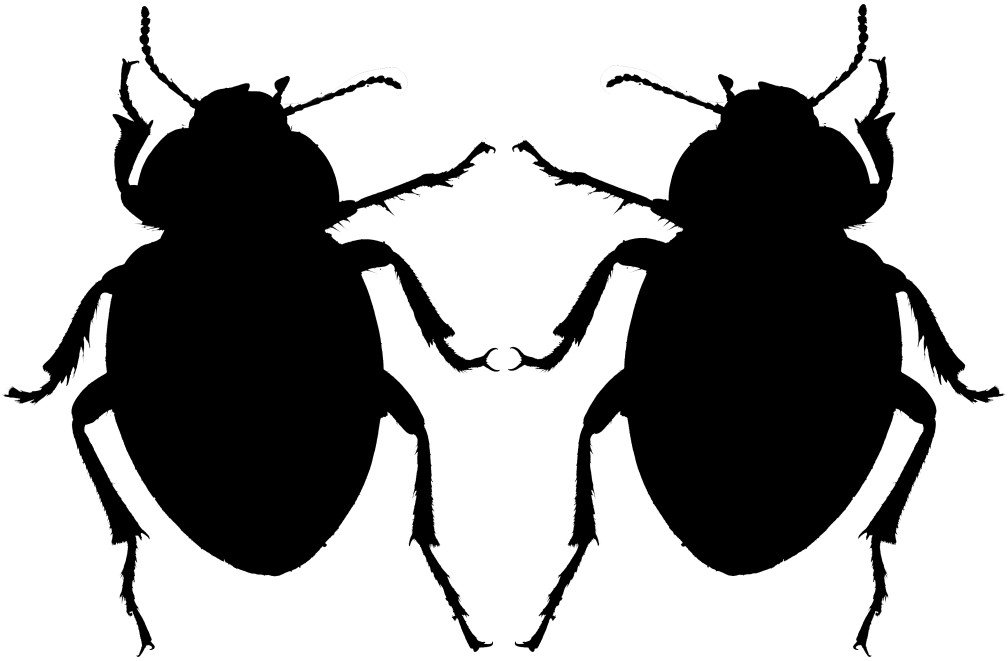
Phylogeny and Taxonomic Revision Of Subtribe Eurynotina (Coleoptera: Tenebrionidae)

Filogeneza i rewizja taksonomiczna chrząszczy z podplemienia Eurynotina (Coleoptera: Tenebrionidae)

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Doctoral Thesis



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Phylogeny and Taxonomic Revision
Of Subtribe Eurynotina (Coleoptera: Tenebrionidae)

PhD dissertation

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Abstract:

Despite a growing number of contributions concerning their taxonomic diversity, many studies of darkling beetles (Coleoptera: Tenebrionidae) still rely on classic morphology that remains untested in modern phylogenetic contexts. Consequently, many taxa have eluded additional scrutiny beyond alpha taxonomic additions. To complicate matters further, specimens unobserved in the wild or represented in collections by scant few specimens compound issues for taxonomists working on classification. New analyses using molecular and morphological methodologies and data are presented here to fill in gaps left by historical contributions, as well as to reevaluate previous classification based solely on morphology. The darkling beetle tribe Platynotini (subfamily Blaptinae) is a grouping with one well-studied lineage (subtribe Platynotina) alongside one which is contrastingly obscure and rare (Eurynotina). Eurynotina has undergone no revisionary work since its original inception over 70 years ago, and includes species described nearly 200 years ago. Originally classified within three informal groupings (*Eurynotus*, *Schyzoschelus*, and *Oncotus*), the 95 species and 16 genera of Eurynotina are largely based upon small series of specimens (>75% of taxa represented only by original type series). To date, specimens remain uncommon in collections and are often damaged or missing important parts that can preclude morphological or molecular analysis. This study focused on leveraging large genomic data sets obtained from next-generation sequencing in tandem with morphology to address gaps in analyses of the phylogenetic status and examine the monophyly of the subtribe, genera, and species of subtribe Eurynotina. Specifically, targeted enrichment (499 nuclear loci / 155,172 amino acids) with museomics (12 mitochondrial loci / 2,395 amino acids) are used alongside classic morphological data from historical specimens to produce a comprehensive, phylogenetically informed backbone classification. As a result of the analyses presented in this thesis, the subtribe is reorganized into five lineages supported by morphological and molecular data: *Eurynotus*, *Phylcastus*, *Schyzoschelus*, *Psectrapus*, and *Oncotus*. Two new genera (*Colophonexsula* Lumen & Kamiński, *Muelleropsectropus* Lumen & Kamiński) and 13 new species (*Eurynotus brunoi* (Lumen & Kamiński), *E. privisolum* Lumen & Kamiński, *Isoncophallus ovanullum* Lumen & Kamiński, *I. crispiformus* Lumen & Kamiński, *Ograbies calumnus* Lumen & Kamiński, *Phaleriderma iwani* Lumen & Kamiński, *Phylacastus ancoralium* Lumen & Kamiński, *Phy. makskacymirowi* Lumen & Kamiński, *Psectrapus byki* Lumen & Kamiński, *Ps. distaticum* Lumen & Kamiński, *Ps. latimentulum* Lumen & Kamiński,

Ps. simplicimentulum Lumen & Kamiński*, Schyzoschelus aetheculus* Lumen & Kamiński) are described along with several neotype and lectotype designations to stabilize the taxonomy of the group, as well as new combinations and redefinitions of genera over five published manuscripts. Non-target subjects such as ovovivipary and new revised terminology for reproductive morphology are also described. Finally, a total revision is presented in the form of an exhaustive monograph including keys to all five phylogenetic lineages, 19 genera, and 94 species. As a result of the body of work presented in this thesis, the subtribe Eurynotina now has a well-documented and tested phylogenetic background upon which future work can scaffold.

Streszczenie:

Pomimo wieloletniego zainteresowania badaczy systematyką chrząszczy z rodziny mącznikowatych (Coleoptera: Tenebrionidae), klasyfikacja wielu jednostek taksonomicznych nadal opiera się na historycznych koncepcjach morfologicznych. Nowo odkrywane taksony są często sztucznie dopasowywane do istniejących definicji rodzajowych, a znaczna część współczesnych opracowań Tenebrionidae ma charakter alfataksonomiczny. Istotnym ograniczeniem badań nad tą grupą jest także fakt, że wiele gatunków znanych jest jedynie z nielicznych okazów muzealnych. W niniejszej pracy przedstawiono wyniki analiz integrujących dane molekularne i morfologiczne, których celem była weryfikacja klasyfikacji opartych wyłącznie na cechach morfologicznych. Plemię Platynotini (Blaptinae) obejmuje jedną dobrze poznaną linię filogenetyczną (podplemię Platynotina) oraz drugą — słabo zbadaną i rzadko odławianą — Eurynotina. Podplemię Eurynotina nie było przedmiotem kompleksowych rewizji od momentu jego ustanowienia w latach 50. XX wieku i obejmuje gatunki opisane nawet 200 lat temu. Tradycyjnie wyróżniano w nim trzy nieformalne grupy rozwojowe (grupy *Eurynotus*, *Schyzoschelus* i *Oncotus*), obejmujące łącznie 95 gatunków w 16 rodzajach. Ponad 75% tych taksonów znanych jest wyłącznie z serii typowych, często ograniczonych do pojedynczego holotypu, nierzadko w złym stanie zachowania, co znacząco utrudnia analizy morfologiczne i molekularne. W celu przezwyciężenia tych ograniczeń zastosowano podejście integratywne, łączące dane genomowe (499 loci, 155 172 aminokwasy) pozyskane z okazów współczesnych z danymi mitochondrialnymi (12 loci, 2 395 aminokwasów), w tym z materiału historycznego Eurynotina. Dane molekularne skonfrontowano z matrycą cech morfologicznych w celu pełnego pokrycia różnorodności rodzajowej podplemienia. W wyniku przeprowadzonych analiz podplemię Eurynotina zostało zreorganizowane w pięć linii filogenetycznych: *Eurynotus*, *Phylacastus*, *Schyzoschelus*, *Psectrapus* oraz *Oncotus*. Opisano dwa nowe rodzaje (*Colophonexsula* Lumen & Kamiński, *Muelleropsectropus* Lumen & Kamiński) oraz 13 nowych dla nauki gatunków: *Eurynotus brunoi* (Lumen & Kamiński), *E. privisolum* Lumen & Kamiński, *Isoncophallus ovanullum* Lumen & Kamiński, *I. crispiformus* Lumen & Kamiński, *Ograbies calumnus* Lumen & Kamiński, *Phaleriderma iwani* Lumen & Kamiński, *Phylacastus ancoralium* Lumen & Kamiński, *Phy. makskacymirowi* Lumen & Kamiński, *Psectrapus byki* Lumen & Kamiński, *Ps. distaticum* Lumen & Kamiński, *Ps. latimentulum* Lumen & Kamiński, *Ps. simplicimentulum* Lumen & Kamiński, *Schyzoschelus aetheculus* Lumen & Kamiński.

Ponadto wyznaczono liczne neotypy i lektotypy w celu stabilizacji nomenklatury, zaproponowano nowe kombinacje i synonimy oraz zidentyfikowano nowe taksony jajożyworodnych mącznikowatych. Dokonano również rewizji terminologii dotyczącej morfologii układu rozrodczego. Wyniki badań zostały opublikowane w serii pięciu prac naukowych, z których ostatnia stanowi kompleksowe opracowanie monograficzne obejmujące klucze do wszystkich pięciu linii filogenetycznych, 19 rodzajów i 94 gatunków. W rezultacie przeprowadzonych badań podplemię Eurynotina uzyskało solidną hipotezę filogenetyczną, stanowiącą podstawę dla przyszłych badań systematycznych i ewolucyjnych.

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ARTICLE 1

Lumen, R.* & Kamiński, M.J. (2023) Taxonomic revision of the genus *Phylacastus* Fairmaire (Tenebrionidae, Eurynotina): shortfalls of anatomical nomenclature with notes on aedeagal homology. **Zookeys**, 1138, 1–27. https://doi.org/10.3897/zookeys.1138.95968

ARTICLE 2

Lumen, R.* & Kamiński, M.J. (2024a) Revision of the darkling beetle genus *Eurynotus* (Blaptinae: Platynotini) and new records of ovovivipary in Tenebrionidae. **Zoological Journal of the Linnean Society**, 201, 358–386. https://doi.org/10.1093/zoolinnean/zlad146. *Awarded the Jean Theodore Lacordaire Prize by The Coleopterists Society, recognizing the best paper derived from a PhD thesis. https://www.coleopsoc.org/society-info/prizes-and-awards/jean-theodore-lacordaire-prize*

ARTICLE 3

Lumen, R.* & Kamiński, M.J. (2024b) Redefining generic boundaries in subtribe Eurynotina (Coleoptera: Tenebrionidae): taxonomy of the *Schyzoschelus* generic group. **The European Zoological Journal**, 91, 122–141. https://doi.org/10.1080/24750263.2023.2300723

ARTICLE 4

Lumen, R., Rork, A.M., Smith, A.D. & Kamiński, MJ*. 2025. Complementary genomic and morphological data elucidate the phylogeny of obscure darkling beetles (Blaptinae: Platynotini: Eurynotina). **Systematic Entomology**, e70012. https://doi.org/10.1111/syen.70012

ARTICLE 5

Lumen R.*, Kamiński MJ. 2025. Revision of subtribe Eurynotina (Coleoptera: Tenebrionidae: Blaptinae). **Natural History Monographs of the Upper Silesian Museum** 5: 1–217. https://doi.org/10.5281/zenodo.17878025

Note: Publications listed above are cited in bold blue throughout the thesis (e.g., **Lumen & Kamiński 2023**) to facilitate navigation and clearly identify published thesis work.

1. Introduction

Darkling beetles (family Tenebrionidae Latreille) are a cosmopolitan group encompassing a wide array of diverse bauplans and ecological niches. Tenebrionids have specialized across a variety of habitats such as tropical rainforests, coastal dunes, and arid deserts; with diets including other invertebrates (predatory), dead wood (saproxyly), detritus (detritivory), and fungus (fungivory) (Matthews *et al*. 2010). Past studies have focused on a variety of topics including: their role as crop pests (Allen 1937, Chittenden & Marsh 1910, Czernej & Fedoranko 2006, Drinkwater 1999, Elmore 1948, LeBoeuf 2002, Medvedev 1968, Papp & Pierce 1960, Reichardt 1936, Roberts 1947, Strauss *et al*. 2002), as adventive species (Aalbu *et al*. 2009, Steiner 2003), indicators of habitat quality (*e.g.*, Fattorini & Salvati 2014), interesting behaviors (such as fog-basking in *Onymacris* Allard) (Hamilton & Seely 1976), and even potential as forensic indicators (Aballay *et al*. 2016). Despite various research foci, and a sizable diversity of over 30,000 described species (Bouchard *et al*. 2021), the systematics of Tenebrionidae remains insufficiently studied (Kergoat *et al*. 2014, Kamiński *et al*. 2021), leaving many lineages with a dearth of information as to their classification, identification, and, consequently, the materials needed to adequately study them.

Many recent studies and the current classification of darkling beetles continue to rely heavily on dated morphological concepts (*e.g.*, Watt 1974, Doyen & Tshickel 1980) or focus on resolving relationships at the subfamily level with molecular data (Kergoat *et al.* 2014, Ragionieri *et al*. 2023). While previous efforts offer valuable reference points for targeted taxonomic work (*e.g*., Aalbu *et al*. 2023; Ragionieri *et al.* 2023; Kamiński *et al.* 2024), many lineages remain unassessed within a robust phylogenetic framework, and older morphological characters are in need of reexamination in updated phylogenetic contexts. For example, the subfamily Blaptinae Leach (grouping nearly 4,000 species) was largely treated as an informal grouping of polyphyletic lineages for many decades with authors disagreeing about the phylogenetic limits based on inconsistent or plesiomorphic morphology (Doyen 1972, Doyen & Tschinkel 1982, Iwan & Bečvář 2000, Schulze 1969, Skopin 1962, 1964, Watt 1974). Recent molecular data (Kamiński *et al*. 2021) provided further evidence to reevaluate and subsequently reinstate the subfamily as a monophyletic entity. Without more rigorous phylogenetic examination, taxa are often difficult or even impossible to identify or classify; further, studies of

ethology or ecology are severely impaired, as they lack phylogenetic data for study in proper evolutionary context.

For example, under current classification, the tribe Platynotini Mulsant & Rey (Blaptinae) contains two sister subtribes: Platynotina Mulsant & Rey and Eurynotina Mulsant & Rey, 1854. Platynotina has received extensive treatment (*e.g.*, Kaszab 1941, Koch 1956, Ferrer 1983, Endrödy-Younga 1988, 2000, Iwan 1990, 1995, 2002, Banaszkiewicz 2007, Iwan & Kamiński 2014, Iwan *et al*. 2012, Ivie *et al*. 2021, Kamiński 2012, 2013, 2014, 2015, 2017, Kamiński & Iwan 2013, Kamiński & Schoeman 2018, Schimrosczyk 2010), whereas Eurynotina has only recently attracted focused attention (*e.g.*, Banaszkiewicz 2006, Kamiński 2016, Kamiński and Schawaller 2019, Kamiński *et al*. 2019). Some species of Platynotina are represented by many specimens, with concepts encompassing variation of individuals within a species (*e.g.*, *Upembarus wittei wittei* Koch with over 8,000 syntype specimens (Koch 1956)); while in Eurynotina, the majority of species are represented by very few specimens (Kamiński 2016), resulting in species concepts hinging on a single sex or even lone specimens (*e.g.*, *Oncotus irrepertus* Koch known only by the type series of seven females, or *Schyzoschelus aeneomicans* Koch known only by the male holotype). Systematic investigations of Eurynotina are additionally hampered by a lack of morphological data in cases where specimens are badly damaged (*i.e.*, missing body parts), precluding full codification into morphology matrices. Despite their original descriptions 70–200+ years ago (Koch 1954, 1955), many species have not been recollected and, as a result, the original diagnostic characters have not been verified and systematic revision of the group has been stalled. The imbalance of taxonomic work betwixt the two subtribes of Platynotini not only limits our understanding of Eurynotina itself, but also constrains broader evolutionary and biogeographic interpretations within the subfamily Blaptinae.

The asymmetry between Platynotina and Eurynotina has also left interesting questions about ecology and behavior difficult to approach. Ovovivipary, for example, is an extremely rare reproductive strategy in beetles, and yet has been recorded for several species in the tribe Platynotini (Iwan 2000). Ovoviviparous species retain eggs, allowing them to hatch internally or shortly after laying. In the case of Platynotini, well-developed larvae have been observed within the bursa copulatrices of dissected female specimens–indicating that such species likely undergo larviposition (laying larvae) rather than oviposition (laying eggs) (Iwan 1996, 2000, Iwan &

Ferrer 2000). While most examples historically are recorded within the subtribe Platynotina, a single example has been recorded from the sister subtribe Eurynotina (*Eurynotus capensis* (Fabricius)) (Tschinkel 1978). To date, it has been impossible to evaluate the extent or degree to which ovovivipary occurs in Eurynotina, or any factors (climactic, ethological, or otherwise) tied to the phenomenon. Closer study of the phenomenon of ovovivipary (*e.g.,* evolutionary history, which species and/or genera exhibit the behavior) is further hampered by our inability to classify or even identify the majority of species of Eurynotina. Additionally, reproductive morphology and behavior are largely unrecorded and unknown; as such, even preliminary investigations are valuable contributions.

Prior to this work, Eurynotina comprised 16 genera and 10 subgenera, and was further classified into 95 described species and subspecies (Koch 1954a, b, 1955, Kamiński 2016). Representatives of the subtribe are morphologically defined within Blaptinae by the presence of a stridulatory gula (a characteristic shared with Platynotini), lack of aedeagal laciniae/clavae, and presence of tubercles on the elytra of many species (Koch 1956). Confined to southern Africa, many species of Eurynotina are largely restricted to extremely arid environments (*e.g.*, *Hirtograbies* Koch or *Phaleriderma* Koch in the Namib desert), some representatives, such as *Eurynotus* Kirby, are present along the coastline or inland from drier to estuary or riparian habitats (Kamiński 2016 and specimen records).

The monophyly of Eurynotina, with regard to Platynotina, has not been fully tested. For instance, Platynotina contains taxa violating its current morphological subtribal definitions (*e.g.*, *Gonopus* Latreille and *Anomalipus* Guérin-Méneville both contain species possessing elytral tubercles, and *Anchopthalmus plicipennis* Péringuey lacks laciniae/clavae on the aedeagus). The most exhaustive morphological examination of Platynotini was unfortunately limited in the diversity of Eurynotina (two species) (Iwan 2002), and the most comprehensive phylogenetic study of the tribe also included an insufficient number of Eurynotina (four species) to properly test the limits of the two subtribes (Kamiński *et al.* 2021).

Generic relationships within Eurynotina also remain uninvestigated. Koch initially treated the subtribe and described the majority of its diversity (1954a, b), before revisiting the group to add the final two genera and some additional species (1955). His resulting, tentative subdivision of the subtribe into the three following morphological generic groups remains untested (Table 1): *Eurynotus* group (clypeal apex deeply emarginated); *Schyzoschelus* group (clypeal apex

straight); *Oncotus* group (clypeal apex shallowly, but clearly emarginate). While the divisions proposed by Koch are promising, the morphology he used has not been thoroughly examined since their original description, and the groupings remain untested in a phylogenetic framework.

Subtribe Eurynotina *sensu* Koch (1954a, b, 1955, 1956)		
***Eurynotus* group (20 spp.)**	***Schyzoschelus* group (23 spp.)**	***Oncotus* group (51 spp.)**
Eurynotus (3 subgenera, 16 spp.)	*Heteropsectropus* (7 spp.)	*Byrrhoncus* (2 spp.)
Phylacastus (4 spp.)	*Schyzoschelus* (16 spp. and subsp.)	*Capidium* (4 spp.)
		Colophonesthes (3 spp.)
		Hirtograbies (7 spp.)
		Isoncophallus (7 spp.)
		Menederes (2 subgenera, 3 spp.)
		Menederopsis (monotypic)
		Ograbies (7 spp.)
		Oncotus (4 subgenera, 10 spp.)
		Phaleriderma (3 spp.)
		Psectrapus (2 spp.)
		Stridigula (2 spp.)

Table 1: Subtribe Eurynotina generic concepts and organization tested by the thesis presented here. Organization of the genera follows the informal classification presented by Koch (1954a, b, 1955, 1956).

Eurynotina is only known from several hundred specimens in total, distributed throughout a handful of museum collections. While some species are relatively common (*e.g.*, *Eurynotus capensis* (Fabricius)), the majority of eurynotines (>75% of species) are known only from their small descriptive series (Kamiński 2016). Additionally, specimens are often damaged or missing extractable tissue, reducing the likelihood of genetic capture/recovery for sequencing and subsequent phylogenetic analyses. Advancements in sequencing technologies have begun to mitigate challenges presented by suboptimally preserved specimens, particularly through museomics—the extraction of DNA from historical specimens for phylogenetic analyses (*e.g.*, Dabney *et al*. 2013; Smith *et al.* 2021; Hagemann *et al*. 2024). Museomics have enabled molecular insights even in beetles long preserved in collections (*e.g.*, Jin *et al*. 2020; Johnston *et*

al. 2022; Kim & Farrell 2025). Unfortunately, for some of the most taxonomically enigmatic and elusive groups, museomics alone remain insufficient for resolving phylogenetic relationships. Integration of molecular and morphological data would provide a more robust, total dataset for addressing the currently patchy data available for the group. The endemic distribution of Eurynotina (southern Africa), the ecological specificity of several species to some of the most extreme environments on earth, and the phenomena of ovovivipary all represent potentially valuable models for understanding patterns of unique life-history adaptations and diversification in arid habitats for Coleoptera. With a well-tested phylogeny and more thoroughly tested classification, further questions about the subtribe's ecology, evolution, behavior, and biogeography would be more approachable and feasibly addressed by future workers.

2. Aims of Study

The aim of this thesis was to test the taxonomic hypotheses of the subtribe Eurynotina and all its genera and species using modern systematic tools. A comprehensive phylogenetic analysis encompassing all previously recognized genera was conducted using a combined dataset of genomic (510 loci / 157,567 amino acids) and morphological data (91 features). After phylogenetic analysis and examination of nearly all primary types belonging to the focal group, a complete revisionary treatment of all known species was undertaken. As a result, a new classification is proposed and is accompanied by updated identification keys and distributional data.

3. Material and Methods

3.1 Order of studies

To begin work on the full revision of Eurynotina, the subtribe was first divided into smaller parts based on Koch's (1954a, b, 1955) groupings for easier management (Table 1): *Eurynotus* group (2 genera, 20 species), *Schyzoschelus* group (2 genera, 23 species and subspecies), and *Oncotus* group (12 genera, 51 species). Each group contained relatively clear, testable sets of taxa and morphology which also conveniently divided the diversity of the whole subtribe roughly into thirds. Each third was then treated to ultimately produce a final, monographic treatment of the group. The order and brief summary of each treatment is as follows:

- The ***Eurynotus* group** was addressed first through a morphological revision of the genus *Phylacastus* Koch, followed by the genus *Eurynotus*. The latter included a preliminary morphological analysis of the subtribe and the phenomena of ovovivipary outside the scope of the thesis goals. The results of this portion of the study are presented in section 4.1, and more specifically in **Lumen & Kamiński (2023)** and **Lumen & Kamiński (2024a)**.
- A morphological investigation of the ***Schyzoschelus* group** with the revision of the genus *Heteropsectropus* Kaszab and a catalog of *Schyzoschelus* Koch with nomenclatural revisions. Additionally, the phenomena of ovovivipary was reported for *Heteropsectropus* and the larval and pupal forms were described–representing the first records of pupal morphology for the subtribe, and for ovovivipary outside of genus *Eurynotus*. The results of this portion of the study are presented in section 4.2, and in detail in **Lumen & Kamiński (2024b)**.
- Using molecular and morphological datasets, testing the **monophyly of the subtribe** and generic and species concepts throughout Eurynotina are combined with analysis of the ***Oncotus* group**. New generic concepts and species are described. The results of this portion of the study are presented in section 4.3, and specifically in **Lumen *et al.* (2025)**.
- A **comprehensive monographic revision** of the entire subtribe Eurynotina down to the species level based upon all the previous work of this thesis, complete with exhaustive catalog, new species descriptions, taxonomic keys, and geographic distribution reports is

presented. The results of this portion of the study are presented in section 4.4, and also in **Lumen & Kamiński (2025)**.

3.2 Taxon sampling

The single largest and most exhaustive collection of specimens for subtribe Eurynotina was gathered from a worldwide query of entomological collections by the author of this thesis (full list of studied material of each taxon is available in the taxonomy section of **Lumen & Kamiński 2025**). One-hundred and twenty-one primary type specimens were examined encompassing all valid genus and species names. Preserved (ethanol and pinned) specimens were acquired from and deposited in the following institutional insect collections (collections personally visited by RL marked*):

BPBM – Bernice P. Bishop museum; Honolulu, Hawaii, United States;

***CASC** – California Academy of Sciences; San Francisco, California, United States;

HNHM – Hungarian Natural History Museum; Budapest, Hungary;

IMSA – Iziko South African Museum; Cape Town, South Africa;

***MIZPAN** – Muzeum i Instytut Zoologii, Polska Akademia Nauk; Warsaw, Poland;

***MNHN**–Muséum National d'Histoire Naturelle; Paris, France;

NHMB – Naturhistorisches Museum, Basel, Switzerland;

NHMUK–Natural History Museum; London, United Kingdom;

NHRS – Swedish Museum of Natural History; Stockholm, Sweden;

NMNW–Windhoek National Museum of Namibia; Windhoek, Namibia;

NRS – Naturhistoriska Riksmuseum; Stockholm, Sweden;

***PERC** – Purdue Entomological Research Collection; West Lafayette, Indiana, USA;

RBINS – Royal Belgian institute of Natural Sciences; Brussels, Belgium;

RMCA – Royal Museum for Central Africa; Tervuren, Belgium;

***SANC** – South African National Collection of Insects; Pretoria, South Africa;

SMNS – Staatliches Museum für Naturkunde; Karlsruhe, Germany;

SU – Stellenbosch University; Stellenbosch, South Africa;

***TMNH**–Ditsong National Museum of Natural History; Pretoria, South Africa;

UUZM – Uppsala University Museum of Evolution; Uppsala, Sweden;

ZMHB – Museum für Naturkunde; Berlin, Germany;

ZMUK – Zoologisches Museum, Universität Kiel; Kiel, Germany.

3.3 Morphological dataset

Morphological terminology follows Matthews *et al.* (2010), with additional specialized terms for terminalia following Banaszkiewicz (2006), Iwan & Kamiński (2016), and **Lumen & Kamiński (2023, 2024a, 2024b)**. Dissections of male and female terminalia followed methodology outlined in Kamiński (2021). Specifically, specimens were relaxed in 10% KOH solution prior to dissection, and genital tubes were stained with chlorazol black and stored in glycerin. Images were taken using a Canon 1000D body with extension rings and a Canon EF 100 mm macro lens, a Nikon D3500 body with adapter for a Nikon SMZ800N microscope, and with a Hitachi S3400N SEM in MIZPAN. Figures were assembled using Photoshop v.23.5.1.

Morphology of adult specimens was evaluated and scored in morphological matrices using MESQUITE v.3.61 (Maddison & Maddison 2019). Operational taxonomic units (OTUs) for morphological analyses were defined during taxonomic study, which included verification of type material and testing of diagnostic features for all previously described species (see Koch 1954a, b, 1955, 1956, and Kamiński 2016). Representatives of all morphologically coherent genera and subgenera of Eurynotina were scored, with additional sampling of genera made for incongruent species, to more densely cover the morphological diversity of the subtribe. Morphological characters were determined and scored based on a synthesis of multiple specimens whenever possible in an effort to capture the average state(s) for each OTU. Morphological features were also scored for all Eurynotina species included in molecular analyses to ensure the compatibility of OTUs from each dataset. Molecular OTUs were initially based on morphological examinations and further refined in light of acquisition and comparison with type material, as well as phylogenetic analysis (*e.g.*, *Oncotus capicola* (Koch) upon closer investigation was determined to be synonymous with *Ograbies capensis* (Solier), see section 4.3).

Morphology matrices produced in this thesis are available in sections 4.1 **(Lumen & Kamiński 2024a)** and 4.3 **(Lumen *et al.* 2025 Supplementary Table S3)**, and represent a progression of study. Specifically, a preliminary morphological matrix was produced for the second publication in 4.1 **(Lumen & Kaminski 2024a)** which included 26 species spanning eight genera and 70 characters; that matrix was later included in the publication in section 4.3

(Lumen *et al*. 2025), where it was expanded to 91 characters and included 63 species encompassing the full generic and subgeneric diversity of the subtribe. The morphological matrix was then additionally incorporated into a combined molecular/morphological analysis **(Lumen *et al.* 2025)**.

Larval features were excluded from morphomatrices, as data on preimaginal stages within Eurynotina remain scarce, with the vast majority (>90%) still unknown (see **Lumen & Kamiński (2025)**).

3.4 Targeted-enrichment (TE) dataset

Ethanol-preserved specimens used for extractions were collected by the Prof. dr hab. Marcin Jan Kamiński (MIZPAN) and Dr. Aaron D. Smith (PERC) (see **Lumen *et al*. 2025** for permit information) or acquired from the wet collection of MIZPAN. Additional historical pinned material with collection dates ranging from 1921 to 2001 originating from MIZPAN were processed to extend the taxonomic coverage of molecular-based analyses. Outgroup taxa to test the monophyly of Eurynotina included representatives of all major lineages of the sister subtribe Platynotina (Koch 1956, Iwan 2002, Kamiński 2015): trigonopoid (*Atrocrates* Koch, *Melanopterus* Mulsant & Rey, *Schelodontes* Koch, *Trigonopus* Mulsant & Rey), melanocratoid (*Sebastianus* Iwan, *Styphacus* Fairmaire), platynotioid (*Asiopus* Sharp, *Anchophthalmus* Gerstaecker), and gonopoid (*Anomalipus* Latreille, *Gonopus* Latreille) lineages. Additionally, two *Stenolamus* Gebien species representing the closely related tribe Opatrini Brullé, and *Blaps mucronata* Latreille of the distantly affiliated Blaptini (Kamiński *et al.* 2023, 2024) were included.

DNA was extracted from the head capsules and pronota of specimens using QIAamp DNA Micro Kits following the manufacturer's protocols. Grinding of the cuticle was avoided to preserve specimens for morphological examination. Extractions were performed in a sterilized laminar flow hood to minimize contamination from non-target DNA (see Kanda *et al*. 2015). Extraction voucher specimens were rearticulated and card-mounted. Additionally, unique identifiers (TB or MEL#s) were assigned to each specimen for referencing and records uploaded to the Sequence Read Archive with accession numbers (SAMN51150149–SAMN51150179). All voucher specimens are preserved in PERC and MIZPAN.

Extracts were sent to Daicel Arbor Biosciences for library preparation, targeted enrichment, and sequencing on a NovaSeq 6000 system using 150 bp paired-end runs. Targeted enrichment was performed using MyBaits probe kits for 620 nuclear loci spanning ~820kb. Loci were chosen from an existing set of protein coding loci used in Pimeliinae (Kanda 2017, Switchtenberg *et al.* 2023) with baits modified based on transcriptomic data from *Eleodes delicata* Blaisdell (Blaptinae), *Eulabis bicarinata* Eschscholtz (Tenebrioninae), *Tenebrio molitor* L. (Tenebrioninae), and *Clamoris americana* (Horn) (Phrenapatinae Solier) and checked using BLAST filtration against the *Tribolium castaneum* Herbst, *T. confusum* Jacquelin du Val, and *T. madens* Charpentier genomes. Final probes (80bp each) were double tiled for fresh material and triple tiled for museum specimens.

Sequence assemblies were performed on Purdue University's Bell community cluster, within Rosen Center for Advanced Computing (McCartney *et al*. 2014). Read quality was assessed with FastQC v.0.11.9 (Andrews 2010). Reads with an average sequence quality across any 4 bases below 20 were removed with Trimmomatic (Bolger *et al*. 2014). HybPiper v. 2.0 pipeline (Johnson *et al.* 2016), operating in DIAMOND mode (Buchfink *et al.* 2015), was used to assemble reads using the set of orthologs designed by Kanda (2017).

