Zootaxa 4942 (4): 543–557
https://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4942.4.3
http://zoobank.org/urn:lsid:zoobank.org:pub:38464B00-0721-4C27-98F9-599D862E4CB1

Proper cleaning of keratin beetles reveals a cryptic species: *Phoberus fumarius* (Haaf, 1953) from southern Africa is reinstated as valid (Coleoptera: Trogidae)

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Abstract

Among the southern African Trogidae, *Trox fumarius* Haaf, 1953 is presently considered a junior subjective synonym of *Phoberus cyrtus* (Haaf, 1953). The availability of more specimens than were seen by previous workers, coupled with thorough removal of cuticular dirt and accumulated debris, allowed in-depth morphological study of these nominal taxa and reassessment of their synonymy. Consistent differences in external morphology and in aedeagal structure are observed. *Trox fumarius* is removed from synonymy with *Phoberus cyrtus*, reinstated as a separate species, and transferred to the genus *Phoberus* MacLeay, 1819. Both species are diagnosed and redescribed. Photographs of their holotypes and of cleaned specimens illustrate them. The distributions of these two putatively sister species are discussed along with their probable habitat associations. The species are allopatric and have non-overlapping associations with biomes and habitats. *Phoberus cyrtus* is reported from Botswana for the first time. The importance of properly cleaning terricolous beetles covered with dirt and debris that obscure taxonomic features is emphasised and guidelines to achieve this are presented.

Key words: Afrotropical Region, Botswana, distribution, habitat associations, Lesotho, revalidated species, Scarabaeoidea, South Africa, specimen preparation, taxonomy, techniques, Troginae

Introduction

Phoberus MacLeay, 1819 (Scarabaeoidea: Trogidae: Troginae) was recently revalidated as a genus separate from *Trox* Fabricius, 1775 (Strümpher *et al.* 2016b; also see Nikolajev 2016). At the inception of this study, the genus comprised 44 valid species and one valid non-nominotypical subspecies. Most *Phoberus* species are confined to the Afrotropical Region (including Madagascar), but two are present in the arid southern Palaearctic with *Phoberus puncticollis* (Haaf, 1953) restricted to the Arabian Peninsula and *Phoberus squamiger* (Roth, 1851) penetrating Arabia from the Afrotropics (Scholtz 1980a, b; Pittino & Bezděk 2016). Like all Trogidae, adult and larval *Phoberus* feed mainly on keratin in various kinds of shed, remnant or excreted animal material, an attribute rare in nature and with Trogidae unique among the Scarabaeoidea (Scholtz & Chown 1995; Sugiura & Ikeda 2014).

In the first part of his landmark treatment of the Afrotropical Trogidae, Haaf (1953) newly described *Trox cyrtus* and *Trox fumarius* on subsequent pages, the former from Lesotho and the latter from the present-day Eastern Cape Province of South Africa. The monograph by Scholtz (1980a) was the next milestone in the study of the Afrotropical keratin beetles. Scholtz (1980a: 97) synonymised *Trox fumarius* and *Trox cyrtus* on the grounds of confusing but similar male genitalia, also stating that the "external morphology of the two forms is identical." Scholtz (1980a) established *Trox cyrtus* as the senior synonym, hence valid. Strümpher *et al.* (2016b) transferred *Trox cyrtus* to the genus *Phoberus*.

Few *Phoberus cyrtus* (Haaf, 1953) specimens, including specimens of what we consider to be the valid species *Phoberus fumarius*, were available for Scholtz's (1980a) study. Subsequently more specimens of *Phoberus cyrtus sensu* Scholtz (1980a) have accumulated in collections, even if they are still comparatively scarce. This larger number of specimens allowed us to study intraspecific variation, especially of the male genitalia, and evaluate the

Accepted by A. Bezděk: 22 Feb. 2021; published: 16 Mar. 2021

synonymy enacted by Scholtz (1980a). Close examination both of specimens examined by Scholtz (1980a) and of the more recently added specimens confirmed the presence of two distinct morphotypes. The consistent differences observed in external morphology and in the shape and structure of the male genitalia of the two nominal species agree with Haaf's (1953) original treatment. This warrants reinstating *Trox fumarius* as a valid species.

The name *Trox fumarius* is hence in this paper removed from synonymy with *Phoberus cyrtus*, reinstated as valid, and newly combined with the genus name *Phoberus*. To clarify differences between *Phoberus cyrtus* and *Phoberus fumarius* and to allow their recognition and identification, both species are redescribed and illustrated with photographs of the holotypes and non-type specimens from which obscuring dirt had been cleared. The geographic occurrences of the two putatively sister species are recorded and discussed along with their probable habitat associations.

Material and methods

This taxonomic study was based on museum material housed in the following institutions:

BMSA—National Museum, Bloemfontein, South Africa
MNHN—National Museum of Natural History, Paris, France
MZLU—Entomological Collections, Lund University, Lund, Sweden
NHMB—Natural History Museum Basel, Basel, Switzerland
SAMC—Iziko South African Museum, Cape Town, South Africa
SANC—South African National Collection of Insects, Pretoria, South Africa
TMSA—Ditsong National Museum of Natural History, Pretoria, South Africa
UPSA—Department of Zoology & Entomology, University of Pretoria, Pretoria, South Africa

Morphological terminology generally follows Scholtz (1980a). Images of type specimens of *Trox fumarius* and *Trox cyrtus* were made, at our request, by curatorial staff of the museums where those specimens are deposited. Preparation and photography of all other specimens and of male genitalia follow the techniques used by Strümpher & Scholtz (2019). Label data of type specimens are cited verbatim: the contents of a single label are enclosed in double parentheses [“”]; a vertical bar [|] separates subsequent lines on a single label; subsequent labels are separated by a double vertical bar [||]; and clarifications and information not on labels are provided between square brackets. The label data of non-type specimens are presented in a standardised format.

For the two nominal species concerned, we re-examined material from all collecting events cited by Haaf (1953) and by Scholtz (1980a). The distribution map herein is based on these specimens, supplemented with one additional locality record published by Haaf (1959), plus all pertaining specimens that had accumulated in collections since the study of Scholtz (1980a) and accessible to us.

We emphasise the importance of properly cleaning adult trogid specimens for taxonomic study. Adult keratin beetles are famously covered with an oily or fatty substance of unknown composition in which environmental dirt accumulates until the beetles are encrusted with soil and gunk. This is a significant handicap in the study of these beetles, since important taxonomic features are obscured. For decades the junior author had considered Trogidae to be muddy, rather featureless and intractable beetles. Over the past two decades, the senior author has increasingly discovered a rich suite of character states visible once the obscuring layer of dirt is cleared away. Were it not for properly removing such dirt, the plumose setal glands on the clypeus and pronotum of the Australian *Omorgus capillamentis* Strümpher & Scholtz, 2011 would not have been discovered—a character hitherto unknown in any other Trogidae (Strümpher & Scholtz 2011).

We strongly recommend the cleaning procedure first suggested by Diéguez (2008) and recently published in English by Costa-Silva & Diéguez (2020). In promoting this procedure, we shamelessly repeat the essence of its three steps:

(1) Work with relaxed specimens. Wash the specimens in a mild solution of detergent at 60–70°C. Rinse with cold water.

(2) Soak a specimen in a weak solution (3–5% by volume) of potassium hydroxide (KOH) or sodium hydroxide (NaOH) at 60–70°C. Simultaneously clear debris from the cuticle with a fine but sturdy brush. Five to ten minutes are reasonable for this step; more dirt requires more time. Rinse the KOH or NaOH from the specimen with cold water.

(3) Neutralise any alkalinity by dunking the specimen in a weak solution of acetic acid. Rinse with cold water again.

