cabo Delgado, Mareja (site 2), P.N. Quirimbas, 200 m; 12°51'41"S 40°09'31"E, 24.xii.2012, eastern Miombo woodlands, dung trap (shaded), leg: F & S. Génier. 2012-08/; /World Scarab database WSD00024355/, /*Sisyphus genierorum* n. sp.; O. Montreuil dét. 2014/.

Distribution: *S. genierorum* is currently only known from Quirimbas National Park (Cabo Delgado, Mozambique) (Fig. 7), where it is associated with the Eastern Miombo Woodlands ecoregion of Olson et al. (2001).



Fig. 6. Images of the aedagi of the *goryi* species-group: **A.** *S. bicuariensis* sp. n.; **B.** *S. caffer*; **C.** *S. genierorum*; **D.** *S. goryi*; **E.** *S. sordidus*.

***Sisyphus goryi* Harold 1859** (Figs. 5, 6D).

Harold 1859:224; Harold 1869:984; Péringuey 1902:106–7; Kolbe 1914: 317; Arrow 1927:460; Haaf 1955:362–3; Ferreira 1972:797; Schäfer & Fischer 2001:53–4; Schäfer & Fischer 1992:121–2.

Sisyphus hirtus Wiedeman, 1823

Wiedeman 1823:21; Gory 1833:14; Harold 1869:984; Arrow 1909:518–9; 1927:460; Haaf 1995:362–3; Schäfer & Fischer 2001:53–4; Schäfer & Fischer 1992:121–2.

S. pygmaeus Dejean, 1837

Dejean 1837: 151; Klug, 1862:219; Harold 1869:984; Haaf 1955:362–3.

Type locality: Senegal

Size: Male: length: 7–4.0 mm, width: 3.4–2.2 mm. Female: Length: 7.0–3.9 mm, width: 3.1–2.4 mm.

Diagnosis: *S. goryi* is similar to *Sisyphus bicuariensis* **sp. n.** However, it differs by the uniform brown colour of the setae compared to the bicoloured setae in *S. bicuariensis* **sp. n.** The male genitalia of both species differ (Figs. 6A, D). Furthermore, it should be noted that larger *S. goryi* specimens resemble those of *S. caffer*. However, *S. goryi* bears well-developed tufts of setae, which emanate from below the abdominal epipleurae (Fig. 5H) (>10 single setae), which differ to those in *S. caffer* where the tufts consist of few single setae (<10).

Examined non-type material: See Supplementary information.

Morphological variation

Head. Antennal club varies in colour between brown or black. **Clypeus.** In some specimens, especially old ones, the lateral edge of the clypeus is worn completely smooth; the third indentation is absent; and the medial surface bears a metallic sheen. **Sternites.** Some populations are completely hairless on the latero-posterior edge of the mesosternum. **Pygidium.** Setae are evenly distributed in some individuals whereas in others they are arranged in a trident pattern.

Populations from highlands and areas of shaded vegetation, such as Inyanga (Zimbabwe), Manyara (Tanzania) and Meru (Kenya) are distinctly larger in size and may, in some cases, resemble *S. caffer*.

Distribution: *S. goryi* is widespread in the Afrotropical region and is associated with a great range of habitats from shaded to open vegetation. Moreover, it has been recorded at a range of different altitudes (Fig. 7). The geographical distribution and morphological variation suggest a species complex. However, as we could not access the type material of *S. goryi*, the putative species complex currently remains undetermined pending further study.

Remarks: The original name of *Sisyphus hirtus* Gory, 1833, is preoccupied by *Sisyphus hirtus* Wiedmann, 1825 (Indian species). Gory's junior homonym was, therefore, renamed as *Sisyphus goryi* Harold, 1859. Subsequently, Péringuey (1901) synonymized

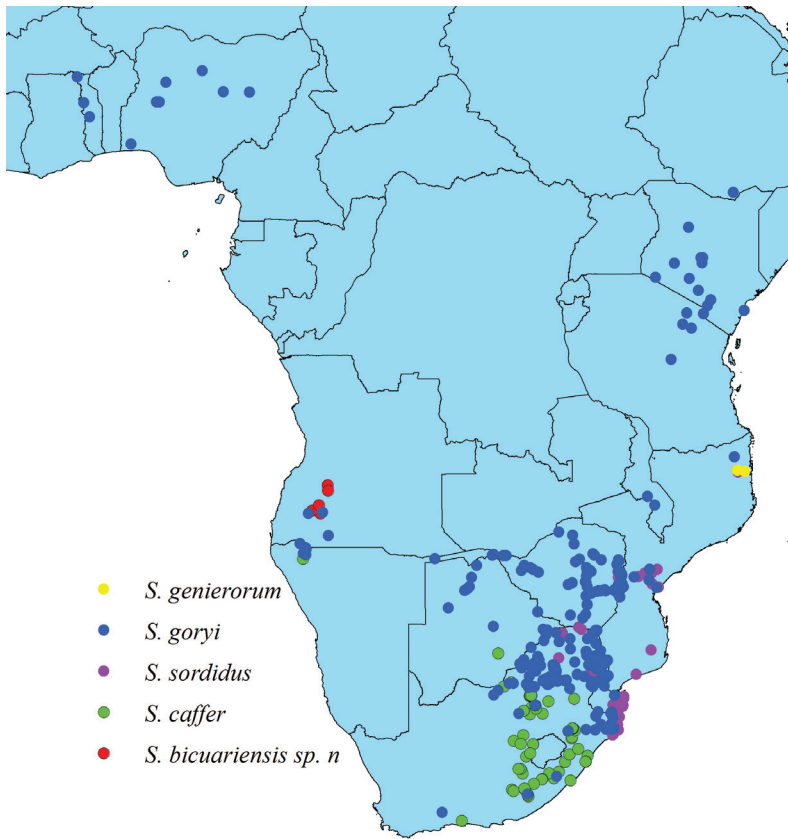


Fig. 7. Distribution map for the *goryi* species-group.

S. caffer Boheman, 1857, and *S. sordidus* Boheman, 1857, with *S. goryi*, whereas, Haaf (1955) and Ferreira (1972) synonymized *S. goryi* with *S. crispatus* Gory, 1833. Based on morphological and biogeographical evidence we have, here, revalidated *S. caffer*, *S. sordidus* and *S. goryi* following the unpublished revision of Paschalidis (1974).

***Sisyphus sordidus* Boheman, 1857** (Figs. 5, 6E).

Boheman 1857: 194; Harold 1869:985; Péringuey 1902: 106–7, Arrow 1927: 465; Haaf 1955: 362–4; Schaefer-Fischer 2001: 54; Schaefer-Fischer, 1992: 123

Sisyphus natalensis Balthazar, 1968 (**syn. n**)

Balthazar 1968: 954

Sisyphus bornemisszanus Endrödi, 1983 (pars) (**syn. n**)

Endrödi 1983:207–210; Daniel et al 2016: 67

Type locality: Caffraria (South Africa).

Size: Male: length: 6.6–4.7 mm, width: 4.3–2.7 mm; Female: length: 6.4–4.0 mm, width: 3.0–2.5 mm.

Diagnosis: *S. sordidus* is similar to *S. caffer* and *S. genierorum*. However, *S. sordidus* is distinguished from the other two species by the thicker setae on the elytra, which are

distributed in non-single rows and form bunches. Although *S. sordidus* is smaller than *S. genierorum*, in both species, the pronotal setae originate from the centre of ocellate punctures, whilst in *S. caffer*, the pronotal setae are inserted between or on the posterior edges of ocellate points.

Examined type material

***Sisyphus sordidus* Boheman, 1857:** Holotype (photograph): (♂ NHRS): /Pt. Nat/, /leg: Tarnier/, /310: 72/, /246: 73/, brown label (handwritten): *sordidus* Bohm/, /19401: E92 +/, /white label (handwritten) /TYPE: *Sisyphus sordidus* Boh, det. J. Ferrer/ NHRS-SRAH 000000218//. Paratypes: (♀ NHRS): /type/, /Caffraria/, /leg: J. Wahlb/, /309: 72/, /245: 73/, red label: /typus/, white label (handwritten): /*Sisyphus sordidus* Boh, det. KM. Paschalidis, 1975/, /Naturhistoriska, Riksmuseet Stockholm; loan 38/90/, /9386 E92+/, /NHRS-SRAH 000000219/.

***Sisyphus natalensis* Balthazar, 1968:** Holotype (♂ HNHM): Natal, Sta. Lucia, Patium, 19–25.ii.1960, leg: Heiia, brown label (handwritten) /*Sisyphus* (*s. str*) *natalensis* n. sp. Balth, Holotypus/, red label (handwritten): /Holotypus, 1966, *Sisyphus natalensis* Balth/, white label (handwritten): /*Sisyphus sordidus* Boh, det. KM Paschalidis 1975/; (♀ HNHM): Paratype, with the same data.

***Sisyphus bornemisszanus* Endrödi, 1983:** Holotype (1♂ TMSA): SOUTH AFRICA, Zululand, St. Lucia 28.22°S 32.25°E, /7.xii.1975, E-Y: 957, groundtraps, 11 days, leg: Endrödy-Younga/, /Holotypus: label with white background and red on border (handwritten): *Sisyphus bornemisszanus* Endrodi/. Paratypes: (1♂, 2♀ TMSA) SOUTH AFRICA, /Zululand, Mfabeni dunes, 28.08°S 32.2°E/, /16. xii.1975, E-Y: 981, groundtraps, 3 days, leg: Endrödy-Younga/, /paratypus: label with white background and red on border (handwritten): *Sisyphus bornemisszanus* Endrodi/. (1♀ TMSA) SOUTH AFRICA, Zululand, St. Lucia 28.22°S 32.25°E, /7.xii.1975, E-Y: 957, groundtraps, 11 days, leg: Endrödy-Younga/. (1♀ TMSA) SOUTH AFRICA, Zululand, Mission Rock 28.16°S 32.29°E, /9.xii.1975; E-Y: 963, groundtraps, hippo dung, leg: Endrödy-Younga/, /Paratypus: label with white background and red on border (handwritten): *Sisyphus bornemisszanus* Endrodi/.

Examined non-type material: See Supplementary information.

Morphological variation

Clypeus. Between the medial teeth, the clypeal edge is mostly concave but, in some specimens, it is somewhat straight. There is a deep notch between the medial and lateral teeth although, in some cases, individuals bear a broad and shallow excavation. Specimens from Gauteng northwards, and inland in KwaZulu Natal, bear a distinct indentation on the lateral clypeal margin, whereas, individuals restricted to the Indian Ocean coastline bear a distinctly smooth clypeus. **Pronotum.** Three depressions are visible, particularly for those specimens from Nylsvley Nature Reserve northwards (24.04°S; 28.42°E). **Colour.** Coastal populations show black setae whereas inland populations show brown setae.

Distribution: *S. sordidus* has been recorded from South Africa, Mozambique and Zimbabwe. Along the coastline, *S. sordidus* has been recorded in grassland and open woodland on dunes from Maputaland (Davis et al. 2002b; Jacobs et al. 2010) up to Sofala Bay (25.11°S; 33.73°E) in Mozambique. Inland in South Africa, it has been recorded in Lowveld savanna vegetation (KwaZulu Natal and Limpopo). In Mozambique, the species has been collected in Gorongosa National Park and Quirimbas National Park under unshaded vegetation (GMD, *personal observation*) (Fig. 7).

Remarks: Peringuéy (1902) regarded *S. sordidus* as a junior synonym of *S. goryi*, whereas it was considered to be a junior synonym of *S. crispatus* by Gillet (1911), Haaf (1955) and Ferreira (1972). Based on the examined type material and the original description, we provide the above diagnosis, which suggests *S. sordidus* should be revalidated at species level. An additional study was conducted on the type material of *S. natalensis* and *S. bornemisszanus*. The holotypes match the diagnosis of *S. sordidus*. Therefore, *S. natalensis* and *S. bornemisszanus* are proposed as new synonyms of *S. sordidus*. It should be noted that synonymy of *S. bornemisszanus* is based solely on the holotype and some paratypes as the allotype and half of the paratypes comprise *S. neobornemisszanus* Daniel & Davis, 2016 (see Daniel et al. 2016).

***umbraphilus* species-group** (Figs. 8, 9A)

***Sisyphus umbraphilus* Daniel & Davis, 2016** (Figs. 8, 9A)

Daniel et al. 2016: 67–69

Size: Male: length: 5.1–7.1 mm, width: 2.9–4.2 mm; Female: length: 5.4–7.4 mm, width 3.2–4.2 mm.



Fig. 8. Images of the habitus of the *umbraphilus* species-group: A. *S. umbraphilus*.



Fig. 9. Images of the aedeagi of the *umbraphilus* species-group: **A.** *S. umbraphilus*.

Type locality: Umfolozi, KwaZulu Natal (South Africa)

Diagnosis: *S. umbraphilus* belongs to its own species-group. However, it is somewhat similar to *S. oralensis*. In this case, *S. umbraphilus* is distinguished by having tufts of epipleural setae. It bears relatively small ocellate punctures on the pronotum. Furthermore, in *S. umbraphilus*, the parameres are simple and attenuated towards the apex (Fig. 9A) whereas, in *S. oralensis* they are somewhat obtuse and truncated towards the apex (Fig. 14A).