The resulting nucleotide sequences were translated to amino acids and then aligned in MAFFT with the L-INS-I algorithm (Katoh *et al.* 2005). Low-quality amino acid sequence sites were masked, while sequences with over 50% gaps per locus were trimmed in trimAl (Capella-Gutiérrez *et al.* 2009). Surviving sequences were concatenated using FASConCAT (Kück & Meusemann 2010) into a partitioned dataset comprising a total of 499 loci spanning 155,172 amino acids (Section 4.3, **Lumen *et al.* (2025)**).

3.5 Mitochondrial dataset

Due to poor recovery of targeted nuclear protein coding genes for pinned historical specimens, bycatch mitochondrial data was harvested for all specimens included in sequencing (see **Lumen *et al.* 2025 supplemental figure S1**). The mitochondrial genomes for selected fresh samples representing Eurynotina (*Byrrhoncus* sp. MEL127, *Eurynotus asperatus* Muslant & Rey TB23375) and Platynotina (*Anomalipus elephas* Fåhraeus TB26363, *Asiopus aciculatus* LeConte MEL147) were assembled de novo using the multi-cell mode in SPAdes v.3.13.035 (Bankevich *et al.* 2012). Prior to this process, raw data were checked for quality and trimmed (see section

3.4). Assembled mitochondrial scaffolds were identified using BLAST searches against the published mitochondrial genome of *Asbolus verrucosus* LeConte (NC_027256). Sequences of 13 protein coding genes of the aforementioned Platynotini species were used in HybPiper v. 2.0 to recover mitochondrial loci from all remaining samples, including extracts taken from museum specimens. The SendSketch script, as implemented in BBMap/36.92 (Bushnell *et al*. 2014), was used to characterize the metagenomic profile of assembled contigs and check for contamination. Similar to the TE dataset, obtained nucleotide sequences were translated to amino acids, aligned with MAFFT, and trimmed in trimAl. Data was concatenated in FASConCAT into a partitioned dataset comprising a final total of 12 loci spanning 2,395 amino acids (see Section 4.3, **Lumen *et al.* (2025)**.

3.6 Data analysis

All phylogenetic analyses based on genomic and combined genomic/morphological data were performed on Purdue University's Bell community cluster, within Rosen Center for Advanced Computing. Morphological traits were analyzed locally. The resulting trees were visualized in FigTree 1.4.4 (Rambaut 2009) and Winclada 1.61 (Nixon 2002).

3.6.1 Monophyly of Eurynotina

Targeted enrichment data from fresh, ethanol-preserved specimens was used to test the monophyly of the subtribe (**Kamiński & Lumen 2025**: Appendix 2). Maximum likelihood (ML) analyses were run in IQ-TREE 2 (Minh *et al.* 2020) using an edge-unlinked partition model (-Q), with the dataset partitioned by loci and the best-fit models for each locus selected *via* ModelFinder (Kalyaanamoorthy *et al.* 2017). Support for the resulting topology was assessed using 10,000 UltraFast Bootstrap (UFB) (Hoang *et al.* 2018) iterations. The molecular matrix was also analyzed using ExaBayes 1.5.1 (Aberer *et al.* 2014). Two independent runs, each with 1 cold chain and 3 heated chains, were performed. Analyses were run for 500,000 generations with a burn-in fraction of 0.25, and convergence was determined by the average standard deviation of the split frequencies; runs were considered to have converged at < 0.01.

3.6.2 Generic relationships of Eurynotina

Most outgroup taxa were trimmed to increase the parsimoniousness of morphological runs by omitting non-focal taxa, and only *Gonopus deplanatus* Fåhraeus (Platynotina) was used as an outgroup reference for morphology-based analyses.

3.6.3 Morphology

The morphological dataset (**Kamiński & Lumen 2025**: Appendix 1) was imported into TNT v.1.5 (Goloboff & Catalano 2016) for phylogenetic inference using maximum parsimony. A setk script, developed by Salvador Arias, was used to identify the most appropriate K value through the formula proposed by Goloboff *et al.* (2008). The resulting k value was then used in the implied weighting scheme for implicit enumeration search. Nodes were evaluated for Bremer support with the Bremer.run script within TNT (Bremer 1994). Performance of characters in parsimony analysis was verified by calculating the consistency (ci) and retention indices (ri) in TNT with *wstats.run* script, whereas the values of CI and retention RI indices for the whole matrix were obtained in the same software with *stats.run* script. Additionally, ML analyses were run in IQ-TREE 2 (Minh *et al*. 2020) as specified above, and the UltraFast Bootstrap values were then mapped onto the cladogram from the parsimony analyses.

3.6.4 Museomics

ML (IQ-TREE 2) and Bayesian (ExaBayes) analyses were performed on the concatenated TE and mitochondrial datasets (see section 3.6.1 *Monophyly of Eurynotina*). The concatenated dataset consisted of 510 loci spanning 157,567 amino acids (**Kamiński & Lumen 2025**: Appendix 3).

3.6.5 Combined analysis

A concatenated dataset of TE, mitochondrial, and morphological data was analyzed both in IQ-TREE 2 and MrBayes v.3.2.7a (**Kamiński & Lumen 2025**: Appendix 1, 3). Data partitions and models of sequence evolution were assessed with IQ-TREE 2. The ML run was performed under the same specifications as stated above (see *Monophyly of Eurynotina*). MrBayes analysis was conducted with models inferred from IQ-TREE 2 model selection analysis. Two independent runs, each with 1 cold and 3 heated chains, were performed. Analyses were run for

1 million generations sampled every 1,000 with a burn-in fraction of 25%. Convergence was evaluated using the average standard deviation of the split frequencies, with a convergence threshold of <0.05.

4. Summary of Thesis and Publication Results

4.1 *Eurynotus* group **(see Lumen & Kamiński 2023, 2024a)**

- *Phylacastus* (four species) was revised first using morphology. All species in the genus were verified and, as a result, one **synonym was proposed** (*P. crypticoides* Koch (=*P. pretoriensis* Koch)) and **two new species** were described (*P. ancoralium* Lumen & Kamiński and *P. makskacymirowi* Lumen & Kamiński). Additionally, new reproductive morphology for the subtribe was described, and new terminology to describe the male reproductive anatomical features was introduced and described. Specifically, accessory structures of the aedeagus, *ancorae*, to replace inadequate terms: lacinia, clavae. Further, the presence of ancorae was recorded in *Phylacastus ancoralium*, which represents the only species in Eurynotina with this trait previously used to diagnose the subtribe from Platynotina.
- While revising *Eurynotus*, a preliminary morphological matrix of 70 characters, including external and internal features, was made for the subtribe *Eurynotina*. Primarily focused on all 16 species from all three subgenera of *Eurynotus*, five other genera from the subtribe were also included to briefly examine generic relationships (totalling 26 species and eight genera examined). *Phylacastus* was not recovered sister *Eurynotus* in the analysis–indicating that while *Eurynotus* and *Phylacastus* are two distinct genera, Koch's (1954a, b, 1955) *Eurynotus* group was not monophyletic. *Eurynotus* was further divided into **two clades recognised as genera** (*Eurynotus* and *Biolus* Mulsant & Rey), and **two new species were described** (*Eurynotus privisolum* Lumen & Kamiński, *Biolus brunoi* Lumen & Kamiński). *Biolus asperipennis* (Mulsant & Rey) was **restored as a valid species** and **two synonyms were proposed** (*Eurynotus asperatus* Mulsant & Rey (=*E. rudebecki* Koch), *E. granulatus* (Fabricius) (=*E. norrisi* Mulsant & Rey)). To further stabilize the taxonomy of the genus, **lectotypes were designated for 10 species**: *Eurynotus alticola* Koch, *E. asperatus*, *E. asperipennis* Mulsant & Rey, *E. capensis*, *E. constrictus* Koch, *E. denticosta* Mulsant & Rey, *E. granulatus*, *E. norrisi*, *E. rudebecki,* and *E. sulcimargo* Koch. Though outside the primary scope of the thesis, an outline for the rare phenomena of ovovivipary was additionally provided along with a preliminary examination of related morphology and a statistical analysis for potential environmental

driving forces for its evolution. While none of the examined environmental factors were statistically relevant, new records of ovovivipary were presented for *Biolus brunoi*, *B. granulatus* (Fabricius), and *E. barbosai* Koch and larval morphology was briefly outlined. Additionally, previous hypotheses from other authors concerning related morphology (*i.e.*, shortened ovipositors for larviposition) were falsified, as all *Eurynotus* without exception, possess elongate ovipositors.

4.2 *Schyzoschelus* group **(see Lumen & Kamiński 2024b)**

- The *Schyzoschelus* group was treated at once with a morphological **revision of the genus *Heteropsectropus*** (7 species) and **reevaluation of the genus *Schyzoschelus*** (16 species and subspecies). The *Schyzoschelus* group is morphologically distinct from the rest of Eurynotina; however, the generic limits between *Heteropsectropus* and *Schyzoschelus* were less clear. The **new genus *Muelleropsectropus* Lumen & Kamiński was described** to receive the species *Muelleropsectropus malaisei* (Koch) (formerly *Schyzoschelus*), which was found to possess morphology between *Schyzoschelus* and *Heteropsectropus*. Closer investigation of both *Schyzoschelus* and *Heteropsectropus* resulted in **four synonymies** within *Heteropsectropus* (*H. difficilis* Koch (= *H. amaroides* Koch, = *H. natalensis* Koch, = *H. transvaalensis* Koch; *H. longantennatus* Koch (= *H. montisdraconis* Koch)), and **two synonymies** within *Schyzoschelus* (*Schyzoschelus dumosicola* Koch (= *S. dumosicola var. diversipenis* Koch; *Schyzoschelus simplicipes* Koch (= *S. simplicipes willowmorensis* Koch)). While the status of most species was sustained, some species of *Schyzoschelus* were exceedingly difficult to evaluate based on a shortage of specimens (*e.g.*, *S. aeneomicans* Koch remains represented only by the singleton male holotype), indicating more work will be required in the future. Finally, a new record of ovovivipary was reported for *Heteropsectropus difficilis* and its **larval and pupal morphology were described for the first time**. As a result, *H. difficilis* is the third species with a described larvae (as well as the first outside genus *Eurynotus*), and the first and only species with a pupal description in the subtribe.

4.3 Monophyly of Eurynotina and treatment of the *Oncotus* group **(see Lumen *et al.* 2025)**

- A comprehensive morphological and molecular analysis of subtribe Eurynotina was provided for the first time. Additionally, the last subunit of Eurynotina *sensu* Koch (1955) was evaluated (*Oncotus* group) using next generation, targeted enrichment sequencing of nuclear loci (499 loci / 155,172 amino acids), mitochondrial loci (12 loci / 2,395 amino acids), and morphological data (91 characters) from a comprehensive set of OTUs representing over 60 species of Eurynotina covering all genera and genus-groups, as well as out-group taxa for the major lineages of Platynotina. The whole generic organization of the subtribe was treated and the monophyly of the subtribe was evaluated and confirmed. A new classification based on phylogenetic lineages recovered in the analyses was also proposed.
- The original composition of the *Oncotus* group designated by Koch (1954a, b) was not monophyletic. Specifically, five genera formed a separate, monophyletic grouping in the combined analysis (subsequently designated the *Psectrapus* lineage: *Byrrhoncus* Koch, *Capidium* Koch, *Colophonesthes* Koch, *Isoncophallus* Koch, *Psectrapus* Solier). Additionally, many genera across the phylogeny were in need of reorganization to restore monophyly. **Two subgenera** of *Oncotus* Solier were **elevated to genus status** (*Menoncotus* Koch, and *Quadroncotus* Koch), a **subgenus** of *Menederes* Solier was **elevated to genus** (*Anamenederes* Koch), and a **new genus** was described (*Colophonexsula* Lumen & Kamiński) to restore monophyly of *Colophonesthes*. **Subgenus** *Cilioncotus* was **synonymized** with the **genus** *Stridigula*. **Three new species were described** as a result of investigating the OTUs and specimens included in the molecular analyses (*Ograbies calumnus* Lumen & Kamiński, *Psectrapus byki* Lumen & Kamiński, and *P. simplicimentulum* Lumen & Kamiński). *Eurynotus* and *Biolus* were reunited and **synonymized** under *Eurynotus* with new information from the molecular and combined dataset. **New combinations** were introduced for several genera as their concepts were revised: *Eurynotus brunoi, Menoncotus chaetotaxicus* (Koch), *M. jokli* (Koch), *M. sinuatipes* (Koch), *Quadroncotus irrepertus* (Koch), *and Stridigula namaquana* (Koch).

4.4 Full taxonomic revision of Eurynotina **(see Lumen & Kamiński 2025)**

- A monograph encompassing the full taxonomic diversity of Eurynotina was presented with dichotomous taxonomic keys for identifying **all 19 genera and 94 species** using the new classification proposed in section 4.3. The genera were reevaluated a final time and new species and generic concepts were presented. The genus *Menederes* was revised using the combined phylogeny from section 4.3 as well as additional morphological scrutiny, and as a result, *Menederopsis* Koch and *Menoncotus* were **synonymized** under *Menederes*. **Six new species are described** (*Isoncophallus crispiformus* Lumen & Kamiński*, Isoncophallus ovanullum* Lumen & Kamiński*, Phaleriderma iwani* Lumen & Kamiński, *Psectrapus distaticum* Lumen & Kamiński*, Psectrapus latimentulum* Lumen & Kamiński*,* and *Schyzoschelus aetheculus* Lumen & Kamiński), and new records of ovovivipary were reported for *Psectrapus* and *Isoncophallus ovanullum*. Color photos are provided for all type species as well as for the general diversity of the subtribe, and diagnostic features are depicted for identificatioin of all species and genera.

5. Discussion

While the goals of this thesis were to investigate the monophyly of subtribe Eurynotina and the coherence of its constituent genera and species, this work has additionally produced unexpected results regarding reproductive strategies and morphology. Previous studies of Tenebrionidae differed on naming conventions for male reproductive morphology and only named them based upon their shape (*i.e.*, lacinia/clavae), rather than on ontological merits, making unifying morphological approaches difficult. See the Hymenoptera Anatomy Ontology (Yoder *et al.* 2010) and the Coleoptera Anatomy Ontology (Girón *et al.* 2024) for ongoing efforts to address such shortfalls in different groups of insects. The new term I proposed (*ancorae*) defines these structures more strictly, based upon the origin of the feature's attachment (*i.e.,* attached to the basal apophysis at the base of the parameres) (**Lumen & Kamiński 2023**). Ovovivipary in Tenebrionidae was also briefly examined (**Lumen & Kamiński 2024a**). It appears to be more common in Eurynotina, and was recorded in the *Eurynotus*, *Schzoschelus*, and *Psectrapus* lineages: three times in *Eurynotus*, once in *Heteropsectropus*, once in *Isoncophallus*, and once in *Psectrapus* (**Lumen & Kamiński 2024a, b, 2025**). In addition to new records of ovovivipary for the subtribe, the first preliminary statistical analysis of the phenomenon with regard to habitat conditions for Tenebrionidae was produced. Though the analysis did not find any strong correlation with climatic factors (**Lumen & Kamiński 2024b**), future studies may use these results to steer their efforts (*e.g.*, include new environmental data or change parameters for analyses). Identification has become less of a hurdle as a result of this thesis work; however, scarcity of specimens for many taxa remains as an impediment to additional research. Future investigations of internal female reproductive physiology in addition to laboratory and microhabitat studies may provide more insights into the evolution of ovovivipary.

On initial investigation, the scant few original descriptions of Eurynotina were found to be either lacking in detail, or otherwise focused on minute details differentiating small series of individuals from overlapping distributions. As a result, many species concepts were weak hypotheses in need of reexamination, and morphology alone was insufficient to fully resolve the phylogenetic relationships below the subtribal level. For example, the *Psectrapus* lineage has no apparent morphological synapomorphies as of this study (**Lumen *et al.* 2025**). Many of the

genera are diagnostic at the generic level (*e.g.*, *Byrrhonchus* with characteristic aedeagal parameres, *Capidium* with cylindrical legs); however, traits that unite the entire lineage remain elusive. If not for molecular evidence uniting them, this group could be divided into lineages represented by as few as a single genus, or render other groups with greater affinity to each other (*i.e.*, *Oncotus* lineage) as paraphyletic. The genus *Eurynotus*, previously divided into subgenera before separation into two separate genera during this thesis (**Lumen & Kamiński 2024a**), was also perturbed by molecular evidence (**Lumen *et al.* 2025**). Morphologically the genus can be divided into two distinct groups (with stronger tuberculation and knobs on the elytral humeri, or weaker/absent tuberculation and lacking knobs). Molecular analyses recover both groups as a single, mixed clade. To reconcile these results, I have opted to restore *Eurynotus* as a single genus without subgeneric classification, as the concerned species (*i.e.*, *E. brunoi* and *E. asperipennis*) violate the classification(s) proposed by Koch (1954a, b), and no morphological evidence to redivide the genus in concurrence with molecular data was found during this investigation (**Lumen *et al.* 2025**).

Incongruencies between morphological and molecular analyses were, by and large, restricted to the aforementioned cases (**Lumen *et al.* 2025**). The subtribe was monophyletic and, aside from the exclusion of the *Psectrapus* lineage and *Phylacastus* lineages from the *Oncotus* and *Eurynotus* lineages respectively, all other genera were recovered well-within their expected regions of both phylogenies (*e.g.*, the *Schyzoschelus* lineage was a distinct and monophyletic lineage, as was the *Oncotus* lineage after the exclusion of the *Psectrapus* lineage).

The molecular methods and results here largely focus on nuclear, protein-coding genes in darkling beetles resulting in topologies with high support using fresh material (**Lumen *et al.* 2025**). Museum specimens were inconsistent in recovery and quality; however, mitochondrial data obtained as bycatch during sequencing made it possible to increase taxonomic representation, as museum samples with viable mitochondrial data could then be compared with fresh material in direct comparison(s) in analyses. Specifically, species which have eluded recollection since their original capture and/or descriptions that were otherwise impossible to evaluate beyond morphology could be included (*e.g., Colophonesthes*), or museum specimens could be compared with fresh material for verifying morphology-based identifications (e.g., *Psectrapus*). As is often the case in museomic studies, future work will benefit as DNA

extraction methodology improves recovery in museum/aged material (e.g. Dabney *et al.* 2013 *v.s.* Dabney & Meyer 2019, and Rohland *et al.* 2004 *v.s.* Rohland *et al*. 2018).

While molecular data is useful for delimiting cases where morphology falls short, morphology provided the opportunity to develop hypotheses for relationships between and amongst taxa which were difficult or impossible to sequence. For example, in cases where recovered genetic material was too low quality or unobtainable–or where few specimens are known (such as *Quadroncotus* (n=4)), morphology served as a means to designate a phylogenetic position for a taxa until such a time where more data becomes available (**Lumen *et al.* 2025**). By using both morphology and next-generation sequencing, I was able to translate my results into a testable classification and generate usable identification material(s) (*i.e*., dichotomous keys) while not expanding phylogeny-classification gaps.

Overall, the results from section 4.3 show that integration of morphological and molecular data can be used to address gaps in data resulting from missing OTU's or characters in multiple datasets. By associating taxa with targeted enrichment nuclear, mitochondrial, and morphological data, a phylogenetic hypothesis could be generated and then rigorously tested for groups where material is difficult to assess or access (*i.e.*, low number of existing specimens, damaged or missing body parts, or poor DNA recovery for certain taxa). Further, by leveraging older museum specimens, identifying species which have not been collected since their original descriptions, and/or describing new species is possible (*e.g.*, the new species *Psectrapus simplicimentulum* was successfully described, extracted, and included in phylogenetic analyses using a specimen collected in 1921) (**Lumen *et al.* 2025**).

As a result of the body of work presented in this thesis, the subtribe Eurynotina now has a well-documented and tested phylogenetic background upon which future work can scaffold, and other workers on rare or difficult to obtain taxa can use the methodology provided in the publications provided here to address systematic and taxonomic queries.

6. Conclusions

- The analyses presented here (section 4.3) strongly support the monophyly of Eurynotina with regard to its sister subtribe Platynotina. Both possess a stridulatory gula (uniting them under Platynotini), while retaining exceptional taxa with regard to their otherwise well-established diagnostic features, such as tubercles of the elytra and presence/absence of ancorae, leaving a simple morphological delineation between the groups difficult; however, Platynotina generally have no tubercles on the elytra, and all but one Eurynotina species lack ancorae on the aedeagus.
- The phylogenies produced from this study allow for subdivision of Eurynotina into five lineages: (*Eurynotus* lineage, *Oncotus* lin.*, Phylacastus* lin., *Psectrapus* lin.*,* and *Schyzoschelus* lin.) (see Table 2), which contrasts with the three groupings originally proposed by Koch (1954a, b, 1955) (*Eurynotus*, *Oncotus,* and *Schyzoschelus*). Specifically, *Phylacastus* is excluded from the *Eurynotus* group, and several genera are excluded from the *Oncotus* group (subsequently referred to as the *Psectrapus* lineage: *Byrrhoncus, Capidium, Colophonesthes, Colophonexsula, Isoncophallus*, and *Psectrapus*).
- As a part of the work on this thesis, nearly all type material for every species-name within Eurynotina was examined (n=121). As a result, many of the genus and species names from older authors (*e.g.*, 1800s Fairmaire and Solier) were confirmed or reestablished through designation of lecto- and neotypes.
- Due to scarcity of data, outdated taxonomy, and a dearth of identification resources, the diversity of Eurynotina was previously underestimated and many taxonomic entities were poorly delineated. While testing the limits of the genera within Eurynotina, I was able to describe two new genera. Specifically, *Muelleropsectropus* and *Colophonexsula* as a result of examining the generic limits of *Schyzoschelus vs. Heteropsectropus*, and *Colophonesthes* vs. *Psectrapus* respectively. A total of 12 new species were described, and six genus-level & 16 species-level synonymies were produced as a result of the investigation of the genus and species concepts of the subtribe.

New Classification of Subtribe Eurynotina				
***Eurynotus* lineage (17 spp.)**	***Phylacastus* lineage (5 spp.)**	***Schyzoschelus* lineage (18 spp.)**	***Psectrapus* lineage (25 spp.)**	***Oncotus* lineage (29 spp.)**
Eurynotus (17 spp.)	*Phylacastus* (5 spp.)	*Heteropsectropus* (3 spp.)	*Byrrhoncus* (2 spp.)	*Anamenederes* (monotypic)
		Muelleropsectropus (monotypic)	*Capidium* (4 spp.)	*Hirtograbies* (5 spp.)
		Schyzoschelus (14 spp.)	*Colophonesthes* (2 spp.)	*Menederes* (5 spp.)
			Colophonexsula (3 spp.)	*Ograbies* (8 spp.)
			Isoncophallus (9 spp.)	*Oncotus* (3 spp.)
			Psectrapus (5 spp.)	*Phaleriderma* (3 spp.)
				Quadroncotus (monotypic)
				Stridigula (3 spp.)

Table 2: Classification of Eurynotina based on publications presented in this thesis.

7. References

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Taxonomic revision of the genus *Phylacastus* Fairmaire (Tenebrionidae, Eurynotina): shortfalls of anatomical nomenclature with notes on aedeagal homology

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Abstract

The genus *Phylacastus* Fairmaire (Tenebrionidae, Blaptinae, Platynotini, Eurynotina) is revised. Two new species and one new synonymy are presented along with new diagnoses, descriptions, a distribution map, and key to species. The resulting species of *Phylacastus* are: *P. ancoralium* **sp. nov.**, *P. crypticoides* Koch (= *P. pretoriensis* Koch **syn. nov.**), *P. makskacymirowi* **sp. nov.**, *P. rhodesianus* Koch, and *P. striolatus* Fairmaire. Lectotypes are designated for the type species, *P. striolatus*, to fix the taxonomic status of the species and genus. As a result of examination and subsequent description of *P. ancoralium* **sp. nov.**, a brief review and treatment of aedeagal morphology is presented. The nomenclature ("clavae" versus "laciniae") and phylogenetic occurrence of accessory structures of the paramere-median lobe area within Blaptinae Leach and Adelinina LeConte (Diaperinae, Diaperini) are discussed. New descriptive terminology (i.e., ancora [singular] and ancorae [plural]) is proposed for these aedeagal structures in Blaptinae to clarify their function and resolve past ambiguities. The morphology within representatives of *Adelina* Dejean, *Alphitophagus* Stephens, *Gnatocerus* Thunberg, and *Sitophagus* Mulsant is also briefly contrasted and outlined.

Keywords

Amphidorini, clavae, Dendarini, laciniae, median lobe, parameres, Pedinini, South Africa

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Introduction

Eurynotina Mulsant & Rey is a subtribe of darkling beetles from Southern Africa within the tribe Platynotini Mulsant & Rey and subfamily Blaptinae Leach (Koch 1954a; Bouchard et al. 2021; Kamiński et al. 2021a). Platynotini are distinguished via the presence of a stridulatory file on the gula (synapomorphy for the tribe; see Koch 1954a, b, 1956). Eurynotina are further diagnosable via their aedeagi, which lack additional "styles", "clavae", or "lacinia" (Antoine 1930; Koch 1954a, b; Lindroth and Palmen 1956) and have a strongly sclerotized medial lobe with reduced basal apophyses (Iwan 2001). Eurynotina has been supported as molecularly distinct by Kamiński et al. (2019, 2021a); however, the taxa included were not fully sufficient to test the monophyly of the group. This paper is the first of a series dedicated to revising subtribe Eurynotina as a part of the first author's Ph.D. dissertation.

Platynotini has received attention from many generations of entomologists (Fairmaire 1897; Gebien 1904, 1910; Reichardt 1936; Español 1945; Koch 1956, 1958; Kaszab 1975; Iwan 1995, 2002, 2006; Endrödy-Younga 2000; Kamiński and Raś 2011; Iwan and Kamiński 2012, 2014; Kamiński 2013, 2015a); however, most contributions concern the subtribe Platynotina Mulsant & Rey. Only a handful of papers concern Eurynotina (Koch 1954a, b, 1955, 1956; Kamiński 2016). For example, *Phylacastus* was erected in Opatrini Brullé by Fairmaire (1897) with a single new species (*P. striolatus* Fairmaire) and remained unstudied for nearly 60 years. In 1954a, Koch described three additional species and assigned the genus to his recently installed subtribe Oncotina Koch, now interpreted as a synonym of Eurynotina (see Kamiński 2016). He hypothesized a relationship between *Phylacastus* and *Eurynotus* Kirby through the following characters: horizontally produced prosternal apophysis, median emargination of epistoma, sharp and rectangular posterior angles of pronotum, and closely jointed prothorax and mesothorax. Prior to the study presented here, the only count of *Phylacastus* specimens was provided by Koch's (1954a) work (34 specimens, 25 of which belonged to one of his new species *P. pretoriensis*, and two syntypes of *P. striolatus*).

After queries to several entomological collections (see list in Materials and Methods) we identified new specimens and species of the genus. These materials provided the opportunity to test the taxonomic concepts of *Phylacastus* and its species. Furthermore, as one of the newly discovered species challenges Koch's (1954a, b) subtribal definition of Eurynotina, male terminalia morphology within subfamily Blaptinae is discussed based on dissected specimens, alongside previous literature (e.g. Koch 1956; Iwan 2001, 2004). Consequently, new terminology is proposed in light of previous application of the terms "clavae" and "laciniae" in the context of their meaning and priority within Blaptinae. They are also briefly contrasted with representatives of Diaperinae Latreille to better describe function, homology, and resolve some ambiguities.

Materials and methods

Revision of genus *Phylacastus*

Pinned material for morphological examination of *Phylacastus* and other taxa was borrowed from the following institutional insect collections: **MNHN** – Muséum national d'Histoire naturelle; Paris, France; and **TMNH** – Ditsong National Museum of Natural History; Pretoria, South Africa. Additional comparative material for redefining the genus and investigating aedeagal morphology was obtained from: **MIIZPAN** – Muzeum i Instytut Zoologii, Polska Akademia Nauk; Warsaw, Poland; **SANC** – South African National Collection of Insects; Pretoria, South Africa. While specimens of Eurynotina are relatively uncommon, the holdings of the aforementioned collections are the most comprehensive for the subtribe, accounting for both the majority of type material, and additional specimens for examination. As a result of specimen loans and contact with collections presented here, all 16 genera and over 90% of the species of Eurynotina are represented by type material and photographs for reference for this project and continued revision of the subtribe.

Original label data for specimens are given in quotation marks and separated by a comma. Morphological terminology follows that of Matthews at al. (2010), with additional specialized terms used for the female terminalia following Kamiński et al. (2022). Dissections were performed following methodology illustrated by Kamiński (2021); specimens were soaked in 10% KOH solution for dissection of genitalia before staining with chlorazol black. Images were taken using a Canon 1000D body with extension rings and a Canon EF 100 mm macro lens, a Nikon D3500 body with adapter for a Nikon SMZ800N microscope, and with a Hitachi S-3400N SEM in MIZ PAS. A species distribution map was produced using QGIS v. 3.16, with vector layers downloaded from the Natural Earth web page (www.naturalearthdata.com). Photographs as well as distribution map figures were edited in Photoshop v. 23.5.1. A table of all localities is presented in Appendix 1.

Male terminalia analysis

Revelation of new structures on the aedeagus of *Phylacastus ancoralium* sp. nov. necessitated a review of aedeagal morphology to confirm its affiliation. To this end, we performed a historical literature review, and assessed aedeagal terminology and morphology (Antoine 1930; Español 1945; Koch 1954a, b; Lindroth and Palmen 1956; Doyen and Tschinkel 1982; Doyen 1984; Iwan 2001, 2004; Kamiński 2014, 2015b). Taxon selection mainly focused on Blaptinae, as various subgroups have historically been defined by the presence or absence of additional structures of the parameres/median lobes (e.g. Platynotina and Eurynotina, Opatrini); however other groups of Tenebrionidae Latreille with structures described as "clavae", "lacinia", "struts", or "styles" were also sampled for morphological study and com-

parison. Taxa were also chosen for potential homology and concurrent terminology based on literature descriptions. Taxa selected were: Blaptinae: *Amatodes* Dejean (Pedinini: Helopinina), *Anomalipus* Guérin-Méneville (Platynotini: Platynotina), *Eleodes* Eschscholtz (Amphidorini), *Heliopates* Dejean (Pedinini: Dendarina), *Trigonopus* Mulsant & Rey (Platynotini: Platynotina), and Diaperinae (Diaperini: Adelinina): *Adelina* Dejean, *Alphitophagus* Stephens, *Gnatocerus* Thunberg, and *Sitophagus* Mulsant.

Taxonomy

Genus *Phylacastus* Fairmaire

Phylacastus Fairmaire, 1897: 116. Koch 1954a: 275; 1954b: 2; 1956: 27; Kamiński 2016: 245.

Type species. *Phylacastus striolatus* Fairmaire; by monotypy.

Diagnosis. Within Eurynotina, *Phylacastus* largely resembles *Eurynotus* and *Capidium* Koch. All three have relatively sharp basal pronotal angles, rather than broadly rounded as is the case in the rest of Eurynotina (Kamiński 2016: fig. 2). The only other exception is *Oncotus* Solier which, while some representatives have basal angles of the pronotum similarly shaped, is separable by prosternal process shape (rounded rather than angular in lateral view (Kamiński 2016), body shape (much rounder/transverse than *Phylacastus*), tibial morphology (foretibia greatly expanded apically and with a sharp lateral projection; Kamiński 2016), and coloration (species may be bicolored and/or very pale or testaceous in color). *Phylacastus* can be easily separated from all other subtribal representatives by the presence of (at most) weak tubercles on the apical declivity of the elytra (Figs 1, 2), the form of the prosternal process which is angular rather than rounded in lateral view (Kamiński 2016: fig. 2D), and the pronotum with basal angles present rather than absent/rounded) (Kamiński 2016: fig. 2J).

