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WELCOME HOME: PHYLOGENETIC PLACEMENT AND TAXONOMY OF AN ENIGMATIC SUBTRIBE STENOLAMINA KOCH, 1956 (TENEBRIONIDAE: BLAPTINAE: OPATRINI)

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Abstract.— The phylogenetic placement of the enigmatic subtribe Stenolamina is investigated based on the analysis of four molecular loci (CAD, wg, 28S, 12S). Historically, the position of Stenolamina remained unfixed, and was listed as *incertae sedis* within the darkling beetle subfamily Blaptinae. Molecular data render Stenolamina as a separate lineage within the tribe Opatrini. The morphology and distribution of Stenolamina are reexamined. Scanning electron microscopy revealed that Stenolamina shares the synapomorphic Opatrini protrochanter structure seen in all other members of the tribe. Furthermore, unique antennal sensoria (placoid / stenolamoid) are reported for Stenolamina – this feature is distinct from all other Blaptinae. This paper presents the first morphological definition of Stenolamina. Finally, *Stenolamus borowieci* **sp. nov.** is described from the surroundings of Port Nolloth (South Africa). The material examined for this species displayed a striking type of sexual dimorphism, which is omnipresent within Stenolamina (females with acute basal angles of the pronotum).

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Key words.— darkling beetles, *Stenolamus*, phylogeny, species discovery, antennal sensoria, Angola, Namibia, South Africa

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INTRODUCTION

Stenolamina Koch, 1956 is one of the most enigmatic subtribes of Afrotropical Tenebrionidae (Coleoptera). It comprises over 20 relatively small (1.75–5.50 mm) species classified within a single genus *Stenolamus* Gebien, 1920 (Table 1). Although formally the phylogenetic distinctiveness of this subtribe has been recognized (Koch 1956, Iwan 2001), no direct morphological definition of this taxon was ever proposed (Koch 1956, Medvedev 1968, Iwan 2001). Namely, while introducing the name, Koch (1956) did not provide any unique morphological features of Stenolamina, nor did he list any previous bibliographic references with such descriptions. As such, his contribution failed to fulfill the requirements of Article 13.1 of the ICZN (1999). Nevertheless, the name has been made available under article 13.2.1., with Koch (1962) and Medvedev (1968) as the supporters of its validity. Both Koch and Medvedev intentionally recognized Stenolamina as valid while listing it as one of the South African subtribes of Opatrini Brullé, 1832 without providing any distinguishing morphological features. Based on a comparative morphological analysis of male terminalia and protrochanters, Iwan (2004) concluded that Stenolamina should be excluded from the tribe Opatrini, as it lacked any synapomorphies proposed for this group. Kamiński *et al*. (2021) then listed Stenolamina as *incertae sedis* within the subfamily Blaptinae Leach, 1815, as no molecular data for the subtribe was available to classify it further.

The majority of current knowledge concerning Stenolamina can be extracted from Koch (1955), in which more than half of the currently recognized species of *Stenolamus* were described (Table 1). According to Koch, *Stenolamus* display some degree of morphological resemblance to *Dilamus* Jacquelin du Val, 1861 (Opatrini Brullé, 1832), as representatives of both genera possess elongated body shape, intermediate sclerites of aedeagus (plates located between parameres and basal part of the tegmen), apically abbreviated epipleura, and dilated anterior tarsi in males. As only the first of these features seemed to be specific to *Stenolamus* and *Dilamus*, Koch (1955) concluded that the general resemblance between these entities might be superficial, and both possibly represent different subtribes. Moreover, according to Koch (1955), *Stenolamus* can be further distinguished from *Dilamus* based on the following morphological traits: the presence of postocular sulcus on the tempora, the abbreviated third segment of the antennae (distinctly shorter than the second segment vs longer than the second one in *Dilamus*), the absence of a scutellum (strongly developed, triangular and dorsally exposed in *Dilamus*), the short metasternum (elongate in *Dilamus*), and by the absence of ancorae (see Lumen & Kamiński 2023) on the aedeagus (well-developed, but concealed, in *Dilamus*). Lacking comparative data, Koch (1955) decided not to introduce any taxonomic decisions concerning their subtribal status.

In summary, a handful of contributions have been published on *Stenolamus* and Stenolamina (Gebien 1920, Koch 1953a, b, 1955, 1956, Medvedev 1968, Ferrer 2000, Iwan 2001), and no comprehensive morphological treatment for this enigmatic lineage exists. The lack of photographs and user-friendly resources for species identification makes the subtribe unappealing to a wider entomological community, which is unfortunate as *Stenolamus* are often plentiful, and easily collected in the field (Kamiński pers. obs.). To address the taxonomic and classification shortfalls presented above, this paper uses molecular and morphological data to propose the first, formal diagnosis of the subtribe Stenolamina, and determine its phylogenetic position. Additionally, a newly discovered *Stenolamus* species is described from the surroundings of Port Nolloth (South Africa).