Examined type material

Holotype: (♂ SANC): SOUTH AFRICA, KZN, Umfolozi 28°15'S 31°55'E, 1–7.x.1970, leg: Bornemissza & Aschenborn. Paratypes: (3♂, 9♀ SANC) with the same data as holotype. (1♂, 2♀ UPSA): SOUTH AFRICA, KZN, Ithala Game Reserve 27°27'53.6"S 31°15'36.1"E, 13.i.1999, leg: Chown, McGeogh & Davis. (2♂ SANC): SOUTH AFRICA, KZN, Jozini 27°26'0"S 32°4'0"E, 15.x.1978, leg: Bornemissza & Aschenborn. (7♂, 14♀ SANC): SOUTH AFRICA, Gauteng, Pretoria, 35 km NE of Pretoria Farm 25°42'0"S 28°13'0"E, 12–13.xii.1983, leg: Davis. (1♂ SANC): SOUTH AFRICA, KZN, Weke-Weke Stream, Shongweni Farm 29°48'S 30°43'E, 11.xi.2010, leg: AJ Armstrong & G Van Bassouw.

Examined non-type material: See Supplementary information.

Distribution: *S. umbraphilus* has been recorded in patches of dense woodland and thicket in KwaZulu Natal (Daniel et al. 2016) as well as in dense riverine woodland in North West Province (South Africa). In Gauteng, it has been collected from shaded vegetation on deep sands (Davis 1996) (Fig. 10).

costatus species-group (Figs. 11A–J, 12A–F).

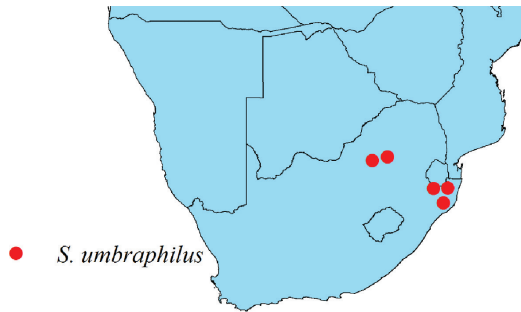


Fig. 10. Distribution maps for the *umbraphilus* species-groups.

***Sisyphus impressipennis* Lansberge, 1886** (Figs. 11, 12A).

Lansberge 1886: 73–74, Gillet 1911: 23; Arrow 1927: 462–5; Haaf 1955: 362; Schefer-Fischer 1992: 124, Schaefer-Fischer, 2001:58, Montreuil 2015a: 96.

Sisyphus transvaalensis Péringuey, 1908

Péringuey 1908: 557; Arrow 1927: 462 ; Haaf 1955: 364 ; Balthasar 1968: 954; Ferreira 1972 : 807; Montreuil 2015a: 96

Sisyphus callosipes Arrow, 1909

Arrow 1909: 517; Arrow 1927: 462; Haaf 1955: 365; Montreuil 2015a: 96.

Type locality: Humpata (Angola).

Size: Male: length: 10.0–7.1 mm; width: 5.6–4.0 mm; Female: length: 10.1–7.5 mm, width 5.1–4.0 mm.

Diagnosis: *S. impressipennis* is easily distinguished from other species in the *costatus* species-group by bearing an anvil-shaped projection on the mid-ventral edge of the metafemur, mainly in males.

Examined type material

***Sisyphus callosipes* Arrow, 1909:** Lectotype: (1♂ NHML), /MOZAMBIQUE, Nyassa/, /coll: Simons & Fry, 1905/, handwritten on brown label /*Sisyphus callopsis*, Arrow *typel*, /*Sisyphus callopsis* det. ME. Bacchus, 1975; Lectotype/. Paralectotype: (1♀ NHML) /Mozambique, Nyassa/, /coll: Simons & Fry, 1905/, handwritten on brown label, /*Sisyphus callopsis* det. ME. Bacchus, 1975; Paralectotype/. (1♂, 1♀ NHML), /RDC, 150–200 miles, W. of Kambove (3500–4500 ft)/, /coll: Neave, 18.10.1907/, /*Sisyphus callopsis* det. ME. Bacchus, 1975. ***Sisyphus transvaalensis* Péringuey, 1908:** Lectotype (designated here): (1♂ SAM): /SOUTH AFRICA, Transvaal, Pietersburg/, handwritten on brown label, /*Sisyphus transvaalensis* Péringuey/, /red label, /TYPE/ (Lectotype det. GM. Daniel 2016).

Examined non-type material: See Supplementary information.

Distribution: *S. impressipennis* was described from south-west Angola. It is distributed in east-central and southern Africa (Davis et al. 2005) where it is associated with shaded areas in savanna and dense miombo woodland. It has been recorded from

lowlands in northern South Africa, in upland Chirinda Forest (Zimbabwe), Mt Mulanje (Malawi), Central Mozambique, Manyara National Park (Tanzania) and Kambove (Republic Democratic of Congo) (Fig. 13C).

Remarks: Examination of *S. callosipes* and *S. transvaalensis* type material showed that the external morphology and genitalia are similar to *S. impressipennis*. Therefore, we regard both species as junior synonyms of *S. impressipennis*, as previously proposed by Paschalidis (1974) and Montreuil (2015a).

***Sisyphus costatus* (Thunberg, 1818)** (Figs. 11, 12B).

Peringuéy 1901:100; Gillet 1912:22; Arrow 1927:458; Haaf 1955:355–6; Ferreira 1972: 794–5; Harold 1869:984

Ateuchus costatus Thunberg, 1818

Thunberg 1818:412

Size: Male: length: 5.3–4.8 mm, width: 3.0–2.0 mm. Female: length: 5.3–4.2 mm, width: 2.6–2 mm.

Type locality: (Cape of Good Hope) South Africa

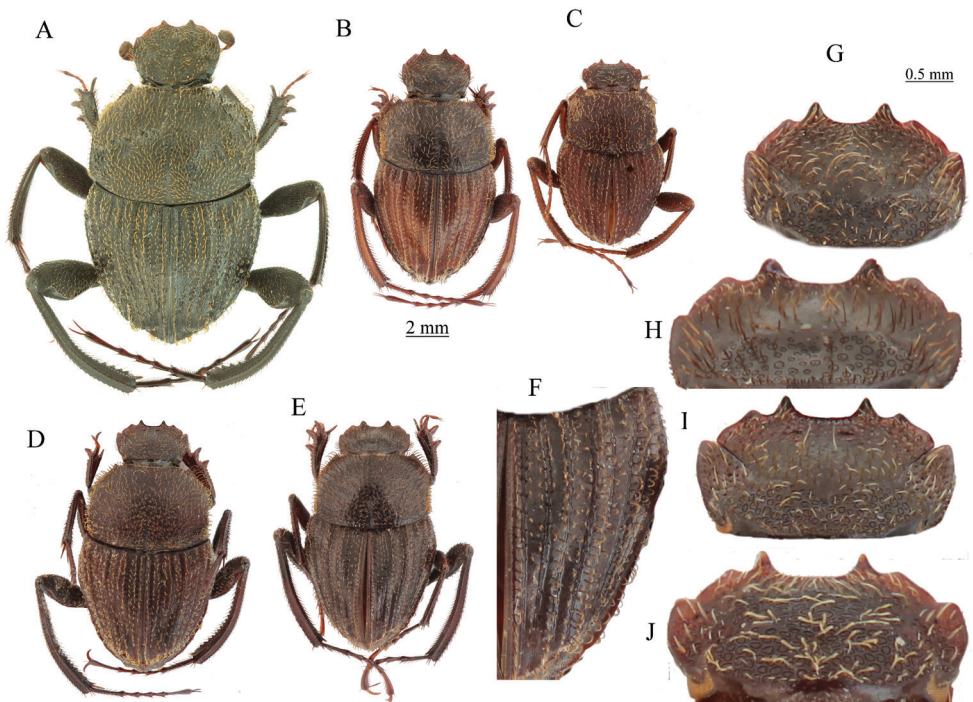


Fig. 11. Images of the habitus of the *costatus* species-group: A. *S. impressipennis*; B. *S. costatus*; C. *S. gazanus*; D. *S. inconspicuus* sp. n.; E. *S. australis* sp. n. F. elytra composed of alternate rows of well and less-developed setae, normally seen in *S. costatus* and *S. australis* sp. n. G. Head of *S. costatus* shows a concavity between the medial teeth on the anterior edge of the clypeus. H. Head of *S. australis* sp. n. shows a straight margin between the medial teeth on the anterior edge of the clypeus; there are defined carinae on the clypeo-frontal suture, and scattered punctation on the vertex. I. Frons of *S. inconspicuus* sp. n. without clear punctation. J. *S. gazanus*: bearing vertex and frons densely and fully punctate.

Diagnosis: *S. costatus* is close in appearance to *S. australis* **sp. n.** In both species, the elytral interstriae bear alternating rows of well-developed or less-developed setae (Fig. 11F). However, *S. costatus* is distinguished by an upcurved anterior clypeal edge and a concavity between the medial clypeal teeth. In addition, it lacks a carina between the clypeus and the frons (Fig. 11G).

Examined type material

(1♀ SMNH) Lectotype (designated here): Red label /Uppsala University Zoology Museum; Thunberg, saml.nr. 3206., *Ateuchus costatus*, Cap. minutus. F. TYP/ /Lectotype, det. GM Daniel, 2016/.

Examined non-type material: See Supplementary information.

Distribution: *S. costatus* has been recorded in moist upland savanna and highland grassland (Davis et al. 1999, Davis et al. 2005) from the Eastern Cape to the north of South Africa (Fig. 13).

Remarks: The species was described by Thunberg (1818) as *Ateuchus costatus*. Gillet (1912) transferred Thunberg's species to the genus *Sisyphus*.

***Sisyphus gazanus* Arrow, 1909** (Figs. 11, 12C).

Arrow 1909: 518; Gillet 1911: 23; Arrow 1927: 461; Haaf 1955: 361; Ferreira 1972: 799; Schäfer & Fischer 1992: 129.

Type locality: Chirinda, Mashonaland (Zimbabwe)

Size: Male: length: 5–4.5 mm; width: 3.1–2.5 mm; Female: length: 5–4.4 mm, width 3.1–2.4 mm.

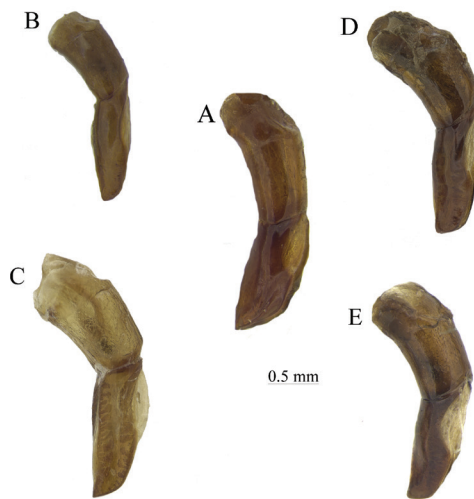


Fig. 12. Images of the aedeagi of the *costatus* species-group: A. *S. impressipennis*; B. *S. costatus*; C. *S. gazanus*; D. *S. inconspicuus* **sp. n.**; E. *S. australis* **sp. n.**

Diagnosis: *S. gazanus* is relatively close in appearance to *S. inconspicuus* **sp. n.** However, it is easily distinguished by a combination of features as follows: *S. gazanus* has a somewhat shallow depression dorsally on the genae; the dorsal surface of the head (vertex and frons) is entirely covered by distinct ocellate punctures (Fig. 11J); the pronotal disc shows a patchwork of bald areas and sparse short setae. In addition, the parameres of both species are distinctly different (Figs. 12C–D).

Examined type material

Lectotype: (♂ NHML): ZIMBABWE, Mashonaland, Chirinda, 05.x.1908. Leg: Marshall (handwritten *Sisyphus gazanus* Arrow 1909), lectotype det: Bacchus, 1976 / violet label/. Paralectotype: (♂ NHML): ZIMBABWE, Mashonaland, Mt. Chirinda, 01.xii.1908, leg: Marshall (handwritten *Sisyphus gazanus* Arrow 1909), lectotype det: Bacchus, 1976; /blue label/.

Examined non-type material: See Supplementary information.

Distribution: *Sisyphus gazanus* is associated with cooler conditions in highland forest in Zimbabwe and Malawi. It was described from Mount Chirinda (Zimbabwe) at the southern end of the Inyanga Highlands and Chimanimani Mountains. This range may have acted as a corridor into Malawi where the species has also been recorded from Mount Mulanje and Mount Gomoloti (Fig. 13). So far, it has not been recorded under cooler, shaded conditions on the intervening Muchinga Mountains (Manica, Mozambique) or Mount Binga (19.78°S 33.30°E).