Eurynotus, the most closely affiliated genus according to Koch (1954a), can be separated from *Phylacastus* by body size (*Eurynotus* ~9–20 mm long and ~5–12 mm wide, versus *Phylacastus* 4–8 mm long and ~2.75–4 mm wide (Koch 1954a; Kamiński 2016); pronotal hind angles (*Eurynotus* prominently produced often rearward projecting; less prominent and not rearwardly projected in *Phylacastus*; Kamiński 2016), tibial morphology (*Eurynotus* with slender/narrow tibiae lacking coarse spines on ventral surface of foretibia; dorsoventrally flattened and apically expanded tibiae with coarse spines on the underside of the foretibia in *Phylacastus* (Kamiński 2016), elytral sculpturing (*Eurynotus* with coarse or well-defined tubercles in most species; while most species of *Phylacastus* lack well-defined tubercles (Kamiński 2016). Finally, *Eurynotus* lacks a subapical sulcus on abdominal ventrite V, which is present in all *Phylacastus* species (Fig. 3F, G).

Capidium can be separated from *Phylacastus* most reliably via the structure of the prosternal process and abdominal ventrite V (prosternal process rounded and not produced in *Capidium*, angular and produced in *Phylacastus* (Kamiński 2016), and subapical sulcus absent in *Capidium* (present in *Phylacastus*); additionally, although *Capidium* also is defined by angular basal angles of the pronotum (Kamiński 2016), the angles are usually more produced. Finally, the elytral sculpturing and tuberculation of representatives of *Capidium* (when present) are stronger than in *Phylacastus*.

Genus redescription. Length 4–8 mm. Shining to dull; colored tenebrous; reddish to dark brown/black. ***Head*****:** epistoma with well-defined median notch. Transition between clypeus and frons gradual and smooth along lateral edge, or with slight depression. Coarsely punctate, punctures large and closely spaced, separated by ≤ 1 feature diameter. Mentum with enlarged, ventrally projecting middle portion parallel-sided to slightly narrowing apically with reduced/slightly hidden lateral wings. Gula with stridulatory file. Eye constricted in middle and reniform, with strong to weakly impressed sulcus situated around posterior perimeter of dorsal lobe. Antennae with 11 antennomeres, terminal members forming weak club. ***Prothorax*****:** pronotum base straight, with basal angles roundly produced. Without lateral depression or flattening along margins. Hypomeron at most only finely sculptured and finely punctured, dull to shining. Prosternal process angulate in lateral view, weakly produced or rounded at apex, with clear sulcus running perimeter, projecting at most only weakly toward midcoxae. ***Pterothorax*****:** scutellar shield small and transversely triangular. Elytra not costate, with or without shallow or weakly defined punctate striae. Intervals punctate, without microtubercles; weak to well-defined tubercles (when present) only on apical declivity. Interval X terminating before reaching elytra base. Epipleura without microtubercules, broad basally, narrowing apically. Apterous. ***Abdomen*****:** punctate. Ventrite V with sulcus running parallel to apical perimeter. ***Legs*****:** femora slightly curved and expanded toward apex. Tibiae dorsoventrally compressed. Meso- and metatibia slightly curved. Foretibia dilated triangularly toward apex with coarse spines underneath. ***Male terminalia*****:** tegmen bipartite with or without ancorae (small ancorae present in one species); basal portion membranous ventrally; dorsally with small, triangular membranous field at base of apical portion. Parameres fused dorsally at base, apical opening (in dorsal view) small or broad (Fig. 4). In lateral view, parameres flattened toward apex, with or without slight curvature. ***Female terminalia*****:** paraprocts nearly as long or slightly longer than coxites I–IV, coxite IV reflected dorsally with gonostyli present (Fig. 5); bursa copulatrix divided into two sections by median constriction (bilobate) or not (Fig. 6), with or without additional "accessory pouch" situated near to spermatheca and accessory glands.

Species included (5). *Phylacastus ancoralium* sp. nov., *P. crypticoides*, *P. makskacymirowi* sp. nov., *P. rhodesianus*, *P. striolatus*.

Distribution. Southern Africa (Lesotho, South Africa, Zimbabwe) (Fig. 7).

Key to the species of the genus *Phylacastus*

1 Well-defined tubercles present on apical declivity of elytra (Fig. 2D) **2**
– Well-defined tubercles absent on apical declivity of elytra (Fig. 2B) **3**
2 Male parameres widely spaced with large dorsal opening exposing median lobe (Fig. 4C); mentum parallel-sided and broad (Fig. 3C); elytral intervals densely punctate; generally larger (6–8 mm) ..... ***P. rhodesianus*** **Fairmaire**
– Male parameres not widely spaced, with small dorsal opening exposing at most only the tip of the median lobe (Fig. 4D); elytral intervals less densely punctate; mentum narrowing apically (Fig. 3B); generally smaller (4–6 mm) ..... ***P. makskacymirowi*** **sp. nov.**
3 Aedeagus with ancorae (Fig. 4G); Ratio of ovipositor coxites I–IV to paraprocts nearly 1:1 (Fig. 5); elytra with at most weakly impressed striae on elytral disc, absent stria on apical declivity (Figs 2A, B) ..... ***P. ancoralium*** **sp. nov.**
– Aedeagus lacking ancorae (Fig. 4); Ratio of ovipositor coxites I–IV to paraprocts distinctly < 1:1 (Fig. 5); more clearly impressed elytral striae (Figs 2E, F) **4**
4 Mentum with narrow carina/keel running up median (Fig. 3A); 5th abdominal sulcus narrowly separated from apex (Fig. 3F) ..... ***P. crypticoides*** **Koch**
– Mentum lacking narrow carina/keel running up median; 5th abdominal sulcus widely separated from apex (Fig. 3G) ..... ***P. striolatus*** **Fairmaire**

Phylacastus ancoralium **sp. nov.**
https://zoobank.org/FDB06FBF-4FCA-4888-B36A-9E9724BDA235
Figs 1A, 2A, B, 3F, 4B, G, 5, 6C

Material examined (data represents single specimens unless otherwise noted). ***Holotype*** (TMNH): "S.Afr.;E. Lesotho Hodson's Peak 300 m 29.37°S, 29.17°E; 11.3.1976;E-Y:1069 fr.und.stones, 3150 m leg. Endrödy-Younga." With an additional label on red paper: "Holotype: *Phylacastus ancoralium* Lumen & Kaminski".

Paratypes (*n* = 11) (TMNH and MIIZPAN): Two specimens with same data as Holotype (MIIZPAN). "S.Afr.Basutoland Makheke Mnts 15 miles ENE Mokhotlong. 8.IV.51 No. 268;Swedish South Africa Expedition 1950–1951; red label." (MIIZPAN), "S.Afr., Lesotho Drakensbg,Black Mt. 29.31°S, 29.12°E; 9.3.1976;E-Y:1060 from under stones leg. Endrödy-Younga.", "S.Afr.;E. Lesotho Hodson's Peak 300 m 29.37°S, 29.17°E; 11.3.1976;E-Y:1067 from under stones leg. Endrödy-Younga" (five specimens)., "S.Afr., E.Lesotho Sani Pass Valley 29.39°S, 29.12°E; 10.3.1976; E-Y:1066 from under stones leg. Endrödy-Younga" (two specimens).

Diagnosis. *Phylacastus ancoralium* is highly modified compared with its congeners. In addition to its wide geographic separation from other species (Lesotho), it can be separated from all other species of *Phylacastus* via the elytra (with extremely weak to absent elytral striae), prosternum (weakly produced between forecoxae, rather

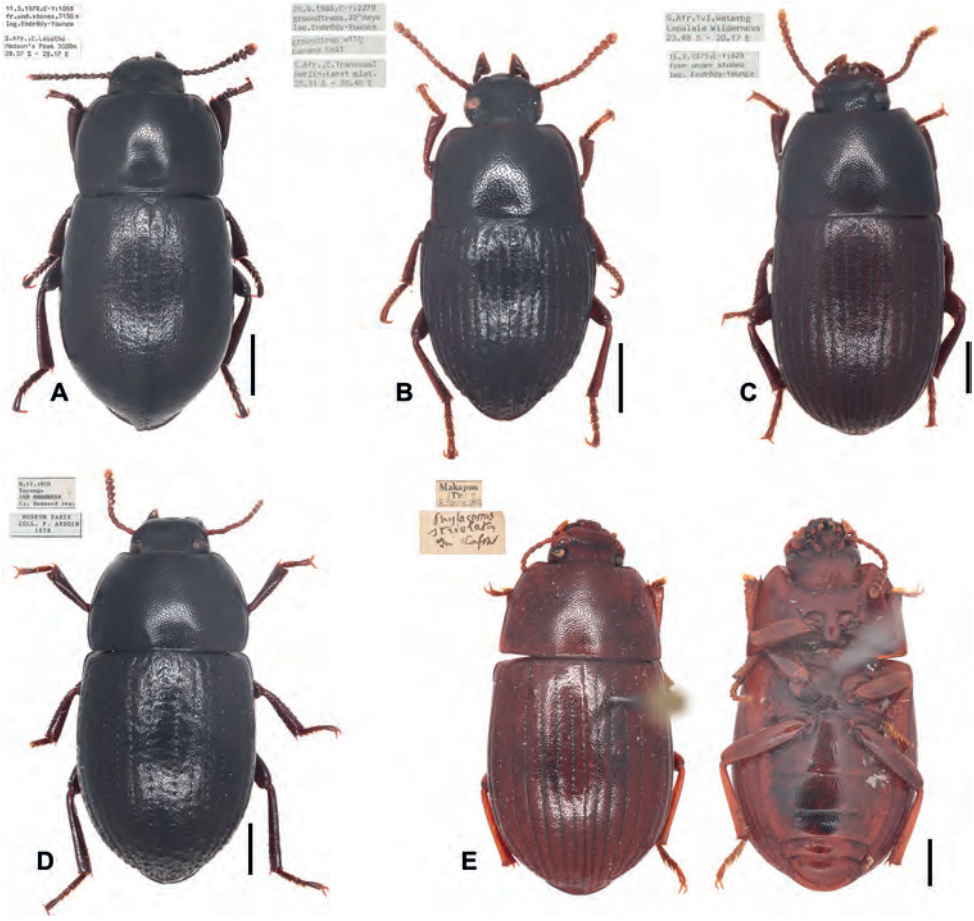


Figure 1. Dorsal habitus of *Phylacastus* species **A** *Phylacastus ancoralium* sp. nov. holotype **B** *Phylacastus makskacymirowi* sp. nov. **C** *Phylacastus crypticoides* **D** *Phylacastus rhodesianus* **E** *Phylacastus striolatus* lectotype. Scale bars: 1 mm.

than projecting more strongly beyond (Fig. 3E)), aedeagus with ancorae on the ventral surface of the parameres (Fig. 4G), and ovipositor relatively short compared to other species (ratio of ovipositor coxites I–IV to paraprocts nearly 1:1, rather than more distinctly < 1:1) (Fig. 5).

Etymology. This species is named for the ancorae of the male aedeagus, which in Blaptinae are hypothesized to anchor the male genitalia during copulation. To date, this is the only species within the subtribe Eurynotina with ancorae.

Description. Length 6–7 mm. ***Head*:** punctures separated by ~1 feature diameter. Mentum midportion slightly narrowing apically, exposing lateral wings, midportion without distinct median carina. ***Prothorax*:** pronotum finely punctate, punctures widely spaced, separated by > 1 feature diameter. Hypomeron lightly wrinkled and finely punctate. Prosternal process weakly produced between forecoxae. ***Pterothorax*:**

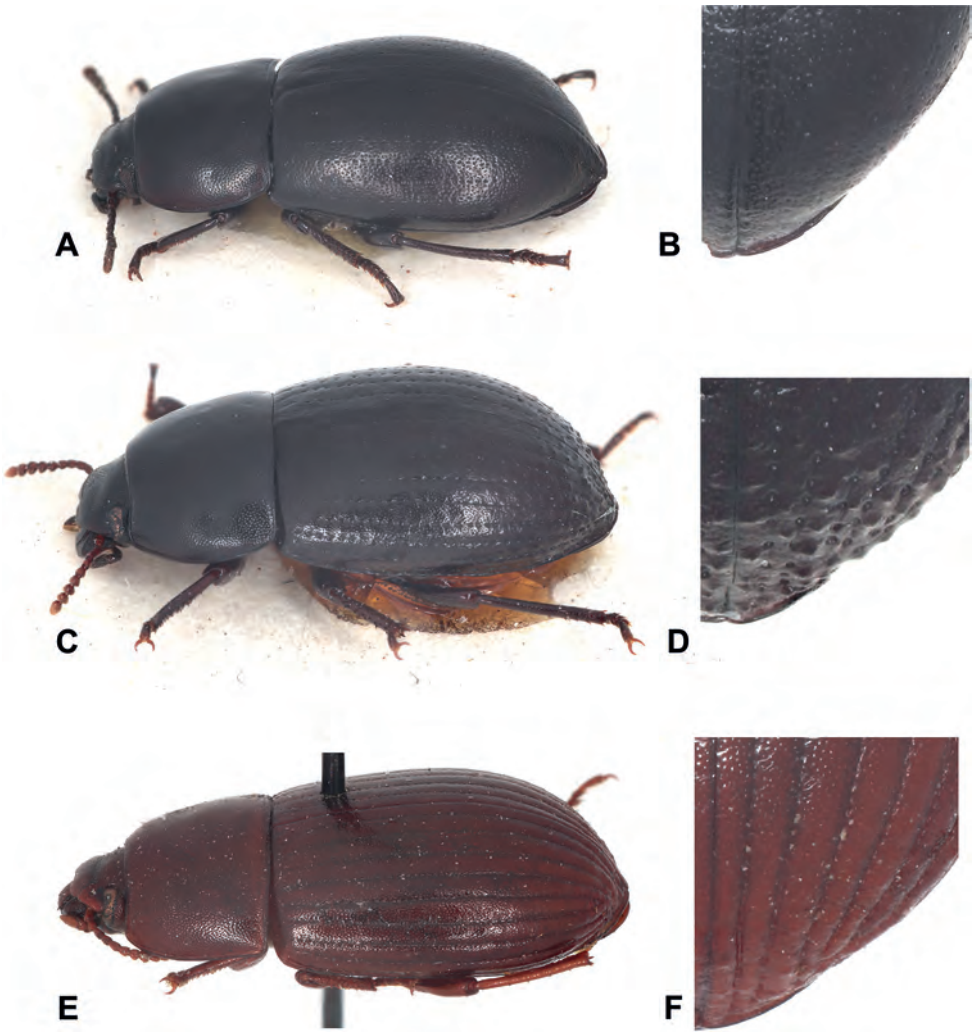


Figure 2. *Phylacastus* lateral aspect photographs and close-up of apical elytral tubercles and striae **A** *Phylacastus ancoralium* lateral angle **B** *P. ancoralium* close-up of elytra apical declivity **C** *P. rhodesianus* lateral angle **D** *P. rhodesianus* close-up of elytra apical declivity **E** *P. striolatus* lateral angle **F** *P. striolatus* close-up of elytra apical declivity.

elytra width about equal to pronotal width. Elytral striae and intervals punctate; striae very weakly impressed or absent. Interval punctures fine and widely spaced (>1 feature diameter), distinctly smaller than strial punctures. Elytral tubercles absent. ***Abdomen*:** ventrite V sulcus narrowly separated from apical border. ***Terminalia*:** male: parameres tapering apically, fused basally with narrow opening at apex exposing median lobe. Each paramere bearing a small, ventral medial ancora. Female: Ratio of ovipositor coxites I–IV to paraprocts nearly 1:1. Bursa copulatrix not bilobate, accessory gland present near-to spermatheca, accessory pouch present.

Distribution. Lesotho.

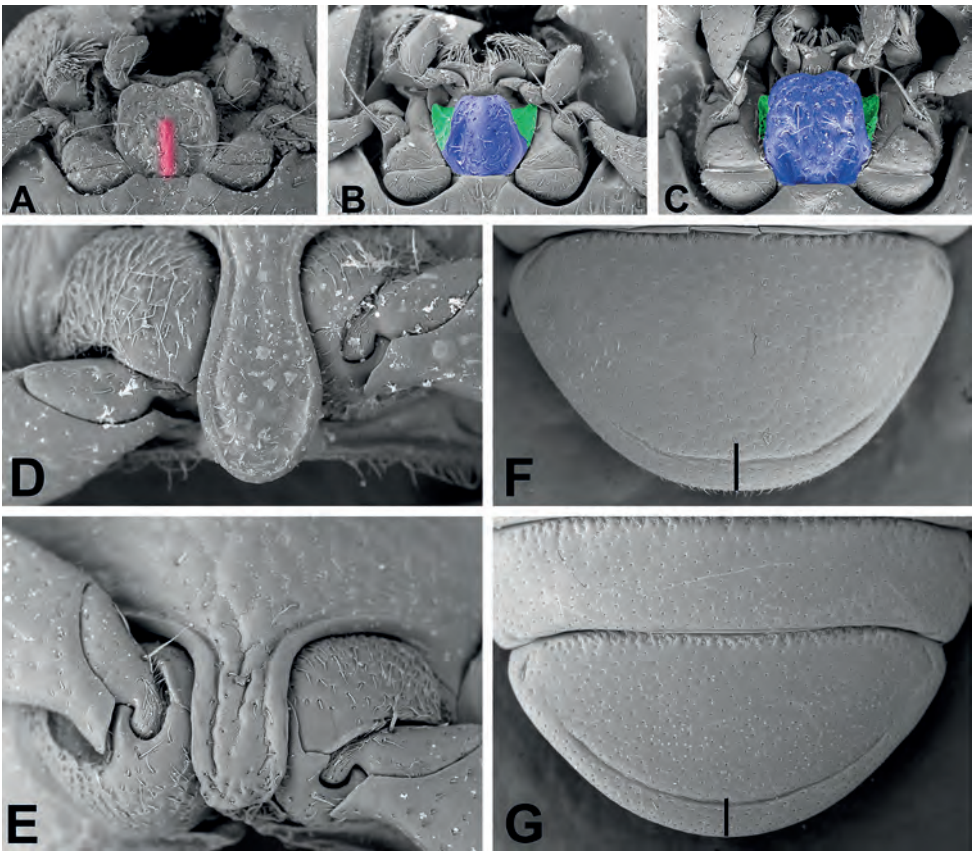


Figure 3. Diagnostic features of *Phylacastus* species **A–C** mentum (Median keel red, middle portion and lateral wings blue and green respectively) **D–E** prosternal process **F–G** abdominal ventrite V **A, D, F** *Phylacastus crypticoides* **B** *P. makskacymirowi* **C** *P. rhodesianus* **E** *P. ancoralium* **G** *P. striolatus*. Scale bars: 0.1 mm

***Phylacastus crypticoides* Koch**

Figs 1C, 3A, D, F, 4E, 5, 6B, 8B

Phylacastus crypticoides Koch, 1954a: 286. Kamiński 2016: 245.
= *Phylacastus pretoriensis* Koch, 1954a: 285, syn. nov. Kamiński 2016: 245.

Material examined (data represents single specimens unless otherwise noted). ***Holotype*** (TMNH): "Lydenburg Distr. 1896 P.A. Krantz; Phylacastus crypticoides DET.C.KOCH 1953; Holotype No: 1873 Phylacastus crypticoides KOCH; crypticoides Koch; Eurynotus? sp.."

Additional material examined (TMNH). "S.Afr.,N.Transvaal Nylsvley Met.Sta. 24.40°S, 28.42°E; 285.1975; E-Y:1160 humus, Berlese, open leg. Endrödy-Younga.", "S.Afr.,N.Transvaal Nylsvley, Smith frm 24.40°S, 24.42°E 15.11.1975; E-Y: 952 cattle dung leg. Endrödy-Younga; trench; rep: 5 cage mesh 9 mm 7 day aft.sett."*, "S.Afr.,N.Transvaal Nylsvley Met.Sta. 24.40°S, 28.42°E; 29.3.1976; E-Y:1112 sifted

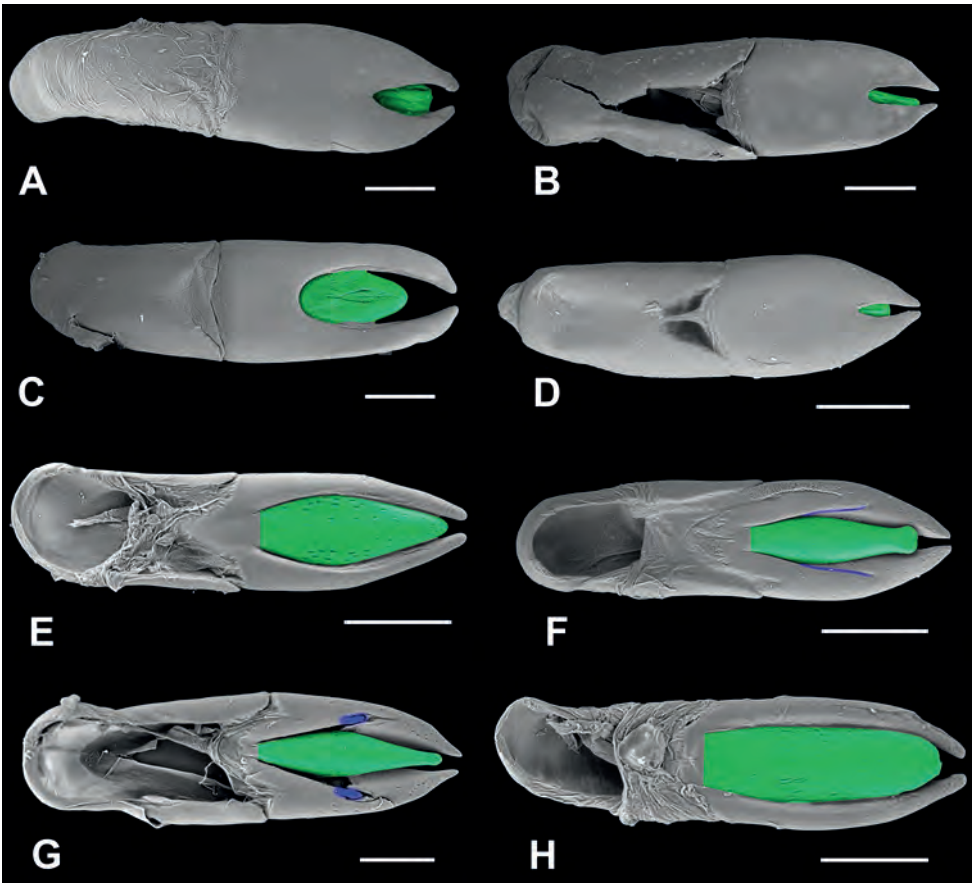


Figure 4. *Phylacastus speciesspp.* aedeagi **A–D** aedeagus dorsal view **E, F** aedeagus Ventral view **A, H** *Phylacastus striolatus* **B, G** *P. ancoralium* (ancorae highlighted blue) **C** *P. rhodesianus* **E** *P. crypticoides* **D, F** *P. makskacymirowi* (subapical sutures highlighted blue). Median lobes highlighted green. Scale bars: 0.2 mm.

litter, open leg. Endrödy-Younga.", "S.Afr.;Limpopo Prov. Lindani Nat Res 1336 m 24.02°S, 28.23°E; 8.12.2005; E-Y:3687 single, bushveld leg.Gusmann, Müller.", "S.Afr.,N.Transvaal Nylsvley, Smith frm 24.40°S, 24.42°E 8.1.1976; E-Y: 990 sifted litter. Endrödy-Younga"*, "S.Afr.Tvl.Waterbg Lapalala Wilderness 23.49°S, 20.17°E; 16.8.1975; E-Y:829 from under stones leg. Endrödy-Younga" (seven specimens)[1].

Notes. Koch described both *Phylacastus crypticoides* and *P. pretoriensis* (1954a), differentiating them from the already described *P. striolatus* and his additional species *P. rhodesianus* based on the following: *P. pretoriensis* with a basal pronotal margin that

1 Some collecting events are likely erroneous in their coordinates (24.40°S, 24.42°E and 23.49°S, 20.17°E). These localities should be represented in northeastern South Africa (circa 24.40°S, 28.42°E); however, the coordinates as written on the labels refer to far-off localities in Botswana. As such, while the labels are recorded here, these points are omitted from the species' range map.

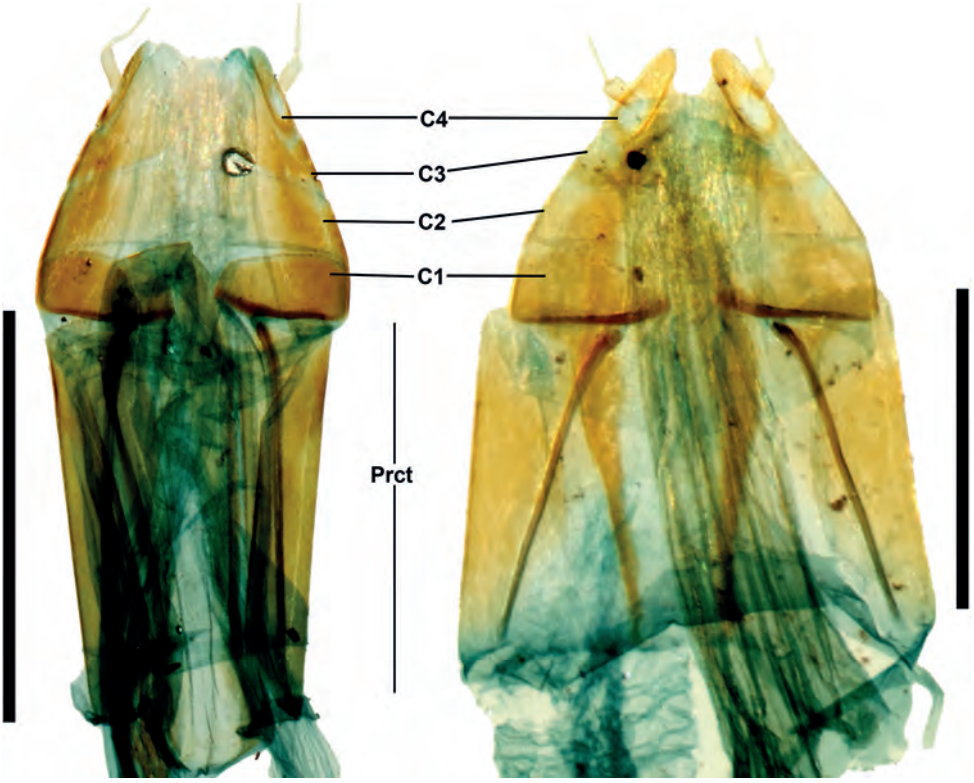


Figure 5. *Phylacastus* ovipositor (dorsal). **Right** *Phylacastus ancoralium* **Left** *P. crypticoides*. Abbreviations: C – Coxae (1–4); Prct – Paraprocts. Scale bars: 1 mm.

is reduced medially, and *P. crypticoides* with a cariniform structure of the mentum and a more apically positioned sulcus on abdominal ventrite V. Upon investigation here, the margination of the pronotal base, while variable, appears to be consistently present in all species with no uniform reduction in restricted populations or collection events examined here. The sulcus of abdominal ventrite V is also consistent between specimens of both of Koch's species. Furthermore, *P. crypticoides* and *P. pretoriensis* specimens compared with his type material bear the carina attributed to *P. crypticoides*. As such, we have decided here to synonymize the two species under *P. crypticoides*.

Redescription. Length 6–7 mm. ***Head*:** punctures separated by < 1 diameter. Mentum broad, lateral wings concealed, midportion with thin, distinct medial carina. ***Prothorax*:** pronotum punctate, punctures closely spaced, separated by ≤ 1 diameter. Hypomeron lightly wrinkled to rugose. Prosternal process produced between forecoxae (Fig. 3D). ***Pterothorax*:** elytra width about equal to pronotal width. Elytral striae, intervals punctate; striae clearly impressed. Interval punctures closely spaced (≤1 diameter), slightly smaller than strial punctures. Elytral tubercles absent; apical declivity with at most weak bumps or callosities (Figs 1C, 2E, F). ***Abdomen*:** ventrite V sulcus narrowly separated from apical border. ***Terminalia*:** male: parameres tapering apically,

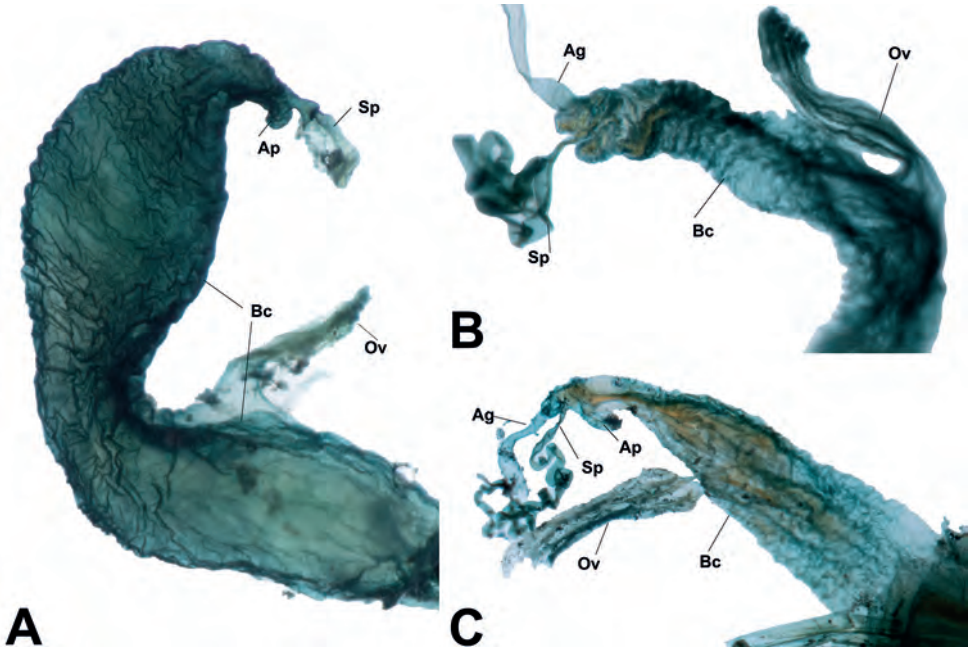


Figure 6. *Phylacastus* internal female structures **A** *Phylacastus striolatus* **B** *P. crypticoides* **C** *P. ancoralium*. Abbreviations: Ag - Accessory gland, Ap - Accessory pouch, Bc - Bursa copulatrix, Ov - Oviduct, *Sp* - Spermatheca.

fused basally with narrow opening at apex exposing median lobe. Female: ovipositor slightly elongate (ratio of ovipositor coxites I–IV to paraprocts < 1:1). Bursa copulatrix not bilobate, accessory gland present near-to spermatheca, accessory pouch absent.

Distribution. South Africa.