Diéguez's (2008) procedure differs from currently commoner practices by adding the alkali treatment. Expanding on Diéguez's (2008) guidelines, we propose a fourth step:

(2a) After the alkali and brush treatment, briefly sonicate the specimen in water in an ultrasonic cleaner. This action allows for loosened debris to be dislodged from punctures and grooves where it may still have been stuck. This step also serves as rinsing.

We recommend similar, fearless cleaning of other terricolous beetles which are also covered with dirt and debris. This phenomenon is seen in numerous beetle families, and even outside the Coleoptera, in some Heteroptera for example. As an example of how taxonomic study of another beetle family is markedly improved by the rigorous cleaning of soiled specimens, we point to the work of Roman Borovec and his collaborators on small South African terricolous weevils (*e.g.* Borovec & Meregalli 2013; Borovec & Skuhrovec 2019).

Phoberus MacLeay, 1819

Phoberus MacLeay, 1819: 137–138 (original description); Strümpher *et al.* 2014: 557–558 (phylogenetics); Strümpher *et al.* 2016b (reinstated as genus); Zídek 2017: 96–113 (checklist).
A bibliography of *Phoberus* was provided by Strümpher *et al.* (2016b: 79–80).

Type species: *Trox horridus* Fabricius, 1775 (by monotypy).

Phoberus cyrtus (Haaf, 1953)
(Figs 1–7, 15, 21)

Trox cyrtus Haaf, 1953: 333 (original description).
Trox (*Trox*) *cyrtus*: Scholtz 1980a: 66, 68, 87, 97 (redescription, illustrations, distribution); Scholtz 1982: 3 (catalogue).
Trox (*Phoberus*) *cyrtus*: Zidek 2013: 9 (checklist).
Phoberus cyrtus: Strümpher *et al.* 2016b: 78 (new combination); Zídek 2017: 99 (checklist).

Type locality. Vallée du Haute Orange [Valley of high Orange River] (border of Mohale's Hoek and Quthing Districts, Lesotho)

Type material examined. All type specimens were examined through detailed photographs. **Holotype** ♂ (MNHN, aedeagus extracted) (Figs 1–3): Rectangle, faded blue cardstock: "MUSEUM PARIS | Basoutoland, Lessouto [Lesotho] | Vallée du H[t] Orange [Valley of high Orange River, 30°17′S 27°46′E], 1500 m. | (legit R. Ellenberger) | E. HAUG 1906" || Rectangle, red cardstock: "HOLOTYPE" || Rectangle, minimally foxing white: "Trox | cyrtus Haaf | det.Dr.E.Haaf 1953" || Rectangular curatorial label, white: "MNHN | EC10025". **Paratypes** 2♂♂ (MNHN): Blue label identical || Rectangle, red cardstock: "PARATYPE" || Foxy white label identical || White curatorial labels: "MNHN | EC10027" and "MNHN | EC10029". **Paratypes** 3♀♀ (MNHN): Labels identical to those of ♂ paratypes, but each specimen with an additional foxy white square: "♀" || "MNHN | EC10028"; "MNHN | EC10026" with red label: "ALLOTYPE"; "MNHN | 10030" with different determination label, white rectangle: "PARATYPE | *Trox* | *cyrtus* Haaf, 1953". **Paratype** 1♂ (MNHB): Blue label identical || Rectangle, white, preprinted red text interspersed with black handwriting: "PARATYPUS | Trox | cyrtus sp.n. | det.Dr.E.Haaf 1953".

Haaf (1953) described this species from six males and four females, all with the same label data. We studied four males and three females of the type series, including the holotype. Haaf (1953) indicated that all ten type specimens would be lodged in the MNHN, but we located one male in the MNHB.

Additional material examined. SOUTH AFRICA. Eastern Cape Province. 1♂ Aliwal North, [30°42′S 26°42′E], 15–25.ii.1971, Snyman & Jones (TMSA). **Free State Province.** 13♂ Nova 667 [farm], near Ladybrand, SE2927Ab [29°07′S 27°22′E], 19–22.i.1976, GW Ferreira, S van Ee (BMSA: BMSA(C)-21032–21044) (Figs 4–7). 3♂, 3♀ *idem* but 01–12.ii.1977, GW & MC Ferreira, A Strydom (BMSA: BMSA(C)-21045–21046; BMSA(C)-21975; BMSA(C)-21978; BMSA(C)-22031; BMSA(C)-22293). 4♂, 4♀ Kerkenberg, near Harrismith, 2829Ac/d [28°30′14″S 29°06′30″E], 08–18.xi.1976, Museum staff (BMSA: BMSA(C)-21020–21027). **KwaZulu-Natal Province.** 1♂ [uKhahlamba-Drakensberg Park World Heritage Site], Mdedelelo Forestry Area, 29°07′S 29°26′E, 13–14.xi.1981, SJ van Tonder, C Kok (SANC). 1♀ [uKhahlamba-Drakensberg Park World Heritage Site], Giant's

Castle Game Reserve, at Bannerman Hut, 29°15′S 29°26′E, 2,300 m, 24.iv.1994, J duG Harrison, R Stals (TMSA). **Mpumalanga Province.** 1♂ Kruger National Park, Skukuza Rest Camp, 24°59′S 31°36′E, 28.i.1994, E-Y:2952, UV light trap, S Endrödy-Younga (TMSA). 1♂ Winkelhaak [mine], Ermelo district, [26°30′S 29°07′E], x.1970, L Schulze (TMSA). **North West Province.** 2♂, 7 unsexed: Rustenburg, [25°39′S 27°14′E], 28.x.1956 (NHMB, through photographs). 7 unsexed: *idem* but 13.viii.1961 (NHMB, through photographs). **BOTSWANA. South-East District.** 1♂ Otse, [25°02′S 25°44′20″E], 02.ix.1963, JA Nagle (TMSA).

Redescription. *Size*: Length: 9–13 mm. Width across humeri: 5–8 mm.

Colour (Figs 1, 4–5): Matt black, with dull reflection. Body setae yellow unless stated otherwise below.

Head (Figs 4–5): Surface sculpted with discrete punctures, surfaces between punctures with dull reflection. Clypeus triangular, straight, apically deflexed and rounded; anterior clypeal margin entire, bare; clypeogenal and frontoclypeal sutures distinctly raised; frontoclypeal suture complete, with a low clypeogenal tubercle on either side, tubercles punctate. Frons raised, with paired, arched, setose frontoclypeal carinae delimiting two semicircular depressions, separated by a distinct, setose median carina. Genal angles obtuse, wide, recurved; genal margin with straight setae. Eyes large and bulbous, barely visible in dorsal view. Antennal scape rounded, longer than wide, punctate, with long light brown setae; pedicel attached apically; antennal club dark brown, velutinous. Setae around mouthparts dense, yellow to rust-brown.

Pronotum (Figs 4–5, 15): Slightly narrower than elytra. Surface with discrete, round punctures, surfaces between punctures dull to shiny. Lateral margins broad and flat, somewhat explanate, entire to irregularly, coarsely dentate, strongly attenuate anteriad, with fringes of long, straight setae. Apex with row of long, recurved, evenly spaced setae. Base with dense fringe of straight setae. Median discal area only slightly raised, broad, narrowing towards base to form a distinct triangular disc; dorsal outline evenly arched in anterior view; median discal depression shallow; median basal tubercles distinct; lateral basal tubercles fused to those in front of them to form a low, broad carina; all tubercles and ridges with setal tufts.