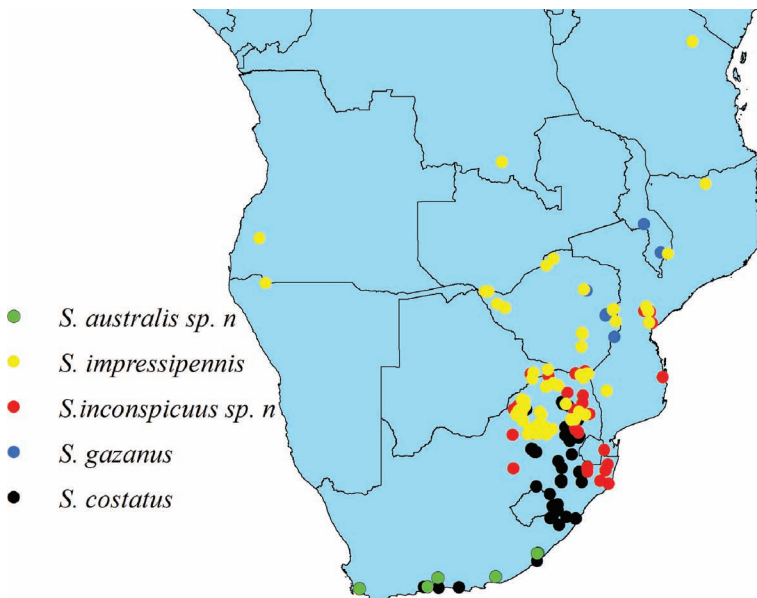


Fig. 13. Distribution map for the *costatus* species-group.

Sisyphus inconspicuus Daniel & Davis sp. n. (Figs. 11, 12D).

ZooBank: <http://zoobank.org/A8C95127-D39B-4DC7-A564-0F77CCA4AB14>

Diagnosis: *Sisyphus inconspicuus* sp. n. is similar to *S. costatus*; both bear inconspicuous ocellate punctation on the dorsal surface of the clypeus and frons, however, the vertex bears scattered ocellate punctures in *S. costatus* and dense ocellate points in the new species. *Sisyphus inconspicuus* sp. n. has a straight margin between the medial clypeal teeth and the anterior margins of the genae are arcuate. In *S. costatus*, the dorsal clypeal margin is distinctly concave and curved upwards between medial teeth whereas the genal margin is virtually straight (Figs. 11G, I). Additionally, the new species bears setae that are uniformly arranged on the elytra whereas, in *S. costatus*, the setae on the elytral interstriae alternate between rows that are dense or less dense.

Description: Male holotype: **Size.** Length: 7 mm; width: 3.9 mm. **Colour.** Body and setae brown; meso- and metasternum black; antennae brown. **Head.** Medial teeth on the clypeus separated by a straight margin; shallowly notched edge between medial and lateral teeth; genal margin arcuate anteriorly. Dorsal surface of the clypeus and frons inconspicuously punctate (Fig. 11I); epicranial suture clearly visible; vertex setigerous with dense ocellate punctation. **Pronotum.** Convex; maximum length equal to maximum width; dorsal surface finely setose with ocellate punctation; setae on the antero-lateral projection well-developed. Complete lateral prothoracic ridge between the prothoracic disc and prothoracic episternum. **Elytra.** Wider and ovoid proximally, narrow posteriorly; elytral striae minutely punctate and crenulate, characterized by a distinct crenulate double line, which is interrupted by fine, ocellate strial punctures. Granulation and notches basally on elytral striae 1–4; setae evenly distributed on the interstriae. Hind wings and venation fully developed. **Pygidium.** Setigerous with ocellate punctation arranged in a U-shape. **Sternites.** Abdominal sternites finely crenulate, setigerous with ocellate punctation; setae arranged in rows laterally; meso-metasternal suture visible, acute laterally; meso- and metasternum densely punctate and setose; a punctate depression present on the postero-medial surface of the metasternum. **Legs.** In ventral view, antero-lateral carina of profemur punctate, internally pubescent with a lateral row of fine and well developed setae; meso- and metafemur with granulation, densely punctate and setose; meso- and metatrochanter contiguous with femur, metatrochanter slightly projected backwards; metacoxa punctate and shagreened ventro-anteriorly; protibia with three teeth and single terminal spine; mesotibia punctate and setose with two terminal spines; metatibia densely setose, serrated laterally with two spurs; pro- meso- and metatarsi five segmented with two claws, setose laterally; first tarsal segment of the meso- and meta-thoracic legs with a row of strong setae on the external edge. **Aedeagus.** Parameres simple, symmetric; truncated basally (Fig. 12D).

Morphological variation

Size: Male: length: 8.2–6.0 mm; width: 3.8–4.1 mm; Female: 8.0–6.0 mm; width: 3.0–3.6 mm. **Head:** In some populations, mainly from the Eastern Cape (The Haven):

lateral side of the clypeus is completely smooth as far as the clypeo-genal suture in some specimens; the lateral margin of the genae tends to be less convex; the surface of the clypeus is less setigerous. **Colour:** Inland populations are black and brown whilst the majority of the coastal population is black although two specimens from Pomene (Mozambique) are brown. **Male:** Meta- and mesotibia curved (Fig. 1H); last abdominal sternite narrowed medially (Fig. 1A). **Female:** Meta- and mesotibia almost straight (Fig. 1G); last visible abdominal sternite not constricted medially (Fig. 1B).

Examined type material

Holotype: (♂ TMSA): SOUTH AFRICA, KZN, Ithala Game Reserve, Ngubu; Dense woodland 27°32'55"S 31°13'32"E. 13.i.1999, dung baited pitfall; leg: Chown, McGeogh & Davis. Paratypes: (6♂, 2♀ SANC): with the same data as the holotype. (12♂, 9♀ UPSA) SOUTH AFRICA, KZN, Ithala Game Reserve 27°31'S 31°14'E, 12–14.i.1999, dung baited pitfall, leg: Davis. (3♂, 3♀ TMSA) SOUTH AFRICA, E. Transvaal, Blyde River Canyon 24°35'S 30° 48'E, 28.xi.1991, dung baited pitfall, leg: Klimaszewski. (3♂, 3♀ TMSA) SOUTH AFRICA, Transvaal, 20 km NE Thabazimbi 24.32°S 27.24°E, 23–24.iii.1985, leg: Vans. (1♂, 1♀ TMSA) SOUTH AFRICA, N. Transvaal, Waterberg, Farm 223; 24.11°S 27.50°E, 28.xi.1991, leg: Strydom. (1♂, 1♀ TMSA) SOUTH AFRICA, E. Transvaal, Barberton 16 km N, 25.44°S 30.59°E, 28.xi.1991, dung baited pitfall, leg: Endrödy-Younga. (1♂ TMSA) SOUTH AFRICA, Transvaal, Nelspruit, Nat. Res. Dry valley, 25.29°S 30.55°E, 09.ii.1987, dung baited pitfall, groundtraps 53 days, leg: Endrödy-Younga. (1♂ TMSA; 1♂ SANC) SOUTH AFRICA, Transvaal, 20 km NE of Pretoria, Farm Roodeplaat, dung baited pitfall, 14–15.xi.1983, leg: Davis. (1♂, 1♀ TMSA) SOUTH AFRICA, E. Transvaal, Klaserie, 23.59°S 31.02°E. 3.v.1981, dung baited pitfall, leg: Endrödy-Younga. (2♂, 2♀ TMSA) SOUTH AFRICA, Transvaal, Nelspruit, 18 km 25.37°S 30.58°E. 24.ix.1986, dung baited pitfall, groundtraps 31 days, leg: Endrödy-Younga. (1♂, ♀ TMSA) SOUTH AFRICA, E. Transvaal, Nelspruit district, Farm de Hoop E, 24.ix.1986, dung baited pitfall, groundtraps, leg: Endrödy-Younga. (1♂, 1♀ TMSA) SOUTH AFRICA, E. Transvaal, Mariepskop, 24.35°S 30.50°E, 2.v.1986, dung baited pitfall, groundtraps 5 days, leg: Endrödy-Younga. (1♂ TMSA) SOUTH AFRICA, E. Transvaal, Nerina Nat. Res. 23.42°S 30.16°E, 2.v.1986, dung baited pitfall, groundtraps 50 days, leg: Breytenbach. (1♂ TMSA) SOUTH AFRICA, Transvaal, Langjan Nature Res, 22.52°S 29.14°E, 10–20.i.1980, leg: Prinsloo. (13♂, 17♀ TMSA) SOUTH AFRICA, Kruger National Park, Sukuza, 1 km NW, 24.59°S 31.37°E, 22.i.1995, dung baited pitfall, groundtraps, leg: Endrödy-Younga. (3♂, 5♀ TMSA) SOUTH AFRICA, Kruger National Park, Pafuri res. Camp, 22.25°S 31.12°E, 31.i.1994, dung baited pitfall, groundtraps 10 days, leg: Endrödy-Younga. (1♂, 2♀ SANC) SOUTH AFRICA, Kruger National Park, Sukuza, 1 km NW, 24.59°S 31.37°E. 22.i.1999, cattle dung, leg: Inward. (1♂, 2♀ TMSA) SOUTH AFRICA, Kruger National Park, Punda Maria, 22.38°S 30.59°E, 11.ii.1994, elephant dung, leg: Endrödy-Younga. (1♂ UPSA) SOUTH AFRICA, Kruger National Park, Sukuza, 24.00°S, 31.00°E, xii.1977, cattle dung, leg: Scholtz. (10♂, 13♀ TMSA) SOUTH AFRICA, N. Transvaal, Mma-bolela Estates, 22.40°S 28.15°E, 10.iii.1973, groundtraps, leg: Endrödy-Younga. (1♂

TMSA) SOUTH AFRICA, Zululand, Sodwana Bay 10 km NW, 27.32°S 32.37°E, 24.xi.1992, groundtraps 5 days, leg: Endrödy-Younga. (7♂, 8♀ TMSA) SOUTH AFRICA, Zululand, Ndumu Game Reserve, 26.54°S 32.17°E. 24.xi.1992, white rhino dung, leg: Endrödy-Younga. (1♂ TMSA) SOUTH AFRICA, KwaZulu Natal, Ngome State Forest, 27.48°S 31.25°E, 12–17.xi.1995, white rhino dung, leg: Endrödy-Younga. (4♂, 6♀ SANC) SOUTH AFRICA, KZN, Mkuze Game Reserve, 24.xi.1981, legs: Doube, MacQueen, Davis & Flanagan. (4♂, 5♀ SANC) SOUTH AFRICA, KZN, St. Lucia Estuary, 26.viii.1978, leg: Bornemissza. (1♂, 3♀ SANC) SOUTH AFRICA, KZN, Hluhluwe Game Reserve (Inzimane), 24.xi.1982, leg: Doube. (4♂, 3♀ SANC) SOUTH AFRICA, KZN, St. Lucia Est. Nat. Res, forest, 23.i.1979, leg: Aschenborn. (9♂, 7♀ UPSA) SOUTH AFRICA, KZN, Ntshondwe, 27°43'S 31°15'E, 24.i.1999, leg: Davis. (2♂, 2♀ TMSA) SOUTH AFRICA, Limpopo, 17 km N Thabazimbi, Kransberg, 20.xii.2009, leg: Beyers. (1♂, 1♀ TMSA) MOZAMBIQUE, Pomene, 22.59°S 35.35°E, 02.v.1974, leg: Strydom. (1♂ UPSA) SOUTH AFRICA, Gauteng, Roodeplaat Nat. Res, 25°37'–39°S 28°20'–21°E. 13–14.xii.2001, leg: Davis & Deschodt. (1♂ UPSA) SOUTH AFRICA, Northwest Province, Rustenburg, 25°43'S 27°10'E. 27.ii.1999, leg: Wagemaker. (1♂ TMSA) SOUTH AFRICA, Zululand, Mtubatuba, 28.22°S 32.19°E, 3.iv.1974, fruit trap, leg: Endrödy-Younga. (1♂ TMSA) SOUTH AFRICA, Zululand, S. Natal, Weza, Ingeri Forest, 30.32°S, 29.41°E, 23.xi.1989, leg: Endrödy-Younga & Klimaszew. (1♀ SANC) SOUTH AFRICA, Limpopo, Murmelende Waters Farm, Kampersrus, Mariepskop 24°32'S 30°17'E, 08–11.iv.1992, leg: Stals. (1♂, 1♀ TMSA) SOUTH AFRICA, Limpopo Prov, Lajuma, southern slope, 900 m, 16.i.2016, leg: Colin Schoeman. (1♂, 1♀ SANC) SOUTH AFRICA, Natal, Umfolozi, 1–7.x.1970, legs: Bornemissza & Aschenborn. (1♂, 1♀ SANC) SOUTH AFRICA, Cape Province, Avontuur (20 km S), 2.ii.1977, leg: Bornemissza. (3♂, 6♀ TMSA): SOUTH AFRICA, Eastern Cape, Transkei, The Haven, 32.15°S 28.55°E, 09.xii.1979, E-Y: 1696, groundtraps, 7 days, leg: Endrödy-Younga. (2♂, 2♀ TMSA): SOUTH AFRICA, Eastern Cape, Transkei, Coast Dwesa forest, 32.17°S 28.50°E, 5.iii.1985, zebra dung, leg: Endrödy-Younga. (1♂ TMSA) SOUTH AFRICA, Zululand, Lake Bangazi, 28.07°S, 32.31°E, 12.xii.1975, groundtraps, 5 days, leg: Endrödy-Younga. (12♂, 8♀ UPSA): SOUTH AFRICA, NW Province, Mooiooi, Maretlwane Bush Camp (near to river) 25°47'07"S 27°34'37"E, 1274 m, 12–14.ii.2016, leg: Daniel. (1♂, 1♀ SANC) MOZAMBIQUE, Sofala, Beira (15 mi N), 19.i.1972, leg: Bornemissza & Kirk. (2♂, 2♀ UPSA) MOZAMBIQUE, Sofala, Gorongosa National Park (Cheringoma), near Claud's waterfall Camp 19°01'43"S; 34°40'24"W, 1–3.v.2013, leg: B de Medeiros. (5♂, 6♀ UPSA) MOZAMBIQUE, Sofala, Gorongosa National Park (near Chitengo) Sandforest 18°57'24"S 34°20'24"E, 26 m, 14.vi.2014, pitfall, h. dung, leg: GM Daniel (1♂, 1♀ SANC): MOZAMBIQUE, Sofala, Dondo 19°37'S 34°45'E. 19.i.1972, leg: Bornemissza & Kirk.