***Phylacastus makskacymirowi* sp. nov.**

https://zoobank.org/D45D3B72-5E44-451F-96B1-35D28A05E555

Figs 1B, 3B, 4D, F

Material examined (data represents single specimens unless otherwise noted). ***Holotype*** (TMNH): **"**S.Afr.,E.Transvaal Berlin;Karst plat. 25.31°S, 30.46°E; 20.9.1986; E-Y:2279 groundtraps, 33 days leg. Endrödy-Younga; ground trap with meat bait." With an additional label on red paper: "Holotype: *Phylacastus makskacymirowi* Lumen & Kaminski"

Paratypes (*n* = 11) (TMNH and MIIZPAN): Three additional specimens with same data as holotype (MIIZPAN). "S.Afr.,E.Transvaal Berlin;Karst plat. 25.31°S, 30.46°E; 23.10.1986; E-Y:2001 groundtraps, 42 days leg. Endrödy-Younga; ground trap with meat bait.", "S.Afr.,E.Transvaal Berlin;Karst plat. 25.31°S, 30.46°E; 4.2.1986 E-Y:2414 under fungous logs leg. Endrödy-Younga.", "S.Afr.; Mpumalanga

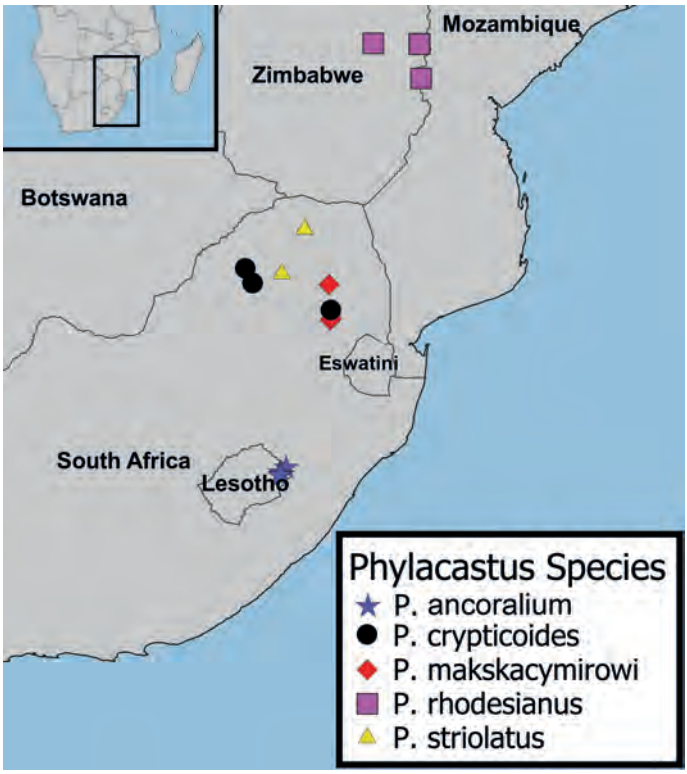


Figure 7. *Phylacastus* species distribution map. *P. ancoralium* (blue star), *Phylacastus crypticoides* (black circle), *P. makskacymirowi* (red diamond), *P. rhodesianus* (pink square), *P. striolatus* (yellow triangle).

10 km E Kaapsehoop 25.36°S, 30.43°E; 4–6.1.2014: E-Y:3943 sifting; indigenous forest leg. Ruth Müller.", "S.Afr.;Mpumalanga Sjonajona, Badplaas 24.44°S, 30.40°E; 11.11.2002; E-Y:3565 general collect. 1410 m leg. TMSA staff" (four specimens), "S.Afr.,E.Transvaal Berlin;Karst plat. 25.31°S, 30.46°E; 8.12.1986 E-Y:2363 fungous Pinus logs leg. Endrödy-Younga."

Diagnosis. As of this revision, this is the smallest species of the genus (4–6 mm). In addition to its size, this species is further defined by the presence of well-defined tubercles on the apical declivity of the elytra—a trait shared only by *P. rhodesianus*, which is larger and can be further differentiated by 1) punctures on elytral intervals (more numerous and dense in *P. rhodesianus*); 2) the shape of the mentum is broad, not tapered, further concealing the lateral wings in *P. rhodesianus* (Fig. 3C), tapers apically, exposing lateral wings in *P. makskacymirowi* (Fig. 3B); 3) aedeagus with a wide space between parameres, exposing large portion of median lobe in P. rhodesianus (Fig. 4C), narrow exposing only the tip of the median lobe in *P. makskacymirowi* (Fig. 4D).

Etymology. Named after young bug enthusiast Maksymilian Jan Kacymirow (born on December 17, 2014 in Warsaw, Poland).

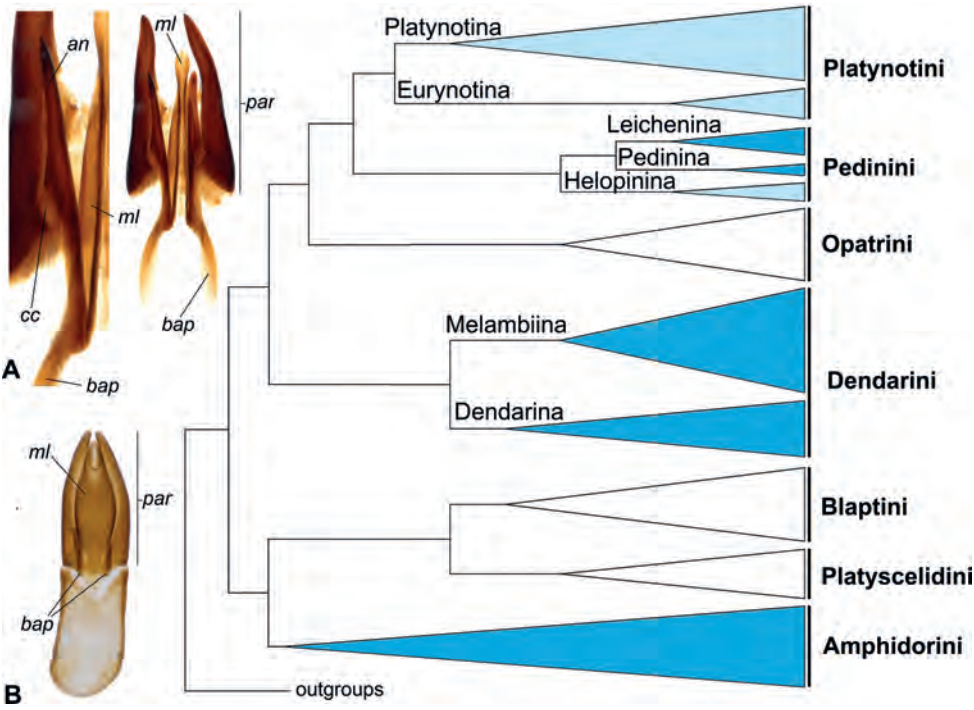


Figure 8. Distribution of *ancorae* in Blaptinae (displayed on Bayesian molecular topology from Kamiński et al. 2021a) **A** *Heliopates ibericus* Mulsant & Rey (Dendarina) apical aedeagus **B** *Phylacastus crypticoides* aedeagus. Dark blue clades = all representatives have ancorae. Light blue clades = exceptions (with or without ancorae). White clades = no ancorae. Abbreviations: an - ancora, bap - basal apophysis, cc - sclerotized connection to parameres, ml - median lobe, par - parameres.

Description. Length 4–6 mm. ***Head*****:** punctures separated by < 1 diameter. Mentum midportion medially raised but without distinct median carina, laterally tapering slightly toward apex, lateral wings exposed. ***Prothorax*****:** pronotum finely punctate, punctures smaller and widely spaced, separated by > 1 diameter. Hypomeron very finely punctate and lightly sculptured/wrinkled. Prosternal process produced between forecoxae. ***Pterothorax*****:** elytra wider than pronotal width. Elytral striae and intervals punctate; striae clearly impressed. Interval punctures fine, widely spaced (>1 diameter), distinctly smaller than strial punctures. Elytra distinctly tuberculate on apical declivity. ***Abdomen*****:** ventrite V sulcus narrowly separated from apical border. ***Terminalia*****:** male: parameres tapering apically, fused basally with narrow opening at apex exposing median lobe. Each paramere bearing a small, weak, subapical suture (Fig. 4F). Female: ovipositor slightly elongate (ratio of ovipositor coxites I–IV to paraprocts < 1:1). Bursa copulatrix not bilobate, accessory gland present near-to spermatheca, accessory pouch absent.

Distribution. South Africa.

***Phylacastus rhodesianus* Koch**
Figs 1D, 2C, D, 3C, 4C

Phylacastus rhodesianus Koch, 1954a: 287. Kamiński 2016: 245.

Material examined (data represents single specimens unless otherwise noted). ***Holotype*** (TMNH): "Marandella Mashld XI.97 GKMarshall; Holotype No: 1877 Phylacastus rhodesianus KOCH; Phylacastus rhodesianus Koch DET.C.KOCH; rhodesianus Koch."

Additional material examined (MNHN). "9.VI.1970 Vumba SUD RHODESIE Cl. Besnard leg. 8.VI.1970 Inyanga SUD RHODESIE Cl. Besnard leg." (10 specimens).

Redescription. Length 6–8 mm. ***Head*****:** punctures separated by ≤ 1 diameter. Mentum midportion broad, concealing lateral wings, midportion without distinct median carina. ***Prothorax*****:** pronotum punctate, punctures closely spaced, separated by ~1 diameter. Hypomeron very lightly textured, without clear punctation. Prosternal process produced between forecoxae. ***Pterothorax*****:** elytra width about equal to pronotal width. Elytral striae and intervals punctate; striae impressed. Interval punctures fine, closely spaced (~1 diameter), distinctly smaller than strial punctures. Elytral tubercles present on apical declivity. ***Abdomen*****:** ventrite V sulcus narrowly separated from apical border. ***Terminalia*****:** male: parameres converging apically, fused basally with deep and wide opening at apex exposing median lobe (Fig. 4C). Female: ovipositor slightly elongate (ratio of ovipositor coxites I–IV to paraprocts < 1:1). Bursa copulatrix bilobate, accessory gland present near-to spermatheca, accessory pouch absent.

Distribution. Zimbabwe.

***Phylacastus striolatus* Fairmaire**
Figs 1E, 2E, F, 3G, 4A, H, 6A

Phylacastus striolatus Fairmaire, 1897: 117. Koch 1954a: 287; 1954b: 2; Kamiński 2016: 245.

Material examined (data represents single specimens unless otherwise noted). Lectotype (MNHN) here designated: "Makapan (TR.) E. Simon 1893; Phylacastus striolatus ? Cafrar?". With an additional label on red paper: "Lectotype: *Phylacastus striolatus* Fairmaire" Paralectotype (MNHN): single specimen with same data as lectotype.

Additional material examined (MIIZPAN). "Transvaal Soutpansberg Mphome Magd Knothe S" (two specimens).

Redescription. Length 8 mm. ***Head*****:** punctures separated by < 1 diameter. Mentum midportion broad, concealing lateral wings, midportion without distinct median carina. ***Prothorax*****:** pronotum punctate, punctures closely spaced, separated by ≤ 1

diameter. Hypomeron lightly wrinkled. Prosternal process produced between forecoxae. ***Pterothorax*:** elytra width slightly greater than pronotal width. Elytral striae and intervals punctate; striae impressed. Interval punctures closely spaced (~1 diameter), smaller than strial punctures. Elytral tubercles absent; apical declivity with at most weak bumps or callosities. ***Abdomen*:** ventrite V sulcus widely separated from apical border. ***Terminalia*:** male: parameres converging apically, fused basally with small opening at apex exposing median lobe. Female: ovipositor slightly elongate (ratio of ovipositor coxites I–IV to paraprocts < 1:1). Bursa copulatrix bilobate, accessory gland present near-to spermatheca, accessory pouch present.

Distribution. South Africa.

Note. While Fairmaire did not specify the number of specimens he examined in his original description, he did make mention of the collector (E. Simon) and locality, making specimens of his syntype series identifiable. Two specimens from MNHN are here designated as the lectotypes to fix the taxonomic status of the species.

Discussion

Revision of genus *Phylacastus*

Overall, there were relatively few specimens available for study (n = 45), which may represent restricted ranges or collecting bias, although the collections we sampled represent older historical collections of their range. Despite the number of specimens, we borrowed and examined all of the type material, as well as additional representatives of all species. As of this revision, many of the traits that Koch (1954a) used to diagnose *Phylacastus* are still supported; however, some characters (e.g. the joining of the pronotum and elytra and the dilated male protarsi) were difficult to reliably confirm in the material gathered for this study. We interpret Koch's (1954a) species *P. crypticoides* and *P. pretoriensis* as synonymous, as the traits used to differentiate them (mentum with sharp median carina in *P. crypticoides* and lack of basal pronotal margination in *P. pretoriensis*) were actually congruent between Koch's type material for both species in the case of the mentum, and inconsistent throughout all the available material in the case of the pronotal margins. As to Koch's (1954a) asserted relationship between *Phylacastus* and *Eurynotus*, additional phylogenetic study using morphological and/or molecular data will be required (Lumen and Kaminski in prep.). Currently, as of this revision their affiliation is not rejected—both genera have angled basal margins of the pronotum, angular prosternal processes, and tubercles on the apical declivity of the elytra (though often reduced in *Phylacastus*). The ovipositor of *Phylacastus* is only diagnostic for one species (*P. ancoralium*), and the genus appears to be overall congruent with other representatives of the subtribe (e.g. *Oncotus*), while also differing from *Eurynotus*, which has extremely long paraprocts (Iwan 2000; Banaszkiewicz 2006). There is some variation in the construction of the internal female anatomy of *Phylacastus*. In particular, *P. striolatus* and *P. rhodesianus* have a bursa copulatrix

which is divided into two "lobes" by a median constriction (Fig. 6A), and there is an additional pouch situated near the spermatheca and accessory glands in *P. striolatus* and *P. ancoralium* (Fig. 6A, C). While the function of these structures is unclear at present, there may be similar structures in other representatives of the subtribe (e.g. *Eurynotus capensis* (Fabricius) appears to have a similarly divided bursa copulatrix; Tschinkel 1978: fig. 1), which may be helpful for diagnosing groups or for phylogenetic inference. Additionally, there were some accessory structures on the aedeagi of *P. ancoralium* and *P. makskacymirowi*. Namely, the former possesses structures historically referred to as "lacinia" or "clavae", and *P. makskacymirowi* has small, preapical sutures or grooves on the ventral side of the parameres. While the case of *P. ancoralium* is discussed in the below section, it is possible that the structures in *P. makskacymirowi* offer additional flexibility in the parameres.

Male terminalia analyses

Our discovery of accessory structures on the parameres of *P. ancoralium* (Fig. 4G) raise questions not only on the phylogenetic placement of the species, but on the concept of Eurynotina and the way such structures have been defined historically in Tenebrionidae (e.g. Koch 1954a, b, 1955, 1956; Iwan 2001, 2002, 2004). The revelation of these structures highlights the necessity of investigating Eurynotina, as well as other enigmatic and poorly understood groups. One such subtribe, Helopinina Lacordaire (Pedinini Eschscholtz), is morphologically similar to Eurynotina, despite molecular evidence separating them (Kamiński et al 2021a, b; Fig. 8). In the case of Helopinina, there is also a marked reduction in accessory structures (similar to Eurynotina), though they can be differentiated in other ways (e.g. scale-like setation, non-reduced or elongate basal apophyses, basal versus apical tegmen length ratio, lack of stridulatory gula). A literary review revealed a myriad of terms used to refer to accessory structures associated with the median lobe, parameres, and tegmen (Antoine 1930; Español 1945; Doyen and Tschinkel 1982; Doyen 1984; Iwan 2001, 2002, 2004; Kamiński et al. 2019). Terms which have garnered the most use historically and recently are "clavae" and "lacinia." Unfortunately, they have not been used uniformly, nor explicitly/formally defined in a way that is easily traceable or consistent. In fact, the two most used terms appear to follow authorship in North America ("clavae"—see Doyen and Tschinkel 1982; Doyen 1984; Aalbu et al. 2012; Johnston 2019) versus elsewhere ("lacinia"—see Español 1945; Iwan 2001). Thus far, the terms appear to have been used in an effort to qualitatively describe their shape. However, "clavae" is misleading in this regard and is much more widely used to refer to antennae (e.g. clava in Hymenoptera, Yoder et al. 2010). Additionally, while lacinia may adequately describe the form in some taxa, it misses the mark in others (e.g. *Anomalipus* spp.) and overlaps with much more widely used anatomical features (lacinia of the maxillary mouthparts of insects; Lawrence et al. 2011). Iwan (2004) gave a definition using the term lacinia (accessory spike- or hook-like structures which connect the median lobe with the inflexed alae of the apical piece), while also outlining their potential function

(a means for the male to anchor itself internally during copulation as they extend/evert)—as well as the change in aedeagal function in groups which lacked them, such as Eurynotina (switching from lateral movement of "lacini" to a dorsoventral motion with a sclerotized median lobe and flexible parameres).

The aforementioned accessory structures to the median lobe and parameres have been recorded in two subfamilies and appear to be uncommon within Tenebrionidae. The first subfamily, Blaptinae, has several tribes (Amphidorini LeConte, Dendarini Mulsant & Rey, Pedinini, and Platynotini), and the second, Diaperinae, has one subtribe (Adelinina LeConte) that seem to have evolved variations of this characteristic morphology (Doyen 1984; Kamiński 2015b; Johnston 2019; Kamiński et al. 2021a). As a result of their unique and varied appearance, "clavae" or "lacinia" have been used to diagnose many tribes and subtribes (see Koch 1958; Doyen 1984; Iwan 2001); though in the case of some subtribes there are representatives that stand out contrastingly with their cohort as either having these structures (e.g. *Phylacastus ancoralium*, unusual in Eurynotina; Fig. 4G) or lacking them (e.g. *Anomalipus heraldicus* Gerstaecker and *Anchophthalmus* spp. of Platynotina or *Amatodes* Dejean (Fig. 9A), *Ametrocera* Fåhraeus, and *Oncopteryx* Gebien of Helopinina).

We examined published records and dissected representatives of Blaptinae (e.g. *Anomalipus* and *Eleodes*) (Fig. 9C, D) to first solidify an anatomical definition for our accessory aedeagal structures of interest. Our dissections reveal these structures always mediate the connection between the parameres and median lobe in some capacity, though the diversity of morphological structures may obfuscate connecting points, giving the illusion they are linked only to the median lobe (Figs 8, 9). Additionally, even in less-closely related taxa, the conglomerate structure of the parameres and median lobe (plus accouterments) possess a median extension connected/merged with the basal apophyses (Fig. 9B–D), giving evidence for homology. To make referring to these structures more uniform, while also making their function more apparent, we propose naming these structures ancorae (singular: ancora) from the Latin *ancor*—in reference to the organ's apparent reproductive function in anchoring the male to the female. We also hope that coining a new name for this feature will provide a means to better investigate homology, evolutionary strategies, and phylogeny. Our definition aims to unify the terminology and enable verification of homology in problematic cases. For example, some species of *Anomalipus* are known to possess several appendages of the tegmen (Endrödy-Younga 1988). Dissections of *Anomalipus mastodon* Fåhraeus (Fig. 9D) revealed most of these appendages are not linked to the median lobe or parameres; therefore, they cannot be regarded as ancorae. All of the extra appendages originate either from the basal piece of the tegmen (Fig. 9D, *pan3*) or are loosely attached by connecting membranes (Fig. 9D, *pan1* and *pan2*). Using the following criterion: connection to the parameres and the median lobe and linkage to the basal apopyses, we conclude that *A. mastodon* possesses only one pair of ancorae homological with the structures in other Platynotina (e.g. Fig. 9B). In another case, the subtribe Adelinina (Diaperinae: Diaperini) is defined by structures coined by Doyen (1984) as "clavae." To test our definition, we also dissected representatives of *Adelina*, *Alphitophagus*, *Gnatocerus*, and

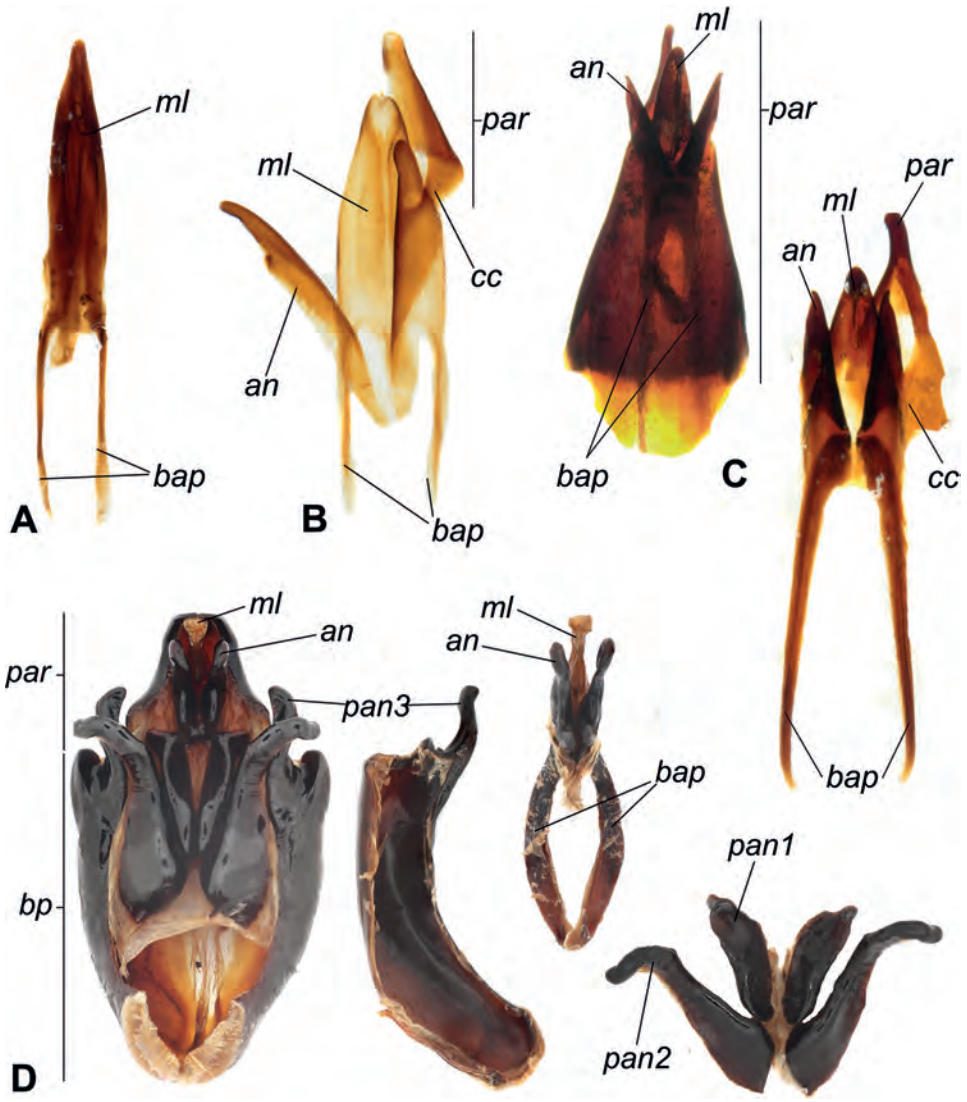


Figure 9. Dissections of ancorae variation and aedeagal morphology from Blaptinae **A** *Amatodes* Dejean (Pedinini, Helopinina) median lobe with basal apophyses **B** *Trigonopus similis* Iwan (Platynotini, Platynotina) parameres, median lobe, and ancorae **C** *Eleodes obscura* (Say) (Amphidorini) intact and extracted parameres, median lobe, and ancorae **D** *Anomalipus mastodon* Fåhraeus, 1870 (Platynotini, Platynotina). Abbreviations: an - ancorae, bap - basal aphophyses, bp - basal portion of tegmen, cc - cuticular connection of ancorae to parameres, ml - median lobe, pan 1–3 - pseudo ancorae, par - parameres.

Sitophagus. While all three possess accessory structures related to the median lobe and apex (parameres) of the aedeagus, there are several differences in comparison with what we observe in Blaptinae: 1) the median lobe is divided into two halves (Fig. 10), rather than fused as in Blaptinae (Figs 4, 8, 9); 2) the "clavae" are strongly connected with

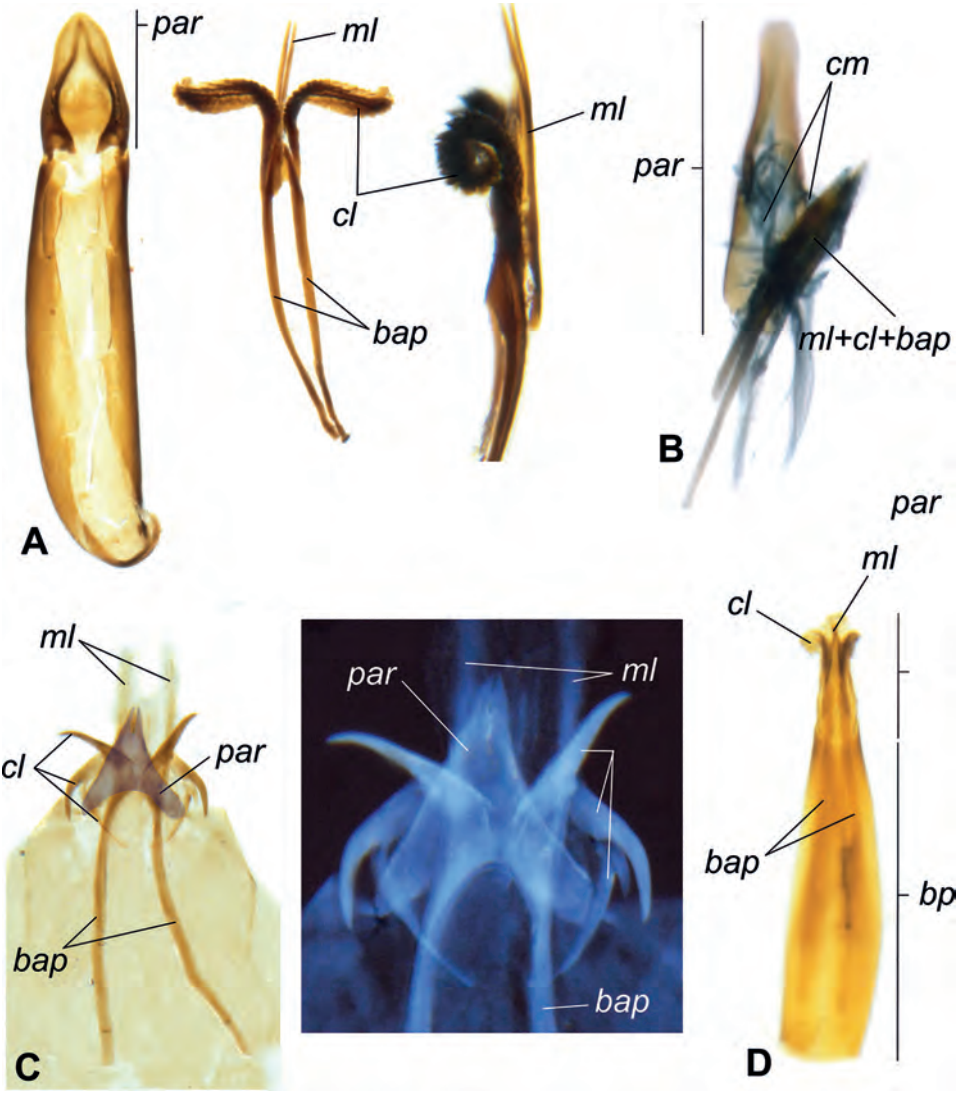


Figure 10. Sampled Adelenina (Diaperinae: Diaperini: Adelinina) aedeagi **A** *Sitophagus hololeptoides* (Laporte) **B** *Adelina plana* (Fabricius) **C** *Alphitophagus bifasciatus* (Say) **D** *Gnatocerus cornutus* (Fabricius) Abbreviations: *bap* - basal apophyses, *cl* - "clavae", *ml* - median lobe, *par* - parameres, *bp* - basal portion of aedeagus, *cm* - connective membrane.

the basal aphophyses, which were long in all dissected specimens, but very weakly attached/associated with the median lobe (Fig. 10A); in Blaptinae all three structures are strongly associated/fused into a conglomerate structure (Figs 4, 8, 9); 3) the connection of the "clavae" to the parameres appears to be mediated by membranous structures (Fig. 10B). All the Blaptinae we observed have a much more strongly sclerotized connection (Fig. 9B, C). As a result, we propose that while these structures may be similar in form and operate in similar function(s), they do not fit our definition of ancorae

focused on Blaptinae in particular. Diaperini Latreille as a tribe is very distantly related to Blaptinae phylogenetically (Kergoat et al. 2014; Kamiński et al. 2021a), and so these structures are likely not homologous, and likely would require additional examination in the future, and potential new terminology of their own. As such, we leave further investigation to other researchers focused on this and other more closely related groups.

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Appendix 1

Table of *Phylacastus* distributional data in .csv format.

Genus, Species,Verbatim Label, date (d.m.y), Determined Lat, Determined Long, note(s)

Phylacastus, *striolatus*, Makapan (TR.) E. Simon 1893; *Phylacastus striolatus* ? Cafrar; , 1893, -24.1586, 29.1769, Type Locality; Point based on Makapan valley archeological site near to Mokopan.

Phylacastus, *striolatus*, Makapan (TR.) E. Simon 1893, 1893, -24.1586, 29.1769, Point based on Makapan valley archeological site near to Mokopan.

Phylacastus, *striolatus*, Transvaal Soutpansberg Mphome Magd Knothe S, -,-23.0084, 29.7690, point based on Soutpansberg Mountain.

Phylacastus, *striolatus*, Transvaal Soutpansberg Mphome Magd Knothe S, -,-23.0084, 29.7690, point based on Soutpansberg Mountain.

Phylacastus, *rhodesianus*, Marandella Mashld XI.97 GKMarshall; Holotype No: 1877 *Phylacastus rhodesianus* KOCH; *Phylacastus rhodesianus* Koch DET.C.KOCH; *rhodesianus* Koch, 11.1897, -18.1897, 31.5467, Type locality; Marondera (Marandella synonym).

Phylacastus, *rhodesianus*, 9.VI.1970 Vumba SUD RHODESIE Cl. Besnard leg.,9. VI.1970, -19.1000, 32.7833, Point based on Bvumba Mts.

Phylacastus, *rhodesianus*, 8.VI.1970 Inyanga SUD RHODESIE Cl. Besnard leg.,8. VI.1970, -18.2100, 32.7400,"Point based on Nyanga, Zimbabwe".

Phylacastus, *rhodesianus*, 8.VI.1970 Inyanga SUD RHODESIE Cl. Besnard leg.,8. VI.1970, -18.2100, 32.7400,"Point based on Nyanga, Zimbabwe".

Phylacastus, *rhodesianus*, 8.VI.1970 Inyanga SUD RHODESIE Cl. Besnard leg.,8. VI.1970, -18.2100, 32.7400,"Point based on Nyanga, Zimbabwe".

Phylacastus, *rhodesianus*, 8.VI.1970 Inyanga SUD RHODESIE Cl. Besnard leg.,8. VI.1970, -18.2100, 32.7400,"Point based on Nyanga, Zimbabwe".

Phylacastus, *rhodesianus*, 8.VI.1970 Inyanga SUD RHODESIE Cl. Besnard leg.,8. VI.1970, -18.2100, 32.7400,"Point based on Nyanga, Zimbabwe".
Phylacastus, *rhodesianus*, 8.VI.1970 Inyanga SUD RHODESIE Cl. Besnard leg.,8. VI.1970, -18.2100, 32.7400,"Point based on Nyanga, Zimbabwe".
Phylacastus, *rhodesianus*, 8.VI.1970 Inyanga SUD RHODESIE Cl. Besnard leg.,8. VI.1970, -18.2100, 32.7400,"Point based on Nyanga, Zimbabwe".
Phylacastus, *rhodesianus*, 8.VI.1970 Inyanga SUD RHODESIE Cl. Besnard leg.,8. VI.1970, -18.2100, 32.7400,"Point based on Nyanga, Zimbabwe".
Phylacastus, *rhodesianus*, 8.VI.1970 Inyanga SUD RHODESIE Cl. Besnard leg.,8. VI.1970, -18.2100, 32.7400,"Point based on Nyanga, Zimbabwe".
Phylacastus, *rhodesianus*, 8.VI.1970 Inyanga SUD RHODESIE Cl. Besnard leg.,8. VI.1970, -18.2100, 32.7400,"Point based on Nyanga, Zimbabwe".
Phylacastus, *makskacymirowi*, "S.Afr.,E.Transvaal Berlin;Karst plat. 25.31 S - 30.46 E; 23.10.1986; E-Y:2001 groundtraps, 42 days leg. Endrödy-Younga; ground trap with meat bait",23.10.1986, -25.52, 30.77.
Phylacastus, *makskacymirowi*, "S.Afr.,E.Transvaal Berlin;Karst plat. 25.31 S - 30.46 E; 20.9.1986; E-Y:2279 groundtraps, 33 days leg. Endrödy-Younga; ground trap with meat bait",20.8.1986, -25.52, 30.77, Type locality.
Phylacastus, *makskacymirowi*, "S.Afr.,E.Transvaal Berlin;Karst plat. 25.31 S - 30.46 E; 20.9.1986; E-Y:2279 groundtraps, 33 days leg. Endrödy-Younga; ground trap with meat bait",20.8.1986, -25.52, 30.77.
Phylacastus, *makskacymirowi*, "S.Afr.,E.Transvaal Berlin;Karst plat. 25.31 S - 30.46 E; 20.9.1986; E-Y:2279 groundtraps, 33 days leg. Endrödy-Younga; ground trap with meat bait",20.8.1986, -25.52, 30.77.
Phylacastus, *makskacymirowi*, "S.Afr.,E.Transvaal Berlin;Karst plat. 25.31 S - 30.46 E; 20.9.1986; E-Y:2279 groundtraps, 33 days leg. Endrödy-Younga; ground trap with meat bait",20.8.1986, -25.52, 30.77.
Phylacastus, *makskacymirowi*, "S.Afr.,E.Transvaal Berlin;Karst plat. 25.31 S - 30.46 E; 4.2.1986 E-Y:2414 under fungous logs leg. Endrödy-Younga",4.2.1986, -25.52, 30.77.
Phylacastus, *makskacymirowi*, "S.Afr.,E.Transvaal Berlin;Karst plat. 25.31 S - 30.46 E; 8.12.1986 E-Y:2363 fungous Pinus logs leg. Endrödy-Younga",8.12.1986, -25.52, 30.77.
Phylacastus, *makskacymirowi*, S.Afr.;Mpumalanga 10km E Kaapsehoop 25.36 S - 30.43 E; 4-6.1.2014: E-Y:3943 sifting; indigenous forest leg. Ruth Müller, 4-6.1.2014, -25.60, 30.72.
Phylacastus, *makskacymirowi*, "S.Afr.;Mpumalanga Sjonajona, Badplaas 24.44 S - 30.40 E; 11.11.2002; E-Y:3565 general collect. 1410m leg. TMSA staff",11.11.2002, -25.73, 30.67.
Phylacastus, *makskacymirowi*, "S.Afr.;Mpumalanga Sjonajona, Badplaas 24.44 S - 30.40 E; 11.11.2002; E-Y:3565 general collect. 1410m leg. TMSA staff",11.11.2002, -25.73, 30.67.