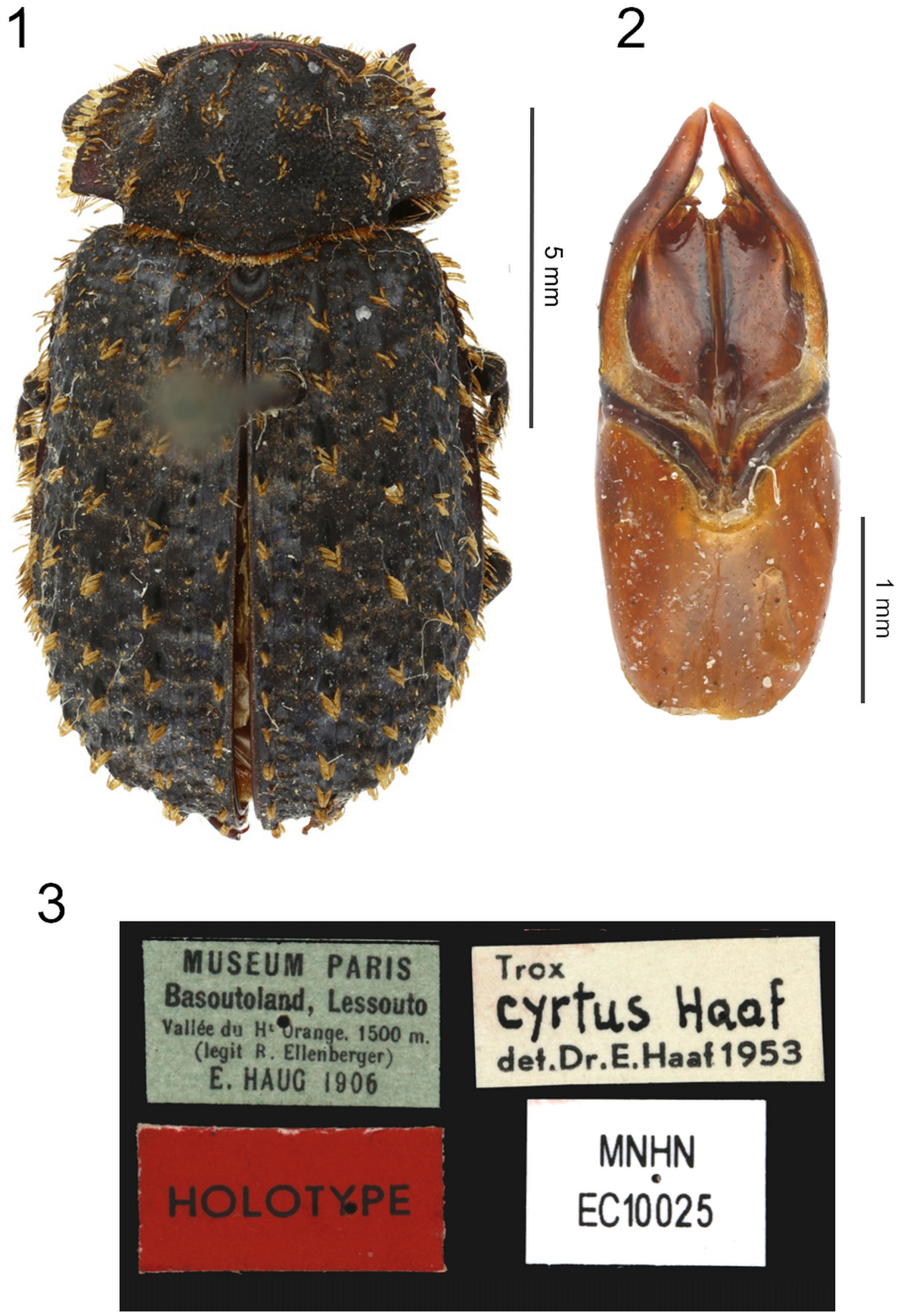
Scutellum (Figs 4–5): Longer than wide; surface smooth; apicolaterally rounded, lateral margins straight; mediobasally depressed, depression weakly sculpted to punctate.

Elytra (Figs 1, 4–5): Elongate, length 2.7–2.8 pronotum length, lateral margins subparallel, sides narrow, lateral margin finely dentate and bearing long setae; widest at c. 0.6 length; profile slightly convex, attaining maximum height approximately in the middle, strongly declivous posteriorly. Humeral calli prominent, with short setae. Sutural margin raised, surface smooth, with low (sometimes flat) round to oval tubercles, widely separated and irregularly distributed along margin, roughly of similar size for 0.75 elytral length, thereafter decreasing in size until barely discernible; these tubercles smooth, dull shiny, each with a posterior setal tuft. Elytral costae distinct, even-numbered costae more prominent than odd-numbered. Even-numbered costae with raised oval tubercles widely and fairly evenly spaced along elytral length; these tubercles smooth, shiny, each with a posterior setal tuft. Apical callosity present on fourth costal interval at top of elytral declivity. Elytral costae 2 and 4 with 5–8 tubercles for 0.75 elytral length (up to apical callosity); odd-numbered costae marked by small round to oval, shiny tubercles, each with one or two short setae, these tubercles regularly spaced, roughly of equal size for 0.75 elytral length, thereafter decreasing in size until barely discernible. Dorsally costae 1–4 separated from intercostae as slightly elevated bands; laterally costae 5–9 barely discernible as bands. Intercostae with very shallow, undulating depressions separated by transverse ridges; dorsally, margins of intercostae 1–4 marked by weak narrow longitudinal ridges; intercostal carinae laterally vestigial, barely discernible or lacking.

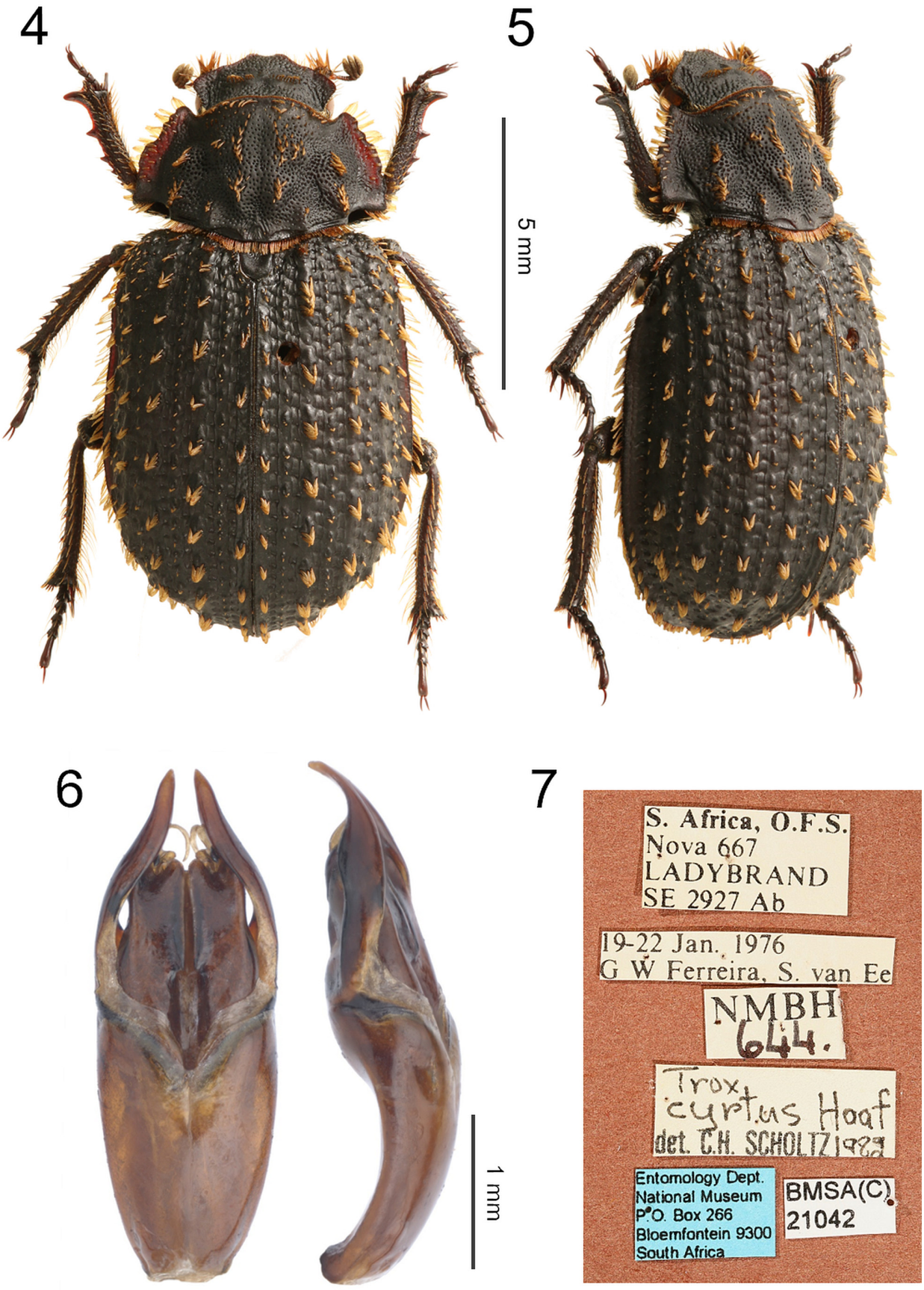
Legs (Figs 4–5): Surfaces rugose and coarsely punctate. Protibia dorsally keeled, with small apical process and row of short, stout transverse setae; outer margin with 2 distinct median teeth and 3–5 smaller basal teeth; inner margin with long, dense setae; protibial apex divided into two spines, distinct in males, females with spines partly fused; protibial spur as long as, or longer than, third tarsomere, flattened laterally, apex pointed and recurved. Mesotibia and metatibia with outer margins dentate and with long, dense yellow setae; with 2 apical spurs on inner margin, spurs as long as, or slightly longer than, second tarsomere. Tarsomeres ventrally with sparse setae. Tarsal claws simple, equal.