Etymology: The species name reflects the inconspicuous punctures on the frons.

Distribution: *Sisyphus inconspicuus* sp. n. occurs in South Africa and Mozambique. It has been recorded from moist savanna or dense woodland and riverine vegetation. It has also been collected in dry shaded vegetation along the coastline, in sand forest, and

in dry, dense savanna from KwaZulu Natal (South Africa) to Sofala Bay (Mozambique) (Fig. 13).

***Sisyphus australis* Daniel & Davis sp. n.** (Fig. 11, 12E).

ZooBank: <http://zoobank.org/762856F2-064A-4B6C-9A1C-BB22BA70A271>

Diagnosis: *Sisyphus australis* sp. n. is similar to *S. costatus*. However, the new species is distinguished by the straight margin between the medial clypeal teeth. It also bears a strong clypeo-frontal carina (Fig. 11H). In addition, the parameres of *S. costatus* and *S. australis* sp. n. are distinctly different (Fig. 12 B, E)

Description: Male holotype: **Size.** Length: 5.7 mm; width: 3.2 mm. **Colour.** Black body; setae brown; meso- and metasternum black; antennae grey. **Head.** Medial teeth not sharp apically; edge between medial teeth separated by a straight margin; a rectangular margin between the medial tooth and lateral indentation; genal margin straight. Dorsal surface of the clypeus setose, without punctation; clypeo-frontal carina distinctly defined; vertex setigerous with scattered ocellate punctures (Fig. 11H). **Pronotum.** Convex; maximum length longer than maximum width; dorsal surface with setation and ocellate punctures of different sizes; setae on the antero-lateral projection well-developed. Complete lateral prothoracic margin between the prothoracic disc and prothoracic episternum. **Elytra.** Elongate, narrow posteriorly; elytral striae minutely punctate and crenulate, characterized by a distinct crenulate double line, which is interrupted by fine ocellate strial punctures; interstriae with alternating rows of well or weakly developed setae; hind wing and venation are fully developed. **Pygidium.** Setigerous with ocellate punctation. **Sternites.** Abdominal sternites finely crenulate, setigerous with ocellate punctation; setae arranged in rows laterally; meso-metasternal suture visible; punctate depression on the postero-medial surface of the metasternum. **Legs.** In ventral view, antero-lateral carina of profemur punctate, with a lateral row of fine and well developed setae; meso- and metafemur with granulation, densely punctate and setose; meso- and metatrochanter contiguous with femur, metatrochanter projected somewhat backwards; protibia with three teeth and single terminal spine; mesotibia punctate and setose with two terminal spines; metatibia densely setose, serrated laterally with two spurs; pro- meso- and metatarsi five segmented with two claws, setose laterally; first tarsal segment of the meso- and meta-thoracic legs with a row of strong setae on the external edge. **Aedeagus.** Parameres simple and symmetrical (Fig. 12E)

Morphological variation

Size: Male: length: 8.2–5.5 mm; width: 3.2–4.0 mm; Female: 8.0–6.0 mm; width: 3.0–3.6 mm. **Head:** Mainly in populations from the Eastern Cape (The Haven), the surface of the clypeus is less setigerous. **Male:** Meta- and mesotibia curved; last abdominal sternite narrowed medially (Fig. 1A). **Female:** Meta- and mesotibia almost straight; last visible abdominal sternite not constricted medially (Fig. 1B).

Examined type material

Holotype: (♂ TMSA) SOUTH AFRICA: /S. Cape Prov (Western Cape), Outeniekwa-berg, 33.50°S; 23.11°E/; 13.12.1977; E-Y: 1422, dung collecting, leg: Endrödy-Younga.

Paratypes: (3♂, 3♀ TMSA) same data as holotype. (1♂, 1♀ TMSA) SOUTH AFRICA: Cape Prov. (Western Cape) George, Saasveld, 205, leg: Breytenbach. (1♀ SANC) SOUTH AFRICA: Cape Prov. (Western Cape) George, Saasveld, 205, leg: Breytenbach. (1♂ SANC) SOUTH AFRICA: C.P. (Western Cape) (10 km SW), 3.iii.1973, leg: Davis. (3♂, 5♀ TMSA) SOUTH AFRICA: Transkei (Eastern Cape), The Haven, 32.15°S 28.55°E, 09.xii.1979, E-Y: 1696, groundtraps, 7 days, leg: Endrödy-Younga. (2♂, 2♀ TMSA): SOUTH AFRICA: Transkei (Eastern Cape), Coast Dwesa forest, 32.17°S 28.50°E, 5.iii.1985, zebra dung, leg: Endrödy-Younga. (1♂ TMSA): SOUTH AFRICA: Transkei (Eastern Cape), Alexandria For. St., 33.43°S 26.23°E, 5.xii.1987, groundtraps with faeces bait, 2 days, leg: Endrödy-Younga. (1♀ SANC) Transkei (Eastern Cape), Wavecrest, 25.xi.1981, leg: Doube.

Etymology: The species name reflects the geographical distribution of the species, which is restricted to the southern part of South Africa.

Distribution: *Sisypbus australis* **sp. n.**, has been recorded along the coastline in association with shaded vegetation of the Western and Eastern Cape Provinces, South Africa (Fig. 13).

Remarks: Detailed study of type and non-type material of *S. gazanus* and *S. costatus* have revealed a species complex composed of *S. costatus*; *S. australis* **sp. n.**; *S. inconspicuous* **sp. n.** and *S. gazanus*. The main distinguishing features for the species complex are presented in Table 1. Furthermore, the shape of the parameres (Figs. 12A–E) and the distributions (Fig. 13) are useful to separate the four species belonging to the *gazanus* complex.

Table 1. Comparative features for the *gazanus* species complex (*S. inconspicuous* **sp. n.**, *S. gazanus*, *S. costatus*, *S. australis* **sp. n.**)

Species	Punctuation on vertex	Shape between medial teeth	Genae dorsal surface	Setae on pronotum	Setae on elytra	Frons dorsal surface
<i>S. inconspicuous</i> sp. n.	Dense	Somewhat straight	Flat	Normally arranged	Normally arranged	Inconspicuously punctate
<i>S. gazanus</i>	Dense	Straight	Shallow depression	Some bare patches	Normally arranged	Conspicuously punctate
<i>S. costatus</i>	Scattered	Upcurved	Flat	Normally arranged	Alternate between rows of dense or less dense setae	Inconspicuously punctate
<i>S. australis</i> sp. n.	Scattered	Straight	Flat	Normally arranged	Alternate between rows of dense or less dense setae	Inconspicuously punctate

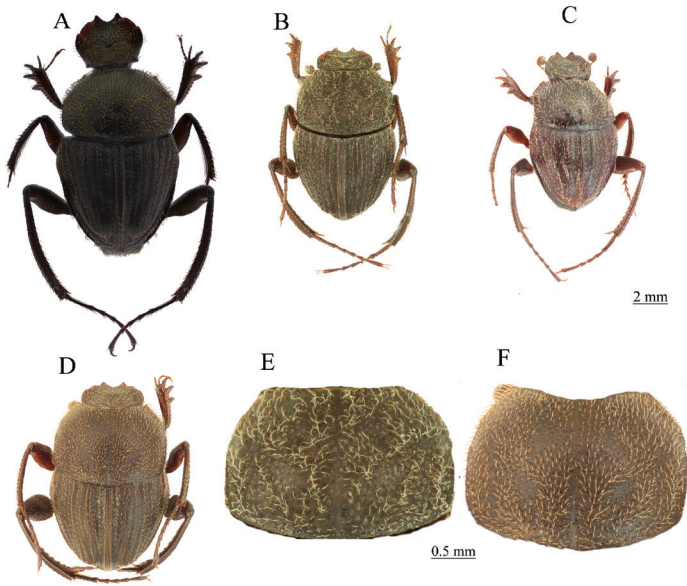


Fig. 14. Images of the habitus of the *seminulum* species-group: **A.** *S. splendidus*; **B.** *S. oralensis*; **C.** *S. nanniscus*; **D.** *S. auricomus* **sp. n.** Pronotal setation and punctation patterns of *S. oralensis* (**E**), and *S. auricomus* **sp. n.** (**F**).

***seminulum* species-group** (Figs. 14A–D, 15A–C).

***Sisyphus splendidus* Montreuil 2015** (Fig. 14A).

Montreuil 2015a: 91–102

Type locality: Otavi mts, Farm Gauss (Namibia)

Size: Female: length: 4.5 mm, width: 2.5 mm.

Diagnosis: *S. splendidus* may be separated from other members of the *seminulum* species-group by the distinct metallic sheen on the pronotal disc.

Examined non-type material: See Supplementary information.

Distribution: *Sisyphus splendidus* is found in unshaded vegetation of northern Namibia and southern Angola (Fig. 16).

***Sisyphus oralensis* Daniel & Davis, 2016** (Figs. 14B, E; 15A).

Daniel et al. 2016: 70

Size: Male: length: 3.4–4.8 mm, width: 2.1–2.5 mm. Female: length: 3.9–4.7 mm, width: 2.1–2.5 mm.

Type locality: Richard's Bay (KwaZulu Natal, South Africa)

Diagnosis: *S. oralensis* resembles *Sisyphus auricomus* **sp. n.** However, it differs by the less dense cover of long yellow setae on the pronotal disc that are not distributed uniformly, but, mostly arranged in a linear pattern separated by bare patches (Fig. 14E). Furthermore, parameres of *S. oralensis* are notched dorso-transversally (Fig. 15A).

Examined type material

Holotype: (♂ TMSA): SOUTH AFRICA, KZN, Richard's Bay 28°39'29.1"S 32°15'19.2"E, 27.i.2000, leg: Davis & Delport. Paratypes: (5♂, 8♀ UPSA): SOUTH AFRICA, KZN Richard's Bay 28°39'S 32°15'E, 26–27.i.2000, leg: Davis & Delport. (4♀ UPSA; 3♂, 2♀ SANC): SOUTH AFRICA, KZN, Thembe Elephant Park 27°01'S 32°24'E, 17.xii.1996, leg: B.J. Van Rensburg. (9♂, 8♀ UPSA): SOUTH AFRICA, KZN, Thembe Elephant Park 27°01'S 32°24'E, 17.vii.1995, leg: B.J. Van Rensburg. (2♂, 3♀ UPSA): SOUTH AFRICA, KZN Thembe Elephant Park 26°55'S 32°23'E, 15–30.x.2008, leg: B.J. Van Rensburg. (2♂ SANC, 1♀ TMSA): SOUTH AFRICA, KZN, Umfolozi 28°15'S 31° 55'E, 25.viii.1971, leg: Bornemissza & Insley. (1♂, 10♀ SANC): SOUTH AFRICA, KZN St Lucia Est. Nat. Reserve, Dune Forest 28°13'S 32°21'E, 27.x.1978, leg: Bornemissza. (1♀ SANC): SOUTH AFRICA, KZN Ntl Kosi Bay Nature Res 26°34'S 32°28'E, 8–11.ii.1990, leg: B. Grobbelaar. (1♀ SANC): SOUTH AFRICA, KZN, Near Richards Bay, 28°36'52"S 32°17'34"E, 27.x.1978, leg: Bornemissza. (1♂ SANC): SOUTH AFRICA, KZN, Thembe Elephant Park 27°01'S 32°24'E, 01–49.ii.1996, leg: Stals. (5♂, 6♀ TMSA): SOUTH AFRICA, KZN, Ntl Kosi Bay Nature Res 26°34'S 32°28'E, 14.xi.2002, leg: Burger, Harrison & Muller. (7♂, 8♀ TMSA): SOUTH AFRICA, Zululand, Sodwana Bay 5km, 27°21'S 32°23'E, 23.xi.1992, leg: Endrödy-Younga. (8♂, 8♀ TMSA): SOUTH AFRICA, N Zululand, Ndumu Game Reserve 26°32'S 32°10'E, 1.xii.1992, leg: Endrödy-Younga. (30♂, 42♀ TMSA): SOUTH AFRICA, N Zululand, Lake Bangazi 28°04'S 32°18'E, 12.xii.1992, leg: Endrodi-Younga. (1♂, 2♀ TMSA): SOUTH AFRICA, Zululand, St. Lúcia. Mission Rock 28°13'S 32°21'E, 23.xi.1992, leg: Endrödy-Younga. (1♂, 2♀ TMSA): SOUTH AFRICA, Natal, Cape Vidal, Forest litter 28°8'S 32°33'E, 23.i.1990, leg: J. Klimaszewski. (1♂, 2♀ TMSA): SOUTH AFRICA, N Zululand, Hluhluwe Game Reserve. 28°03'S 32°02'E, 20.xi.1992. leg: Endrödy-Younga. (12♂, 30♀ SANC); SOUTH AFRICA, KZN St Lucia Est. Nat. Reserve, Forest 28°13'S 32°21'E, 24–23.i.1979, leg: NH Aschenborn. (1♂, 2♀ TMSA): MOZAMBIQUE, Inhambane, Pomene, 22°35'S 35°21'E, 04.v.1974, leg: A. Strydom. (5♂, 5♀ UPSA): MOZAMBIQUE, Maputo Elephant Reserve 26°39'S 32°43'E, 10–16.xi.2007, leg: W. Strümpher & C. Deschodt.