MATERIAL AND METHODS

Specimens used in this study were collected by the authors in South Africa (permits in acknowledgments) or contributed by collaborators. Voucher specimens are preserved in the Ditsong National Museum of Natural History (TMSA) and the Museum and Institute of Zoology PAS (MIZ PAS). Specimens used in molecular analyses have been assigned unique identifiers (TB#s) linked to sequence data in the Sequence Read Archive (NCBI-SRA). Morphological identifications were made using the following resources: Gebien (1920), Koch (1953a, b, 1955), and Ferrer (2000). Images of specimens were taken using a Nikon D3500 body with an adapter for a Nikon SMZ800N microscope, and with a Hitachi S-3400N Scanning Electron Microscope in MIZ PAS. Species distribution maps were produced based on previously published records and newly collected data (Appendix) using QGIS v. 3.16, with vector layers downloaded from the Natural Earth web page (www.naturalearthdata.com).

DNA was extracted from two specimens representing *Stenolamus reichenspergeri* Koch, 1955 (TB26395) and *S. stenammaphilus* Koch, 1955 (TB26386) respectively. Extraction was performed with DNeasy Blood & Tissue Kit (Qiagen, Germantown, MD, USA) following the manufacturer's protocols. Specimens were disarticulated into three parts (head, thorax, and abdomen) and inserted into a buffer for proteinase K digestion. Extracts were sent to Daicel Arbor Biosciences for library preparation, and targeted enrichment using MyBaits probes designed to capture 618 genetic loci from Blaptinae/Tenebrioninae

Table 1. A list of the species of the genus *Stenolamus* displayed on an informal classification proposed by Koch (1955); * – type species.

I. *azurescens* species group	II. *sulciceps* species group	III. *dentimanus* species group	Species not assigned to any species groups
Diagnosis. Anterior tibiae triangularly and straightly dilated, spatuliform (Fig. 3I,J, 4C). Parameres mostly not diverging (Fig. 2F), except *S. borowieci* sp. nov. (Fig. 2G)	***Diagnosis***. Anterior tibiae slender or with a median tooth. Parameres diverging, subfurcate	***Diagnosis***. Anterior tibiae slender or with a median tooth (Fig. 3K). Parameres subparallel, not diverging, and not compressed	***Remarks***. Described based on female specimens exclusively. The only representative of *Stenolamus* reported from the eastern part of Southern Africa (Fig. 5B)
azurescens Koch, 1955	*deserticus* Koch, 1953b	*ashmoleorum* Ferrer, 2000	*lundholmi* Koch, 1955
borowieci **sp. nov.**		*brincki* Koch, 1953a	
caudatus Koch, 1955	*filum* Koch, 1953b	*dentimanus* Gebien, 1920	
reichenspergeri Koch, 1955	*furciphallus* Koch, 1955	*dentitibia* Koch, 1953a	
semirufus Koch, 1955	*halli* Koch, 1955	*machadoi* Koch, 1953b	
spinipes Koch, 1955	*kalaharicus* Koch, 1955	*malacodermus* Koch, 1955	
vanzylorum Koch, 1955	*magnificatus* Koch, 1953a	*spinicauda* Koch, 1955	
	sulciceps Gebien, 1920*	*stenammaphilus* Koch, 1955	

(modified from Kanda 2017 and Switchtenberg *et al.* 2023). Libraries were sequenced with NovaSeq 6000 system for 150 bp paired-end runs.

The quality of sequencing data was assessed with FastQC v.0.11.9 (Andrews 2010). Reads with an average sequence quality across any 4 bases below 20, using the sliding window approach, were removed from further analyses with Trimmomatic (Bolger *et al.* 2014). Surviving reads were assembled by using the HybPiper v.1.3.1 (Johnson *et al.* 2016) bioinformatic pipeline with the bait probe markers for carbamoyl-phosphate synthetase domain of rudimentary (CAD) (723 bp), wingless (wg) (438 bp), nuclear ribosomal 28S (1059 bp), and mitochondrial ribosomal 12S (363 bp). Retrieved data were integrated into the matrix generated for the subfamily Blaptinae (Kamiński *et al.* 2021), with taxa trimmed for subtribal representation. The final matrix comprising 2,583 bp and 81 taxa was prepared in Mesquite 3.61 (Maddison & Maddison 2019) and is available online (Kamiński 2023).

IQ-TREE 2 was used to run maximum likelihood (ML) analyses using an edge proportional partition model (-spp), with the dataset partitioned by loci and the models for each locus applied from ModelFinder (Kalyaanamoorthy *et al.* 2017). Support for the resulting topology was assessed using 10,000 UltraFast Bootstrap (Hoang *et al.* 2018) iterations. All sequence assembly and IQ-TREE 2 analyses were performed on Purdue University's community cluster, Bell, within ITaP Research Computing (McCartney *et al.* 2014). The dataset, with the same partitions, was also analyzed using ExaBayes 1.5.1 (BI) (Aberer *et al.* 2014) run through the CIPRES portal (Miller *et al.* 2010). Two independent runs of 20 million generations, each with 1 cold chain and 2 heated chains, were performed with a burn-in fraction of 0.25.

RESULTS

Phylogeny

The recovered ML topology is largely congruent with that presented by Kamiński *et al.* (2021). The subfamily Blaptinae was retrieved as monophyletic, containing the following tribes: Amphidorini LeConte, 1862, Blaptini Leach, 1815, Dendarini Mulsant & Rey, 1854, Opatrini, Pedinini Eschscholtz, 1829, Platynotini Mulsant & Rey, 1853, and Platyscelidini Lacordaire, 1859. Although the BI also rendered Blaptinae as monophyletic with the same tribal composition, both inference methods returned conflicting topologies concerning the relations within the opatrinoid clade. In particular, in the ML runs the following relation has been recovered: ((Platynotini + Pedinini) + Dendarini) + Opatrini (Fig. 1). Contrarily, the BI analysis rendered the following topology: ((Opatrini + Platynotini) + Pedinini) + Dendarini. Regardless, in both types of analyses, representatives of *Stenolamus* were deeply rooted within Blaptinae, particularly the tribe Opatrini (Fig. 1). Within Opatrini, the two analyzed Stenolamina species were projected as a separate phylogenetic lineage between Blapstinina and the remaining members of the tribe.