Metathoracic wings: Complete.

Male genitalia (Figs 2, 6): Symmetrical, slender; phallobase arched, slightly longer than parameres. Parameres long, extending beyond median lobe, apices pointed, long and decurved. Median lobe divided into two symmetrical parts, these narrow, subparallel, in dorsal view concave upward; apices acutely rounded; two bladelike projections and hooks visible between parameres and median lobe.



FIGURES 1–3. Holotype of *Trox cyrtus* Haaf, 1953 (MNHN). 1, habitus, dorsal view; 2, aedeagus, dorsal view; 3, holotype labels. Photographs by Antoine Mantilleri, copyright MNHN.



FIGURES 4–7. *Phoberus cyrtus* (Haaf, 1953), specimen with obscuring layer of dirt removed (BMSA). 4, habitus, dorsal view; 5, habitus, lateral view; 6, aedeagus, dorsal and lateral views; 7, labels.

Diagnosis. *Phoberus cyrtus* and *Phoberus fumarius* are very similar, but the former can be distinguished from the latter in having a less coarsely punctate pronotum (Figs 15–16). Additionally, the arrangement of the tubercles on elytral costae 2 and 4 differs between the species: *Phoberus cyrtus* has these tubercles widely separated, with 5–8 tubercles between the elytral base and the apical callosity, whereas these tubercles in *Phoberus fumarius* are close together, with 8–12 tubercles between the elytral base and the apical callosity. The male genitalia of the two species are distinctive with the most important differences found on the median lobes. *Phoberus cyrtus* have the lobes narrow and their apices sharper or angular, whereas in *Phoberus fumarius* the lobes are broad and their apices more rounded (as described in the text and as shown in Figs 2 and 6 versus Figs 9 and 13). Available information strongly suggests that the two species are allopatric and existent only in different, non-overlapping biomes, *Phoberus cyrtus* in the summer rainfall area of southern Africa and *Phoberus fumarius* in the winter rainfall area (see text and Fig. 21).

Phoberus sulcatus (Thunberg, 1787) (Figs 17–20) is widespread and common throughout South Africa (Scholtz 1980a). Both *Phoberus cyrtus* and *Phoberus fumarius* have an external appearance similar to that species, and the three may be confused. In collections they have certainly been confused. Of the two species treated in this work, *Phoberus fumarius* is more likely to be confused in this way. *Phoberus sulcatus* differs from both the other species in bearing a distinct median pronotal depression (Fig 19) and having the pronotal and elytral carinae and tubercles more pronounced and higher (Figs 17, 19). The male genitalia of *Phoberus sulcatus* are indubitably different with the median lobe of this species divided into two broadly curved lobes (Fig 18). We found that *Phoberus sulcatus* can readily be distinguished from these other two species by the larger shadows cast under oblique lighting by its more prominent paramedian pronotal carinae; specimens should not be too soiled for this comparison to succeed.

Geographic distribution. *Phoberus cyrtus* is known from South Africa, Lesotho and Botswana (Fig. 21). In South Africa the species has been recorded from the Eastern Cape, KwaZulu-Natal, Mpumalanga and North West Provinces.

Broad habitat associations. As far as it is known, *Phoberus cyrtus* is restricted to the summer rainfall region of southern Africa, in contrast to its putative sister species *Phoberus fumarius*, which is confined to the winter rainfall region. *Phoberus cyrtus* is known from two biomes. In the south of its known distribution, the species lives in the Grassland Biome, where it is present in the Mesic Highveld Grassland–, Drakensberg Grassland– and Dry Highveld Grassland Bioregions (biomes and bioregions following Mucina & Rutherford 2006; Dayaram *et al.* 2019). Towards the north and west of its range, the species occurs in the Savanna Biome (Central Bushveld– and Lowveld Bioregions). Whereas the grassland habitats are cool and mesic, the savanna habitats are warm to hot and experience extended dry periods. This discordant distribution among two sets of habitats with significantly different bioregional climate regimes may indicate a eurytopic species.

Phoberus fumarius (Haaf, 1953), revalidated and new combination

(Figs 8–14, 16, 21)

Trox fumarius Haaf, 1953: 334 (original description); Haaf 1959: 473 (checklist, localities); Scholtz 1980a: 97 (new junior synonym of *Trox* (*Trox*) *cyrtus*); Scholtz 1982: 3 (catalogue, as synonym of *Trox* (*Trox*) *cyrtus*); Zidek 2013: 9, 10 (checklist, as synonym of *Trox* (*Phoberus*) *cyrtus*); Zídek 2017: 99, 101 (checklist, as synonym of *Phoberus cyrtus*).

Type locality. Willowmore (Sarah Baartman District Municipality, Eastern Cape Province, South Africa)

Type material examined. **Holotype** ♂ (NHMB, aedeagus extracted, examined through detailed photographs) (Figs 8–10): Rectangle, greyish white: "[South Africa, Eastern Cape Province] Willowmore [33°17′S 23°29′E] | 30.10.[19]48." || Rectangle, white: "Süd-Afrika | leg. C. Koch" || Rectangle, white: "Museum Frey | Tutzing" || Rectangle, white with red bars at top and bottom, preprinted red text interspersed with black handwriting: "HOLOTYPUS | Trox | fumarius sp.n. | det.Dr.E.HAAF 1953" || Rectangle, white, preprinted black text interspersed with black handwriting: "Trox fumarius | Haaf (= Trox | cyrtus Haaf. | det. C.H. SCHOLTZ 1979" || Rectangle, white cardstock with black margin: "*Phoberus fumarius* | (Haaf, 1953) | stat. rev., comb. nov. | Strümpher & Stals 2021". **Paratype** 1♂ (TMSA, aedeagus extracted): Rectangle, yellowing white: "Willowmore, | Capland. | Dr. H. Brauns." || Narrow rectangle, red: "PARATYPE" || Rectangle, white, preprinted text interspersed with handwriting: "Trox | fumarius Haaf | det.Dr.E.Haaf 1953" || Rectangle, white cardstock with orange margin: "Paratypus 1953 | Trox fumarius sp.n | E. Haaf" || Rectangle, white cardstock with black margin: "*Phoberus fumarius* | (Haaf, 1953) | stat. rev., comb. nov. | Strümpher & Stals 2021".