Examined non-type material: See Supplementary information.

Distribution: *S. oralensis* is a coastal and sandforest endemic (Jacobs et al. 2010; Daniel et al. 2016). It has been observed in dense coastal woodlands and forest from Maputaland, north-east South Africa, to south-east Mozambique (Maputo Elephant Reserve and Pomene) (Fig. 16). Furthermore, recently, we found new distribution records from uMkhuze Game Reserve in South Africa (see Supplementary information). The species was collected in shaded deep sand vegetation, under pitfalls baited by dead diplopods.

Remarks: Revision of *S. oralensis* type material has revealed that specimens from Mozambique (Dondo, Beira and Gorongosa) with distinct golden hair on the pronotum

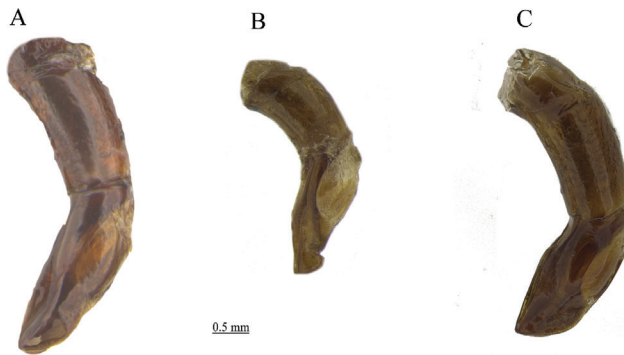


Fig. 15. Images of the aedeagi of the *seminulum* species-group: **A.** *S. oralensis*; **B.** *S. nanniscus*; **C.** *S. auricomus* sp. n.

belong to a new species of the *seminulum* species-group that is described below. In addition, it should be noted that in the original description of *S. oralensis* (Daniel et al. 2016), three specimens (a male and two females) from Ithala Game Reserve (Kwa-Zulu Natal, South Africa) were cited in error as paratypes of *S. oralensis*. These same three specimens were also cited correctly as paratypes of *S. umbraphilus* in the same publication.

***Sisyphus nanniscus* Péringuey, 1901** (Figs. 14C, 15B).

Péringuey 1901: 107–8; Gillet 1911:23; Arrow, 1909: 519; Arrow 1927: 465; Haaf: 355–6; Montreuil 2017: 3

Sisyphus ocellatus nanniscus Péringuey, 1901

Haaf 1995: 357–8; Ferreira: 1972: 807;

Type locality: Durban (South Africa)

Size: Male: length: 3.0–3.8 mm; width: 1.7–1.5 mm; Female: length: 3.0–4.0 mm, width 1.8–1.5 mm.

Diagnosis: *S. nanniscus* resembles *S. seminulum*. However, it can be easily distinguished as it bears large, dense ocellate punctures on the pronotum, unlike in *S. seminulum* where the punctures are relatively smaller and clearly separated from each other. Additionally, in *S. nanniscus* the internal margin of the metatibia is weakly dentate whilst, in *S. seminulum*, it is distinctly serrated.

Examined type material

***Sisyphus nanniscus* Péringuey, 1901:** (♂ SAM): Lectotype (designated here): handwritten on brown label /*Sisyphus nanniscus*, type/, red label /type, SAM, ento: 2672/, /Lectotype, det. GM Daniel, 2016/. (♂ SAM): Paralectotype (designated here): /Durban, x. 1896 leg: undetermined/, (white label) /*Sisyphus seminulum* Gerstaecker, det. K.M. Paschalidis, 1975/, (handwritten on brown label) /*Sisyphus nanniscus*, type/, (handwritten on brown label bordered by blue colour) /*Sp. nanniscus* Pér/, red label /type/, /Lectotype, det. GM Daniel, 2016/.

***Sisyphus seminulum* Gerstaecker, 1871:** Lectotype (designated here): (1♀ MNHUB): /Zanzibar/, (brown label) /*typus*/, /56381/; handwritten on blue label /*seminulum* Gerst/; (red label) /Syntypus *Sisyphus seminulum* Gerstaecker 1871, labelled by MNHUB 2016/, /leg: Cooke/; /Lectotype, det. GM Daniel, 2016/. Paralectotype (designated here): (1♂ MNHUB): /Zanzibar/; brown label /*paratypus*/, /56381/; handwritten on blue label /*seminulum* Gerst, det: Muller/, red label /Syntypus *Sisyphus seminulum* Gerstaecker 1871, labelled by MNHUB 2016/, leg: Cooke, /Paralectotype, det. GM Daniel, 2016/. (3♂, 2♀ MCZ): /Zanzibar/ C. Cooke/, (red label written) /*type*/ *S. seminulum*!, *costatus*, det. PFS Pereira/ Paralectotype, det. GM Daniel, 2017/.

Examined non-type material: See Supplementary information.

Distribution: *Sisyphus nanniscus* is found primarily under shaded vegetation in southern Africa (Fig. 16).

Remarks: Type material has been studied of both *S. nanniscus* and *S. seminulum*. External morphology and parameres are sufficiently different for separation into two species. Therefore, we support the revalidation and new status of *S. nanniscus* proposed by Montreuil (2017).

***Sisyphus auricomus* Daniel & Davis sp. n.** (Figs. 14D, F; 15C)

ZooBank: <http://zoobank.org/B1E48C14-84C3-487F-AC44-E1728AAA1C7D>

Diagnosis: *Sisyphus auricomus* sp. n. is close in appearance to *S. oralensis*. However, the new species differs by bearing thick and short golden setae on the pronotum. The directional projection of setae is well-defined (Fig. 14F). Furthermore, the genitalia differ from those of *S. oralensis* by lacking a dorso-transverse notch on the apex of the parameres (Fig. 15C).

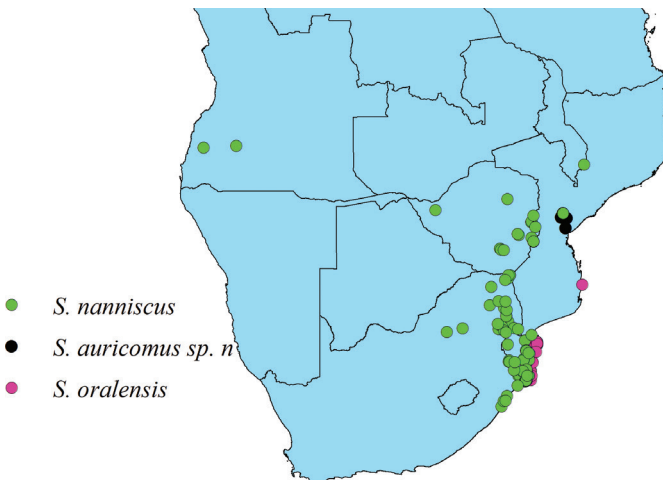


Fig. 16. Distribution map for the *seminulum* species-group.

Description: Male holotype: **Size.** Length: 4.2 mm; width: 2.2 mm. **Colour.** Body brown with golden setae; antennal club and setae brown. **Head.** Long setae on dorsal surface; anterior edge of clypeus cleft between medial teeth, convex lateral sinuosity extending to clypeo-genal suture; no indentation at the clypeo-genal suture; rounded protrusion antero-laterally on genae. Surface of frons and vertex setose with ocellate punctation. **Pronotum.** Maximum width as long as maximum length; golden setae arranged evenly between punctation, setae absent from the distinct rounded bald spots on central disc (Fig. 14F); coarse ocellate punctation. Complete lateral prothoracic ridge separating pronotal disc and prothoracic episternum. **Elytra.** Ovoid, interstriae with evenly distributed setae; striae with distinct crenulate double line, which is interrupted by fine, minute and ocellate punctures; granulation and depressions basally on elytral striae 1–4. Hind wing and venation fully developed. **Pygidium.** Narrow basally; densely setose with ocellate punctation. **Sternites.** Edges between abdominal sternites finely crenulate with setigerous punctures; setae arranged in rows laterally; meso-metasternal suture visible; meso- and metasternum densely punctate and setose. Mesepimerum and metepisternum finely punctate and setose. **Legs.** In ventral view, profemur carinate antero-laterally, punctate and internally pubescent with a lateral row of fine and well-developed setae; meso- and metafemur densely punctate and setose; meso- and metatrochanter contiguous with femur, metatrochanter projected slightly backwards; metacoxa punctate and shagreened ventro-anteriorly; protibia with three teeth and single terminal spine; mesotibia punctate and setose with two terminal spines; metatibia densely setose, serrated laterally with two spurs; pro-, meso- and metatarsus five-segmented, with two claws, setose laterally; first tarsal segment of meso- and metathoracic legs with a row of strong setae on the external edge. **Aedeagus.** Phallobase weakly sclerotized; parameres simple, lacking dorso-transversal excavation; apex relatively truncated (Fig. 15C).

Morphological variation

Size: Male: Length: 3.9–5.0 mm; width: 2.0–2.5 mm; Female: Length: 3.7–5.0 mm; width: 1.9–2.6 mm

Male. Meta- and mesotibia curved; last abdominal sternite narrowed medially (Fig. 1A). **Female.** Meta- and mesotibia almost straight; last visible abdominal sternite not constricted medially (Fig. 1B).

Examined type material

Holotype: (♂ TMSA) MOZAMBIQUE, Sofala, Gorongosa National Park (near Chitengo) Sandforest 18°57'24"S 34°20'24"E, 26 m, 14.vi.2014, pitfall, h. dung, leg: GM Daniel Paratypes: (23♂, 20♀ TMSA; 25♂, 18♀ SANC; 18♂, 25♀ UPSA) with the same data as the holotype. (1♂ SANC) with the same data as the holotype, except: 11–28.i.1972, leg: Bornemissza & Kirk. (3♂, 4♀ TMSA; 4♂, 4♀ SANC; 4♂, 4♀ UPSA) MOZAMBIQUE, Sofala, Gorongosa National Park (Cheringoma), near Claud's waterfall Camp 19°01'43"S; 34°40'24"E, 1–3.v.2013, leg: B de Medeiros. (7♂, 10♀ SANC): MOZAMBIQUE, Sofala, Dondo 19°37'S 34°45'E. 19.i.1972, leg:

Bornemissza & Kirk. (1♂, 1♀ SANC): MOZAMBIQUE, Sofala, Beira 19°50'S 34°51'E 19.i.1972, leg: Bornemissza & Kirk.

Additional examined non-type material: *Sisyphus weneri* Montreuil 2017. (2♂, 3♀ HNHM) **KENYA:** Sachu, 3.5844°S 39 4496°E; 28.x–14.xi.2001. leg: Kontschán. (1♂, 1♀ HNHM) **TANZANIA:** Usambaras Mts, Mafi Hills Plateau, 1200 m, 26.xii.1985, Usambara rain Forest Project. Peregovits

Distribution: *S. auricomus* **sp. n.** may be restricted to Central Mozambique (Beira, Cheringoma, Dondo and Gorongosa) where it is associated with shaded vegetation between the Zambeze and Púnguè rivers (Fig. 16). It was recorded from sandforest and dense woodland in Gorongosa National Park (10 km from northern Chitengo), but was completely absent from surrounding grassland of the same area (Daniel, 2014, unpublished data). In Cheringoma, it has been collected in dense riverine forest (de Medeiros, *pers. communication*).

Etymology: The species name refers to the setae, which are distinctly golden-coloured.

Remarks: It should be noted that *S. auricomus* **sp. n.** is similar to the eastern African species *Sisyphus weneri* Montreuil, 2017. However, they can be easily separated by the presence of yellow setae and strong serration on the mid-internal margin of the metatibia in *S. weneri* whereas, in *S. auricomus* **sp. n.**, the internal margins of the metatibiae are weakly dentate with golden setae. Furthermore, *S. weneri* differs by the two distinct patterns of punctation on the pronotum, smaller medially and larger laterally, unlike in *S. auricomus* **sp. n.** where punctures are roughly of the same size. In addition, the genitalia in *S. weneri* are markedly different compared to *S. auricomus* **sp. n.**

Neosisyphus Müller, 1942

Müller 1942: 86; Haaf 1955: 346; Ferreira 1972: 810–844; Schaefer & Fisher 1992: 130; Montreuil 2015b: 1–44

Type species: *Neosisyphus spinipes* (Thunberg, 1818)

barbarossa species-group (Figs. 17A–D)

Neosisyphus barbarossa (Wiedemann, 1823) (Figs. 17, 18A)

Montreuil 2015b:16

Sisyphus barbarossa Wiedemann, 1823

Wiedemann 1823:23; Harold 1869:984, Péringuey 1901: 100; Gillet 1911:38; Arrow 1927: 464; Haaf 1955: 368; Ferreira 1972: 829

Sisyphus rugosus Gory, 1833

Gory 1833:12

Type locality: Cape of Good Hope (South Africa)

Size: Male: length: 10.2–8.0 mm; width: 4.5–4.0 mm; Female: length: 10.0–7.5; width: 4.5–3.0

Diagnosis: *N. barbarossa* resembles *N. calcaratus* but differs by having brown setae on the elytra. Furthermore, the projection of the metatrochanter is shorter even though major males of *N. barbarossa* are larger than those of *N. calcaratus*.