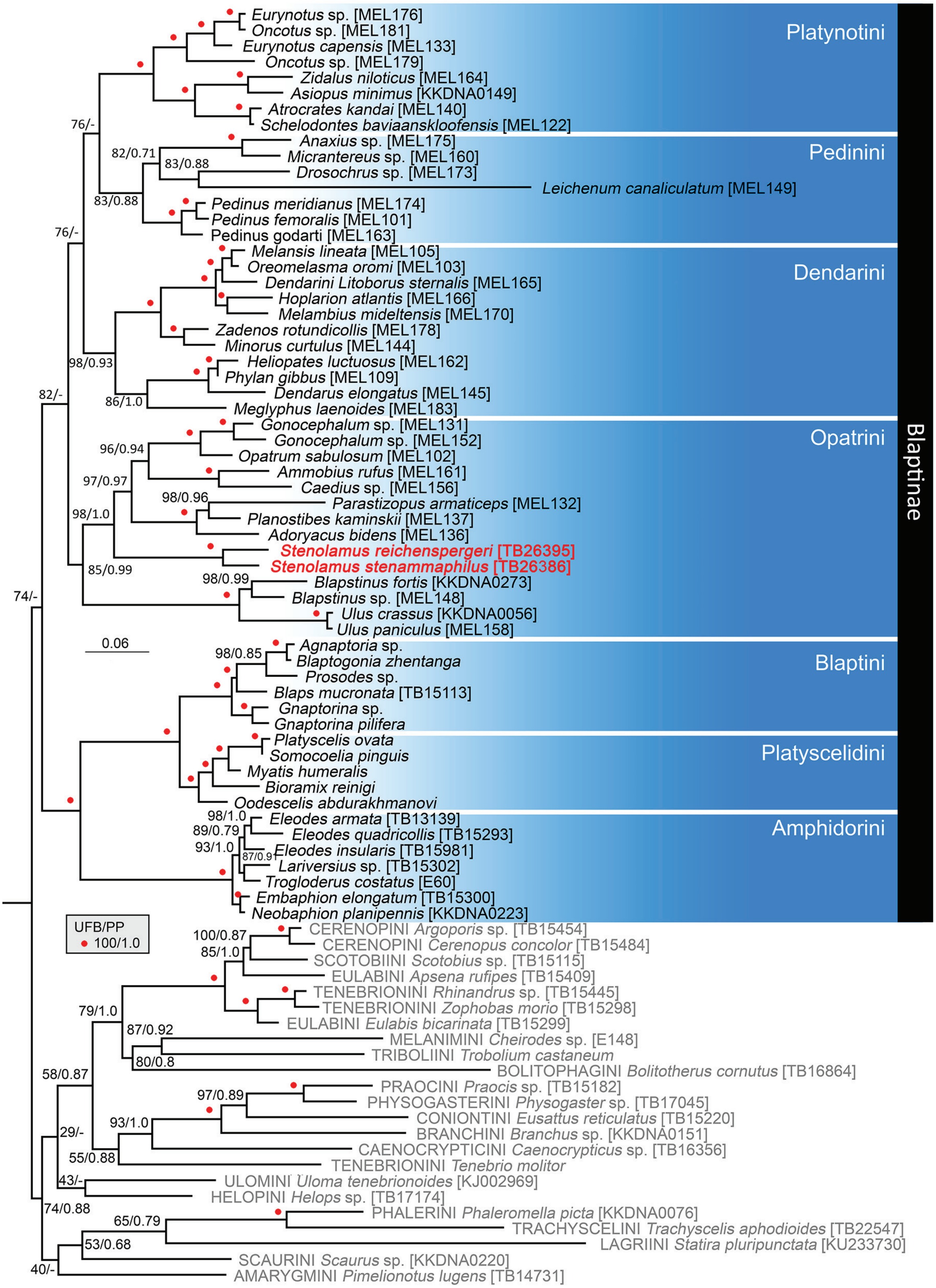

Figure 1. Phylogenetic placement of the genus *Stenolamus* within the subfamily Blaptinae. Strict consensus tree derived from maximum parsimony analysis of concatenated CAD, wg, 12S, and 28S matrix is presented. Gray taxon names represent subfamilies outside Blaptinae, and *Stenolamus* representatives are in red. Branch support displayed as ultrafast bootstrap (UFB) and posterior probability (PP).

Morphology

Morphological investigation revealed that adult forms of *Stenolamus* display the following combination of features assigned to Blaptinae, i.e. procoxal cavities externally and internally closed, intersternal membrane of abdominal ventrites 3–5 visible, and presence of paired, not annulated, abdominal defensive glands. Additionally, the presence of specific antennal stenolamoid sensoria seems to be unique for the genus across the whole subfamily (Fig. 2B–D). Within Blaptinae, based on the specific structure of the protochanters (elongated base), *Stenolamus* can be unambiguously assigned to the tribe Opatrini (Fig. 2E). Within this tribe, this genus does not display strong affiliations toward any of the already designated subtribes.