Haaf (1953) described *Trox fumarius* from three males and one female, deposited in NHMB (among these we studied the male holotype); one male in the Hungarian Natural History Museum, Budapest (not seen by us); and one male and one female in TMSA, of which we studied the male paratype but could not locate the female.

Additional material examined. SOUTH AFRICA. Northern Cape Province. 1♂ Richtersveld, Paradieskloof [*recte* Paradyskloof], 28°19′S 17°00′E, 06.ix.2001, E-Y:3412, light trap, TMSA staff (TMSA). 1♀ *idem* but E-Y:3413, on vegetation [*sic*] (TMSA). 2♀ Richtersveld, Gelykswerf [Mountain], [c. 28°22′S 17°08′E], x.1955, C Koch (TMSA). 1♂ Namaqualand, Swart Doring River, [30°48′S 17°54′E], 02–03.x.1966, S.A.M. [South African Museum] (TMSA). 1♂ Namaqualand, Dermbergsdraai Farm, 30°47′S 17°43′E, pitfall traps: 24.viii.1979–26.x.1979, E-Y:1589, S Endrödy-Younga (TMSA). 1♂ Kamieskroon, 30°12′S 17°56′E, 01–13.ix.2003, A Frolov, C Deschodt (UPSA, preserved in 99% ethanol). 1♀ Namaqualand, Garies, [30°33′30″S 17°59′E], vi.1930, Museum staff (SAMC: SAM-COL-A082505). **Western Cape Province.** 1♂, 1♀ Farm Zeekoeivlei [*recte* Seekoevlei], near Clanwilliam, [32°09′S 18°45′E], 27.xi.2003, farm staff (TMSA). 1♂ Saldanha Bay, Jutten Island, [33°05′0.5″S 17°57′19″E], 25.i.[19]51, Swedish South African Expedition, 1950–1951, P Brink, G Rudebeck (MZLU: MZLU-COL00007061, through photographs). 1♂, 4♀ Cape Town, 65 km N, 33°21′S 18°15′E, pitfall traps: 30.viii.1983–01.xi.1983, E-Y:1999, S Endrödy-Younga, M-L Penrith (TMSA). 20 unsexed: Dassen Island, 33°25′24″S 18°05′14″E, 18.ix.2009, WP Strümpher, CH Scholtz (UPSA, preserved in 99% ethanol); 6♂, 3♀ *idem* but dry-mounted (SANC); 1♂ *idem* but dry-mounted (SAMC: SAM-COL-A082509). 2♂ Citrusdal, [32°35′S 19°01′E], v.1974, Honiball (TMSA). 1♀ Cape Town, [33°55′S 18°25′E], 1913 (TMSA). 1♂ CPT [Cape Town], Green Point, [33°54′25″S 18°24′23″E], 16.vi.1958, JA Nagle (TMSA). 2♂ Cape-Karoo, Farm Zwartskraal, 33°10′S 22°32′E, pitfall traps: 08.xi.1978–17.i.1979, E-Y:1540, S Endrödy-Younga (TMSA); 1♂ *idem* but 01.ii.1979–02.iii.1979, E-Y:1545, R Oosthuizen (TMSA); 1♂ *idem* but 02.iii.1979–31.iii.1979, E-Y:1552, R Oosthuizen (TMSA); 1♂ *idem* but 23.vii.1979–05.ix.1979, E-Y:1637, R Oosthuizen (TMSA); 1♂ *idem* but 05.ix.1979–25.x.1979, E-Y:1639, R. Oosthuizen (TMSA); 1♂ *idem* but 25.x.1979–09.xii.1979, E-Y:1672, R. Oosthuizen (TMSA); 1♂ *idem* but 01.i.1980–18.ii.1980, E-Y:1699, R Oosthuizen (TMSA); 1♂ *idem* but 22.ix.1980–08.xi.1980, E-Y:1717 (TMSA). 1♀ Touws R[iver], [33°20′15″S 20°02′E], 1896, Purcell (SAMC: SAM-COL-A082507). 1♂, 2♀ Zwartberg Pass [*recte* Swartberg Pass], [33°21′S 22°03′E], Prince Albert district, xii.1968, RH Jones, JH Potgieter (TMSA); 1♂, 1♀ *idem* (SAMC: SAM-COL-A082508, SAM-COL-A082510). 1♀ Swartberge [Swartberg Mountains], Blesberg East, 2,000 m, 23°25′S [*recte* 33°25′S] 22°41′E, pitfall traps: 16.xii.1976–02.iii.1977, E-Y:1532, S Endrödy-Younga (TMSA). 1♀ Gamkaberg Nature Reserve, [33°43′S 21°54′E], ii–iii.1994, T Berry (TMSA). 1♂ Riversdale, [34°02′45″S 21°15′45″E], RJ Power (TMSA) (Figs 11–14); 2♂, 1♀ *idem* (SAMC: SAM-COL-A082503–A082505).

Redescription. *Size*: Length: 13–14 mm. Width across humeri: 6–8 mm.

Colour (Figs 8, 11–12): Matt black. Body setae yellow-brown (amber) to light rust-brown.

Head (Figs 11–12): As in *Phoberus cyrtus*, except surface coarsely sculpted and densely punctate, surfaces between punctures smooth, dull matt; antennal scape with long yellowish-brown to rust-brown setae.

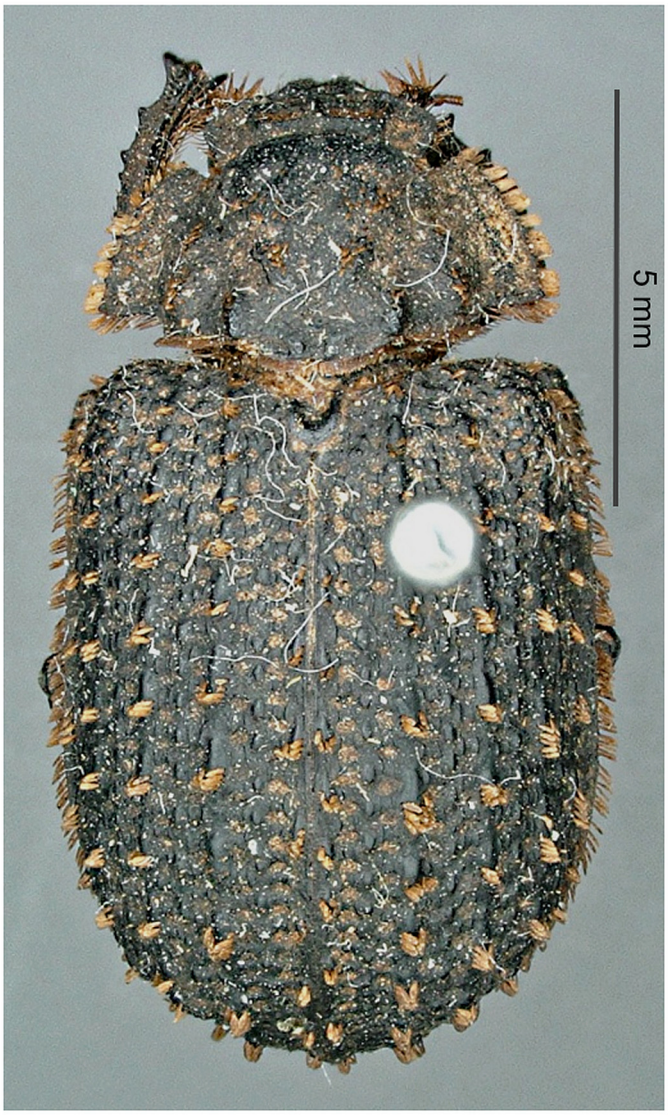
Pronotum (Figs 11–12, 16): As in *Phoberus cyrtus*, except surface coarsely punctate; punctures prominent, round; surfaces between punctures smooth, dull matt.