Examined type material

Lectotype (*designated here*): (♀ NHMD): /Mus. Western/, red label, /Type/, Cap. bon. Sp., febr.1817, *barbarossa* Wied/. /Lectotype, det. GM Daniel, 2016/.

Examined non-type material: See Supplementary information.

Distribution: *N. barbarossa* is considered to be endemic to moist highland grassland and southern coastal uplands in South Africa (Fig. 19). This contrasts with distribution records sourced from Montreuil (2015b).

Remarks: There is no collection locality for the individual in the habitus photograph of “*N. barbarossa*” provided by Montreuil (2015b). Although it resembles the photograph of *N. barbarossa* provided in Fig. 17A, most of the distribution data in Montreuil (2015b) is at odds with that cited, here, from cool areas of the Cape type locality and highlands of South Africa (see Supplementary information). Therefore, on the basis of

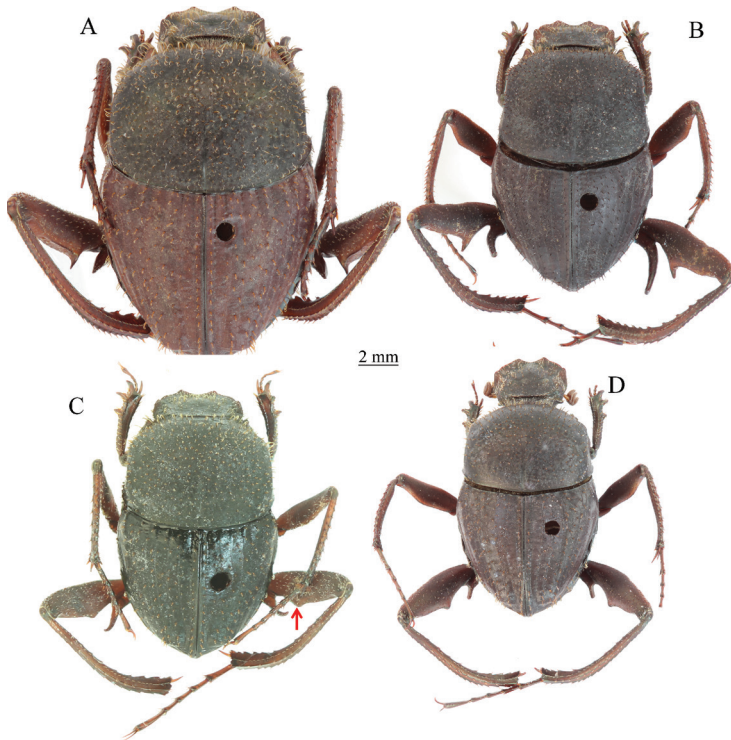


Fig. 17. Images of the habitus of the *barbarossa* species-group: **A.** *N. barbarossa*; **B.** *N. calcaratus*; **C.** *N. tembyi* sp. n., arrow showing a diagnostic feature for the new species; **D.** *N. setiger*.

restriction to cooler regions, it would be justified to dispute Montreuil's interpretation of the species distribution as extending into warmer savanna regions.

***Neosisyphus calcaratus* (Klug, 1855)** (Figs. 17, 18B)

Montreuil 2015b: 15

Sisyphus calcaratus Klug, 1855

Klug 1855: 651; Harold 1869: 984; Arrow 1927: 464; Boucomont 1933: 3; Haaf 1955: 377, Ferreira 1972: 829.

Sisyphus rubripes Boheman, 1857

Boheman 1857:193

Size: Male: length: 7.1–6.6 mm; width: 4.5–3.0 mm. Female: length: 7.0–6.5 mm; width: 4.0–3.8 mm.

Type locality: Sena (Sofala, Mozambique).

Diagnosis: *N. calcaratus* is similar to *N. barbarossa*. Males of both species bear a sharp pointed spine on the mid-posterior edge of the metafemur, which is absent in the female. However, the elytra of *N. calcaratus* bear black setae that are bent over at the tip whilst the elytra of *N. barbarossa* are covered by brown setae. Furthermore, compared to *N. barbarossa*, major males of *N. calcaratus* are smaller but the projection of the metatrochanter is twice as long.

Examined type material

***Sisyphus rubripes* Boheman, 1857:** (1♀ NHRS): /Caffraria/, /Typus/; /*rubripes* Bohem/; /*Sisyphus rubripes* Boh =*armatus* Gory, det. E. Haaf, 1954/; /*Sisyphus calcaratus* Klug, det. KM, Paschalidis 1975/; /NHRS_JLKB: 000025221.

Examined non-type material: See Supplementary information.

Distribution: *N. calcaratus* has been recorded in dry lowland savanna and mixed woodland in the lowveld of South Africa, Botswana, Zimbabwe and Swaziland. It has also been observed on the coastal plain and interior of southern central Mozambique (Fig. 19).

***Neosisyphus tembyi* Daniel & Davis sp. n.** (Figs. 7, 8C)

ZooBank: <http://zoobank.org/476EBD87-13C2-4DE0-A31E-883EEC69DA66>

Diagnosis: *N. tembyi* sp. n. is similar to *Neosisyphus jossoi* Montreuil, 2015. Both species are roughly the same size and lack sharp spines on the posterior margin of the metafemur. However, *N. tembyi* sp. n. bears a small angled protuberance on the mid-posterior margin of the metafemur in males. The metatrochanter projection in major males of the new species is $\frac{1}{2}$ of the total length of the metafemur and is somewhat inwardly projected at the tip. Unlike in *N. jossoi*, in which the metatrochanter projection is $\frac{3}{4}$ of the total length of the metafemur in major males and strongly inwardly



Fig. 18. Images of the aedeagi of the *barbarossa* species-group: **A.** *N. barabrossa*; **B.** *N. calcaratus*; **C.** *N. tembyi* **sp. n.**; **D.** *N. setiger*.

projected. Southern African specimens of *N. setiger* Roth (1851) differ from the new species by bearing a shorter metatrochanter in males, which is $\frac{1}{4}$ of the total length of the metafemur. Furthermore, the metatrochanter in Southern African *N. setiger* projects straight and is never bent on the tip. The phallobase and parameres of all of the above species are distinctly different.

Description: Male Holotype: **Size.** Male: length: 7.3 mm; width: 4.5 mm. **Colour.** Black body with brown setae; meso- and metasternum black; antennal club brown. **Head.** Anterior edge of clypeus with shallow sinuosity between medial teeth; lateral extreme of clypeal margin simply arcuate. Clypeo-genal suture markedly cleft; genae elongate. Frons and vertex dorsally granular, setose and minutely punctate, epicranial suture clearly visible. **Pronotum.** Convex with a sheen on dorsal surface; maximum width as long as the maximum length; setae inserted between ocellate punctures. Incomplete lateral prothoracic ridge between pronotal disc and prothoracic episternum. **Elytra.** Broad proximally and narrow posteriorly; well-spaced setae on interstriae; elytral surface shiny, distinct antero-lateral humeral callus; striae fine with double marginal lines interrupted by smooth ocellate strial punctures; granulation basally on elytral striae 4–7. **Pygidium.** Bearing U-shaped, ocellate punctuation, a metallic sheen and setation. **Sternites.** Margins between abdominal sternites setigerous laterally, and glabrous medially with minute ocellate punctation; meso-metasternal suture visible; meso- and metasternum finely punctate and setose; metasternum with a punctate depression on the postero-medial edge. Mesepimeron and metepisternum finely punctate and setose. **Legs.** In ventral view, profemur carinate antero-laterally, punctate and internally pubescent with a lateral row of fine and well-developed setae; mesofemur finely punctate and setose, lacking any projection posteriorly; metafemur with an angled-protuberance mid-posteriorly with fine punctation and setae; metatrochanter projected backwards

almost reaching top of angled protuberance; tip of metatrochanter slightly projected inward, but always parallel with metafemur. Metacoxa punctate and shagreened ventro-anteriorly. Protibia with three teeth and single terminal spine; meso-metatarsus densely setose, serrated laterally, with two terminal spines on mesotibia, and two terminal spurs on metatarsus; pro-, meso- and metatarsus five-segmented, with two claws; mostly setose. **Aedeagus.** Parameres separated by visible dorsal membranous portion extending nearly to the middle; arciform ridge bordering the membrane laterally, deeply notched medially; inwardly curved on the apex (Fig. 18C).

Morphological variation

Males bear a backwardly projected metatrochanter that is curved inwardly at the tip; this projection is absent in females where the metatrochanter is contiguous with the metafemur. The pronotum in males is larger than in females.

Examined type material

Holotype: (1♂ SANC) /Angola, Paiva Coucero (14.816667°S 15.55°E) (50 & 45 km E), 18.xii.1974, leg: Davis & Temby/, /Ex coll CSIRO, Div. Entomology S. African Station/. Paratypes: (1♀ SANC) same data as holotype.

Distribution: The species is only known from woodland vegetation in southern Angola (Paiva Coucero) (Fig. 19).

Etymology: The patronym is named after Ian Temby, a former researcher at the CSIRO, Division of Entomology, South African station; who was one of the collectors of the type material.

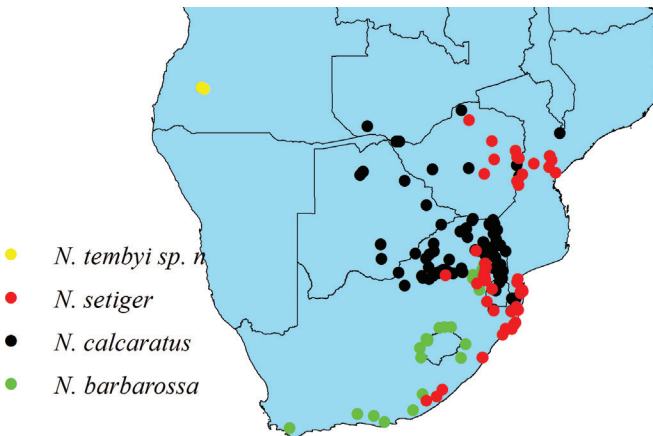


Fig. 19. Distribution map for the *barbarossa* species-group.

***Neosisyphus setiger* Roth (1851)** (Figs. 7, 8D)

Montreuil 2015b: 11

Sisyphus setiger Roth, 1851

Roth 1851: 124; Montreuil 2015b: 11

Neosisyphus confrater (Kolbe, 1914)

Montreuil 2015b: 11

Sisyphus confrater Kolbe, 1914

Kolbe 1914: 317; Haaf 1955: 376;

Type local: Bukoba (Tanzania)**Size:** Male: length: 9.0–5.0 mm; width: 4.8–3.0 mm. Female: length: 9.2–5.0 mm; width: 4.5–3.0 mm**Diagnosis:** *N. setiger* is distinguished from other members of the *barbarossa* species-group, by a combination of the following features: a triangular protrusion on the mid-posterior edge of the metafemur in males. Additionally, the projected metatrochanter is relatively short, comprising $\frac{1}{4}$ of the total length of the metafemur in males.**Examined non-type material:** See Supplementary information.**Distribution:** As defined by Montreuil (2015b), *N. setiger* is distributed in moist lowland and upland vegetation from northeast to southern Africa (Fig. 19).**Remarks:** We have compared Kenyan specimens identified as *N. setiger* with southeast African specimens identified as *N. confrater* by Paschalidis (1974). Females of *N. confrater* and *N. setiger* are close morphologically making it difficult to separate them into species. However, we have observed that males of southern Africa “*N. confrater*” bear a short blunt triangular projection on the mid-posterior edge of the metafemur and a short projecting metatrochanter. By contrast, males of east African “*N. setiger*” have a sharp projecting spine on the mid-posterior edge of the metafemur and a metatrochanter as large as in *Neosisyphus josoi* Montreuil, 2015.Montreuil (2015b) synonymized *N. confrater* with *Neosisyphus setiger* (Roth 1851). The synonymy seems to be based on the holotype female of *N. setiger* from Ethiopia and a lectotype male of *N. confrater* from Tanzania. This is questionable as females are often difficult to separate into species as stated above. Furthermore, although the photograph of a major male of *N. setiger* (Montreuil 2015b) closely resembles “*N. confrater*”, there is no indication of where the individual was collected. Nevertheless, we have retained the name *N. setiger* for southern African material as we have not been able to compare it with the type and non-type material used in Montreuil’s study (2015b).***spinipes* species-group** (Figs. 20A–C)***Neosisyphus fortuitus* (Péringuey, 1901)** (Figs. 20, 21A)*Sisyphus fortuitus* Péringuey, 1901

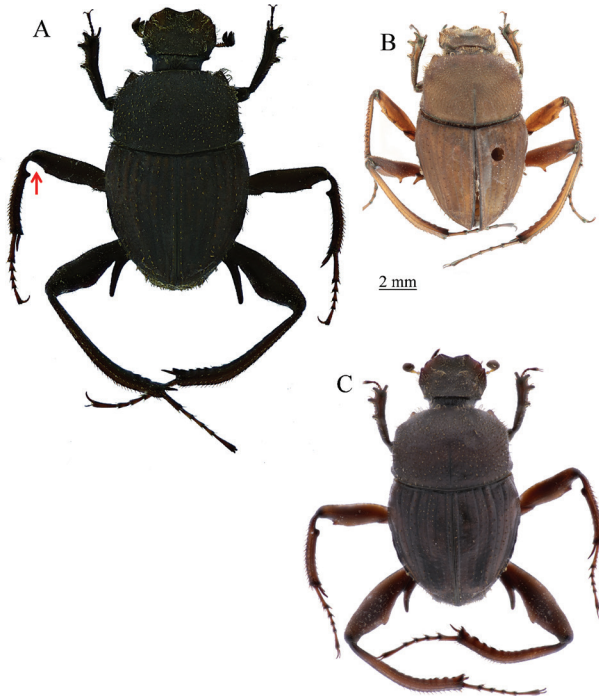


Fig. 20. Images of the habitus of the *spinipes* species-group: **A.** *N. fortuitus*, arrow indicating the main diagnostic feature of the species-group; **B.** *N. infuscatus*; **C.** *N. spinipes*.