TAXONOMY

Subtribe **Stenolamina** Koch, 1956

Diagnosis. The presence of opatrinoid protrochanters places Stenolamina in Opatrini (Fig. 2E, see Iwan & Kamiński 2016). Among the tribe, Stenolamina is clearly diagnosable by the presence of stenolamid sensoria on the antennae (Fig. 2B–D), and the postocular sulcus on the tempora (Fig. 3E–G). Furthermore, Stenolamina is well-recognizable superficially by the small body size (1.75–5.50 mm) and elongated habitus of its representatives. See the discussion for additional details.

Distribution (Fig. 5). Angola, Namibia, and South Africa.

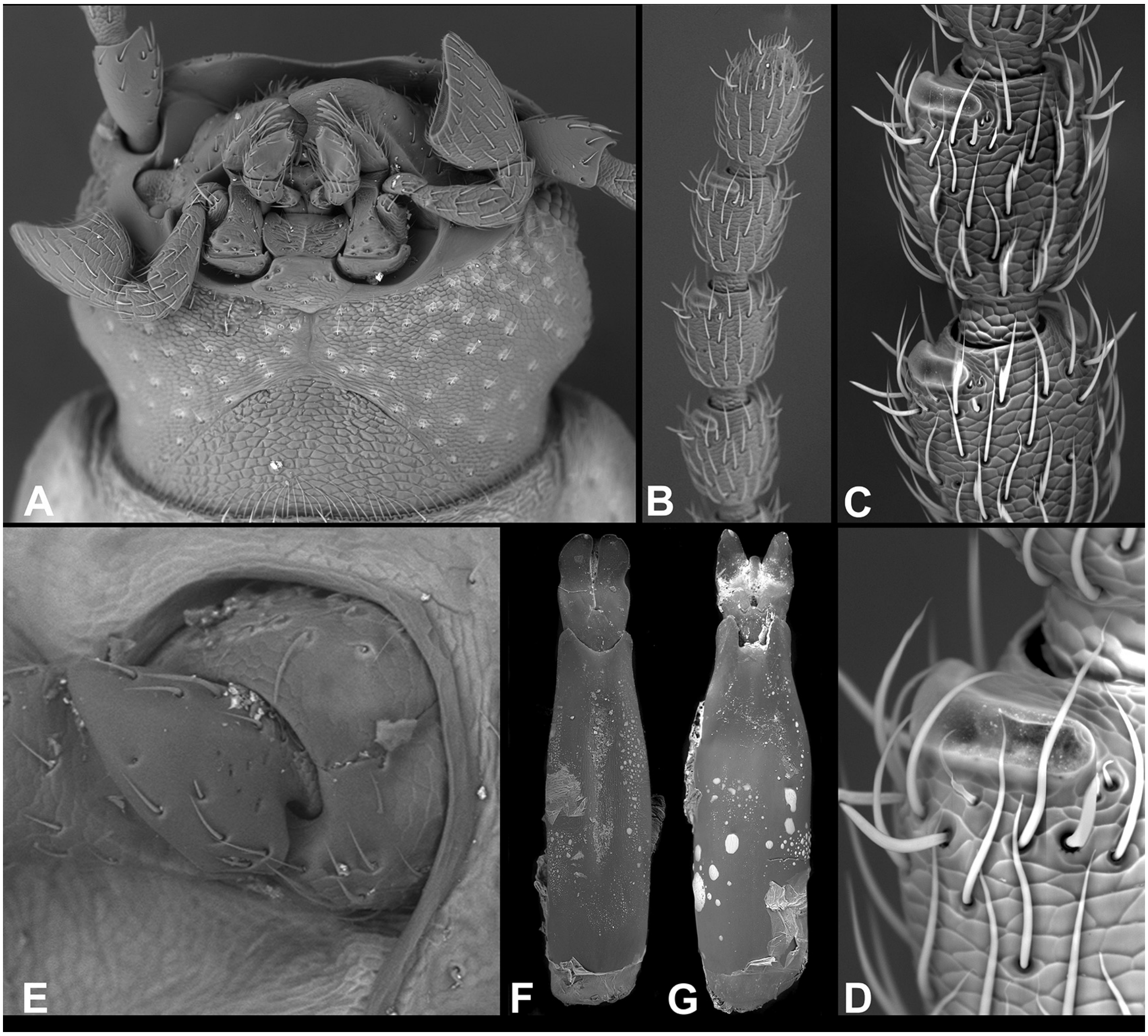

Figure 2. Ultrastructure of the genus *Stenolamus*. (A–F) *Stenolamus spinipes* Koch, 1955, (G) *S. borowieci* sp. nov. Head: (A) ventral view, (B) apical piece of antennae, (C) antennomeres 9–10, and (D) antennomere 10. Legs: (E) protrochanter. Aedeagus: (F, G) dorsal view.

Genera included (monogeneric). *Stenolamus* Gebien, 1920 (Table 1).

Stenolamus borowieci sp. nov.
(Fig. 2G; 3A–J, L–N; 5C)

Type data. Holotype (male TMSA): "-29.24S, 17.27E, 23 January 2022, under stones". Paratypes (5 males and 1 female TMSA, male and female MIZ PAS), same data as holotype.