Phylacastus, *makskacymirowi*, "S.Afr.;Mpumalanga Sjonajona, Badplaas 24.44 S - 30.40 E; 11.11.2002; E-Y:3565 general collect. 1410m leg. TMSA staff",11.11.2002, -25.73, 30.67.

Phylacastus, *makskacymirowi*, "S.Afr.;Mpumalanga Sjonajona, Badplaas 24.44 S - 30.40 E; 11.11.2002; E-Y:3565 general collect. 1410m leg. TMSA staff",11.11.2002, -25.73, 30.67.

Phylacastus, *crypticoides*, Lydenburg Distr. 1896 P.A. Krantz; *Phylacastus crypticoides* DET.C.KOCH 1953; Holotype No: 1873 *Phylacastus crypticoides* KOCH; *crypticoides* Koch; Eurynotus? sp.,1896, -25.0960, 30.4460, Approximated in Google Earth.

Phylacastus, *crypticoides*, "S.Afr.,N.Transvaal Nylsvley Met.Sta. 24.40 S - 28.42 E; 285.1975; E-Y:1160 humus, Berlese, open leg. Endrödy-Younga",28.5.1975, -25.67, 28.70.

Phylacastus, *crypticoides*, "S.Afr.,N.Transvaal Nylsvley, Smith frm 24.40S-24.42E 15.11.1975; E-Y: 952 cattle dung leg. Endrödy-Younga; trench; rep: 5 cage mesh 9mm 7 day aft.sett.",15.11.1975, -25.67, 28.70.

Phylacastus, *crypticoides*, "S.Afr.,N.Transvaal Nylsvley Met.Sta. 24.40 S - 28.42 E; 29.3.1976; E-Y:1112 sifted litter, open leg. Endrödy-Younga",29.3.1976, -25.67, 28.70.

Phylacastus, *crypticoides*, "S.Afr.;Limpopo Prov. Lindani Nat Res 1336m 24.02 S - 28.23 E; 8.12.2005; E-Y:3687 single, bushveld leg.Gusmann, Müller",8.12.2005, -24.03, 28.38.

Phylacastus, *crypticoides*, "S.Afr.,N.Transvaal Nylsvley, Smith frm 24.40S-24.42E 8.1.1976; E-Y: 990 sifted litter. Endrödy-Younga",8.1.1976, -25.67, 28.70.

Phylacastus, *crypticoides*, S.Afr.Tvl.Waterbg Lapalala Wilderness 23.49 S- 20.17 E; 16.8.1975; E-Y:829 from under stones leg. Endrödy-Younga, 16.8.1975, -23.82, 20.28.

Phylacastus, *crypticoides*, S.Afr.Tvl.Waterbg Lapalala Wilderness 23.49 S- 20.17 E; 16.8.1975; E-Y:829 from under stones leg. Endrödy-Younga, 16.8.1975, -23.82, 20.28.

Phylacastus, *crypticoides*, S.Afr.Tvl.Waterbg Lapalala Wilderness 23.49 S- 20.17 E; 16.8.1975; E-Y:829 from under stones leg. Endrödy-Younga, 16.8.1975, -23.82, 20.28.

Phylacastus, *crypticoides*, S.Afr.Tvl.Waterbg Lapalala Wilderness 23.49 S- 20.17 E; 16.8.1975; E-Y:829 from under stones leg. Endrödy-Younga, 16.8.1975, -23.82, 20.28.

Phylacastus, *crypticoides*, S.Afr.Tvl.Waterbg Lapalala Wilderness 23.49 S- 20.17 E; 16.8.1975; E-Y:829 from under stones leg. Endrödy-Younga, 16.8.1975, -23.82, 20.28.

Phylacastus, *crypticoides*, S.Afr.Tvl.Waterbg Lapalala Wilderness 23.49 S- 20.17 E; 16.8.1975; E-Y:829 from under stones leg. Endrödy-Younga, 16.8.1975, -23.82, 20.28.

Phylacastus, *pseudoclavum*, S.Afr.Basutoland Makheke Mnts 15 miles ENE Mokhotlong. 8.IV.51 No. 268;Swedish South Africa Expedition 1950-1951; red label, 8.IV.1951, -29.19, 29.29, Approximated in Google Earth.

Phylacastus, *pseudoclavum*, "S.Afr.;E. Lesotho Hodson's Peak 300m 29.37S - 29.17 E; 11.3.1976;E-Y:1069 fr.und.stones, 3150m leg. Endrödy-Younga",11.3.1976, -29.62, 29.28, Type locality.

Phylacastus, *pseudoclavum*, "S.Afr.;E. Lesotho Hodson's Peak 300m 29.37S - 29.17 E; 11.3.1976;E-Y:1069 fr.und.stones, 3150m leg. Endrödy-Younga",11.3.1976, -29.62, 29.28.

Phylacastus, *pseudoclavum*, "S.Afr.;E. Lesotho Hodson's Peak 300m 29.37S - 29.17 E; 11.3.1976;E-Y:1069 fr.und.stones, 3150m leg. Endrödy-Younga",11.3.1976, -29.62, 29.28.

Phylacastus, *pseudoclavum*, S.Afr.;E. Lesotho Hodson's Peak 300m 29.37S - 29.17 E; 11.3.1976;E-Y:1067 from under stones leg. Endrödy-Younga, 11.3.1976, -29.62, 29.28.

Phylacastus, *pseudoclavum*, S.Afr.;E. Lesotho Hodson's Peak 300m 29.37S - 29.17 E; 11.3.1976;E-Y:1067 from under stones leg. Endrödy-Younga, 11.3.1976, -29.62, 29.28.

Phylacastus, *pseudoclavum*, S.Afr.;E. Lesotho Hodson's Peak 300m 29.37S - 29.17 E; 11.3.1976;E-Y:1067 from under stones leg. Endrödy-Younga, 11.3.1976, -29.62, 29.28.

Phylacastus, *pseudoclavum*, S.Afr.;E. Lesotho Hodson's Peak 300m 29.37S - 29.17 E; 11.3.1976;E-Y:1067 from under stones leg. Endrödy-Younga, 11.3.1976, -29.62, 29.28.

Phylacastus, *pseudoclavum*, S.Afr.;E. Lesotho Hodson's Peak 300m 29.37S - 29.17 E; 11.3.1976;E-Y:1067 from under stones leg. Endrödy-Younga, 11.3.1976, -29.62, 29.28.

Phylacastus, *pseudoclavum*, "S.Afr., Lesotho Drakensbg, Black Mt. 29.31 S - 29.12 E; 9.3.1976;E-Y:1060 from under stones leg. Endrödy-Younga",9.3.1976, -29.52, 29.20.

Phylacastus, *pseudoclavum*, "S.Afr., E.Lesotho Sani Pass Valley 29.39 S - 29.12 E; 10.3.1976; E-Y:1066 from under stones leg. Endrödy-Younga",10.3.1976, -29.52, 29.20.

Phylacastus, *pseudoclavum*, "S.Afr., E.Lesotho Sani Pass Valley 29.39 S - 29.12 E; 10.3.1976; E-Y:1066 from under stones leg. Endrödy-Younga",10.3.1976, -29.52, 29.20.

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Revision of the darkling beetle genus *Eurynotus* (Blaptinae: Platynotini) and new records of ovoviviparity in Tenebrionidae

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ABSTRACT

The taxonomic concepts and monophyly of the southern African genus *Eurynotus* and its subgeneric components (*Biolus* and *Neosolenopistoma*) are tested using cladistic analyses. Seventy morphological characters were scored and analysed using maximum parsimony and Bayesian inference for 26 Eurynotina species, including all *Eurynotus*. Comprehensive revision of *Biolus* and *Eurynotus* resulted in *Neosolenopistoma* becoming a junior synonym of the genus *Biolus* stat. nov. (elevated to generic rank), restoration of one species (*B. asperipennis* stat. res.), recognition of seven new combinations, and descriptions of two new species (*Biolus brunoi* sp. nov. and *Eurynotus privisolum* sp. nov.). Lectotypes are designated for previously described species from syntype material, and a key to species of *Biolus* and *Eurynotus* is provided. Three species were confirmed as ovoviviparous (two *Biolus* and one *Eurynotus*) bringing the number of recorded ovoviviparous Tenebrionidae to 14. Shortened ovipositors are discounted as requisite for ovoviviparity based on elongate paraprocts in *Biolus* and *Eurynotus*. Principal component analyses were used to examine three lineages of ovoviviparous tenebrionids; however, no single set of climatic variables was correlated with ovoviviparity. Southern African, Malagasy, and Guadeloupe lineages of ovoviviparous Tenebrionidae probably have additional and/or separate evolutionary origins and selection pressures to consider when examining this reproductive strategy.

Keywords: bursa copulatrix; ovipositor; Southern Africa; phylogeny; Eurynotina

INTRODUCTION

Eurynotina is a southern African endemic subtribe of darkling beetles classified within Platynotini of the subfamily Blaptinae (Kamiński *et al.* 2019, 2021). Currently, it groups nearly 100 species distributed in 16 genera (Kamiński 2016, Lumen and Kamiński 2023). Monophyly of Eurynotina seems well-grounded morphologically (presence of a stridulatory file on the gula) and has been supported by molecular data (Kamiński *et al.* 2019). Compared to Platynotina, subtribe Eurynotina remains largely understudied, with only a handful of modern contributions (Banaszkiewicz 2006, Kamiński 2016, Kamiński and Schawaller 2019, Kamiński *et al.* 2019, 2021, Lumen and Kamiński 2023). The last comprehensive treatment was over 65 years ago (Koch 1954a, b, 1955, 1956). Presently, most taxonomic concepts of the genera remain ambiguous (see: Kamiński 2016), impeding meaningful biological investigation on the subtribe. For example, although ovoviviparity has been observed in *Eurynotus capensis* (Tschinkel 1978), without proper phylogenetic analysis it is difficult to evaluate taxa for biological study. As a result, ovoviviparity in Eurynotina has remained unexplored and whether other examples of this reproductive strategy in the subtribe exist remained uninvestigated.

Though it has been reported in representatives of Carabidae, Cerambycidae, Chrysomelidae, Micromalthidae, Staphylinidae, and Tenebrionidae (Hagan 1948, 1951, Tschinkel 1978, Liebherr and Kavanaugh 1985, Iwan 2000, Gabriš *et al.* 2016, Zilberman *et al.* 2019), ovoviviparity is extremely rare and restricted to few representatives among beetles. For example, within Tenebrionidae, all but one case (see:Dutrillaux *et al.* 2010) occur in one tribe (Platynotini Mulsant and Rey) (Tschinkel 1978, Iwan 2000). Specifically, first instar larvae were found in the bursa copulatrix of a single species of Eurynotina Mulsant and Rey and nine species of Platynotina (Fig. 1; Table 1). The evolutionary drivers of ovoviviparity within Platynotini have avoided comprehensive investigation largely due to data scarcity. Uncovering evidence of ovoviviparity requires

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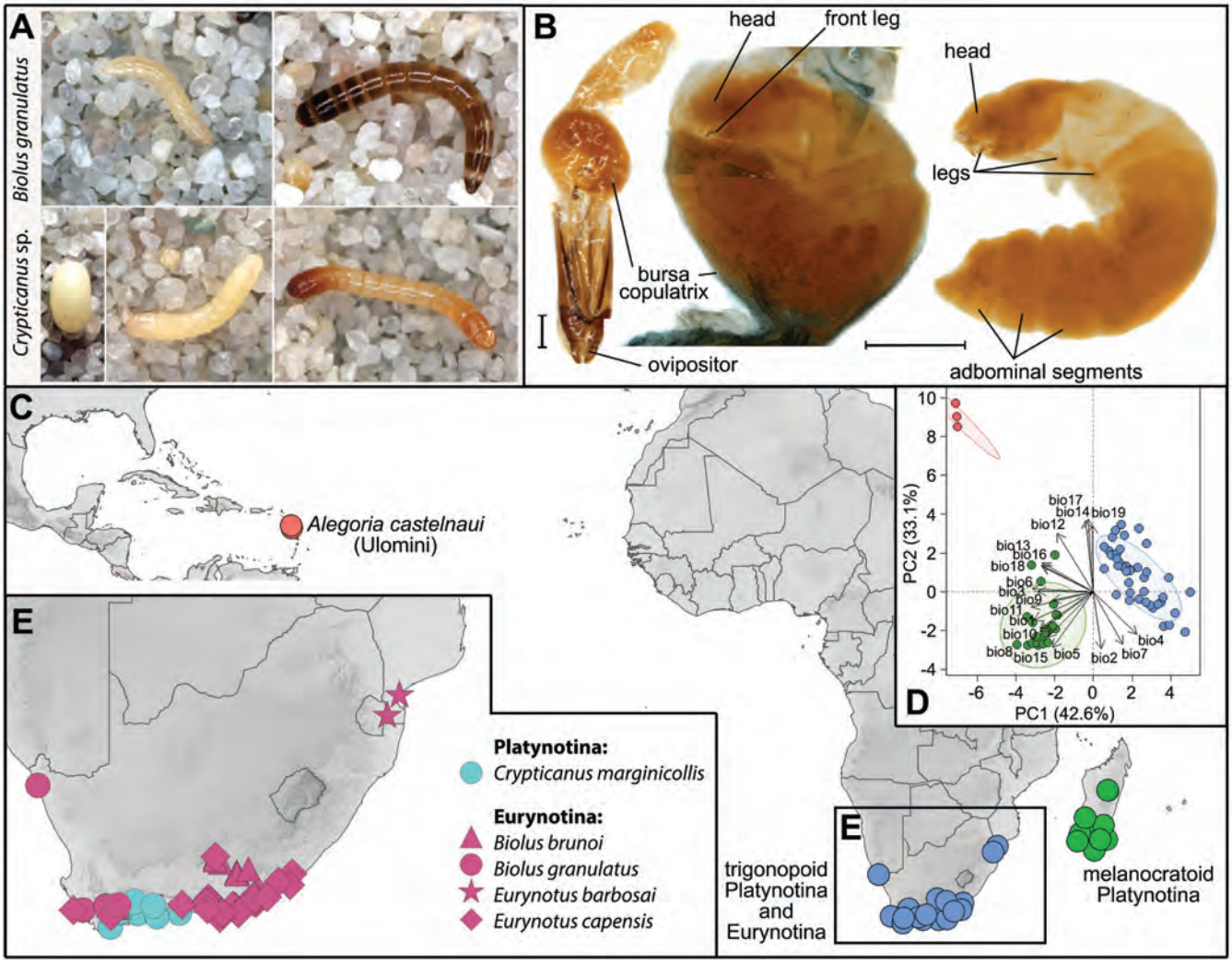


Figure 1. Ovoviviparity in Tenebrionidae and its geographical distribution. A, sympatric Platynotini species displaying different reproduction strategies: *Biolus granulatus*–ovoviviparous, *Crypticanus* sp.–oviparous. B, female genital tract of *Biolus brunoi* sp. nov. with developed 1st instar larva. Scale bar = 1.0 mm. C, distribution of known ovoviviparous Tenebrionidae (Tschinkel 1978, Iwan 2000, 2010, Dutrillaux *et al.* 2010, present paper). D, PCA of the 19 bioclimatic variables in known occurrence records of ovoviviparous Tenebrionidae. Environmental variable contributions to both axes are represented on the same graph. 95% confidence ellipses are presented for three geographical clusters (green: Malagasy Platynotina, blue: trigonopoid Platynotina and Eurynotina, red: Alegoria castelnaui). E, distribution of known ovoviviparous Tenebrionidae species in continental Africa.

behavioural observations (e.g. 'laying' larvae; to date unrecorded) or dissection of fresh or well-preserved specimens that are gravid. Additionally, the evolutionary drivers and origins of ovoviviparity in Tenebrionidae remain unresolved. Iwan (2000, 2010) hypothesized that ovoviviparity may have evolved in response to low humidity and large diurnal temperature ranges characterizing platynotine habitats. Specifically, he asserted that reductions in oviposition (e.g. reduced ovipositor morphology) and characteristics associated with lengthening egg development (such as increased egg retention and larger egg size) may be preadaptations to ovoviviparity (Iwan 2000, 2010). In the case of Malagasy Platynotina, Iwan (2010) noted a shortening of paraprocts and first coxal plates of the ovipositor. He considered these features beneficial for larviposition, alhough he also made note of the ovipositor of the only known oviviparous Eurynotina species—*Eurynotus capensis* (F.)—diverging from this bauplan by having relatively long paraprocts (see: Tschinkel 1978, Banaszkiewicz 2006).

This study constitutes the second contribution to a series dedicated to revising the subtribe Eurynotina as a part of the first author's Ph.D. dissertation (see: Lumen and Kamiński 2023). While reviewing the morphology and taxonomy of the species classified within the genus *Eurynotus* Kirby, three taxa were discovered to be ovoviviparous (Table 1). As previous taxonomic concepts were insufficient to unambiguously identify them to species-level, a comprehensive review of the genus *Eurynotus* was necessary. A morphology-based phylogeny, together with redefined species concepts, and brief ecological analysis, provides a thorough revision of *Eurynotus* and insight into the phenomenon of ovoviviparity in darkling beetles.

MATERIAL AND METHODS

Morphological studies and species' distribution

Pinned material for morphological examination was acquired from the following institutional insect collections: BPBM,

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Table 1. Checklist of known ovoviviparous darkling beetle species.

Tribe	Subtribe\Species	Paraproct/coxites length	Distribution	Source
Platynotini	**Platynotina**			
	melanocratoid lineage			
1	*Clastopus aberlenci* Iwan	1.30	Madagascar	Iwan 2005
2	*Melanocratus ferreri* Iwan	1.10	Madagascar	Iwan 1996, 2000
3	*Sebastianus projectus* Iwan	0.80	Madagascar	Iwan 1996, 2000
4	*Sebastianus simplex* Iwan	0.60	Madagascar	Iwan 2000
5	*Styphacus bartolozzii* Iwan	1.04	Madagascar	Iwan 2000
6	*Styphacus decorsei* Fairmaire	1.20	Madagascar	Iwan 1996
7	*Styphacus kochi* Iwan	1.20	Madagascar	Iwan 1996, 2000
	trigonopoid lineage			
8	*Atrocrates medvedevi* Iwan et Ferrer	0.90	South Africa	Iwan and Ferrer 2000
9	*Crypticanus marginicollis* (Mulsant et Rey)	1.10	South Africa	Tschinkel 1978
	EURYNOTINA			
10	*Biolus brunoi* sp. nov.	2.18	South Africa	present paper
11	*Biolus granulatus* (F.) comb. nov.	1.90	South Africa	present paper
12	*Eurynotus barbosai* Koch	2.00	Mozambique, South Africa	present paper
13	*Eurynotus capensis* (F.)	2.63	South Africa	Tschinkel 1978, present paper
ULOMINI				
14	*Alegoria castelnaui* Fleutiaux and Sallé	1.0*	Guadeloupe	Dutrillaux *et al.* 2010

*in the case of *Alegoria castelnaui* the paraprocts shield the coxites laterally.

Bernice P. Bishop Museum; Honolulu Hawaii; HNHM, Hungarian Natural History Museum; Budapest, Hungary; MIIZPAN, Muzeum i Instytut Zoologii, Polska Akademia Nauk; Warsaw, Poland; MNHN, Muséum National d'Histoire Naturelle; Paris, France; NHMUK, Natural History Museum; London, United Kingdom; NMNW, Windhoek National Museum of Namibia; Windhoek, Namibia; RBINS, Royal Belgian institute of Natural Sciences; Brussels, Belgium; RMCA, Royal Museum for Central Africa; Tervuren, Belgium; SANC, South African National Collection of Insects; Pretoria, South Africa; SMNS, Staatliches Museum für Naturkunde; Karlsruhe, Germany; TMNH, Ditsong National Museum of Natural History; Pretoria, South Africa; ZMUK, Zoologisches Museum, Universität Kiel; Kiel, Germany. Private collections are indicated without codons. Original label data for studied specimens are condensed into single entries after their repositories (in bold) (see Supporting Information, Appendix S1 for non-type material data). Each institution's holdings are separated by a full stop, and each record separated by quotation marks, comma, and spaces (ex: SANC: 'specimen record 1', 'specimen record 2'. MIZPAN: 'specimen record 1'.).

Adult morphological terminology follows Matthews *et al.* (2010), with additional specialized terms for male and female terminalia following Banaszkiewicz (2006), Iwan and Kamiński (2016), and Lumen and Kamiński (2023). Dissections followed methodology outlined in Kamiński (2021). Specimens were soaked in 10% KOH solution before dissection of genitalia, which were then stained with chlorazol black. Images were taken using a Canon 1000D body with extension rings and a Canon EF 100 mm macro lens, a Nikon D3500 body with adapter for a Nikon SMZ800N microscope, and with a Hitachi S3400N SEM in MIZPAN. Species' distribution maps were produced based on specimen label data using QGIS v.3.16, with vector layers downloaded from the Natural Earth web page (www.naturalearthdata.com). Photographs, as well as distribution maps, were edited in Photoshop v.23.5.1.

A principal component analysis (PCA) was performed using environmental conditions within specimen distribution data to compare the environmental requirements of three geographical clusters of ovoviviparous Tenebrionidae (Fig. 1). Analysis was conducted using the 'ellipse' package in R environment v.4.0.250 (R Core Team 2020). Variables for PCA data were extracted from all 19 WorldClim bioclimatic raster layers (Fick and Hijmans 2017) in QGIS v.3.16 (see Supporting Information, Appendix S2).

Phylogenetic analysis

Morphology of adult specimens was evaluated and scored in a morphological matrix in MESQUITE v.3.61 (Maddison and Maddison 2019). Operational taxonomic units representing *Eurynotus sensu* Koch (17 species; Figs 2, 3) were defined in a preliminary taxonomic study, which included verification of type material morphology and testing of diagnostic features for all previously described species (see: Kamiński 2016). To test the monophyly of *Eurynotus*, nine species representing all currently recognized lineages within Eurynotina were added to the phylogenetic analysis as outgroups, i.e. *Oncotus* generic complex (*Capidium tuberculatum* Koch, *Oncotus cedrimontis* Koch), *Schyzoschelus* generic complex [*Heteropsectropus amaroides* Koch, *Schyzoschelus africanus* (Kaszab)], and

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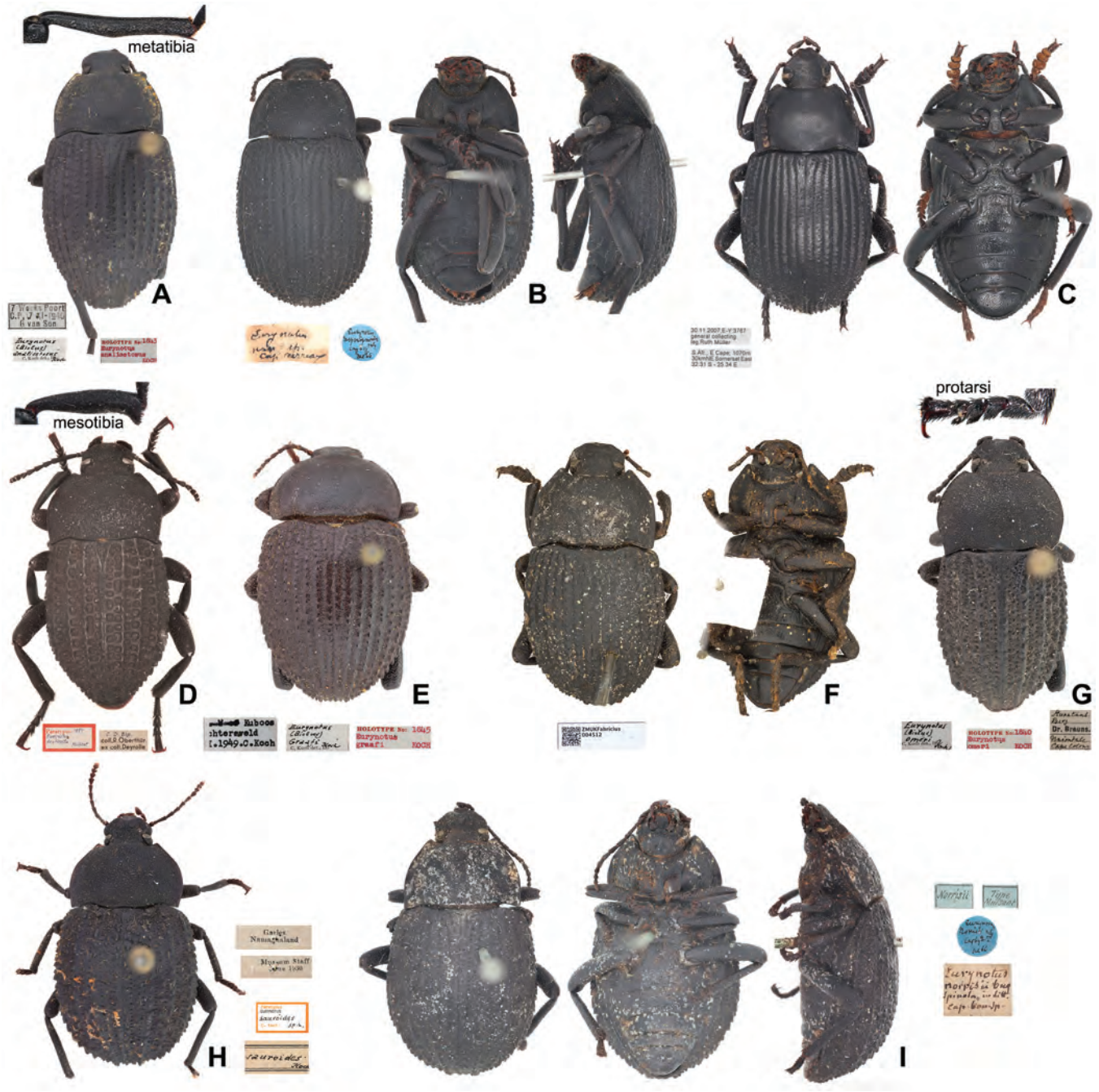


Figure 2. *Biolus* stat. nov. species. A, *Biolus analisetosus* (Koch) **c**omb. nov. Holotype; B, *B. asperipennis* (Mulsant and Rey) stat. res., comb. nov. Lectotype; C, *B. brunoi* sp. nov. Holotype; D, *B. denticosta* (Mulsant and Rey) comb. nov. Lectotype; E, *B. graafi* (Koch) comb. nov. Holotype; F, *B. granulatus* (Fabricius) comb. nov. Lectotype; G, *B. omeri* (Koch) comb. nov. Holotype; H, *B. sauroides* (Koch) comb. nov. Holotype; I, *Eurynotus norrisi* Mulsant and Rey syn. nov. of *B. granulatus*, Lectotype.

Eurynotus generic complex (Figs 4, 5). The '*Eurynotus* group' also includes all representatives of the genus *Phylacastus* Fairmaire, which has been defined as the most closely affiliated with *Eurynotus* (Koch 1954a, b, Lumen and Kamiński 2023). *Gonopus* (*Gonopus*) *tibialis skeletonensis* Endrödy-Younga (Fig. 4E) was also added as the most distant outgroup for character polarization (Iwan 2002). Morphological characters and states were adapted from previous publications (see: Koch 1954a, b, 1955, 1956, Iwan 2002), as well as being newly generated during this investigation.

The morphological matrix (see Supporting Information, Appendix S3) was imported into TNT v.1.5 (Goloboff and Catalano 2016) for phylogenetic inference using parsimony. A setk script, developed by Salvador Arias, was used to identify the most appropriate K value throughout the formula proposed by Goloboff *et al.* (2008), which was subsequently used in the implied weighting scheme for implicit enumeration search. Nodes were evaluated for Bremer support with the Bremer.run script within TNT. Additionally, Bayesian analysis was performed in MrBayes v.3.2.7 (Ronquist *et al.* 2012) using the following

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Figure 3. *Eurynotus* sens. nov. species. A, *Eurynotus alticola* Koch Lectotype; B, *E. asperatus* Mulsant and Rey Lectotype; C, *E. rudebecki* Koch syn. nov. of *E. asperatus* Holotype; D, *E. barbosai* Koch Holotype; E, *E. capensis* (Fabricius) Lectotype; F, *E. constrictus* Koch Lectotype; G, *E. graniderma* Koch Holotype; H, *E. privisolum* sp.nov. Holotype; I, *E. sulcimargo* Koch Lectotype; J, *E. thermarum* Koch Holotype.

parameters: Standard Discrete model; mcmc ngen = 10 000 000; samplefreq = 10; sump burnin = 15; sumt burn-in = 15. Two simultaneous and completely independent analyses starting from different random trees (Nruns = 2) were performed using three hot chains and one cold chain (Nchains = 4). Posterior probabilities were displayed on to the most parsimonious topology (Fig. 5). Phylogenetic trees were visualized and characters mapped in FigTree 1.4.4 (Rambaut 2009) and Winclada 1.61 (Nixon 2002), respectively.

Captive beetle rearing

Live beetles gathered in the field were kept in captivity to examine for evidence of ovovivipary. Four individuals (one male/three female) of *Biolus granulatus* and *Crypticanus* sp. were placed into separate plastic containers (125 × 125 × 67 mm) filled with aquarium sand (layer of 1 cm). Water and food (apple peels) were provided ad libitum. Beetles were kept at room temperature (~20°C) without specific humidity modifications. Containers were inspected and substrate filtered daily for eggs

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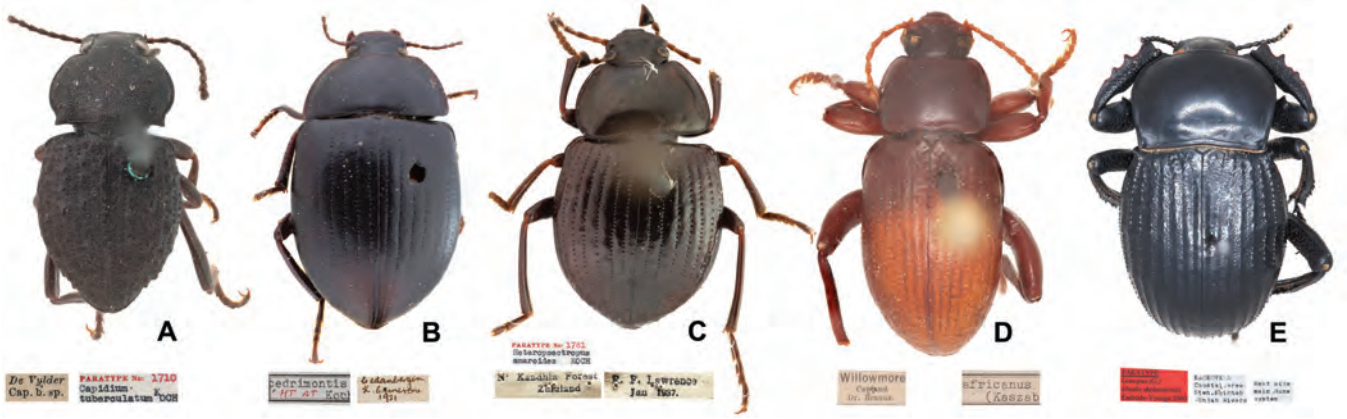


Figure 4. Outgroup taxa used in cladistic analysis. A, *Capidium tuberculatum* Koch Paratype; B, *Oncotus cedrimontis* Koch Holotype; C, *Heteropsectropus amaroides* Koch Paratype; D, *Schyzoschelus africanus* (Kaszab); E, *Gonopus tibialis skeletonensis* Endrödy-Younga Paratype.

and larvae. All beetles had died after 2 months and were subsequently dissected for identification, morphological examination, and to check for eggs and/or larvae in the bursa copulatrix. Larvae and adults are deposited at TMNH.