Péringuey 1901: 103; Arrow 1927: 464; Gillet 1911: 23; Haaf 1955: 371; Ferreira 1972: 819; Montreuil 2015b: 9.

Type locality: Durban, Natal (South Africa)

Size: Male: length: 11.1–9.0 mm; width: 5.7–5.0 mm. Female: length: 11.5–9.0 mm; width: 6.0–4.4 mm.

Diagnosis: *Neosisyphus fortuitus* is distinguished from other members of the *spinipes* species group in southern Africa by lacking a spine or projection on the mid-posterior edge of the metafemur. In addition, the projecting metatrochanter is almost $\frac{1}{2}$ of the length of the metafemur in major males. The parameres are distinctly different to those of the other two species within the group (Fig. 21A).

Examined type material

Lectotype: (1♂ SAM) /Natal, Durban/ (red label) /*S. fortuitus* Pér, Lectotype, det. E. Haaf, 1954/.

Examined non-type material: See Supplementary information.

Distribution: *N. fortuitus* occurs in shaded vegetation in southern (South Africa, Mozambique, Zimbabwe) and East Africa (Kenya) (Fig. 22).



Fig. 21. Images for the the aedeagi of the *spinipes* species-group: **A.** *N. fortuitus*; **B.** *N. infuscatus*; **C.** *N. spinipes*.

***Neosisyphus infuscatus* (Klug, 1855)** (Figs. 20, 21B)

Montreuil 2015b: 10;

Sisyphus infuscatus Klug, 1855

Klug 1855: 651; Harold 1869: 984; Gillet 1911: 23; Arrow 1927: 464; Haaf 1955: 344; Ferreira 1972: 811.

Size: Male: length: 8.1–7.1 mm; width: 4.8–3.6. Female: length: 8.0–7.0 mm; width: 4.5–3.0 mm

Type locality: Sena, Sofala, Mozambique

Diagnosis: *N. infuscatus* bears a sharp mid-posterior metafemoral spine as opposed to the more obtuse spine in *N. spinipes*. *N. infuscatus* also differs by lacking the prominent sharp-angled protrusion on the basal-posterior edge of the mesotibia. Parameres of *N. infuscatus* are distinctly bent inwards at the apex (Fig. 21B).

Examined type material

Paralectotype (designated here): (♂ SAM) /Senal, *Sisyphus fortuitus*, PJJ/, red label /Type SAM, 2677/ *spinipes* Thunb, det. Haaf 1954/, /*Sisyphus infuscatus* Klug, det. KM. Paschalis 1975/, /Paralectotype, det: GM, Daniel, 2016/.

Examined non-type material: See Supplementary information.

Distribution: *N. infuscatus* is an East to southern African species, associated with lowland dry savanna (Fig. 22).

***Neosisyphus spinipes* (Thunberg, 1818)** (Figs. 20, 21C)

Montreuil 2015b: 9

Ateuchus spinipes Thunberg, 1818

Thunberg, 1818: 411

Sisyphus spinipes (Thunberg, 1818)

Boheman, 1857: 190; Harold 1869: 985; Péringuey 1901: 100; Gillet 1911: 24; Arrow 1927: 458; Haaf 1955: 368; Ferreira 1972: 811;

Sisyphus hessii Gory, 1833

Gory 1833: 8; Klug, 1855: 651; Boheman, 1857: 190; Harold 1869: 985; Péringuey 1901: 100; Gillet 1911: 24; Arrow 1927: 458; Haaf 1955: 368; Ferreira 1972: 811;

Sisyphus atratus Klug, 1855

Klug 1855: 651; Boheman, 1857: 190; Harold 1869: 985; Péringuey 1901: 100; Gillet 1911: 24; Arrow 1927: 458; Haaf 1955: 368; Ferreira 1972: 811;

Sisyphus appendiculatus Boheman, 1857

Boheman 1857: 190; Harold 1869: 985; Péringuey 1901: 100; Gillet 1911: 24; Arrow 1927: 458; Haaf 1955: 368; Ferreira 1972: 811; Montreuil 2015b: 9.

Type locality: South Africa

Size: Male: length: 10.4–8.0 mm; width: 4.7–3.0 mm. Female: length: 10.7–8.4 mm; width: 4.7–4.0 mm.

Diagnosis: *N. spinipes* is close in appearance to *N. infuscatus*. Both bear projecting spines mid-posteriorly on the metafemur in males. However, in *N. spinipes* the spine is obtuse rather than acute. *N. spinipes* also bears a distinct triangular projection on the basal posterior edge of the mesotibia and the apex of the parameres is simple (Fig. 21C).

Examined type material

***Ateuchus spinipes* Thunberg, 1818:** Lectotype (*designated here*): (♂ UUZM), /Thunberg, sam nr.2744, *Ateuchus spinipes* (= *Neosisyphus spinipes* **Thunb.**), Cap. TYP/, /Lectotype, det. GM Daniel, 2016).

***Sisyphus appendiculatus* Boheman, 1857:** (1♀ NHRS): /Caffraria/, /J. Wahlb./, /Typus/, /*appendiculatus* Bohem/, /*Sisyphus appendic*= *spinipes* Thunb., det. E. Haaf, 1954/, /NHRS_JLKB: 000025219.

Examined non-type material: See Supplementary information.

Distribution: *N. spinipes* is associated with upland or lowland moist grassland (Davis et al. 2002b; Davis et al. 1999). It is a widespread species, recorded from east to southern Africa (Fig. 22).

tibialis species-group (Fig. 23A)

***Neosisyphus mirabilis* (Arrow 1927)** (Figs. 23, 24A)

Sisyphus spinipes Gory 1833

Gory 1833: 8; Harold 1869: 985; Péringuey 1901: 87; Arrow 1927: 459; Haaf 1955: 345; Ferreira 1972: 825; Paschalidis 1974: 21; Montreuil 2015: 3;

Sisyphus mirabilis Arrow 1927

Arrow 1927: 459; Haaf 1955: 345; Ferreira 1972: 825; Paschalidis 1974: 21; Montreuil 2015: 3;

Size: Male: length: 11.0–8.0 mm; width: 5.2–3.0 mm; Female: length: 11.2–8.3 mm; width: 5.5–3.0 mm

Type locality: Cape of Good Hope

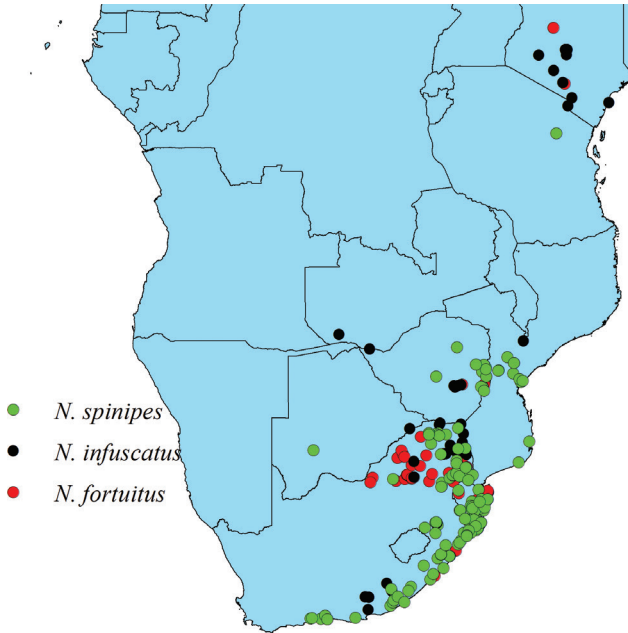


Fig. 22. Distribution map for the *spinipes* species-group.

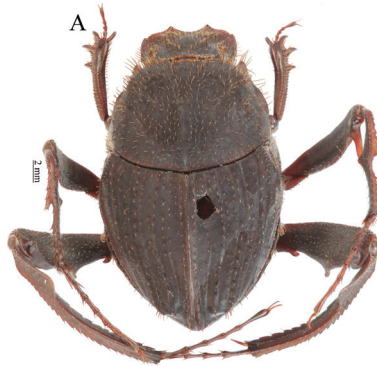


Fig. 23. Image of the habitus of the *tibialis* species-group: A. *N. mirabilis*.



Fig. 24. Image of the aedeagus of the *tibialis* species-group: A. *N. mirabilis*.

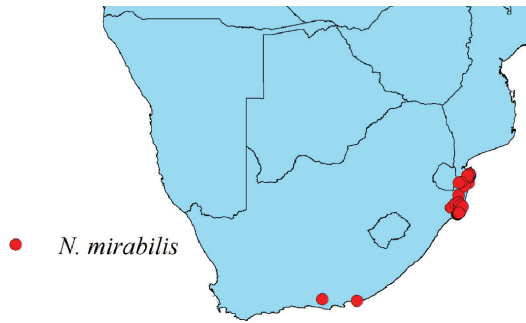


Fig. 25. Distribution map for the *tibialis* species-group.

Diagnosis: *N. mirabilis* is distinguished from other southern African species by having mesotibiae that are strongly modified by indentations and protrusions including a spine projecting from the anterior edge. *N. mirabilis* differs from the similar east African species, *N. tibialis* (Raffray, 1877), by lacking tubercles on the pygidium.

Examined non-type material: See Supplementary information.

Distribution: Although the type locality of this species is cited as Cape of Good Hope (South Africa) (Gory 1833) it is more likely that the type specimen was originally collected from the Eastern Cape coastline. *N. mirabilis* is a summer rainfall species associated with coastal forest (Davis et al. 2002) and, possibly, upland woody vegetation in the Eastern Cape (South Africa). However, it is primarily found in the Maputaland Coastal Forest Mosaic in KwaZulu Natal (South Africa) and in Maputo Elephant Reserve (Mozambique) (Fig. 25).

Remarks: *N. mirabilis* was described by Gory (1833) as *Sisyphus spinipes* but the name was preoccupied by *Sisyphus spinipes* (Thunberg, 1818). Arrow (1927) recognized the homonymy and renamed Gory's species as *Sisyphus mirabilis*.

Conservation status: *N. mirabilis* is listed as a Least Concern species on the IUCN Red Data List (Davis 2013d). However, a potential major threat is clearance of native habitats (woodland and forest).

***quadricollis* species-group** (Figs. 26A–B)

***Neosisyphus quadricollis* (Gory, 1833)** (Figs. 26, 27A)

Montreuil 2015b: 20.

Sisyphus quadricollis Gory, 1833

Gory 1833: 9; Harold 1869: 985; Péringuey 1901: 87; Arrow 1927: 459; Haaf 1955: 345; Ferreira 1972: 829.

Type locality: Cape of Good Hope.

Size: Male: length: 13.5–11; width: 6.5–5.4; female: length: 13.8–11; width: 6.5–5.5.

Diagnosis: *N. quadricollis* is close in appearance to *N. kuehni*. However, *N. quadricollis* may be separated by a combination of the following characters: elytra emarginated laterally with the concavity of the margin distinctly deep in the middle; the projecting metatrochanter in males is one-third of the total length of the metafemur; the metafemur lacks spines.

Examined non-type material: See Supplementary information.

Distribution: *N. quadricollis* has been recorded from deep sands and natural shrubland under drier, warmer winter rainfall climate on the southwest coast of South Africa (Western Cape) (Davis 1987, 1997; Davis et. al. 2008). In this region, it is active for a short period between late October to late December. It also has been collected between November and March at Willowmore and Lemoenkloof (Eastern Cape) in karoo vegetation of the late summer rainfall region (Fig. 28).

Neosisyphus kuehni (Haaf, 1955) (Figs. 26, 27B)
Montreuil 2015: 28.

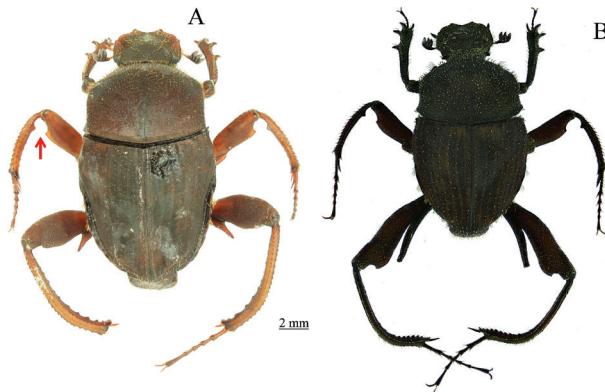


Fig. 26. Image of habitus of the *quadricollis* species-group: **A.** *N. quadricollis*, arrow showing the main diagnostic feature of the species-group; **B.** *N. kuehni*.