Etymology. This new species is dedicated to Prof. Lech Borowiec, a prominent Polish entomologist.

Diagnosis. On account of having triangularly and straightly dilated spatuliform anterior tibiae, this new species can be assigned within the *azurescens* species group. The characteristic color pattern of the body (head and pronotum reddish, elytra dark brown) put it close to *S. caudatus* Koch, 1955, *S. semirufus* Koch, 1955, and *S. vanzylorum* Koch, 1955. From all these species and also other members of *azurescens* species group, *S. borowieci* can be easily separated by its relatively large body size (4.0–4.3 mm vs 1.75–3.0 mm) and the characteristic shape of the parameres (narrowing towards the apex in other members of the *azurescens* species group, bifurcate in *S. borowieci*).

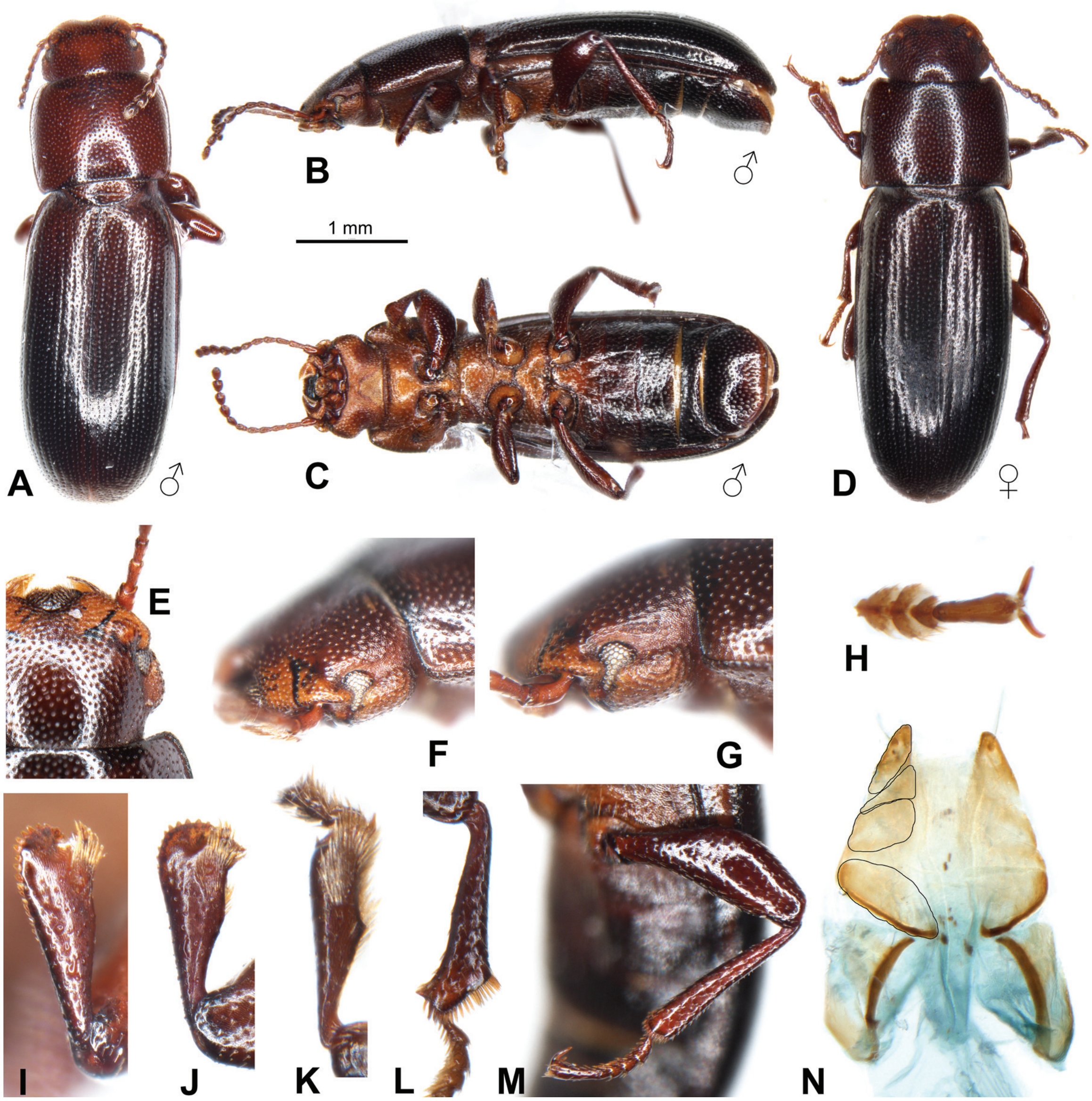

Figure 3. Morphology of the genus *Stenolamus*. (A–J, L–N) *Stenolamus borowieci* sp. nov., (K) *S. dentimanus*. Habitus: (A, D) dorsal, (B) lateral, and (C) ventral views. Head: (E) dorsal, (F) dorsolateral, and (G) lateral views. Male legs: (H) protarsus, (I) protibia, (J) protibia, (K) protibia, (L) mesotibia, and (M) metatibia. Ovipositor: (N) ventral view.

The latter feature projects the newly discovered species close to the species of *sulciceps* group. However, it can be easily distinguished from all species of this complex by different protibial structure (triangularly and straightly dilated, spatuliform in *S. borowieci*, slender in the remaining taxa).