RESULTS

Here we employ the newly proposed classification of *Biolus* sens. nov. and *Eurynotus* sens. nov.. Taxonomic decisions at the species-level are introduced based on taxonomic revision and classification changes at the generic-level are the result of phylogenetic analysis.

Character list and analysis

A total of 70 characters were scored for 26 Eurynotina species, including all currently recognized representatives of *Eurynotus* and *Biolus*. The complete dataset is composed of 15 characters of the head, 18 of the prothorax, 15 of the pterothorax, eight of the legs, and 14 of the abdomen and genitalia. Characters 4, 41, 59, 62, and 67 are parsimony-uninformative and/or constitute diagnostic features of selected species. The character matrix is provided in the Supporting Information, Appendix S3.

Head (0–14)

0. Head punctation spacing: (0) fine (≥1 diameter apart) (Fig. 6B); (1) coarse (≤1 diameter apart) (Fig. 6A). All representatives of Eurynotina sampled here possess some level of punctation on the head capsule. All species representing the newly reinterpreted genus *Biolus* possess coarse (1) punctures, while all but one *Eurynotus* (*E. privisolum* sp. nov.) possess fine (0) punctation.

1. Frons: (0) not elevated from lateral eye area; (1) strongly elevated from lateral eye area (Fig. 6A). Many of the analysed taxa possess a sulcus, groove, or impression situated around the dorsal surface of the eye (see character #13). As a result of this, some have a resulting 'shelf-like' appearance to the frons wherein it appears more exaggeratedly elevated above the plane of the lateral eye area. State (1) is observed in more robustly sculptured species of *Biolus* [*B. granulatus* (Fabricius), *B. omeri* (Koch), *B. sauroides* (Koch), and *B. denticosta* (Mulsant and Rey)].

2. Transition between clypeus and frons: (0) without depression along lateral edge; (1) with lateral depression at frons/clypeal suture. Along the portion of the head where the frons meets with the clypeus there is often a faintly visible suture. The lateral edge of the head is usually continuous without any depression or divot (0); however, in some cases at the point of this suture there is a slight dip or divot (1). State 1 is observed in *Oncotus cedrimontis*, *Capidium tuberculatum*, *Eurynotus constrictus* Koch, *Phylacastus striolatus* Fairmaire, and *Biolus sauroides*.

3. Mentum apical notch: (0) absent; (1) present (Fig. 6D). The structure of the mentum has been an important characteristic for phylogenetic and taxonomic work throughout Blaptinae (e.g. Iwan 2002). Within similar taxa there are sometimes still minute differences. Most taxa in this study lacked a clearly defined notch of the mentum (0), while the few that did were not consistent at the generic level (e.g. 4/8 *Biolus*, 1/9 *Eurynotus*, and 2/5 *Phylacastus*). However, taxa with a notch are also diagnosable with other characteristics (e.g. *Biolus sauroides* with diagnostic tubercles, *Eurynotus capensis* with diagnostic abdominal ventrite V and male leg modifications, and *P. makskacymirowi* Lumen and Kamiński and *P. ancoralium* Lumen and Kamiński, which are separable from congeners by size and unique aedeagal morphology).

4. Mentum median keel: (0) absent; (1) present. A keel running down the midline of the midpiece of the mentum is diagnostic in one species of *Phylacastus* (*P. crypticoides* Koch). This feature is absent in all other taxa investigated here.

5. Mentum stipe from middle portion dividing lateral wing into top and bottom half: (0) absent; (1) present; from the lateral view, a small connecting strip of chitin can be observed connecting the middle portion of the mentum to the lateral wings, making a clear division between a top and bottom half. Present (1) in all species with long/exposed lateral wings of mentum (*P. ancoralium*, *P. makskacymirowi*, *O. cedrimontis*, *C. tuberculatum*, *Heteropsectropus amaroides*, and *Schyzoschelus africanus*) and in three species of *Eurynotus* with short/concealed lateral wings (*E. graniderma* Koch, *E. barbosai* Koch, and *E. thermarum* Koch). Absent (0) in all *Biolus*.

6. Mentum lateral wings: (0) short, or mostly hidden (Fig. 6C, D); (1) long, or exposed and visible from the base. Adapted from Iwan (2002) (character #21). Historically, this character has been used

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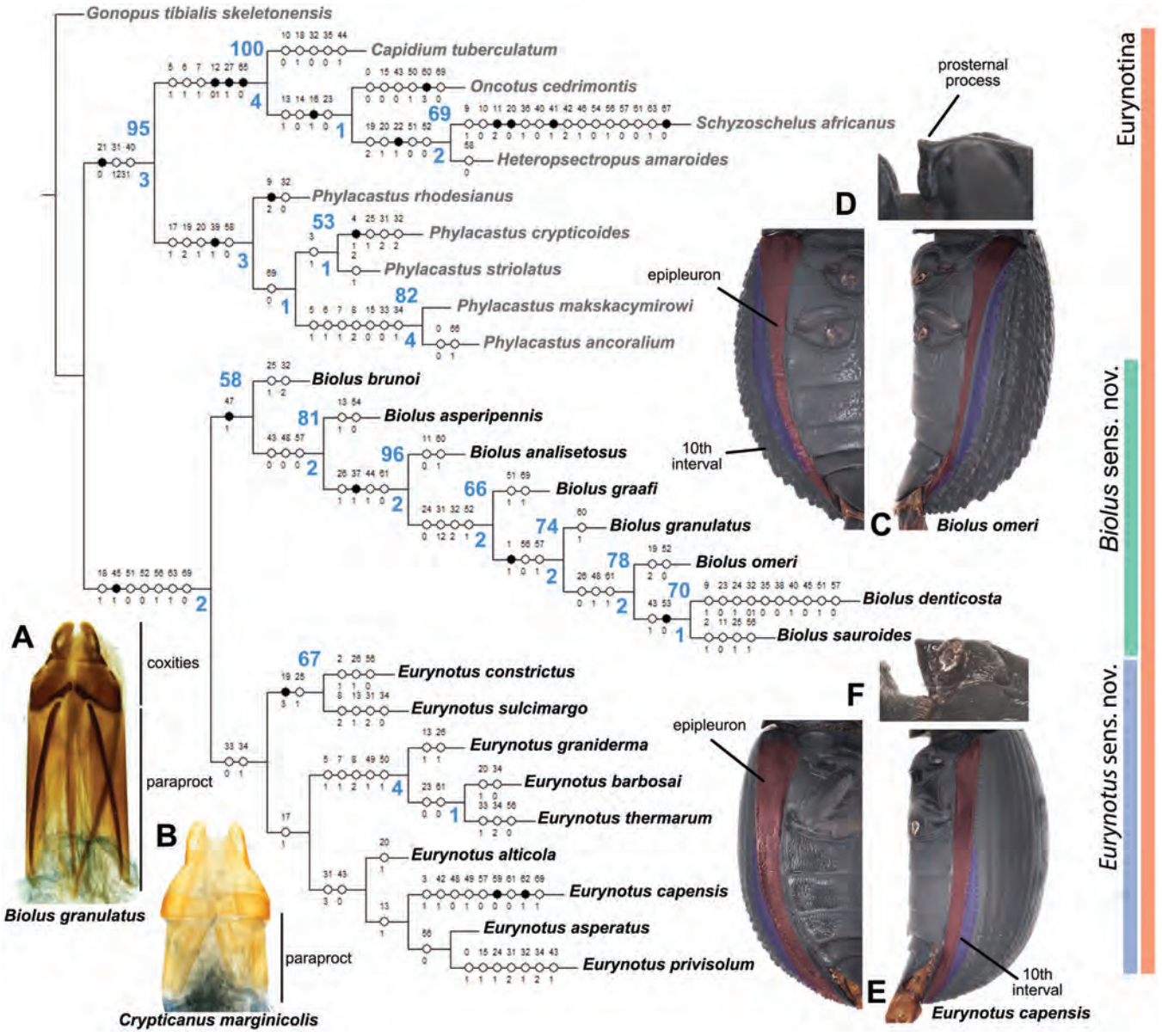


Figure 5. Phylogeny of the subtribe Eurynotina based on morphology. The most parsimonious cladogram obtained in TNT analysis (CI = 0.381, RI = 0.613), with synapomorphies (filled circles) and homoplasies (empty circles). Numbers above and below circles indicate the number and states of characters respectively. Blue numbers above represent posterior probabilities in nodes recovered in bayes analysis. Blue numbers below nodes represent Bremer Support values above 0. (A) Ovipositor with elongated paraprocts of the ovoviviparous Eurynotina species. (B) Ovipositor with reduced paraprocts of the ovoviviparous Platynotina species. (C, D) Diagnostic features of the genus Biolus: (C) elongate 10th elytral interval, (D) "Biolus-type" prosternal process. (E, F) Diagnostic features of the genus Eurynotus: (E) shortened 10th elytral interval, (F) "Eurynotus-type" prosternal process.

to diagnose groups within Platynotini (Koch 1956, Iwan 2002). All *Biolus*, *Eurynotus*, and *Gonopus tibialis skeletonensis* have short or hidden lateral wings of the mentum (0). Additionally, three species of *Phylacastus* (*P. crypticoides*, *P. rhodesianus* Koch, *P. striolatus*) also have short or concealed wings of the mentum. All other species examined have long or otherwise exposed mentum wings (1).

7. Mentum mid part strongly widened, lateral wings not visible: (0) yes; (1) no. Adapted from Iwan (2002) (character #25). Unlike taxa with long wings of the mentum (visible from the base), taxa with a widened mid-portion conceal the majority of the lateral wings. At most, only the apical points are visible. All taxa with long or exposed lateral wings (character #6) lack this trait (1). Other taxa without a widened midpart concealing the lateral wings are *E. barbosai*, *E. thermarum*, and *E. graniderma*.

8. Mentum mid part shape: (0) widening apically; (1) more-or-less parallel; (2) narrowing apically. Adapted from Iwan (2002) (character #26). The majority of Eurynotina had more-or-less parallel mentum mid parts (1). *Gonopus tibialis skeletonensis*, *B. omeri*, and *B. sauroides* all had widening mentum midparts (0). *Phylacastus makskacymirowi*, *P. ancoralium*, *E. sulcimargo* Koch, *E. barbosai*, *E. graniderma*, and *E. thermarum* had narrowing mentum mid parts (2).

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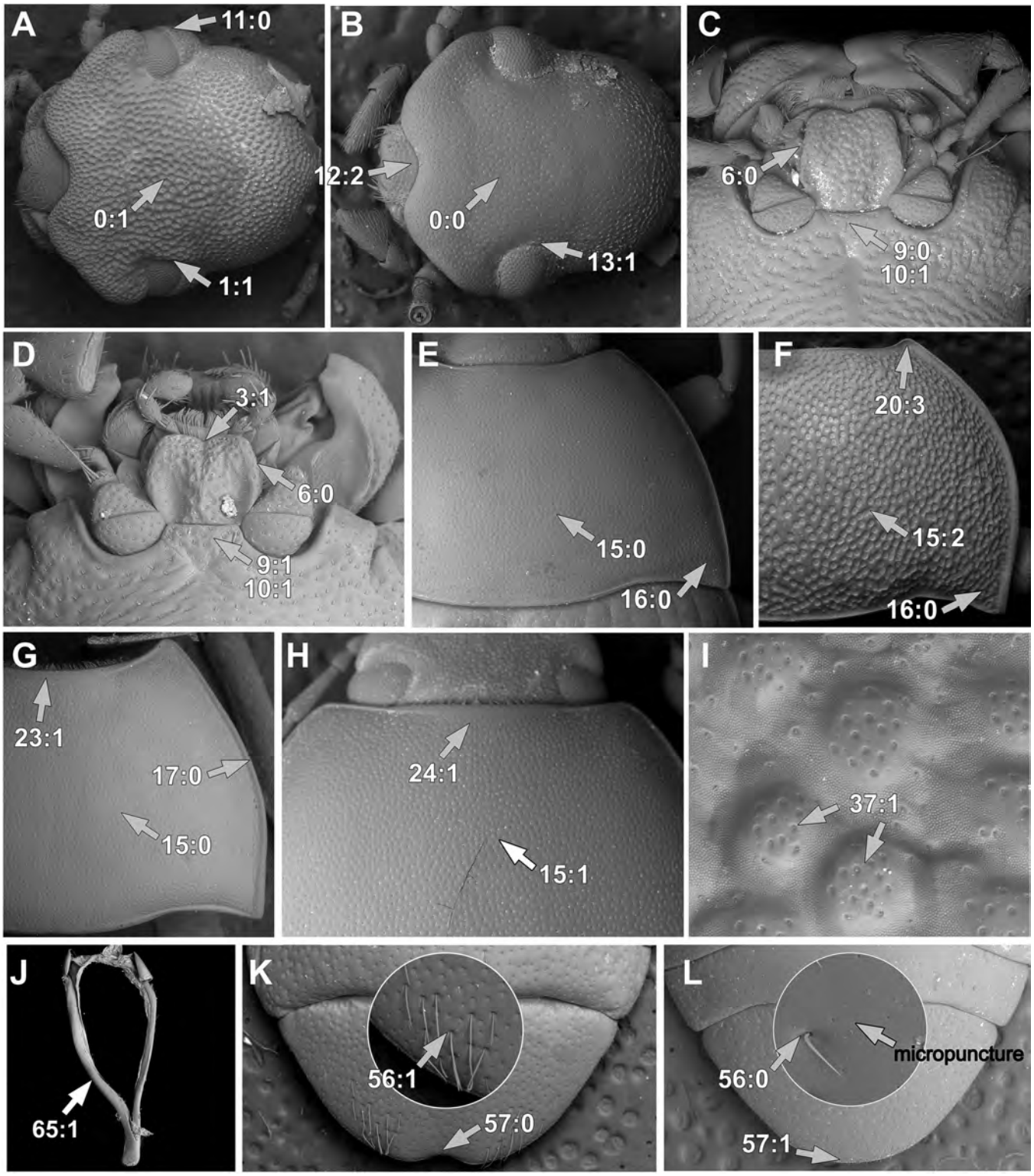


Figure 6. Characters used in the cladistic analysis. Arrows indicate particular states of given characters from the morphological matrix [e.g. 0:1 = head punctation spacing coarse (≤1 diameter apart); 0:0 = head punctation spacing fine (≥1 diameter apart)]. A, B, dorsal head view; C, D, ventral head view; E–H, pronotum; I, macrotubercles on elytral disc; J, spiculum gastrale; K, L, abdominal ventrite V. A, I, *Biolus sauroides*; B, *Eurynotus asperatus*; C, *Biolus analisetosus*; D, F, *Biolus denticosta*; E, *Eurynotus graniderma*; G, *Biolus asperipennis*; H, L, *Eurynotus privisolum*; J, *Biolus brunoi*; K, *Biolus graafi*.

9. Submentum shape: (0) triangular (Fig. 6C); (1) pentagonal (Fig. 6D); (2) U-shaped. All but three representatives sampled here possess a triangular submentum (0). Exceptions to this were: *Schyzoschelus africanus* and *Biolus denticosta* with pentagonal submenta (1), and *Phylacastus rhodesianus* with a U-shaped submentum (2)—see: Lumen and Kaminski (2023).

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10. Submentum shape: (0) elongate; (1) transverse (Fig. 6C, D). Adapted from Iwan (2002) (character #28). All but two taxa examined here have a transverse (1) submentum. *Schyzoschelus africanus* and *C. tuberculatum* both have elongate submenta (0).

11. Genal canthus: (0) strongly widened (Fig. 6A); (1) subequal/narrower than eyes; (2) much narrower than eyes. Adapted from Iwan (2002) (characters #4 and #5). The majority of taxa examined here had a genal canthus width subequal (1) to the eye width; however, exemptions are: *B. analisetosus* Mulsant and Rey and *B. sauroides* (0), *S. africanus* (2).

12. Clypeus emargination characterization: (0) absent/straight; (1) shallow; (2) deep/not shallow (for images see Kamiński 2016). Emargination of the clypeus is characteristic of Blaptinae, with variations being used (to varying degrees of success) to characterize groupings (e.g. Kamiński 2016). All *Biolus*, *Eurynotus*, and *Phylacastus* have a deep clypeal emargination (2). *Oncotus cedrimontis* has a shallower emargination (1). *Schyzoschelus africanus*, *Heteropsectropus amaroides*, and *C. tuberculatum* all lack the distinct emargination (0).

13. Circumocular depression: (0) absent; (1) weak (Fig. 6B); (2) present. As of this examination, all representatives of Eurynotina had some presence of a depression, sulcus, or groove circumscribing the dorsal lobe of the eye. The groove was absent (0) in *Gonopus tibialis skeletonensis*. Most species of *Biolus* [all except *B. asperipennis* Mulsant and Rey with a weak depression (1)] have a well-defined depression (2), while weak depressions (1) were also observed in *H. amaroides*, *S. africanus*, and some *Eurynotus* (*E. asperatus* Mulsant and Rey, *E. sulcimargo*, *E. privisolum*, *E. capensis*, and *E. graniderma*).

14. Eye between tempus and genal canthus: (0) very wide (>8 ommatidia visible); (1) not wide (<8 ommatidia visible). Adapted from Iwan (2002) (character #9). A count of the number of individual ommatidia between the tempus and genal canthus. In the majority of taxa the number of ommatidia was <8 (1). Three species of *Eurynotus* (*E. asperatus*, *E. privisolum*, and *E. capensis*), *O. cedrimontis*, *S. africanus*, *and H. amaroides* were scored as having >8 ommatidia visible (0). Note: This character was left unscored for *Eurynotus alticola*, as the photograph used was of insufficient quality to count, and additional physical specimens were unavailable for examination.

Prothorax (15–32)

15. Pronotal punctation spacing: (0) separated (>1 diameter) (Fig. 6E, G); (1) close (<1 puncture diameter) (Fig. 6H); (2) confluent (Fig. 6F). All taxa examined here have punctures on the pronotum. However, in some taxa punctures are so closely affiliated that they appear to merge into one another (e.g. confluent). Some taxa have both close and confluent punctation and, as a result, are scored for both states (1 and 2) (*B. omeri*, *B. sauroides*, *B. analisetosus*, *B. graafi*, and *B. granulatus*). *Biolus denticosta* comb. nov. was the only taxa with mostly confluent punctation (2). Taxa with close (but not confluent) punctation (1): *S. africanus*, *C. tuberculatum*, *E. privisolum*, *H. amaroides*, *P. crypticoides*, *P. rhodesianus*, and *P. striolatus*. Most taxa with separated punctation (0) were within *Eurynotus* (*E. alticola*, *E. asperatus*, *E. capensis*, *E. constrictus*, *E. sulcimargo*, *E. barbosai*, *E. graniderma*, and *E. thermarum*). Others were *Gonopus tibialis skeletonensis*, *O. cedrimontis*, *P. makskacymirowi*, *P. ancoralium*, and *B. asperipennis*.

16. Basal angles of pronotum: (0) produced or triangular (Fig. 6E, F); (1) rounded. The only taxa with rounded basal pronotal angles (1) were: *O. cedrimontis*, *S. africanus*, and *H. amaroides*. See Kamiński (2016) for images.

17. Pronotum lateral shape: (0) arcuate (Fig. 6G); (1) straight. The shape of the lateral edge of the pronotum. In all *Biolus* the lateral shape is arcuate (0). In all *Phylacastus* and all but two species of *Eurynotus* (*E. constrictus* and *E. sulcimargo*), the lateral shape is straight (1). *Gonopus tibialis skeletonensis*, *S. africanus*, *O. cedrimontis*, *C. tuberculatum*, and *H. amaroides* all have arcuate pronotal sides (0).

18. Basal angles of pronotum produced posteriorly: (0) absent; (1) present. Only *Eurynotus*, *Biolus*, and *C. tuberculatum* had pronotal basal angles that could be considered to be produced posteriorly (1).

19. Lateral margin of pronotum: (0) without depression, groove, or explanate edge; (1) with depression; (2) with groove; (3) extremely explanate. Structure along the lateral edge of the pronotum manifested as a depression, groove, or flattening. While there is a code for absence of any of these (0), no taxa here lacked all of the aforementioned structures. All but one species of *Biolus* (*B. omeri*) possess a depression (1). *Eurynotus* has representatives with a depression (1: *E. barbosai*, *E. alticola*, and *E. capensis*), groove (2: *E. graniderma*, *E. thermarum*, *E. asperatus*, and *E. privisolum*), or were extremely explanate in comparison (3: *E. sulcimargo* and *E. constrictus*). All *Phylacastus* species, *S. africanus*, and *H. amaroides* have a groove (2). *Gonopus tibialis skeletonensis*, *O. cedrimontis*, and *C. tuberculatum* have a depression (1).

20. Pronotum anterior angles: (0) absent (round pronotum); (1) weak angles (barely protruding); (2) strong angles (weakly protruding); (3) strong angles (protruding) (Fig. 6F). Adapted from Iwan (2002) (characters #37 and 38). Only *S. africanus* had a completely round pronotum with no angles (0). All *Biolus* (except *B. brunoi*), *Gonopus tibialis skeletonensis*, *E. sulcimargo*, and *E. constrictus* have strong, protruding angles (3). *Biolus brunoi*, along with *C. tuberculatum* and *O. cedrimontis*, has strong angles that are weakly protruding (2). All *Phylacastus* species, *E. alticola*, *E. barbosai*, and *H. amaroides* have weak angles that barely protrude (1).

21. Pronotum posterior angles projecting posteriorly: (0) no; (1) yes. Previously used character to separate *Eurynotus* from other Eurynotina (specifically *Phylacastus*) (see: Koch 1954a, b, 1955, 1956). All *Eurynotus* and *Biolus* have posterior angles projecting posteriorly (1), as did *Gonopus tibialis skeletonensis*. All other taxa sampled lacked posterior pronotum angles projecting posteriorly (0).

22. Pronotum posterior angles widely rounded: (0) absent; (1) present. Similar to character #20 and also used to separate *Eurynotus*

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and *Phylacastus* from the rest of Eurynotina. However, in this analysis, in addition to *Phylacastus* and *Eurynotus*, *C. tuberculatum*, *G. tibialis skeletonensis*, and *O. cedrimontis* lacked widely rounded posterior pronotal angles (0).

23. Anterior pronotum border demarcation reduced medially: (0) no; (1) yes (Fig. 6G). On the anterior border of the pronotum the border may be unclear or reduced in the middle area. All *Phylacastus*, *C. tuberculatum*, all but a single *Biolus* (*B. denticosta*), and all but two *Eurynotus* (*E. barbosai and E. thermarum*) had a medial reduction (1). *Oncotus cedrimontis*, *S. validus*, *H. amaroides*, and *G. tibialis skeletonensis* also had an anterior border that was not interrupted or reduced (0).

24. Anterior pronotal margin markedly widened medially: (0) no; (1) yes (Fig. 6H). The anterior margin or border may be widened in the middle, rather than the same size throughout (Fig. 6H). Taxa with a widened margin (1): *E. privisolum*, *E. sulcimargo*, *B. denticosta*, *B. brunoi*, *B. asperipennis*, *B. analisetosus*, and *G. tibialis skeletonensis*.

25. Posterior pronotal border demarcation reduced medially: (0) no; (1) yes. Posterior border of the pronotum is sometimes reduced in the middle. See anterior border (character #23). *Phylacastus crypticoides*, *B. sauroides*, *E. constrictus*, *B. brunoi*, and *E. sulcimargo* all had a reduction in the posterior pronotal border (1). *Eurynotus capensis* had individuals with both states: reduced (1) and not reduced (0).

26. Pronotum base convex-arcuate past posterior angles: (0) absent; (1) present. Basal margin of the pronotum rounded—extending beyond the posterior angles. Absent (0) in all taxa except: *E. graniderma*, *E. constrictus*, *B. granulatus*, *B. graafi*, *B. analisetosus*, and *E barbosai* [which also had individuals with state (1)].

27. Intercoxal process of prosternum: (0) produced; (1) rounded. The intercoxal process was produced (0) in all *Eurynotus*, *Biolus*, and *Phylacastus*. The intercoxal process was rounded (1) in: *S. africanus*, *O. cedrimontis*, *H. amaroides*, *and C. tuberculatum.*

28. Intercoxal prosternal process: (0) protruding towards mesosternum; (1) rounded without protrusion. Adapted from Iwan (2002) (character #95). All of *Eurynotus* and *Biolus* had a protruding prosternal process (0), as did *P. ancoralium*, *P. striolatus*, *P. crypticoides*, and *G. tibialis skeletonensis*. The prosternal process was rounded (1) in *O. cedrimontis*, *S. africanus*, *H. amaroides*, *P. rhodesianus*, *P. makskacymirowi*, and *C. tuberculatum.*

29. Intercoxal prosternal process (in lateral view): (0) *Eurynotus*-type (Fig. 5F) triangular laterally; (1) *Biolus*-type (Fig. 5D) more pinched in the lateral view—with a depression along the topside; (2) rounded (see: Kamiński 2016); (3) other. The structure of the prosternal process differentiates most *Biolus* from *Eurynotus*. All *Eurynotus* and *Phylacastus* had the (0) state; while all *Biolus* (except *B. brunoi*) had the (1) state. *Oncotus cedrimontis*, *S. africanus*, *C. tuberculatum*, and *H. amaroides* had a rounded-absent (2) prosternal process. *Gonopus tibialis skeletonensis* has a more uniquely sculptured prosternum absent in all examined Eurynotina (3).

30. Anterior aspect of prosternum in lateral view: (0) convex; (1) flat or depressed; (2) other. In lateral view, the area in front of the forecoxae differs in shape between groups. In particular, it is convex (0) in the case of *Eurynotus* (left unscored in the case of *E. alticola*), *Biolus*, *Phylacastus*, *C. tuberculatum*, and *H. amaroides*. *Schyzoschelus africanus* and *O. cedrimontis* are flattened or depressed (1) in lateral view. In the case of *G. tibialis skeletonensis*, the area is sculptured and depressed vastly differently (2) from the aforementioned groups (see: Endrody-Younga 1988, 2000). *Note: E. alticola* was left unscored, as specimens for examination of this character from this angle were not available for analyses.

31. Hypomeron punctation characterization: (0) shallow; (1) deep; (2) confluent; (3) no punctures. For some species of *Biolus* and *Eurynotus*, differences in the punctation of the hypomeron can be distinguishing. All but one species of *Phylacastus* (*P. crypticoides*), *Eurynotus alticola*, *E. asperatus*, and *E. capensis* had no punctures (3). *Eurynotus barbosai*, *E. graniderma*, *E. thermarum*, and *E. constrictus* had shallow (1) punctation. Many *Biolus* had shallow, deep and/or confluent punctures of the hypomeron (0, 1, 2, or all of the states); however, *B. asperipennis* and *B. analisetosus* differed in having shallow (0) punctation.

32. Hypomeron sculpturing: (0) absent; (1) lightly sculptured/wrinkled; (2) rugose. In addition to differences in punctation, there are some trends in hypomeron sculpturing. Most *Eurynotus* (except *E. constrictus* and *E. privisolum*) lacked sculpturing (0). Similarly, all but three species of *Biolus* (*B. denticosta*, *B. asperipennis*, and *B. analisetosus*) had rugose sculpturing of the hypomeron (2). *Biolus denticosta* had two states of hypomeron sculpturing (0) and (1).

Pterothorax (33–47)

33. 10th elytral interval termination: (0) relatively early (between the elytral apex and hind coxae) (Fig. 5C); (1) not early (between the elytral base and hind coxae) (Fig. 5E). All taxa examined here have at least 10 elytral intervals; the 10th terminates before reaching the elytral base and differs in where this termination occurs. All *Biolus*, *O. cedrimontis*, *S. africanus*, and *G. tibialis skeletonensis* terminate between the elytral base and hind coxae (1). Additionally, *H. amaroides* and *C. tuberculatum* exhibit the same morphology as of this study. All but two species of *Phylacastus* (*P. makskacymirowi* and *P. ancoralium*) exhibit this trait as well. All but one species of *Eurynotus* (*E. thermarum*) have a 10th interval that ends early (0).

34. Epipleura width in ventral view: (0) wider than combined width of elytral intervals 9 + 10; (1) subequal to combined width of intervals 9 + 10; (2) narrower than combined width of intervals 9 + 10. *Eurynotus sulcimargo* and *E. barbosai* both have a wider interval (0). *Phylacastus ancoralium*, *P. makskacymirowi*, and most of *Eurynotus* (*E. alticola*, *E. asperatus*, *E. capensis*, *E. graniderma*, and *E. constrictus*) have subequal epipleura (1). All of *Biolus*, the rest of *Phylacastus*, *E. privisolum*, *E. thermarum*, *O. cedrimontis*, *S. africanus*, *G. tibialis skeletonensis*, *H. amaroides*, and *C. tuberculatum* have narrower epipleura (2).

35. Epipleura shoulder: (0) produced; (1) rounded. At the base of the elytra (the humeral angle) the epipleura can be produced

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or rounded. Of all the taxa examined here, only *B. denticosta*, *G. tibialis skeletonensis*, and *C. tuberculatum* had produced epipleura shoulders (0).

36. Lateral elytral intervals visible ventrally: (0) yes (see: Koch 1956); (1) no. Lateral intervals of the elytra visible from below (0), or obscured by the epipleuron (1). The lateral intervals of the elytra were visible in all taxa except for: *E. sulcimargo*, *E. barbosai*, *E. alticola*, *E. asperatus*, *E. graniderma*, *S. africanus*, and *H. amaroides*.

37. Macrotubercles on elytral disc: (0) absent; (1) present (Figs 2A, G, H, 6I). Many taxa have tubercles; however, the presence of large, distinct tubercles on the elytral disc varies. All but two *Biolus* (*B. brunoi* and *B. asperipennis*) have distinct macrotubercles on the elytral disc (1). All other taxa lacked (0) these tubercles.

38. Costate elytra: (0) present; (1) absent. Only two taxa have costate elytra (0): *G. tibialis skeletonensis* and *B. denticosta*.

39. Base of epipleura forming slight border parallel to base of elytra: (0) absent; (1) present (ventrally). The epipleura can end in a carina or ridge, making a slight border at the base of the elytra that (when present) is visible ventrally. Absent (0) in most taxa; however, it is present ventrally (1) in *Phylacastus*.

40. Elytral base more-or-less straight between humeri: (0) absent; (1) present. Absent (0) in most taxa; present (1) in *B. denticosta*, *O. cedrimontis*, all *Phylacastus*, *H. amaroides*, and *C. tuberculatum*.