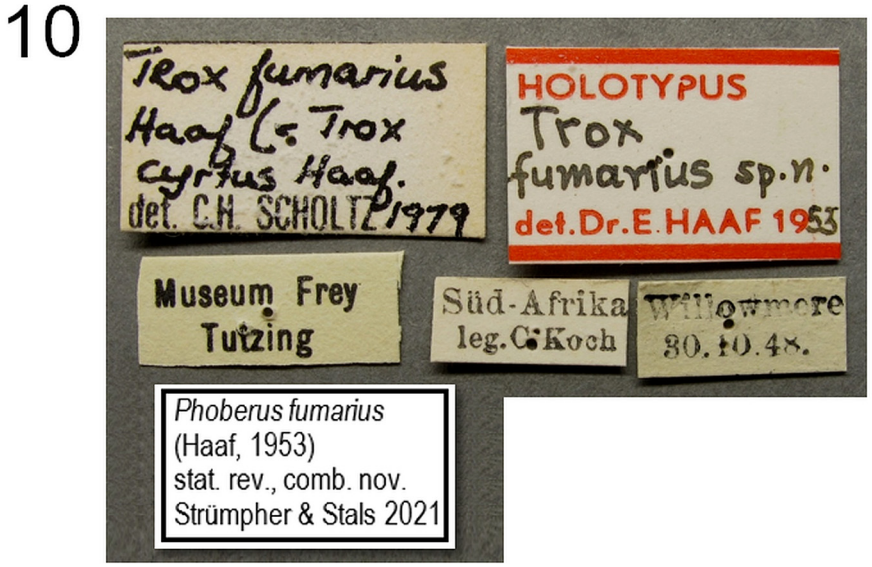
Scutellum (Figs 11–12): Oval, rounded; surface smooth; lateral margins flat; mediobasally depressed, depression punctate.

Elytra (Figs 8, 11–12): Relative dimensions, margins and profiles as in *Phoberus cyrtus*. Humeral calli as in *Phoberus cyrtus*. Sutural margin raised, surface smooth, with distinct round to oval tubercles regularly distributed along margin, roughly of similar size for 0.75 elytral length, thereafter decreasing in size until barely discernible; these tubercles as in *Phoberus cyrtus*. Elytral costae distinct; even-numbered costae with prominently raised oval to elongate tubercles, roughly of equal size and height, evenly spaced along elytral length; these tubercles smooth, dull, each with a posterior setal tuft. Apical callosity as in *Phoberus cyrtus*. Elytral costae 2 and 4 with 8–12 tubercles for 0.75 elytral length (up to apical callosity); odd-numbered costae marked by small round to oval, dull shiny tubercles like in *Phoberus cyrtus*, but these tubercles closely spaced. Costae 1–8 separated from intercostae as well-defined elevated bands. Intercostae with undulating depressions separated by transverse ridges, the margins of intercostae 1–7 marked by distinct, narrow longitudinal ridges, thereafter intercostae with carinae vestigial, barely discernible or lacking.

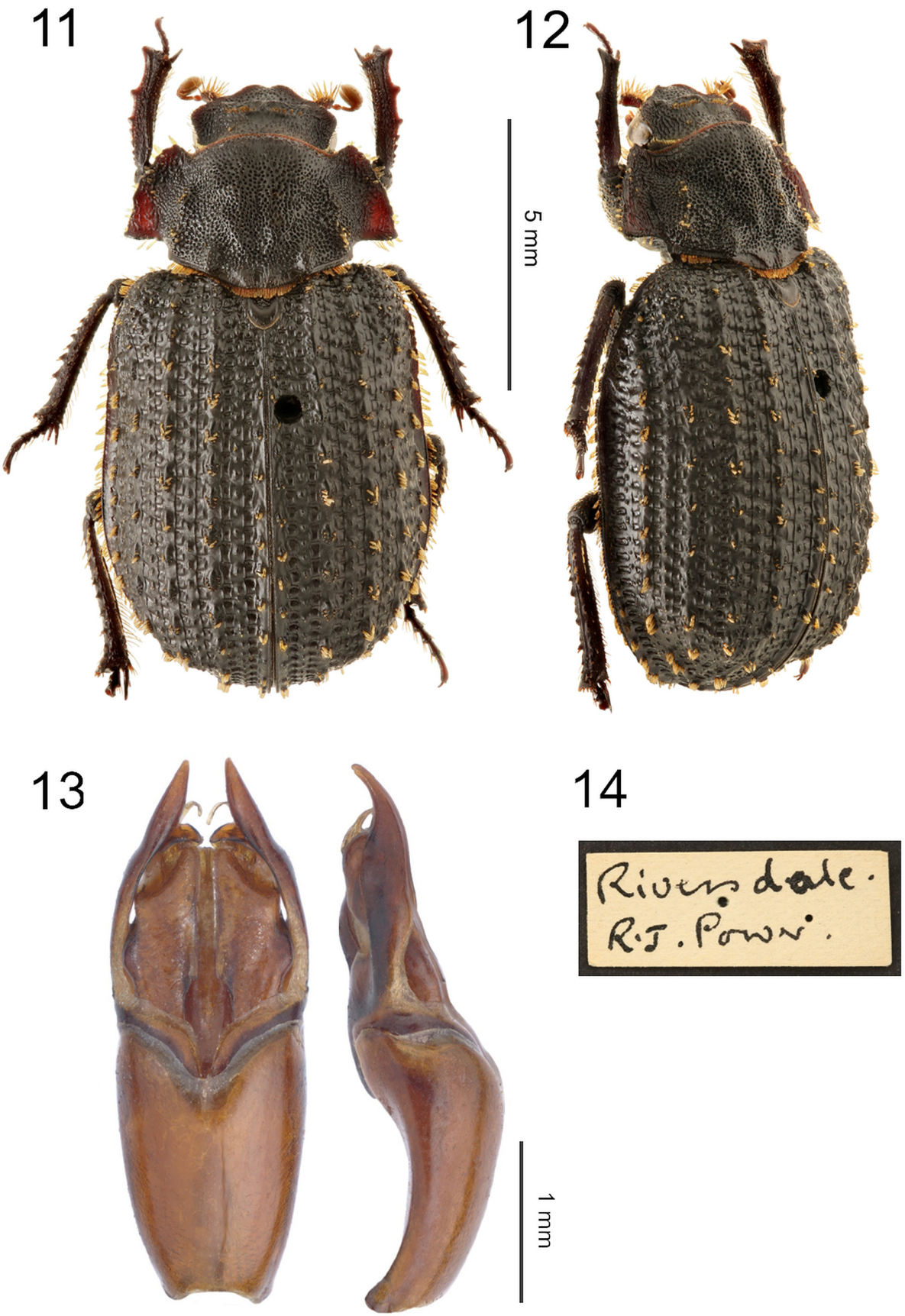
Legs (Figs 11–12): As in *Phoberus cyrtus*.

Metathoracic wings: Complete.