Description. Description. Length 4.0–4.3 mm. Head: widest near base; punctures well-noticeable (1.5–2.0 diameters apart); clypeal emargination deep; postocular sulcus on tempora strongly highlighted. Antennomeres 8–10 with pairs of stenolamoid sensoria. Mentum midportion flat, with indistinct median carina; submentum with elongate base. Prothorax: pronotum punctate, punctures well-noticable (1.5–2.0 diameters apart). Hypomeron very finely punctate, covered with sparse setae. Legs: protibiae (both sexes) flat, widended towars apex, preapically with tuft of setae (Fig. 3I, J); mesotibiae (in males) with preapical denticle on inner side (Fig. 3L); metatibiae (both sexes) simple (Fig. 3M). Prosternal process rounded (lateral view) and impressed (dorsal view). Pterothorax: scutellum visible, rounded. Elytra slightly wider than pronotum; elytra darker in apical portion; elytral rows distinct, punctate; interrows covered with noticeable punctures (2–3 diameters apart). Epipleura abbreviated at level of ventrite 5. Metaventrite relatively short (length ratio cavity of hind coxa / metaventrite between the insertions of mid and hind coxae = 0.8). Process of first abdominal ventrite narrow (ratio of distances between mid- and metacoxae = 1.0). Abdomen: sulcus of fifth ventrite narrowly separated from apical border. Male terminalia: aedeagus elongate (length ratio aedeagus / body = 0.4), parameres short (ratio parameres / basal piece = 0.28), diverging apically, subfurcate (Fig. 2G). Female terminala: ovipositor slightly shortened (ratio ovipositor coxites I–IV / paraprocts = 1.43) (Fig. 3N). Bursa copulatrix simple, not bilobate, accessory gland present, accessory pouch absent.

Sexual dimorphism. Female specimens were found to have acute basal pronotal angles that slightly extend towards the back of the body (Fig. 3D). Furthermore, males are characterized by having wide protarsi (Fig. 3H).

Distribution (Fig. 5C). Arid ecosystems between Port Nolloth and Steinkopf, South Africa (Fig. 5A).

Stenolamus spinipes Koch, 1955
(Fig. 2A–F, 4, 5C)

New record. 3 males and single female (TMSA): "-29.28, 17.27, 23 January 2022, under stones".

Distribution (Fig. 5C). The western part of the Northern Cape, South Africa.

DISCUSSION

The structure of protrochaters (presence of elongated base) and molecular evidence places *Stenolamus* in Opatrini, where it constitutes a distinct phylogenetic lineage (Fig. 1). As the classification of Opatrini is strongly based on female terminalia morphology (Iwan & Kamiński 2016), at this point it is challenging to find any reliable morphological traits linking Stenolamina to other subtribes of Opatrini, especially in the

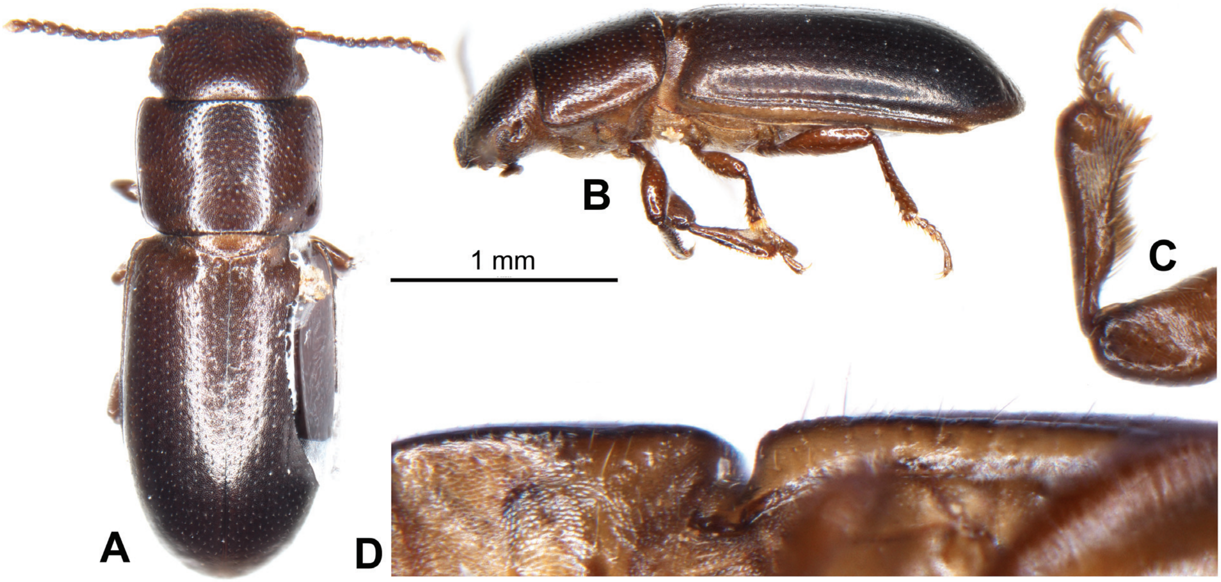

Figure 4. Morphology of *Stenolamus spinipes* Koch, 1955. Habitus: (A) dorsal and (B) lateral views. Male leg: (C) protibia. Setation: (D) hypomeron and epipleura.