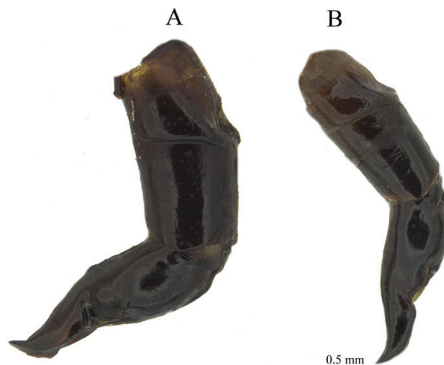


Fig. 27. Images of the aedeagi of the *quadricollis* species-group: **A.** *N. quadricollis*; **B.** *N. kuehni*.

Sisyphus kuehni Haaf, 1955

Haaf 1955: 345; Montreuil 2015: 28.

Type locality: Natal (Griqualand), South Africa.

Size: Male: length: 13.5–10; width: 6.5–5.5; Female: length: 13.0–11; width: 6.5–5.6.

Diagnosis: *N. kuehni* bears a gibbosity apically on the metafemur, which is lacking in the closely-related *N. quadricollis*. The projecting metatrochanter in males of *N. kuehni* is also longer, comprising over half of the total length of the metafemur. Unlike in *N. quadricollis*, the elytra in *N. kuehni* are not laterally emarginate.

Examined non-type material: See Supplementary information.

Distribution: *N. kuehni* occurs in highland grassland under the moist to wet conditions of the eastern escarpment of South Africa (Eastern Cape, KwaZulu Natal and Mpumalanga) (Fig. 28).

Conservation status: *N. kuehni* was assessed as a Data Deficient species for the IUCN Red Date List (Davis 2013g). Further collecting and monitoring is required to accurately assess the conservation status of this species.

***rubrus* species-group** (Figs. 29A–B)

***Neosisyphus macrorubrus* (Paschalidis, 1974)** (Figs. 29, 30A)

Montreuil 2015b: 20, 28

Sisyphus macrorubrus Paschalidis 1974

Paschalidis, 1974b: 300

Size: Males: length: 10.2–7.5 mm; width: 4.5–3.0 mm. Females: length: 10.5–7.0 mm; width: 4.5–3.0 mm.

Type locality: Vanstandensrus, OFS (Free State, South Africa)

Diagnosis: *N. macrorubrus* is very close in appearance to *N. rubrus*. However, it shows simple parameres (Fig. 30A) that lack the lateral protrusions, which typify *N. rubrus*.

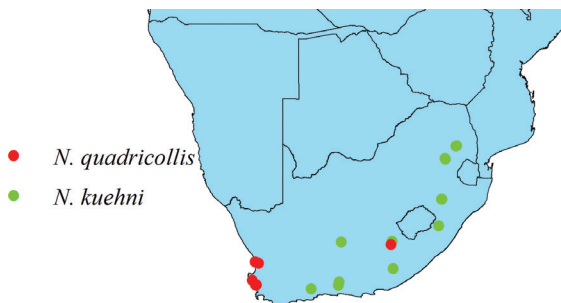


Fig. 28. Distribution map for the *quadricollis* species-group.

It also shows a different geographical distribution pattern and minimal overlap with *N. rubrus*.

Examined type material

Holotype: (♂ SANC) /SOUTH AFRICA, OFS, Vanstadensrus, 10.xii.1971, leg: Kirk/, /457/1/, /ex coll. CSIRO, Div. Entomology; S. African Station/; red label / Holotype ♂, *Sisyphus macrorubrus* **spec. nov.**, det. KM Paschalidis, 1974/, white label /SANC TYPH 00724/ Paratypes: (4♂, 4♀ SANC; 1♂, 1♀ SAM) SOUTH AFRICA, OFS, Ladybrand (Maseru Rd), 27.xi.1971, leg: Bornemissza & Aschenborn. (3♂, 3♀ SANC; 1♂, 1♀ SAM) SOUTH AFRICA, OFS, Zastron (21 mi N), 12.v.1972, leg: Olsen. (2♂, 1♀ SANC; 1♂, 1♀ SAM) SOUTH AFRICA, OFS, Caledon River (3 mi W Maseru), 2.iii.1971, leg: Aschenborn. (9♂, 6♀ SANC) SOUTH AFRICA, CP, Aliwal North (North), 3.iii.1971, leg: Aschenborn. (3♂, 3♀ SANC) SOUTH AFRICA, OFS, Wepener (22 mi N), 11.v.1971, leg: Aschenborn. (4♂, 3♀ SANC) SOUTH AFRICA, CP, Kimberley (25 mi S), 14.iii.1971, leg: Bornemissza & Kirk. (2♂, 1♀ SANC) SOUTH AFRICA, OFS, Rouxville, 01.xi.1971, leg: Bornemissza & Kirk. (1♂, 2♀ SANC) SOUTH AFRICA, OFS, Bloemfontein (11 mi N), 03.xi.1971, leg: Bornemissza & Kirk. (1♂, 3♀ SANC) SW.AFRICA (NAMIBIA), Outjo (15 kms N), 10.iv.1974, leg: Aschenborn.

Examined non-type material: See Supplementary information.

Distribution: *N. macrorubrus* is distributed in dry savanna, karoo and grassland, under cooler conditions in South Africa (Northern Cape and Free State), Namibia (Etosha Pan Okaukuejo) and Botswana (near Kanye) (Fig. 31).

Remarks: The type series of *S. rubripes* Boheman 1857 contained specimens belonging to two different species. Péringuey (1901) described one of Boheman's type specimens

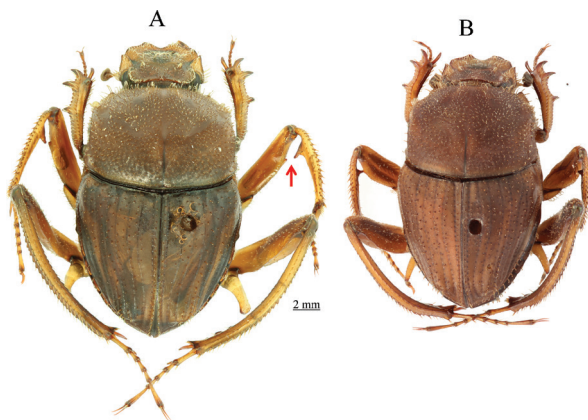


Fig. 29. Images of the habitus of the *rubrus* species-group, arrow showing the main diagnostic feature for the species-group: **A.** *N. macrorubrus*; **B.** *N. rubrus*.

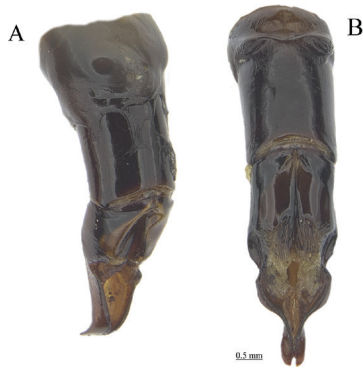


Fig. 30. Images of the aedeagi of the *rubrus* species-group: **A.** *N. macrorubrus*; **B.** *N. rubrus*.

under the name *S. rubripes*. However, the characters which Péringuey discussed did not match those of the holotype of *S. rubripes* (Arrow 1927), which means that, Péringuey was describing an unnamed species. The Péringuey species was recognized as new by Haaf (1955), Ferreira (1972), and later, Paschalidis (1974b) who proposed the current official name for the species.

***Neosisyphus rubrus* (Paschalidis, 1974)** (Figs. 29, 30B)

Montreuil 2015b: 20, 28

Sisyphus rubrus Paschalidis 1974

Paschalidis, 1974b: 299

Type locality: Castle Gorge (South Africa)

Size: Male: length: 9.0–6.0 mm; width: 4.1–3.0 mm. Female: length: 8.7–6.0 mm; width: 4.0–3.0 mm.

Diagnosis: *N. rubrus* closely resembles *N. macrorubrus* (Paschalidis 1974). However, the species can be distinguished by the lateral protrusions at the apices of the parameres in *N. rubrus* (Fig. 30B), which are lacking in *N. macrorubrus*.

Examined type material

Holotype: (♂ SANC) /SOUTH AFRICA, TVL, Castle Gorge (42 mi W Pretoria), 15.v.1971, leg: Bornemissza & Insley; /283a/, /ex coll. CSIRO, Div. Entomology; S. African Station;/ red label /Holotype ♂, *Sisyphus rubrus* **spec. nov.**, det. KM Paschalidis, 1974/, white label /SANC TYPH 00723/.

Paratypes: (5♂, 1♀ SAM) /RHODESIA, Sebakwel/, /*Sisyphus rubripes* Pér, det. Dr. Haaf, 1954/. (15♂, 15♀ SANC) SOUTH AFRICA, TVL, Castle Gorge (42 mi W Pretoria), 15.v.1971, leg: Bornemissza & Insley. (2♂, 1♀ SANC) SOUTH AFRICA, OFS, Vredefort (20 mi S), 03.xi.1971, leg: Bornemissza & Kirk. (3♂, 5♀ SANC) SOUTH AFRICA, CP, Mafeking, 22.v.1972, leg: Davis. (2♂, 1♀ SANC) SOUTH AFRICA, SE. TVL, Bergen, 1.v.1972, leg: Kirk. (1♂, 5♀ SANC) SOUTH AFRICA, N. TVL, Louis Trichardt (11 mi N), 14.xii.1971, leg: Olsen. (2♂, 1♀ SANC)

SOUTH AFRICA, CP, Aliwal North (22 mi S), 4.iii.1971, leg: Aschenborn, (50♂, 47♀ SANC) SOUTH AFRICA, E. TVL, Bosbokrand (5 mi N), 6.ii.1971, leg: Olsen. (2♂, 3♀ SANC) SOUTH AFRICA, Transkei, Umtata (10 mi N), 19.v.1971, leg: Aschenborn. (1♂, 2♀SANC) MOZAMBIQUE, Vila Pery, (5 mi E), 10.iv.1971, leg: Bornemissza & Aschenborn. (1♂ SANC) SOUTH AFRICA, Vryburg, N. CP, (15 mi E, Leeuwrand Farm), 7.x.1972, leg: Kluge.

Sisyphus rubripes Péringuey, 1901: Lectotype: (♂ SAM) /Natal, Durban;/ *Sisyphus rubripes* Pér, det. Dr. Haaf, 1954/; red label *Sisyphus rubripes* Pér, Lectotype, det: E. Haaf, 1954/.

Examined non-type material: See Supplementary information.

Distribution: *N. rubrus* is distributed in upland and coastal, moist grassland and savanna (Davis et al. 1999) in southeast Africa (Fig. 31).

Conservation status: *N. macrorubrus* and *N. rubrus* are listed as Least Concern species on the IUCN Red Data List (Davis 2013e, f).

Remarks: It has been suggested that on grounds of gender, the spelling of *N. rubrus* and *N. macrorubrus* should be changed to *N. ruber* and *N. macroruber* respectively (Davis et. al. 1999; Davis et al. 2008, Davis 2013e, f). It should be noted that; “*ruber*” is a masculine classical adjective, which has been used in a rare case as an alternative form of ‘*rubrus*’ (Brown, 1954). However, the original description of each species does not specify the etymological meaning of the specific name ‘*rubrus*’ (Paschalidis, 1974b). According to ICZN (article: 31.2.2) “Where the author of a species-group name did not indicate whether he or she regarded it as a noun or as an adjective, and where it may be regarded as either and the evidence of usage is not decisive, it is to be treated as a noun in apposition to the name of its genus”. Therefore, *rubrus* and *macrorubrus* must be treated as indeclinable names.

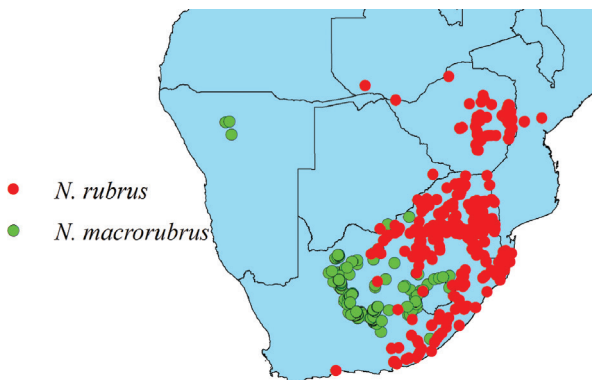


Fig. 31. Distribution map for the *rubrus* species-group.

Concluding Remarks

The southern African dung beetle species in the tribe Sisyphini *sensu stricto*, are revised taxonomically. Southern African sisyphines comprise 33 valid species, belonging to the genera *Sisyphus* and *Neosisyphus*. Of these, six species are described as new. Nevertheless, the *S. goryi* complex of species remains unclear due to the unavailability of type material. Therefore, both alpha taxonomic (including type material examination) and molecular approaches should be addressed in future studies. In addition, further clarification is required concerning the identity of *N. setiger* in comparison with southern African material now included under *N. setiger*, but formerly identified as *N. confrater*.

In southern Africa, five species-groups are proposed for each genus. It should be noted that the species groups comprise only taxonomic arrangements. However, a phylogenetic analysis of the tribe is required to test hypothetical relationships between and within the species groups proposed herein.

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