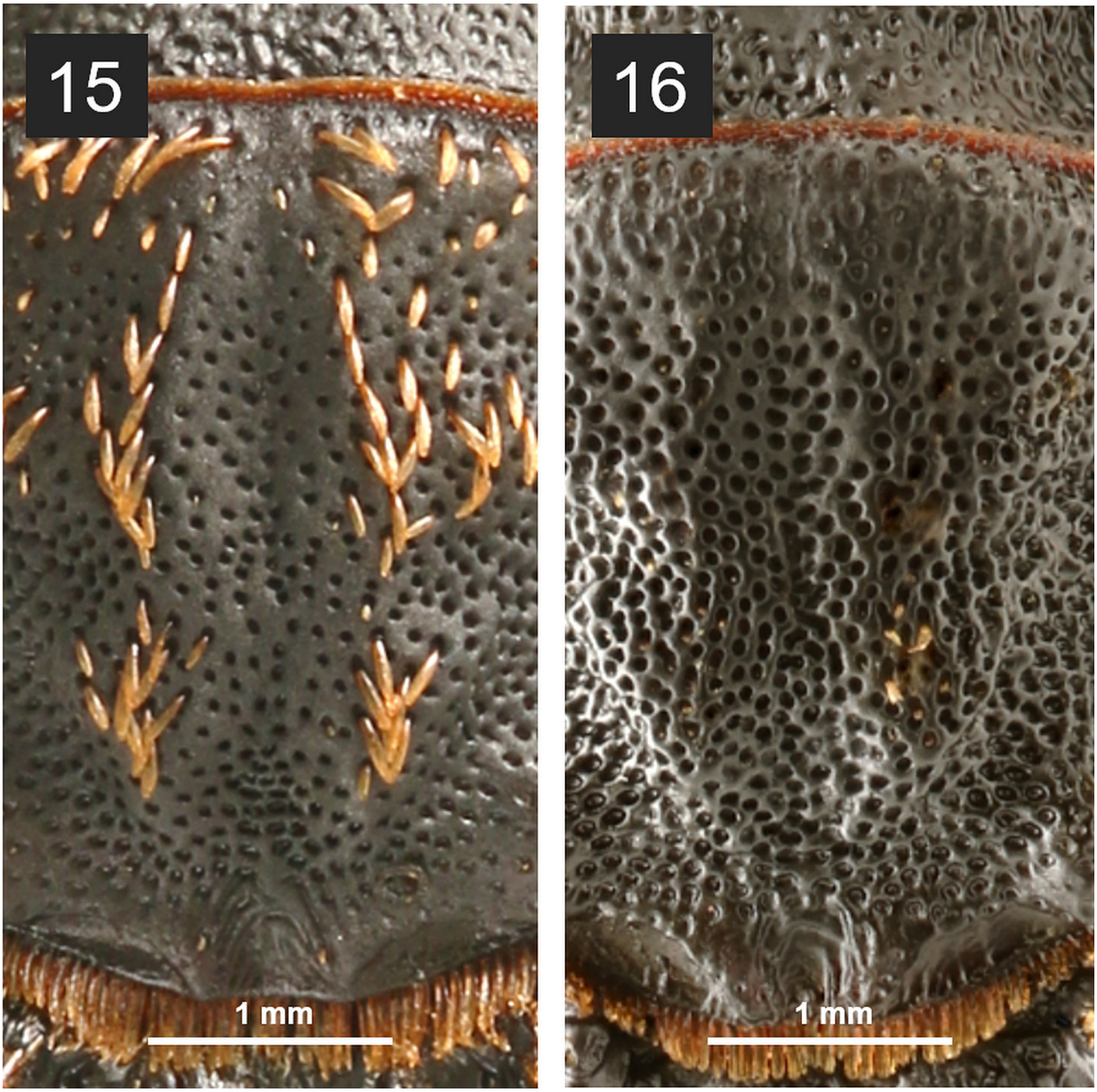




FIGURES 8–10. Holotype of *Trox fumarius* Haaf, 1953 (NHMB): 8, habitus, dorsal view; 9, aedeagus, dorsal view; 10, holotype labels. Photographs by Christoph Germann, copyright NHMB.



FIGURES 11–14. *Phoberus fumarius* (Haaf, 1953), **revalidated and new combination**, specimen with obscuring layer of dirt removed (TMSA). 11, habitus, dorsal view; 12, habitus, lateral view; 13, aedeagus, dorsal and lateral views; 14, locality label.

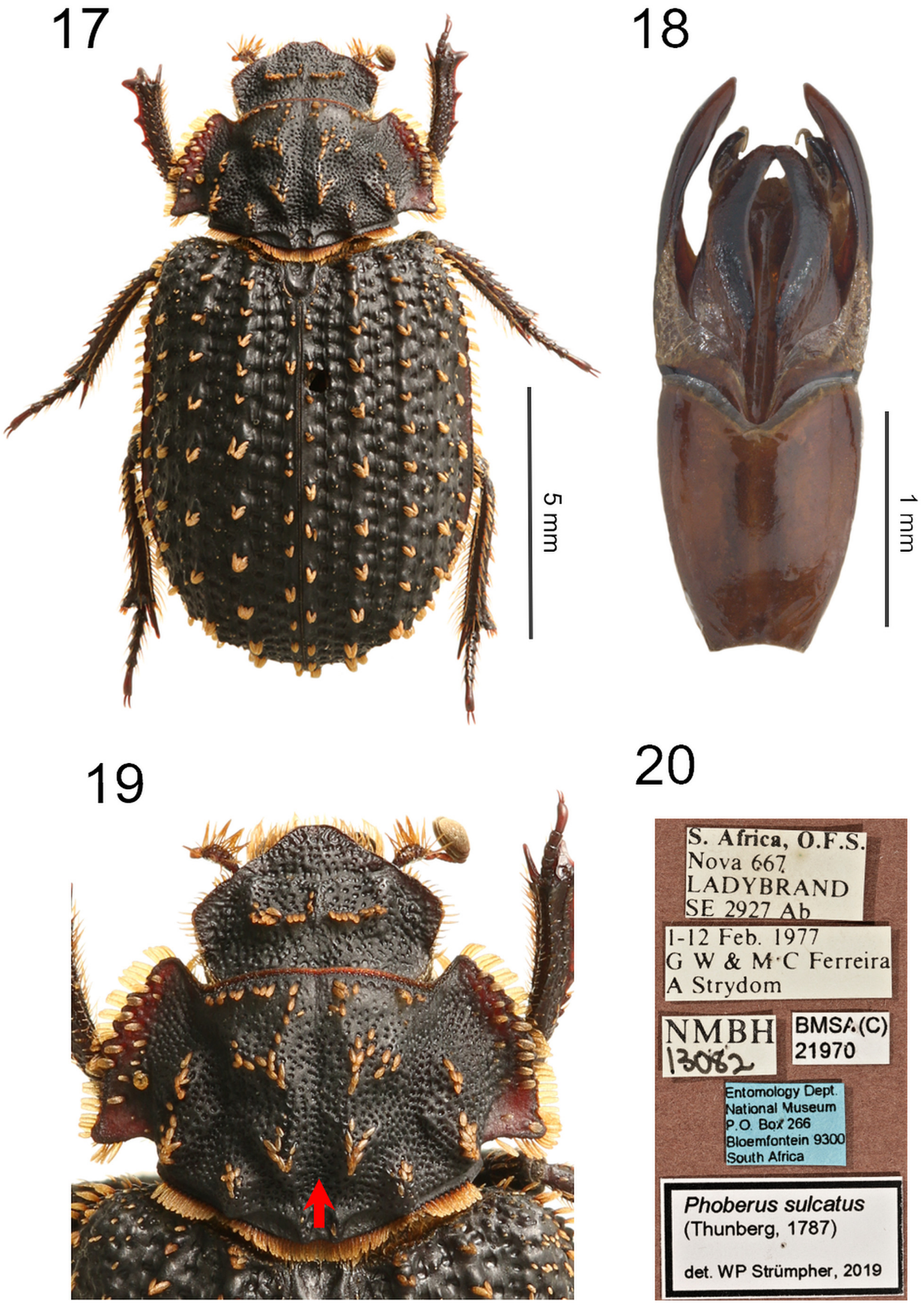


FIGURES 15–16. Pronotal disc, dorsal view. 15, *Phoberus cyrtus* (Haaf, 1953); 16, *Phoberus fumarius* (Haaf, 1953).