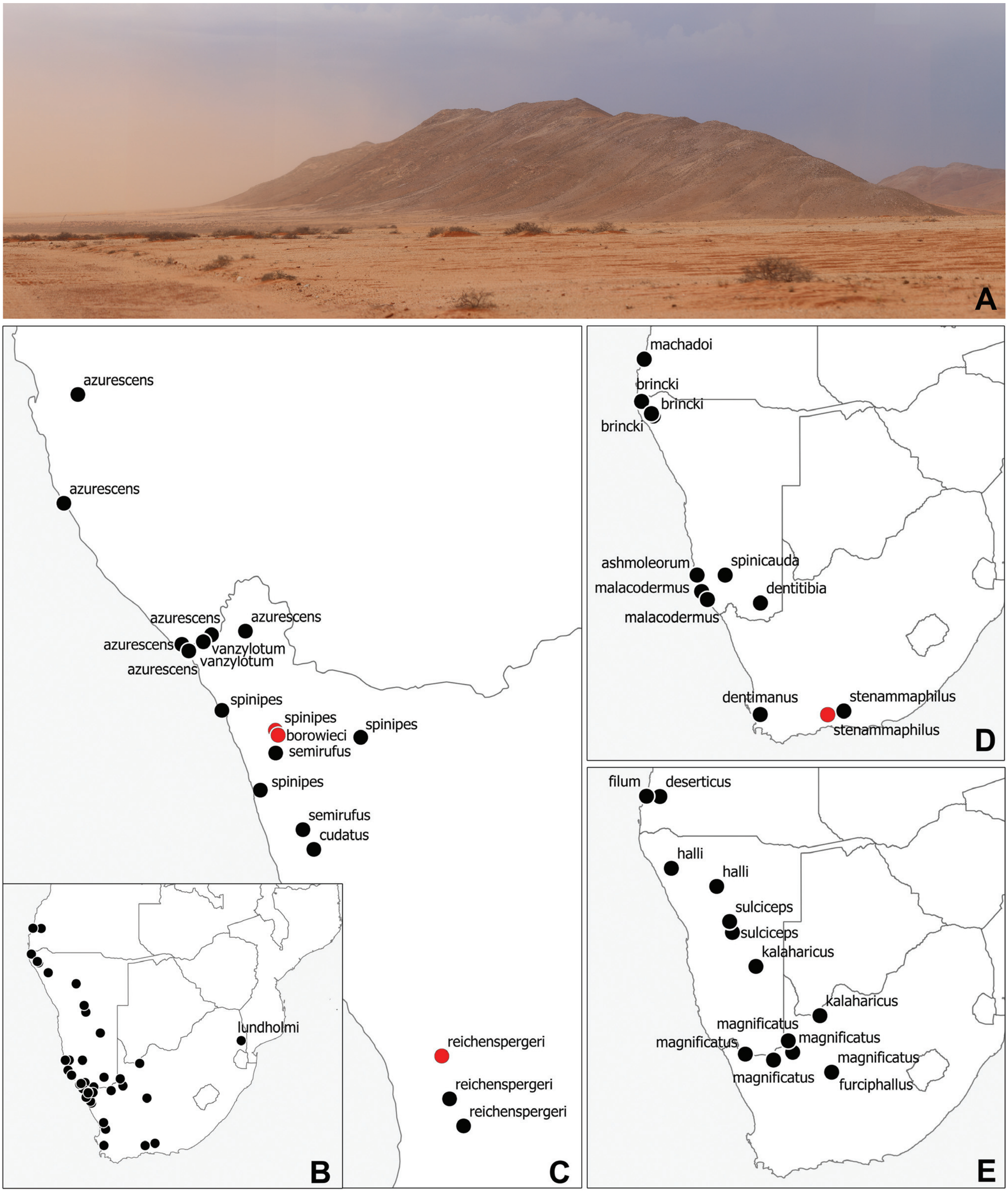

Figure 5. Occurrence records of the genus *Stenolamus*. (A) habitat for *Stenolamus borowieci* sp. nov. (B) general distribution of the genus. Detailed distributional records for (C) *azurescens*, (D) *dentimanus*, and (E) *sulciceps* species groups. New distributional records are marked in red.

context of the rather plesiomorphic structure of the ovipositor of *Stenolamus* (Fig. 3N, see Kamiński *et al*. 2023). Nevertheless, within the tribe, the genus displays some degree of morphological similarity toward representatives of Blapstinina Mulsant and Rey, 1853 (Lumen *et al*. 2019, Kamiński *et al*. 2022). Namely, the constriction of the eyes in both lineages is a result of the expanding genae (Fig. 3E–G). Although, contrary to *Stenolamus*, all Blapstinina possess eyes fully divided into the dorsal and ventral portions (Lumen *et al*. 2019). Furthermore, both share a similar structure of aedeagi, i.e. blapstinoid type (see Iwan 2001). On the other hand, *Stenolamus* can be easily separated from Blapstinina by having abbreviated epipleurae – a common feature of non-blapstinoid Opatrini (Koch 1956, Lumen *et al*. 2019). Additionally, *Stenolamus* differs by having only a slightly sclerotized dorsal side of the basal piece of the tegmen and a ventrally located gap for the median lobe protrusion (Iwan 2001, 2004).