41. Number of elytral rows: (0) 10; (1) 11. Only *S. africanus* has 11 elytral rows (1).

42. Inner margin of apical part of epipleuron: (0) entirely bordered; (1) partially bordered; (2) unbordered. In ventral view there may be a slight carina running the perimeter of the elytral apex which (when present) may run partially or entirely to the apex. Entirely bordered (0) in *Phylacastus*, *H. amaroides*, *O. cedrimontis*, *C. tuberculatum*, and some species of *Eurynotus* (*E. privisolum*, *E. thermarum*, *E. barbosai*, *E. alticola*, *E. asperatus*, and *E. graniderma*) and *Biolus* (*B. brunoi*, *B. sauroides B. analisetosus*, and *B. denticosta*). *Biolus granulatus* had both entirely (0) and partially (1) bordered states. *Eurynotus capensis*, *E. constrictus*, *E. sulcimargo*, *B. asperipennis*, *B. omeri*, and *B. graafi* had partially bordered states (1). *Gonopus tibialis skeletonensis* and *S. africanus* were unbordered (0).

43. Elytral striae with large and dense punctation: (0) no; (1) yes. Most taxa here had dense and relatively large punctation (1) within the elytral striae. Exceptions are *E. alticola*, *E. asperatus*, *E. capensis*, *B. analisetosus*, *B. granulatus*, *B asperipennis*, *B. omeri*, *B. graafi*, *O. cedrimontis*, and *G. tibialis skeletonensis*.

44. Elytral intervals with sparse macrotubercles: (0) absent; (1) present. Many taxa have tubercles on the elytra; however, the size (large/macro or small/micro) and density (sparse or dense) may differ. All but two species of *Biolus* (*B. asperipennis and B. brunoi*) and *C. tuberculatum* have the present (1) state. The rest have either no tuberculation or micro-/fine tuberculation (which is often densely spaced).

45. Elytral base arcuately concave between humeri: (0) absent; (1) present. Adapted from Iwan (2002) (character #71). Present (1) in all *Biolus* (except *B. denticosta*) and *Eurynotus*. Absent in all other taxa.

46. Elytral base arcuately convex anteriad between humeri: (0) absent; (1) present. Adapted from Iwan (2002) (character #72). Present (1) only in *G. tibialis skeletonensis* and *S. africanus*.

47. Dorsal humeri of elytra with large, knob-like tubercles: (0) absent; (1) present. Only present (1) in *Biolus*.

Legs (48–55)

Note: Eurynotus constrictus, *E. sulcimargo*, and *E. thermarum* were left unevaluated for male characteristics, as males were not available for examination.

48. Tarsal setae colour excluding male pads: (0) gold (Fig. 3E); (1) dark (Fig. 2G). In lateral view, the setae of the tarsi can be golden or dark (often brown/black). Mostly diagnostic at species level for *Biolus* and *Eurynotus*, as both have representatives within both states; however, all *Phylacastus*, *O. cedrimontis*, and *S. africanus* have golden tarsal setae (0), and *G. tibialis skeletonensis*, *C. tuberculatum*, and *H. amaroides* have dark tarsal setae (1).

49. Male hind tibia setal patch: (0) absent; (1) present. Some taxa have modifications to the male hind tibiae (e.g. Fig. 3E, G). Only present (1) in *O. cedrimontis*, *E. capensis*, *E. barbosai*, *E. graniderma*, *E. thermarum*, and *H. amaroides*.

50. Male midtibial setae patch: (0) absent; (1) present (Fig. 3E, G). Only present (1) in *O. cedrimontis*, *E. barbosai*, *E. graniderma*, and *E. thermarum*.

51. Male foretarsus expanded: (0) yes; (1) no. Male modification of the foretarsus, present (0) in most taxa. Absent (1) in *Phylacastus*, *G. graafi*, *G. tibialis skeletonensis*, *B. denticosta*, *O. cedrimontis*, and *C. tuberculatum*.

52. Male midtarsus expanded: (0) yes; (1) no. Same as foretarsus; with the exceptions of *B. granulatus* and *B. sauroides*, which lack (1) expanded midtarsi.

53. Male midtibia with apical projection: (0) present; (1) absent. Present only in *B. denticosta* and *B. sauroides* (Fig. 2D).

54. Male hind tibia with slight curvature and distal expansion: (0) Present (Fig. 2A); (1) Absent. Present only in *B. asperipennis* and *S. africanus*.

55. Foretibia shape: (0) slender; (1) strongly widened with sharp lateral projection; (2) widened distinctly triangularly; (3) modified otherwise. Leg modifications are common throughout Tenebrionidae [and diagnostic for many groups within Blaptinae (e.g. Iwan 2002)]. Overall, the foretibia can be categorized based on modifications (often for fossoriality). Taxa with widened foretibia: *Phylacastus* widened triangularly (2). *Oncotus cedrimontis* strongly widened with an additional sharp, lateral projection (1). *Gonopus tibialis skeletonensis* has a distinctly different, scalloped and sculptured protibia (3). All

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Biolus, *Eurynotus*, *Schyzoschelus africanus*, *H. amaroides*, and *C. tuberculatum* have less-modified/specialized, slender tibiae (0).

Abdomen and genitalia (abdomen: 56–59, genitalia: female 60–63, male 64–69)

Note: Eurynotus privisolum and *Eurynotus alticola* were not scored for some female structures as female specimens were unavailable. *Eurynotus thermarum*, *E. privisolum*, *E. constrictus*, and *E. sulcimargo* were left unscored for some male characters due to lack of specimens or intact structures. When possible, evidence from literature (e.g. Koch 1954a, b) was used to score some of these taxa.

56. Abdominal ventrite V punctation types: (0) single (Fig. 6L); (1) dual (Fig. 6K). Not taking into account micropunctation, having two punctation types (1) is the state where alongside the majority type of punctation are larger, setigerous punctures (Fig. 6K). Mostly diagnostic at the species-level, *Eurynotus* and *Biolus* make up the majority of taxa with two puncture types (1); however, *Schyzoschelus africanus* also has this punctation type. *Oncotus cedrimontis*, *C. tuberculatum*, *G. tibialis skeletonensis*, *Phylacastus*, *H. amaroides*, and some species of *Eurynotus* and *Biolus* have only one punctation type (0).

57. Female abdominal ventrite V notch: (0) present (Fig. 6K); (1) absent (Fig. 6L). Apical notch or emargination in abdominal ventrite V. absent (1) in most taxa. Present (0) in *S. africanus*, *B. denticosta*, *B. analisetosus*, *B. graafi*, *B. asperipennis*, and *E. capensis*.

58. Abdominal ventrite V submarginal sulcus: (0) present; (1) absent. Sulcus running along the perimeter of abdominal ventrite V. Present only in *Phylacastus* (see: Lumen and Kamiński 2023) and *H. amaroides*.

59. Abdominal ventrite V laterally sinuate: (0) present; (1) absent. In *Eurynotus capensis* the lateral margins of abdominal ventrite V are distinctly sinuate (0). Absent (1) in all other taxa.

60. Bursa copulatrix sclerite: (0) absent; (1) single; (2) paired plates; (3) paired spikes. Sclerites observed in few taxa, but with varying forms: as single, solitary structures (1) (Fig. 7E, F) (*B. granulatus* and *B. analisetosus*), as paired structures (*E. asperatus* with paired, plate-like sclerites) (2) (Fig. 7G), and *O. cedrimontis* with paired, spike-like structures (3) (Fig. 7H).

61. Bursa copulatrix accessory pouch: (0) present (Fig. 7D–F); (1) absent. Additional sac-like structure of the bursa copulatrix (when present) situated near-to the spermatheca/accessory gland. Present (0) in some species of *Biolus*, *Eurynotus*, *Phylacastus*, and *C. tuberculatum*.

62. Bursa copulatrix initially sac-like, further branched and bent: (0) absent; (1) present (Fig. 7D). This particular construction of the spermatheca is only observed here in *Eurynotus capensis* [previously recorded in Tschinkel (1978)].

63. Ovipositor paraprocts: (0) short; (1) long. Previously hypothesized to represent a modification for taxa with ovoviviparous proclivities (Iwan 2000, 2010), short paraprocts (0) (coxites subequal to paraprocts) are common in Eurynotina—with most representatives examined here displaying this feature. All *Eurynotus* sensu nov., *Biolus* sens nov., and *S. africanus* have long paraprocts (1) (>length of coxites).

64. Dorsal membranous field below parameres: (0) present; (1) absent. Present in most taxa (Fig. 8A–L, P). Absent in *O. cedrimontis*, *C. tuberculatum*, and *G. tibialis skeletonensis*.

65. Spiculum gastrale: (0) roughly symmetrical; (1) asymmetrical (Fig. 6J). Most taxa had asymmetrical spiculum gastrale—with one arm clearly longer, thicker, and/or more bent than the other (1). Taxa with the nearly symmetrical state (0) were: *H. amaroides*, *O. cedrimontis*, *S. africanus*, and *C. tuberculatum*.

66. Aedeagal ancorae: (0) absent; (1) present. Present (1) only in the outrgroup *G. tibialis skeletonensis* and *Phylacastus ancoralium* (see: Lumen and Kamiński 2023).

67. Tegmen entirely opened ventrally: (0) absent; (1) present. The basal portion of the tegmen either membranous (1), or closed with chitin (0). The only taxa with the tegmen closed ventrally (0) was *S. africanus*.

68. Dorsal paramere window: (0) small, parameres separated narrowly; (1) large, wide separation between parameres (Fig. 8M). Only three taxa (*O. cedrimontis*, *P. rhodesianus*, and *C. tuberculatum*) had parameres widely separated (1).

69. Apical paramere opening: (0) shallow, situated apically (Fig. 8J); (1) deep, running nearly or more than halfway down the length of the parameres (Fig. 8E, K). Most taxa had shallow, apically situated paramere openings (0). *Gonopus tibialis skeletonensis*, *P rhodesianus*, *E. capensis*, *B. graafi*, *S. africanus*, *H. amaroides*, and *C. tuberculatum* had deep (1) openings.

Phylogenetic analysis

The morphological matrix analysed in TNT returned a single topology with a score of 19.47307 after 6 962 741 rearrangements. Eurynotina was recovered with two main clades (Fig. 5). The first groups *Capidium*, *Oncotus*, *Schyzoschelus*, *Heteropsectropus*, and *Phylacastus*. The second clade contains all species previously assigned to *Eurynotus*. Both lineages were supported by single synapomorphies, i.e. pronotum posterior angles not projecting posteriorly (21:0) and elytral base arcuately concave between humeri (45:1), respectively. Within the first clade, the *Capidium*, *Oncotus*, *Schyzoschelus*, and *Heteropsectropus* grouping was supported by three synapomorphies: clypeus emargination absent/straight or shallow (12:0/1, respectively), intercoxal process of prosternum rounded (27:1), and spiculum gastrale roughly symmetrical (65:0). The following synapomorphies were also recovered within this grouping: pronotum posterior angles widely rounded (22:1) for *Schyzoschelus* + *Heteropsectropus*; basal angles of pronotum rounded (rather than triangular) (16:1) for *Oncotus* + *Schyzoschelus* + *Heteropsectropus*. Monophyly of *Phylacastus* was supported by the synapomorphic structure of the base of the epipleura, which forms a slight border parallel to the base of the elytra ventrally (39:1).

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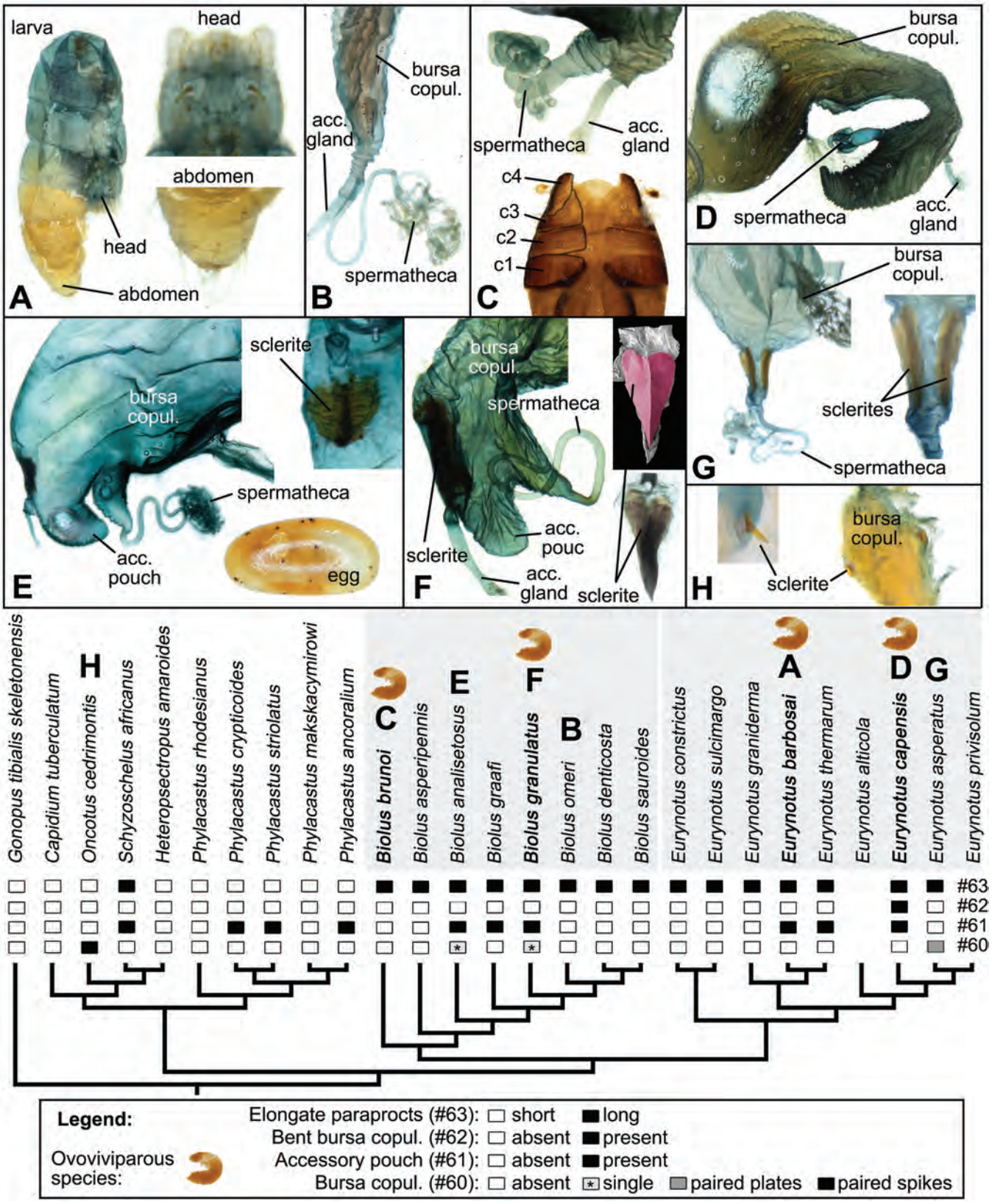


Figure 7. Phylogeny of morphology, ovovivipary, and female reproductive structures of Eurynotina. A, *Eurynotus barbosai*, 1st instar larva dissected from bursa copulatrix. B, *Biolus omeri*, genital tubes. C, *B. brunoi*, spermatheca and ovipositor. D, *E. capensis*, genital tubes of two individuals. E, *B. analisetosus*, sclerite and egg dissected from bursa copulatrix. F, *B. granulatus*, sclerite from bursa copulatrix. G, *E. asperatus*, paired sclerites on distal part of bursa copulatrix. H, *Oncotus cedrimontis*, bursa copulatrix. Abbreviations: c1–c4, lobes of coxities. Numbers in parentheses represent characters and states used in analysis.

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Two major subclades were recovered within the '*Eurynotus*' clade (Fig. 3). The *Biolus* subclade is supported by a single synapomorphy: dorsal humeri of elytra with large, knob-like tubercles (47:1). This lineage contains the type species of *Biolus* (*Eurynotus asperipennis*) and *Neosolenopistoma* (*Eurynotus denticosta*). The latter was recovered as sister to *Biolus sauroides*. The newly discovered *Biolus brunoi* sp. nov. was also recovered within this lineage. The *Eurynotus* subclade as of this reconstruction lacks formal synapomorphies (Fig. 3). However, the early position of the elytral interval 10 termination (33:0) is consistent for all except for *E. thermarum* [which terminates later (1)]; and the width of the epipleura is subequal in most species (34:1), but wider in *E. barbosai* and *E. sulcimargo* (34:0) and narrower in *E. thermarum* (34:2). Two lineages were recovered within the *Eurynotus* subclade. The first consists of *E. constrictus* and *E. sulcimargo*, and is supported by a synapomorphic structure of pronotum (19:3). The second groups the remaining species historically assigned to *Eurynotus*, including *Eurynotus capensis*—the type species of the genus. *Eurynotus sulcimargo*, *E. constrictus*, and *E. thermarum* were previously assigned to *Biolus* by Koch (1954a, b, 1955), but were here recovered within *Eurynotus* [probably as a result of their lack of elytral humeral tubercles (47:0)].

The highly supported clades from the TNT run were also recovered in the Bayesian analysis (Supporting Information, Appendix S4). Branch support values for particular lineages are presented in Figure 5.

Ovoviviparity

First instar larvae were dissected from the bursae of the following species: *Biolus granulatus*, *Eurynotus barbosai*, *Eurynotus brunoi* sp. nov., and *Eurynotus capensis* (see Fig. 7). The first three species are newly reported here, significantly extending the list of ovoviviparous darkling beetles (Table 1). Observation of captive adults of *Biolus granulatus* recovered no eggs or egg shells, contrary to the oviparous specimens of *Crypticanus* (Fig. 1A), though larvae were recovered from both. In *Eurynotus asperatus*, a single large egg was dissected from the bursa copulatrix.

In addition to phylogenetic relationships concerning the placement of *Eurynotus*, *Biolus*, and other genera previously aligned

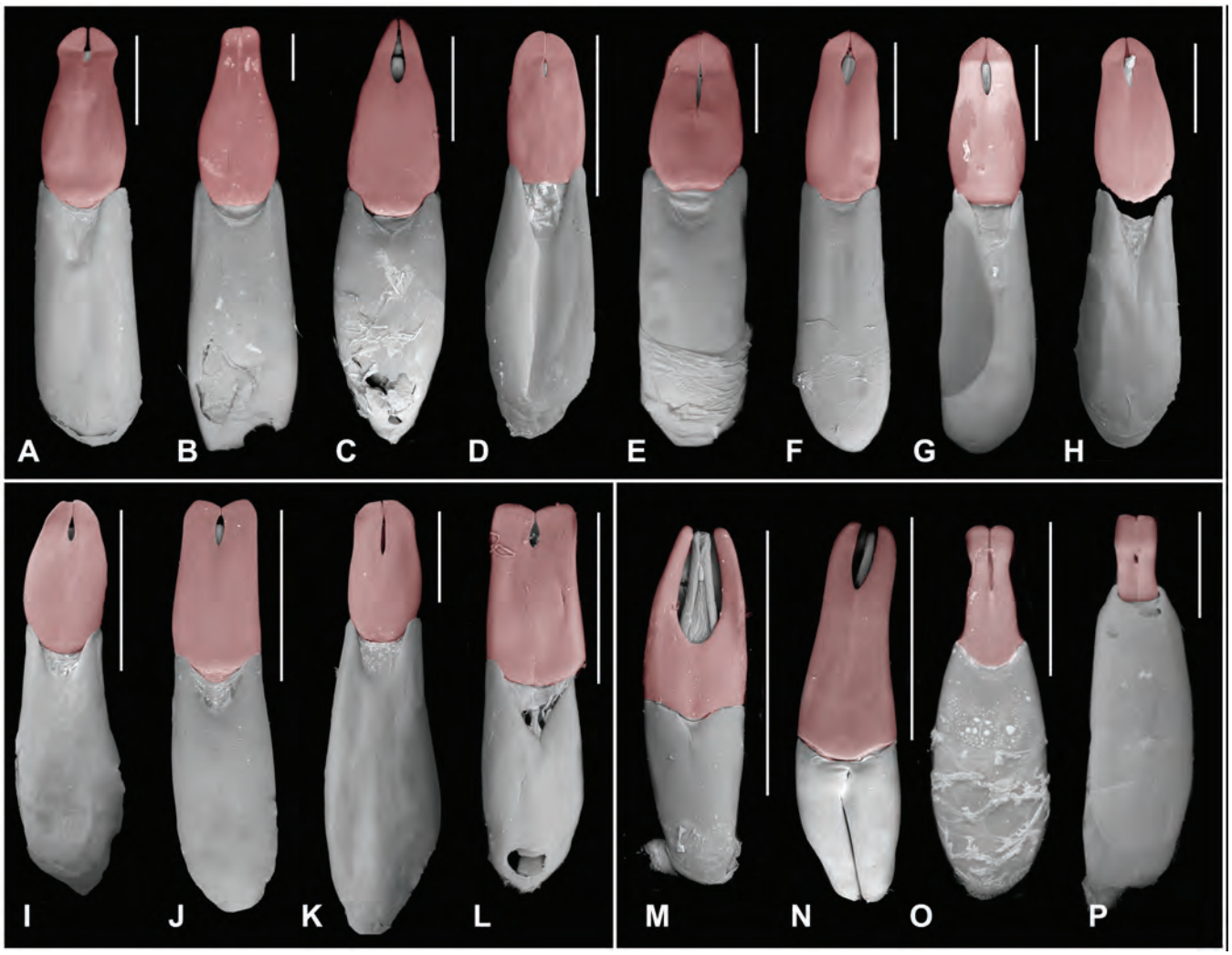


Figure 8. Aedeagal morphology of Eurynotina species. A, *Biolus analisetosus*; B, *B. asperipennis*; C, *B. brunoi* sp. nov.; D, *B. denticosta*; E, *B. graafi*; F, *B. granulatus*; G, *B. omeri*; H, *B. sauroides*; I, *Eurynotus asperatus*; J, *E. barbosai*; K, *E. capensis*; L, *E. graniderma*; M, *Capidium tuberculatum*; N, *Oncotus cedrimontis*; O, *Heteropsectropus amaroides*; P, *Schyzoschelus africanus*. Parameres highlighted red. Scale = 1mm.

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with them (e.g. *Phylacastus*), unique structures of the internal female anatomy for the tribe are recorded here and given within a phylogenetic context for the first time. In particular, *Oncotus*, *Eurynotus*, and *Biolus* have representatives with sclerites within the bursa copulatrix (60:1/2/3). Four different sclerite shapes are recorded here (Fig. 7E–G, H): single, axe-shaped sclerite (*Biolus granulatus*); single, chevron-shaped sclerite (*Biolus analisetosus*); paired, plate-like sclerites (*Eurynotus asperatus*); and paired, spike-shaped sclerites (*Oncotus cedrimontis*). These sclerites constitute reliable diagnostic features for the above-mentioned *Biolus* and *Eurynotus* species and remain stable regardless of the collecting circumstances (i.e. seasonality, geographic locality). Similarly, presence of an accessory pouch in the terminal part of the bursa copulatrix is reported here for some species of *Biolus* stat. nov., and *Eurynotus* (Fig. 7D–F). The present investigation has not revealed any direct relations between the presence of these structures and ovoviviparity (Fig. 7); however, *Eurynotus capensis*, which was the first reported ovoviviparous darkling beetle and possesses a uniquely bent bursa copulatrix, has a relatively large accessory pouch (Fig. 7D; Tschinkel 1978). Furthermore, in ovoviviparous species of *Eurynotus* and *Biolus*, the paraprocts of the ovipositor were not reduced in length and were, on average, twice as long as the combined length of the coxites (see Figs 1B, 5A for examples, and Table 1).

Our PCA to examine environmental effects on ovoviviparity in Tenebrionidae recovered three distinct climactic envelopes encompassing three geographic lineages (South Africa, Madagascar, and Guadeloupe) ($P < 0.001$). Lineages were opposed on the first PCA axis by temperature descriptors such as the minimum temperature of the coldest month (bio6), isothermality (bio3), and temperature seasonality (bio4). On the second PCA axis, lineages were opposed by precipitation descriptors such as the annual precipitation (bio12), precipitation of the driest month (bio14), precipitation of the driest quarter (bio17), and the mean diurnal range of temperature (bio2) (Fig. 1D).

DISCUSSION

Ovoviviparity

Of the currently described ~30 000 species, most Tenebrionidae are probably oviparous (Bouchard *et al.* 2021). Only 11 species have been recorded as ovoviviparous prior to this paper (Iwan 2000, 2010, Dutrillaux *et al.* 2010). The small body of literature examining female terminalia morphology in taxonomic works on darkling beetles (however, for in-depth and/or broad treatments of specific groups, see: Tschinkel and Doyen 1980, Iwan and Kamiński 2016, Kamiński *et al.* 2022) and difficulty in finding well-preserved material in the correct state (i.e. gravid with egg/larvae) has probably resulted in low detection of ovoviviparity. However, it is still likely that ovoviviparity is a rare mode of reproduction within the family. A similar pattern (oviparity > ovoviviparity) is also observed within the whole order Coleoptera and other lineages of holometabolous insects (see: Meier *et al.* 1999, Iwan 2000, Dutrillaux *et al.* 2010). Here we introduce three new detections of ovoviviparous Tenebrionidae (Table 1).

In general, ovoviviparity in insects may involve neotenic or climatic mechanisms. Some ovoviviparous insects (e.g. in Dictyoptera Latreille or Hemiptera Linnaeus) display reductions in adult morphology (Roth 1997, Gavrilov-Zimin 2021). Iwan (2000) considered the shortening of paraprocts as essential for 'larviposition', and a potential morphological indicator of ovoviviparity for Malagasy Platynotina. However, there are lineages of darkling beetles with fully reduced or shortened ovipositors (e.g. *Phrenapates* Gray) that are oviparous (Hinton 1981, Iwan and Kamiński 2016). Additionally, our data show that elongate ovipositors do not exclude ovoviviparity, as all ovoviviparous Eurynotina species examined here have elongate ovipositors (Figs 1B, 5A). Discounting the shortening or reduction of ovipositors in some taxa (Table 1), there appears to be no other obvious neotenic-morphological mechanisms co-occurring with ovoviviparity in darkling beetles (Iwan 2000, 2010). Alternatively, ovoviviparity could be a response to climatic variables (e.g. retaining eggs for favourable conditions or desiccation avoidance). Tenebrionidae are well-known to thrive in arid ecosystems (Koch 1962, Wang *et al.* 2014, Cheli *et al.* 2022, Johnston *et al.* 2022, Pinto *et al.* 2022, Purchart 2022, Silvestro *et al.* 2022, Ragionieri *et al.* 2023). While most species (including those linked to extreme habitats) are oviparous, known ovoviviparous species (*Alegoria castelnaui* excepted) are closely linked to arid environments (Dutrillaux *et al.* 2010, Kamiński and Raś 2012, Kamiński 2016). However, environmental conditions are not fully convergent across all known ovoviviparous Tenebrionidae (Fig. 1). Climate envelopes recovered by PCA for the phylogenetically distinct Malagasy, South African, and Caribbean taxa (Fig. 1D) suggest that the evolution of ovoviviparity cannot be reduced to the group of climatic factors examined here for Tenebrionidae. However, reductions in clutch size and increases in egg size remain to be more closely examined as crucial preadaptations for ovoviviparity in tenebrionids (Iwan 2000, 2010). Regardless, it is likely that each lineage (i.e. South Africa, Madagascar, and Guadeloupe) of ovoviviparous tenebrionids has separate evolutionary origins and selection pressures; this is also supported by other phylogenetic data (Kamiński *et al.* 2021).

Overall, ovoviviparity may be more prevalent in Eurynotina than previously recorded or recognized. As mentioned previously, few dissections of female taxa are recorded in the literature (see: Banaszkiewicz 2006; Lumen and Kamiński 2023). While the extreme diversity of genital tube morphology recorded here was not linked to ovoviviparity (Fig. 1), it may prove useful for phylogenetic inference with further taxon sampling. Male terminalia may also be worth investigation in terms of correlation with ovoviviparity. Eurynotina is unique within Blaptinae due to strong sclerotization of the median lobe and reduction or lack of ancorae (Lumen and Kamiński 2023). Furthermore, all species of *Biolus* and *Eurynotus*, when compared to other representatives of the subtribe, are characterized by having an elongate basal piece of the aedeagus. Additional comparative and observational studies are needed to evaluate the true extent of these phenomena; and such studies should additionally be followed by or include genetic comparative analysis.

Phylogeny, taxonomy, and classification

Historically, three lineages have been designated among Eurynotina (Koch 1954a, b, 1955): the *Eurynotus*, *Oncotus*, and *Schzyzoschelus* generic complexes. This subdivision was proposed largely for identification purposes, and was based on features related to the head

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(depth of clypeal emargination), pronotum (posterior angles sharp or not), and intercoxal process of prosternum (projecting towards abdominal ventrites or not). Additional sexually dimorphic features have been proposed to distinguish genera within the *Oncotus* and *Schzyzoschelus* generic complexes (i.e. bordering on abdominal ventrite V in females) (Kamiński 2016). The phylogenetic analysis presented here does not reflect the above-described subdivision of Eurynotina, especially in the context of the *Eurynotus* generic group (Fig. 5). The close phylogenetic affinity between *Biolus* + *Eurynotus*, and *Phylacastus* is not supported by the obtained topologies, despite a similar gestalt of all three genera (Koch 1954a, b, 1955, Lumen and Kamiński 2023). Contrarily, *Phylacastus* was recovered as more closely affiliated with the *Oncotus* and *Schzyzoschelus* generic complexes (Fig. 1). The distinctness of *Biolus* + *Eurynotus* among Eurynotina is well-grounded in several characters [i.e. basal angles of pronotum produced posteriorly (18:1), elytral base arcuately concave between the humeri (45:1), male foretarsus (51) and midtarsus (52) expanded (0), abdominal ventrite V with two puncture types (56:1), long ovipositor paraprocts (63:1), and paramere opening shallow and situated apically 69:0)]. However, this study was not designed to fully investigate the relations within the subtribe, as taxonomic sampling was largely biased towards *Biolus* and *Eurynotus*, so no new subdivisions were introduced at this level.

In his treatments Koch (1954a, b, 1955) listed 16 species of *Eurynotus*, and divided the genus into three subgenera: *Biolus*, *Eurynotus*, and *Neosolenopistoma* (described as *Solenopistoma*, see: Bouchard *et al.* 2021). Koch's delineations between the subgenera were largely based on the construction of the elytra: ventral visibility of lateral/reflected portions of the elytra (almost entirely visible in *Biolus* and *Neosolenopistoma*; concealed in basal third in *Eurynotus*) and pseudopleural crest position and broadness. Additionally, *Neosolenopistoma* was separated from the other subgenera solely by elytral costae (Fig. 2D). Though some of Koch's characters were used in this study (see Fig. 5), the phylogenetic topologies from our analyses impose a critical need for substantial changes to the classification of *Eurynotus sens* Koch (1955). In particular, the monotypic subgenus *Neosolenopistoma* was recovered deeply embedded within *Biolus* (sister to *Biolus sauroides*); this relationship is supported by several synapomorphies (Fig. 5): frons strongly elevated from lateral eye area (1:1, Fig. 6A), macrotubercles on elytral disc (37:1, Fig. 6I), dorsal humeri of elytral with large, knob-like tubercles (47:1, Fig. 5C), and male midtibia with apical projection (53:0, Fig. 2D). Furthermore, the monophyly of *Biolus sens* Koch (1955) was not supported, as the following species were shown to have greater affiliation to *Eurynotus s.s.*: *E. constrictus*, *E. sulcimargo*, and *E. thermarum*. Interestingly, while providing their descriptions, Koch (1954a, b) noted that these species blur the concepts of *Biolus* and *Eurynotus*. To accommodate the above-mentioned phylogenetic findings, *Neosolenopistoma* is hereby synonymized with *Biolus*, which, due to its substantial morphological distinctiveness and diagnostic features, is elevated to generic rank. Furthermore, *E. constrictus*, *E. sulcimargo*, and *E. thermarum* are excluded from *Biolus*.