Male genitalia (Figs 9, 13): Symmetrical, slender, phallobase arched, as long as parameres. Parameres long, extending beyond median lobe, apices pointed and curved. Median lobe divided into two symmetrical parts, these broad, not parallel, with distinct basolateral swelling, in dorsal view concave upward; apices angularly rounded and incurved; two bladelike projections and hooks visible between parameres and median lobe.

Diagnosis. *Phoberus fumarius* and *Phoberus cyrtus* are very similar to each other. The two species can be told apart as elaborated under the diagnosis of *Phoberus cyrtus*, above. Whereas both species can be confused with the common and widespread *Phoberus sulcatus*, *Phoberus fumarius* is more likely to cause such confusion. Again see the discussion under *Phoberus cyrtus*, above.

Geographic distribution. *Phoberus fumarius* is presently known only from the Northern Cape and Western Cape Provinces of South Africa, apart from its type locality that marginally falls in the westernmost Eastern Cape Province. The known distribution of the species follows the Cape Fold Mountains, along the western mountain chain from the Richtersveld southwards through Namaqualand to the West Coast Peninsula and the Cape Peninsula; and from there eastwards along the southern mountain chains as far east as the town of Willowmore (Fig. 21). This is a distribution pattern that broadly repeats among many beetle species and higher categories. Another example from the Trogidae is the *Phoberus capensis* species-group (Strümpher *et al.* 2016a).



FIGURES 17–20. *Phoberus sulcatus* (Thunberg, 1787), cleaned specimen (BMSA). 17, habitus, dorsal view; 18, aedeagus, dorsal view; 19, pronotal disc, with red arrow indicating distinct median pronotal depression; 20, specimen labels.

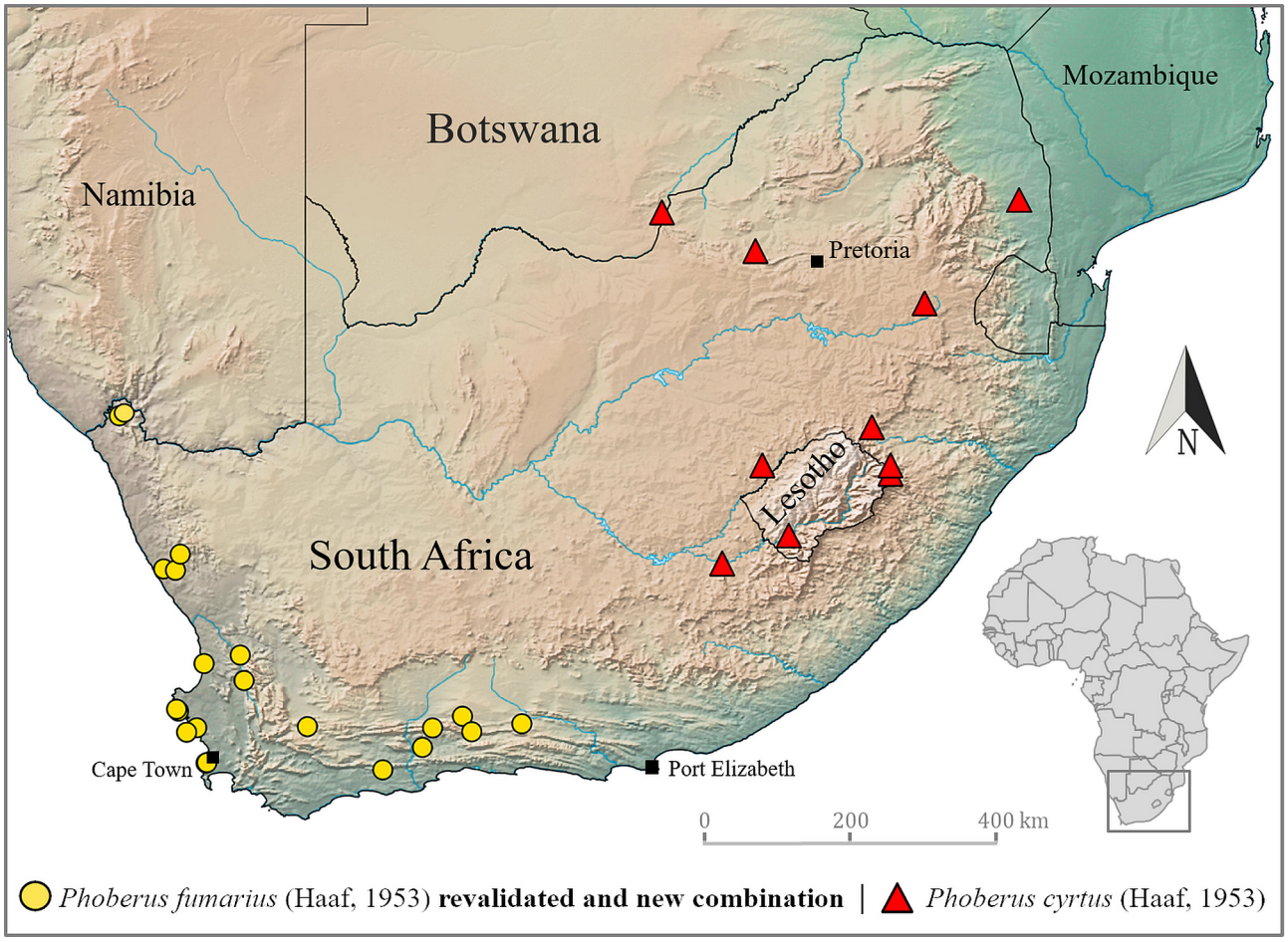


FIGURE 21. Known distribution of *Phoberus cyrtus* (Haaf, 1953) and *Phoberus fumarius* (Haaf, 1953).

The distribution of this species may well reach further east into the eastern Cape Floristic Region; and it may well extend into southern Namibia, since it is known from the Richtersveld on the southern side of the Gariep River, while identical habitat is present on the northern side of the river in Namibia (Fig. 21). *Phoberus fumarius* is present on off-shore islands on the Western Cape Atlantic coast. Two of these 'guano islands' are noted above; Haaf (1959) additionally reported this beetle species from Malgas Island (33°03′10″S 17°55′31″E) in Saldanha Bay.

Broad habitat associations. The known distribution of *Phoberus fumarius* is confined to the Greater Cape Floristic Region of Born *et al.* (2007), falling entirely in the winter rainfall region of southern Africa, whereas the range of the putative sister species *Phoberus cyrtus* is confined to the summer rainfall region. *Phoberus fumarius* has been recorded at an altitude of 2,000 m above sea level in the Swartberg Mountains and close to sea level on the West Coast and the Cape Peninsula. No field-collected information about habitat associations exists for this species, and the possible vegetation types in which it occurs are geographically complexly arranged, necessitating caution when inferring where the species lives.

The distribution of *Phoberus fumarius* is in the northwest centred on the Succulent Karoo Biome (Richtersveld to Namaqualand) and on the Fynbos Biome in the south and towards the east (biomes, bioregions and vegetation units *sensu* Mucina & Rutherford 2006; Dayaram *et al.* 2019). In the Fynbos Biome the species may likely occur in both Fynbos and Renosterveld vegetation units, but dedicated collecting is required to confirm or refute this. At higher altitudes along the southern mountains the species may again be found in Succulent Karoo habitats, and specifically in the Rainshadow Valley Karoo Bioregion. In the Swartberg and Little Karoo it possibly occurs in intrusions of the Albany Thicket Biome. On the off-shore islands the species occurs in Western Strandveld, a vegetation unit of the Fynbos Biome.

Acknowledgements

We are grateful to the following curators who made specimens available for this study: Burgert Muller and Gimo Daniel (BMSA), Aisha Mayekiso (SAMC) and Catherine Sole (UPSA); and grateful to Antoine Mantilleri (MNHN), Christoffer Fägerström (MZLU) and Christoph Germann (NHMB) for photographing specimens in their museums at our request. We thank the reviewers whose comments and suggestions improved the quality of the manuscript.

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