Currently, morphological data does not support a close relationship between *Stenolamus* and *Dilamus* as postulated by Koch (1955). Both genera are clearly distinguished by the different structures of antennae (stenolamoid sensoria in *Stenolamus* vs simple sensoria in *Dilamus*), and temporae (postocular sulcus on tempora in *Stenolamus* vs rounded tempora in *Dilamus*). The first of these features seems to be exclusively assigned to *Stenolamus* within the whole Blaptinae, which all lack compound sensoria (Kamiński *et al*. 2019). In fact, similarly structured sensoria have not been reported for any of the lineages within the whole family of Tenebrionidae (Medvedev 1977). In conclusion, the phylogenetic distinctiveness of Stenolamina among Opatrini is well grounded in both molecular and morphological data. As a result, the subtribal status of this lineage is hereby sustained, while this taxon is reinstalled as an eighth subtribe Opatrini (see Iwan & Kamiński 2016).

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Appendix. Analyzed distributional data in CSV format. Presented records were acquired from literature (Gebien 1920, Koch 1953a, b, 1955, Ferrer 2000) as well as from the studied specimens

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Stenolamus ashmoleorum,Agata beach,-26.605435071627223,15.180604138090581
Stenolamus azurescens,Brandkaross,-28.478001598854803,16.68606843140415
Stenolamus azurescens,Grootderm,-28.53109361349182,16.614400999983452
Stenolamus azurescens,Alexander Bay,-28.610584978215897,16.487438120557076
Stenolamus azurescens,10 miles west of Kuboos,-28.45,16.98333
Stenolamus azurescens,20 miles north of Orangemund,-28.551667,16.426389
Stenolamus azurescens,Bogenfels,-27.460556,15.391944
Stenolamus azurescens,10 miles west of Haalenberg,-26.61196810081174,15.514610365208886
Stenolamus borowieci,Sourrodings of Port Nolloth,-29.248372506576136,17.270079999172214
Stenolamus brincki,Kaokoveld,-17.500559117968763,12.000932408601868
Stenolamus brincki,Sanitatas,-18.28274214177884,12.666580869572453
Stenolamus brincki,Orupembe,-18.159421109434508,12.561085210951621
Stenolamus caudatus,Soebatsfontein,-30.117,17.583
Stenolamus dentimanus,Malmesbury,-33.45,18.733333
Stenolamus dentitibia,Karasburg,-28.020503776429397,18.744220843236935
Stenolamus deserticus,near Rio Giraul,-15.217820021095246,12.914596659273348
Stenolamus filum,between Mocamedes and Rio Coroca,-15.2,12.15
Stenolamus furciphallus,Prieska,-29.717287504427023,22.726680718463616
Stenolamus halli,Zesfontein,-19.138950695134966,13.568008251763635
Stenolamus halli,Outjo,-20.11033362085527,16.15925788438666
Stenolamus kalaharicus,Stamprietfontein,-24.343645769555913,18.40038835447486
Stenolamus kalaharicus,Van Zyls Rust,-26.878732595565516,22.05576779421362
Stenolamus lundholmi,Lower Sabi River,-24.985731770854752,31.47503424904522
Stenolamus machadoi,Mocamedes,-15.2,12.15
Stenolamus magnificatus,Prieska,-29.717287504427023,22.726680718463616
Stenolamus magnificatus,Niekerk Hope,-28.72411131330991,20.500539313350213
Stenolamus magnificatus,65 Meilen W von Upington,-28.150446167628225, 20.24825798184778
Stenolamus magnificatus,Pofadder,-29.11198607218149, 19.405797249335244
Stenolamus magnificatus,10 miles north of Vioolsdrift,-28.817830164849944, 17.79491661907044
Stenolamus malacodermus,Bogenfels,-27.444656374832142,15.406328895348514
Stenolamus malacodermus,30 miles northwest of Chameis,-27.849891078397366,15.735237521507774
Stenolamus malacodermus,Luederitzbucht,-26.616667,15.15
Stenolamus reichenspergeri,10 miles north of Clanwilliam,-31.988186697044515,18.77261567934764
Stenolamus reichenspergeri,Clanwilliam,-32.18936076774761,18.89571655342603
Stenolamus reichenspergeri,Anysberg Nature Reserve,-31.669914,18.704527
Stenolamus semirufus,Oograbies,-29.211358996325398,17.246800591624453
Stenolamus semirufus,Soebatsfontein,-29.967187276433243,17.48729287935
Stenolamus spinicauda,Kuibis,-26.61869452876539,16.744466263451862
Stenolamus spinipes,Buffels River near Grootmist,-29.64916660795951,17.078769014078347
Stenolamus spinipes,Steinkopf,-29.25599573055868,17.725241106518506
Stenolamus spinipes,Holgat,-28.947164311809942,16.784405854766575
Stenolamus spinipes,Sourrodings of Port Nolloth,-29.288232521327473, 17.26907927030032
Stenolamus stenammaphilus,Willowmore,-33.287584013958444,23.475345977108088
Stenolamus stenammaphilus,Gamkaberg Nature Reserve,-33.697852323024016, 21.896222268895393
Stenolamus sulciceps,Windhoek,-22.561061295229468,17.056732942083812
Stenolamus sulciceps,Okahandja,-21.986277868171502,16.89748849468526
Stenolamus vanzylotum,2 miles east of Alexander Bay,-28.602598260074533,16.486965610780878
Stenolamus vanzylotum,Grootderm,-28.531395241268793,16.614358084689417
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