The revisionary part of this study has revealed substantial problems with some species' concepts of *Biolus* and *Eurynotus*, caused by scarcity of materials available to the preceding authors or lack of access to historical types. For example, Koch (1954a) synonymized *E. asperipennis* with *E. granulatus* without providing details. As *E. asperipennis* is the type species of *Biolus*, Koch's decision had important implications for the generic classification. Both *E. asperipennis* and *E. granulatus* are historic names, and it is clear that Koch (1954a, b, 1955) did not examine the types. While looking for material at MNHN, we located a single syntype specimen of *E. asperipennis* from Mulsant's collection. Upon examination of this individual and the type specimen for *E. granulatus* (ZMUK), we found that both are highly divergent (see Fig. 2B, F). Based on material identified by Koch stored in TMNH, it appears Koch's (1954a) concept of *E. granulatus* was based on a hitherto undescribed species that we found to also be distinct from *E. asperipennis*. As a result, *E. asperipennis* is restored to a valid species (stat. res.) and, as the type species of the subgenus *Biolus*, which is now raised to full generic status, becomes *Biolus asperipennis* (comb. nov.). Also, the previously undescribed species is described under the name *B. brunoi* sp. nov.. While this revision is based on newer and redefined traits (e.g. humeral elytral tubercles), more classic characteristics (e.g. the narrowing of the epipleura) affiliated this species to Koch's subgenus *Biolus*. It is likely that Koch's misdiagnosis of *B. brunoi* as *B. granulatus* was the reason he synonymized *B. asperipennis*, as they can be superficially similar (see Fig. 2B, C). Furthermore, Koch's inability to study the above-mentioned historical types resulted in yet another misidentification. Namely, examination of types for *B. granulatus* and *B. norrisi* reveal that they share all diagnostic characteristics proposed by Koch (1954a, b) (e.g. simple punctation of abdominal ventrite V, large punctures of the pronotum and head, and presence of defined tubercles on the disc of the elytra), as well as new characters uncovered as a result of this investigation [e.g. presence and characterization of the sclerite in the bursa copulatrix (Fig. 7F)]. As a result, *B. norrisi* is synonymized here with *B. granulatus*.

In Koch's (1955) treatment of *Eurynotus*, he includes a description of a new species (*E. rudebecki*), while citing a close affiliation to the already described *E. asperatus*. In addition to cuticular texture, epipleural, and leg structure, Koch (1955) also mentions that the two species seem to be allopatric in distribution, and may be 'subspecifically related'. Upon examination of type material of *E. rudebecki* (TMNH) and *E. asperatus* (syntype found in MNHN), and comparison with specimens gathered from a wider distribution (see Supporting Information, Appendix S1), Koch appears to have described geographic variation within a single species. In particular, there appears to be some variation in body size and shape of the pronotum (see Fig. 3B, C). Strikingly, dissections of newer and historical material have revealed that, despite small external differences, all females had uniquely 'paired' sclerites within the bursa copulatrix (Fig. 7G) and similarly shaped aedeagi in males (Fig. 8I). As a result, *E. rudebecki* is here synonymized under *Eurynotus asperatus*.

While examining variation within species, we have uncovered some morphological differences within *E. capensis* that could have greater implications in future investigations. Specifically, in some female specimens the patches of setae on the fore/midtarsus are larger and undivided down the middle—similar to male tarsi (expanded with large pads). Males and females can be differentiated more reliably using abdominal ventrite V (with an apical notch in females; Fig. 6K) and the hind tibiae (modified with a patch of dense setae in males, Fig. 3E). Additionally, there is variation in specimens

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with regard to size (both male and females with wider size ranges than in other species) and opacity/dullness of the cuticle (some specimens 'shinier' than others). However, taking this into account, there appear to be no clearly delimited differences separating these entities to the same degree as other species within this revision (e.g. all males and females share the same external and internal reproductive configurations distinct from all other species).

Taxonomy

KEY TO GENERA *BIOLUS* AND *EURYNOTUS*:

Substitution of couplet 3 in Kamiński (2016).

I. Dorsal humeri of elytra with large and raised, well-defined knob-like tubercles, callosities, or costae (Fig. 5C). Macrotubercles present or absent on elytral disc. Prosternal process in lateral view with or without well-defined protuberance and/or depression on descending surface between forecoxae, giving a 'pinched' appearance to prosternal process apex (Fig. 5D). Epipleura narrower than elytral intervals 9 + 10 (Fig. 5C). Lateral elytral intervals visible ventrally.....genus *Biolus*

II. Dorsal humeri without well-defined large knob-like tubercles (some weakly raised tubercles in *E. constrictus*). Elytral macrotubercles absent from disc. Prosternal process in lateral view with weak or absent protuberance, lacking well-defined depression on descending surface between forecoxae. Epipleura wider or subequal to elytral intervals 9 + 10 (Fig. 5E). Lateral elytral intervals visible ventrally or not.....genus *Eurynotus*

I. Genus *Biolus* Mulsant and Rey stat. nov.

(Fig. 2A–I)

Biolus Mulsant and Rey, 1854a: 25.– Mulsant and Rey 1854b: 169; Lacordaire 1859: 239; Koch 1954a: 276; 1954b: 2; Kamiński 2016: 234.

=*Neosolenopistoma* Bouchard and Bousquet, 2021: 265 (in: Bouchard *et al.* 2021) syn. nov. (type species: *Eurynotus denticosta* Mulsant and Rey, 1854).

Note: Neosolenopistoma has been previously referred to as '*Solenopistoma*' Mulsant and Rey, 1854b: 29.– Mulsant and Rey 1854b: 173; Lacordaire 1859: 239; Koch 1954a: 276; 1954b: 2; Kamiński 2016: 237. However, the name is unavailable (see: Bouchard *et al.* 2021).

Type species: Eurynotus asperipennis Mulsant and Rey; by subsequent designation (Koch 1954a: 276).

Redescription: Length 9–22mm, width 3–12mm. Shining to dull; coloured tenebrous; dark brown to black. Head: Punctate, punctures widely (≥1 puncture diameter) or closely (≤1 puncture diameter) spaced, and/or confluent. Epistoma with well-defined median notch. Mentum middle portion expanded, with two depressions on either side with or without apical notch; lateral wings reduced. Gula with stridulatory file. Eye constricted in middle and reniform, with strong to weakly impressed sulcus situated around perimeter of dorsal lobe. Antennae 11 segmented, terminal segments forming weak club. Prothorax: scutellum small and transversely triangular. Pronotum strongly bisinuate with basal angles pointed posteriorly. Lateral depression or flattening along anterior margin weak to strong. Hypomeron coarsely rugose to smoothed or finely sculptured and with small or large, shallow punctation, with or without microtuberculation. Prosternal process rounded at apex, with clear sulcus running perimeter, projecting weakly to strongly toward midcoxae in lateral view; in lateral view with preapical depression and similar depression on descending surface between forecoxae, giving a 'pinched' appearance to prosternal process apex. Pterothorax: Elytra costate, or not. Striae deep or shallow, with similarly deep or shallow punctures. Intervals punctate, with or without microtuberculation; macrotubercles present on disc in some species, and on apical declivity in all species. Elytral intervals not obscured by epipleuron in ventral view; humeri with large knob-like tubercles, or raised bumpy ridges; interval X terminating between hind coxae and elytral base. Epipleura broad basally, narrowing apically; distinctly narrower than elytral intervals 9 + 10; with or without microtubercles. Apterous. Abdomen: Finely to coarsely punctate with punctures closely (≤1 puncture diameter) or sparsely (≥1 puncture diameter) spaced. Abdominal ventrite V with or without additional, larger setigerous punctures intermixed with smaller punctures and with or without scattered micropunctures in the interstices, females in some species with median apical notch. Legs: femurs slightly curved and expanded toward apex. Meso and meta tibia straight to slightly curved and dilated toward apex. Tarsi with dark brown, black, or golden setae; males of some species with expanded pro- and mesotarsi with large, ventral, tomentose pads and/or slightly modified hind tibiae. Male terminalia: Aedeagus sclerotized dorsally, with small membranous field at base of parameres. Bipartite and without ancorae; basal portion membranous ventrally. Parameres fused dorsally at base with variable shape (e.g. tapered, truncate, or slightly curved inward before dilating again toward apex in dorsal view). In lateral view, parameres flattened toward apex, with or without slight curvature. Female Terminalia: Ovipositor with paraprocts longer than coxites 1–4. Coxite 4 bearing lateral gonostyli. Bursa copulatrix with or without additional 'accessory pouch' situated near to spermatheca and accessory glands, and in some species bearing sclerites.

Species included (eight): Biolus asperipennis (Mulsant and Rey), *B. analisetosus* (Koch), *B. brunoi* sp. nov., *B. denticosta* (Mulsant and Rey), *B. graafi* (Koch), *B. granulatus* (Fabricius), *B. omeri* (Koch), and *B. sauroides* (Koch).

Distribution: Namibia and South Africa (Fig. 9).

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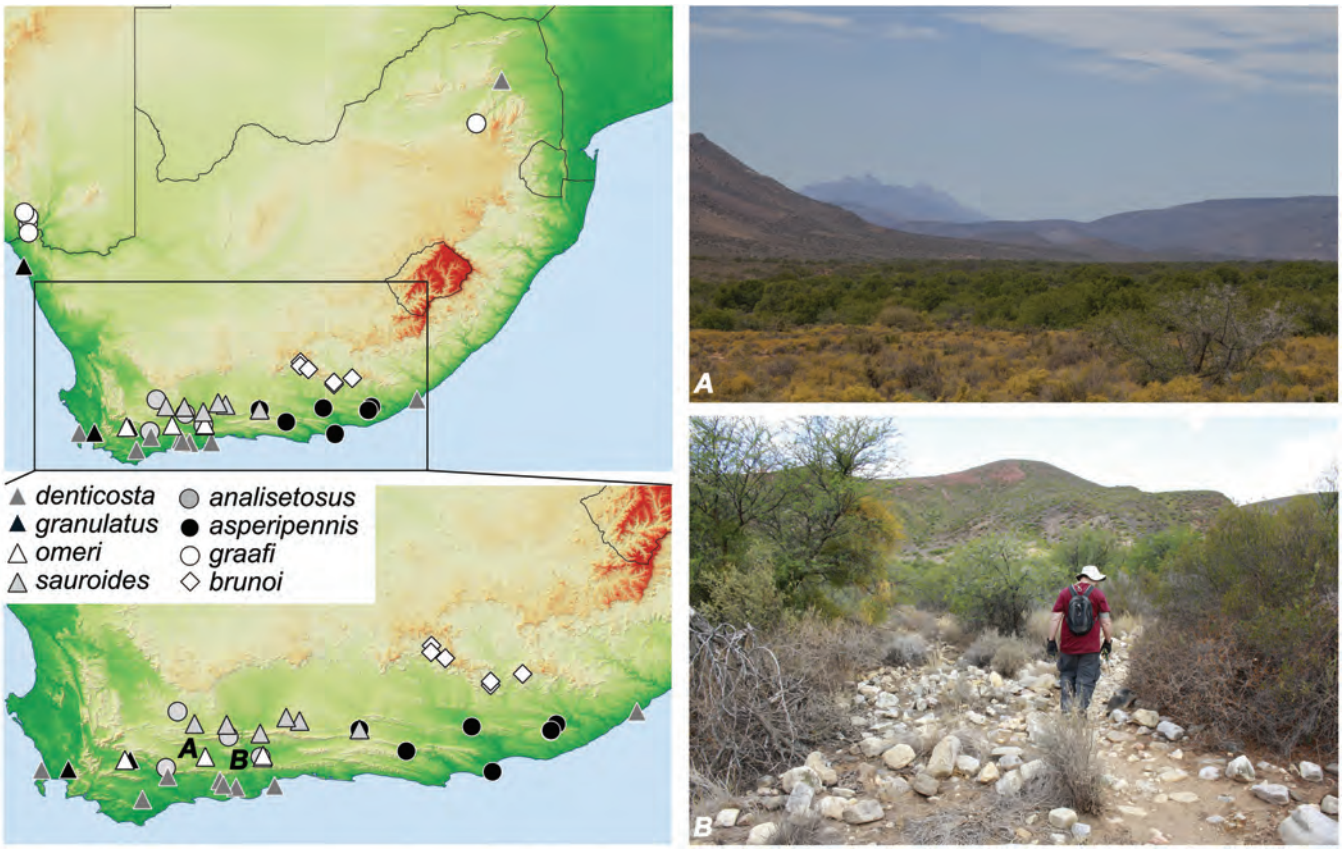


Figure 9. Distribution and sample habitats of *Biolus*. Sample photographs of habitat for *Biolus* species marked by A and B.

KEY TO THE SPECIES OF THE GENUS *BIOLUS*

1. Elytra costate (Fig. 2D), or elytral disc with distinct macrotubercles (Fig. 2G) or with shining bumps/callosities (Fig. 2A) 2
- Elytral disc lacking obvious macrotubercles or callosities (Fig. 2C) 7
2. Tarsal setae (excluding male pads on pro- and mesotarsi) black or dark 3
- Tarsal setae (excluding male pads on pro- and mesotarsi) golden 5
3. Elytra costate, with large punctures giving a lattice-like appearance (Fig. 2D) ..... *Biolus denticosta*
- Elytra not costate, without large punctures giving lattice-like appearance 4
4. Elytral tubercles not reaching base; tubercles subdentate. Male midtibia unmodified ..... *Biolus omeri*
- Elytral tubercles reaching base; tubercles large and knob-like. Male midtibia with apical spur-like projection ..... *Biolus sauroides*
5. Abdominal ventrite V without large, setigerous punctation or micropunctation (Fig. 6L). Bursa copulatrix with axe-shaped sclerite (Fig. 7F) ..... *Biolus granulatus*
- Abdominal ventrite V with large, setigerous punctation interspersed with smaller punctures (Fig. 6K); with or without micropunctation. Bursa copulatrix without sclerites, or sclerite differently shaped 6
6. Pronotum and abdominal ventrite V with micropunctation interspersed between larger punctation (Fig. 6L). Elytra and epipleura intensely microtuberculate (Fig. 2E). Males without expanded tarsi. Bursa copulatrix without sclerite ..... *Biolus graafi*
- Pronotum and abdominal ventrite V without micropunctation. Elytra and epipleura less intensely microtuberculate (Fig. 2A). Males with expanded pro- and mesotarsi. Bursa copulatrix with chevron-shaped sclerite (Fig. 7E) ..... *Biolus analisetosus*
7. Prosternal process with distinct produced protuberance. Pronotal punctation widely spaced (>1 puncture diameter). Male hind tibiae usually strongly modified. Tarsal setae golden in lateral view. Circumocular depression weak. Female abdominal ventrite V with notch (Fig. 6K) ..... *Biolus asperipennis*
- Prosternal process with at most weakly produced protuberance. Pronotal punctation closely spaced (≤1 puncture diameter). Male hinditibae at most weakly modified. Tarsal setae black or dark in lateral view. Circumocular depression present. Female abdominal ventrite V without notch ..... *Biolus brunoi* sp. nov.

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1. ***Biolus analisetosus*** (Koch) comb. nov.

(Figs 2A, 6C, 7E, 8A)

Eurynotus (*Biolus*) *analisetosus* Koch 1954a: 278.– Kamiński 2016: 235.

Diagnosis: Biolus analisetosus is most similar to other species with tubercles on the elytral disc (e.g. *B. granulatus*, *B. graafi*, *B. omeri*, *B denticosta*, and *B. sauroides*). External features to separate them include the colour of the tarsal setae (*B. analisetosus* = golden; *B. omeri*, *B. denticosta*, and *B. sauroides* = black or brown/dark), sculpturing of abdominal ventrite V (with two puncture types and apical median notch in females; simple and without female notch in *B. granulatus* and *B. omeri*), microtuberculation (more intense in *B. graafi*), elytral costae (present only in *B. denticosta*). Internally, the female bursa copulatrix of *B. analisetosus* has a sclerite situated near to the apex (all species except for *B. granulatus* lack sclerites) and an 'accessory' pouch (present in *B. analisetosus*, *B. graafi*, and *B. granulatus*; absent in, *B. omeri*, *B. sauroides*, *B. denticosta*, *B. asperipennis*). *Biolus graafi* can be differentiated by the surface sculpturing (much more intense microtuberculation than in *B. analisetosus*). Other species with bursa copulatrix sclerites (*Biolus granulatus*) can be further separated by the shape of the sclerite (chevron-shaped, versus axe-like in *B. granulatus*).

Redescription: Length 16–17mm, width 7–8mm. Head: Coarsely punctate, punctures closely spaced, separated by ≤1 puncture diameter to confluent. Mentum with apical notch. Eye with impressed sulcus situated around perimeter of dorsal lobe. Prothorax: Pronotum coarsely punctate, punctures closely spaced, separated by ≤1 puncture diameter to confluent. Hypomeron rugose, with large and shallow punctures. Pterothorax: Elytron not costate, with distinct tubercles or raised/shining callosities on disc. Epipleuron with few to no microtubercles. Abdomen: Punctate, punctures separated by ≥1 puncture diameter. Abdominal ventrite V punctures separated by ≤1 puncture diameter with larger, setigerous punctures intermixed. Females with median apical notch. Legs: Male and female legs unmodified. Tarsi with golden setae. Males: pro- and mesotarsi robust with large, ventral, tomentose pads. Male terminalia: Parameres strongly tapered and 'vase-shaped' (tapering apically with sharp subapical constriction, expanding slightly toward apex). Female terminalia: Bursa copulatrix with accessory pouch and chevron-shaped sclerite near spermathecal opening.

Type material examined: Holotype (TMNH): '7 weeks Poort C.P, 17-XI-1940 G van Son; Eurynotus (Biolus) analisetosus C. Koch det., 195 Koch; analisetosus Koch; Holotype No: 1843 Eurynotus analisetosus KOCH'.

(See Supporting Information, Appendix S1 for additional material examined.)

Distribution: South Africa (Fig. 9).

2. ***Biolus asperipennis*** (Mulsant and Rey) stat. res., comb. nov.

(Figs 2B, 6G, 8B)

Eurynotus asperipennis Mulsant and Rey, 1854a: 23.– Mulsant and Rey 1854b: 169; Lacordaire 1859: 239; Gebien 1938: 414; Koch 1954a: 280; 1954b: 2; Banaszkiewicz 2006: 63; Kamiński 2016: 235.

Diagnosis: Lacks sclerite in bursa copulatrix (present in *B. analisetosus* and *B. granulatus*). *Biolus asperipennis* has two puncture types on ventrite V (single type in *B. omeri* and *B. granulatus*), and golden setae on the tarsi (dark/black in *B. omeri*, *B. sauroides*, and *B. brunoi*). Without close inspection, *B. brunoi* (length 15–18 mm; width 7.5–10 mm) specimens may appear similar to smaller specimens of *B. asperipennis* (length 19–22 mm; width 8–11 mm); however, *B. asperipennis* has golden tarsal setae (black or dark in *B. brunoi*), a weaker circumocular depression, the pronotal process is more pronounced, and the male tibiae are also at most only slightly modified in *B. brunoi*, while in *B. asperipennis* they are more strongly curved. See the diagnosis of *B. brunoi* below for more details.

Redescription: Length 19–22mm, width 8–11mm. Head: Punctate; punctures closely spaced, separated by ≤1 puncture diameter. Mentum without apical notch. Eye with weakly impressed sulcus situated around perimeter of dorsal lobe. Prothorax: Pronotum punctate, punctures separated by ≥1 puncture diameter. Hypomeron lightly sculptured/wrinkled with small punctation and microtuberculation. Pterothorax: Elytra not costate, without macrotubercles on disc. Elytral intervals with or without microtuberculation. Epipleuron with many small, faint microtubercles. Abdomen: Finely punctate, punctures separated by >1 puncture diameter. Abdominal ventrite V punctures separated by ≥ 1 puncture diameter with larger, setigerous punctures intermixed, females with median, apical notch. Legs: Male hind tibiae slightly flattened/twisted, appearing bent. Female legs unmodified. Tarsi with golden setae. Males: pro/meso tarsi robust with large, ventral, tomentose pads. Male terminalia: Parameres 'bottle-shaped', strongly tapered and truncate apically. Female terminalia: Bursa copulatrix without accessory pouch or sclerites.

Material examined: Lectotype, here designated (MNHN): 'Eurynotus? sp. cap.?; blue circle label 'Eurynotus asperipennis Muls cap. b. sp.?' also with a red label with handwriting: 'Type'.

(See Appendix S1 for additional material examined.)

Note: As the original description lacks information defining the number or specificity of specimens used, one from the presumed syntype series is here designated as the lectotype to fix the taxonomic status of the species and genus (Fig. 2B).

Distribution: South Africa (Fig. 9).

3. ***Biolus brunoi*** sp. nov.

(Figs 1B, 2C, 6J, 7C, 8C)

urn:lsid:zoobank.org:act:57A85549-53E4-4EA1-ADF2-DDE094DD4D91.

Diagnosis: This taxon is most similar to some specimens of *Biolus asperipennis*. In addition to characteristics provided above, *B. brunoi* can be separated from other *Biolus* species via: tarsal setae dark/black rather than golden; tubercles absent on elytral disc; abdominal ventrite V with large setigerous punctures; head

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punctation coarse and closely spaced (separated by ≤1 puncture diameter). Additionally, *B. brunoi* aedeagal parameres are distinctly pointed (truncate or apically blunted or rounded in all other species of *Biolus* and *Eurynotus*).

Description: Length 15–18 mm; width 7.5–10 mm. Head: Coarsely punctate, punctures closely spaced, separated by ≤1 puncture diameter. Mentum without apical notch. Eye with impressed sulcus situated around perimeter of dorsal lobe. Prothorax: Pronotum coarsely punctate, punctures separated by ≤1 puncture diameter. Hypomeron shallowly and coarsely punctate and lightly sculptured/wrinkled. Pterothorax: Elytron not costate, without tubercles on disc. Elytral interval X terminates between hind coxae and elytra base. Epipleuron narrower than width of elytral intervals 9 + 10. Elytral intervals not obscured by epipleuron in ventral view. Abdomen: Punctate. Abdominal ventrite V coarsely punctate, punctures separated by ~1 puncture diameter with larger, setigerous punctures intermixed. Females without median apical notch. Legs: Male hind tibiae very slightly flattened/twisted, appearing bent. Female legs unmodified. Tarsi with black or dark setae. Males: pro/meso tarsi enlarged, with ventral, tomentose pads. Male terminalia: Parameres strongly tapered and pointed apically. Female terminalia: Bursa copulatrix sac-like and without sclerites, spermatheca thick and coiled, accessory pouch absent.

Material examined: Holotype (TMNH): S. Afr.; E Cape; 1070m 30km NE Somerset East 32.31 S—25.34 E/ 30.11.2007; E-Y:3767 general collecting leg. Ruth Müller. Paratypes (*N* = 17): TMNH: 'S. Afr., Cape-Karroo Woodcliff farm 31.57 S - 24.38 E; 13.9.1983;E-Y:2004 singled day leg. Penrith (2 specimens)', 'S.Afr.; E Cape 1450m 50km NE Graaf Reinet 32.09 S - 24.51 E; 27.11.2007.E-Y: 3766 under stones leg. Ruth Müller (5 specimens)', 'S. Afr.; E Cape; 1070m 30km NE Somerset East 32.31 S - 25.34 E/ 30.11.2007; E-Y:3767 general collecting leg. Ruth Müller (4 specimens)', 'S.Afr., E.Cape Prov. Swaershoek Pass 32.17 S - 25.32 E, 10.10.1984; E-Y:2142 ground and vegetation leg. R. Müller', 'S.Afr.;E Cape; 1070m 30km N Bedford 32.24 S - 26.05 E, 12.12.2007; E-Y 3768 general collecting leg. Ruth Müller (3 specimens)'. MNHN: 'Cap. B. Esp.'.

Etymology: Named after Bruno, dear friend of Ruth Müller (Pretoria, South Africa).

Distribution: South Africa (Fig. 9).

4. ***Biolus denticosta*** (Mulsant and Rey) comb. nov.

(Figs 2D, 6D, F, 8D)

Eurynotus denticosta Mulsant and Rey, 1854a: 29.– Mulsant and Rey 1854b: 173; Gebien 1938: 414; Koch 1954a: 276; 1954b: 2; 1955: 420; Banaszkiewicz 2006: 63; Kamiński 2016: 237.

Diagnosis: Biolus denticosta is arguably the most straightforward to diagnose species (along with *B. sauroides*). The structure of the elytra is unique within the genus (with extremely large punctation and costae giving the appearance of a lattice-like structure). A redescription is provided here along with our morphological analyses to help support this species' inclusion in *Biolus*, outline differences with other, more distantly related but morphologically similar taxa (e.g. genus *Zadenos* Laporte from subtribe Melambiina; see: Kamiński 2015), and provide a more detailed, up-to-date description.

Redescription: Length 9–12 mm; width 3–5 mm. Head: Intensely, coarsely punctate, punctures closely spaced, separated by ≤1 puncture diameter to confluent. Mentum with apical notch. Eye with strongly impressed sulcus situated around perimeter of dorsal lobe. Prothorax: Pronotum coarsely punctate, punctures separated by ≤1 puncture diameter to confluent. Hypomeron rugose, with large and shallow punctures. Pterothorax: Elytron costate, with macrotubercles on disc on intervals between costae. Without microtuberculation on disc or epipleura. Abdomen: Punctate. Abdominal ventrite V coarsely punctate, punctures separated by ≥1 puncture diameter without larger, setigerous punctures. Faint marginal groove on apex. Females with median apical notch. Legs: Male midtibia with large spur-like projection at apex. Tarsi unmodified in males and females. Tarsal setae dark or black. Male terminalia: Parameres weakly tapered and broad, rounded apically. Female terminalia: Bursa copulatrix without sclerites or accessory pouch.

Material examined: Lectotype, here designated (HNHM): 'C. B. Esp. Coll. R. Oberthür ex. Coll. Deyrolle/ Paratypus 1854 Eurynotus denticosta Mulsant/ Red LECTOTYPE label' Note: As the original description lacks information defining the number or specificity of specimens used, a specimen from the presumed syntype series is here designated as a lectotype to fix the taxonomic status of the species. Paralectotype (HNHM): Same labels as Lectotype, with additional yellow 'PARALECTOTYPE' label.

(See Supporting Information, Appendix S1 for additional material examined.)

Distribution: South Africa (Fig. 9).

5. ***Biolus graafi*** (Koch) comb. nov.

(Figs 2E, 6K, 8E)

Eurynotus (*Biolus*) *graafi* Koch 1954a: 279.– Kamiński 2016: 235.

Diagnosis: Koch (1954a) noted this species size in his original description, crediting *B. graafi* with the status as the largest species. With the reinstatement of *B. asperipennis* (length 19–22 mm; width 8–11 mm), *B. graafi* can no longer be clearly separated by size. However, *B. graafi* can be separated from other species by the nature of the punctation of the head and pronotum (coarse and confluent); and from similar species using the sculpturing of the elytra and epipleura (both with intense microtuberculation). Additionally, the pronotum and abdominal ventrite V bear small, micropunctures; absent in other species.

Redescription: Length 17–20 mm; width 10–12 mm. Head: Coarsely punctate, punctures confluent. Mentum without apical notch. Eye with impressed sulcus situated around perimeter of dorsal lobe. Prothorax: Pronotum punctures closely spaced to confluent, with smaller interstitial micropunctures.

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Hypomeron rugose, with large and shallow punctures. Pterothorax: Elytron not costate, with macrotubercles on disc with microtubercles distributed between. Epipleura with many, large microtubercles along entire length. Abdomen: Coarsely punctate, with small interstitial micropunctures. Abdominal ventrite V punctures closely spaced by ≤1 puncture diameter with larger, setigerous punctures and smaller micropunctures intermixed. Females with median apical notch. Legs: Male and Female legs unmodified. Tarsi with golden setae. Males: pro/meso tarsi without large, ventral, tomentose pads. Male terminalia: Parameres broadly tapered and rounded apically. Female terminalia: Bursa copulatrix with accessory pouch and without sclerites.

Material examined: Holotype (TMNH): 'Kuboos?chtereveld.1949.C.Koch; graafi Koc; Eurynotus (Biolus) Graafi Koch C. Koch det., 195?; Holotype No: 1845 Eurynotus graafi KOCH'.
(See Supporting Information, Appendix S1 for additional material examined.)

Distribution: Namibia and South Africa (Fig. 9).

6. ***Biolus granulatus*** (Fabricius) comb. nov.

(Figs 1A, 2F, I, 5A, 7F, 8F)

Helops granulatus Fabricius 1787: 214.

Blaps granulata (Fabricius 1787).– Fabricius 1792: 107.

Eurynotus granulatus (Fabricius 1787).– Gebien 1906: 230, 1938: 414; Koch 1954a: 280; 1954b: 2; 1956: 25; Banaszkiewicz 2006: 63; Kamiński 2016: 235.

=*Eurynotus norrisi* Mulsant and Rey 1854a: 27 syn. nov.– Mulsant and Rey 1854b: 171; Lacordaire 1859: 239; Gebien 1938: 414; Koch 1954a: 277; 1954b: 2; Kamiński 2016: 235.

Diagnosis: Can be difficult to differentiate from other species, but is most similar to *B. omeri* (e.g. both have simple punctation of abdominal ventrite V, and are similar in size, with tubercles/raised callosities on elytral disc). The two can be differentiated based on setation of the tarsi (*B. norrisi* golden; *B. omeri* black/dark brown), the sclerite within the bursa copulatrix (present in *B. granulatus*; absent in *B. omeri)*, and characterization of the dorsal surface (*B. norrisi* blunter/shorter and more crowded tubercles; while *B. omeri* has sharper/taller and more widely spaced tuberculation with a slightly more lustrous surface). Insofar as other species are concerned, the abdominal ventrite V punctation (simple) separates it from *B. analisetosus*, *B. asperipennis*, *B. graafi*, and *B. sauroides* (with two or more types of punctation). The tubercles/raised callosities present on the elytral disc further separate it from *B. asperipennis* (lacking discal tubercles). The presence of a sclerite in the bursa copulatrix separates this species from all but *B. analisetosus* (which, in contrast to *B. granulatus*' axe-shaped sclerite, has a flatter, chevron-shaped sclerite).

Redescription: Length 14–16 mm; width 7–9 mm. Head: Coarsely punctate, punctures closely spaced, separated by ≤1 puncture diameter to confluent. Mentum with apical notch. Eye with impressed sulcus around margin. Prothorax: Pronotum coarsely punctate, punctures separated by ≤1 puncture diameter to confluent. Hypomeron rugose, with large and shallow punctures. Pterothorax: Elytron not costate, with macrotubercles and with distinct or faint microtuberculation in interstices on disc. At most, a few widely spaced, small microtubercles in basal region of epipleura. Abdomen: Punctate. Abdominal ventrite V punctures separated by ≥1 puncture diameter without larger, setigerous punctures intermixed. Females without median apical notch. Legs: Male and Female legs unmodified. Tarsi with golden setae. Males: pro/meso tarsi robust with large, ventral, tomentose pads. Male terminalia: Parameres weakly tapering with tips sharply tapering and directed medially. Female terminalia: Bursa copulatrix with accessory pouch and axe-shaped sclerite near spermathecal opening.

Material examined: Helops granulatus: Lectotype, here designated (ZMUK): QR code label 'ZMUKFabricius 004512'. *Note:* As the original descriptions lack information defining the number or specificity of specimens used, a specimen from the presumed syntype series is here designated as lectotype to fix the taxonomic status of the species.

Eurynotus norrisi Lectotype (MNHN): 'Eurynotus norrisii buq? spinola in litt. cap.bon.sp./ small blue circular label: Eurynotus norrisi Mls Cap. B. Sp. 2 T?/ Type Mulsant/ Norrisii/ Red label: Type'.
(See Supporting Information, Appendix S1 for additional material examined.)

Note: As the original descriptions lack information defining the number or specificity of specimens used, a specimen from the presumed syntype series is here designated as lectotype to fix the taxonomic status of the species.

Distribution: South Africa (Fig. 9).

7. ***Biolus omeri*** (Koch) comb. nov.

(Figs 2G, 5C, 7B, 8G)

Eurynotus (*Biolus*) *omeri* Koch 1954a: 277.– Kamiński 2016: 235.

Diagnosis: Like *B. granulatus*, separating this species from others with similar characteristics is best done through a suite of characters. *Biolus omeri* is most similar to *B. granulatus*. In fact, specimens identified in the past as the here synonymized *Eurynotus* (*Biolus*) *norrisi* are at first glance difficult to differentiate. The most glaring differences and distinctive traits of *B. omeri* are the tarsal setae (black), the sharp well-defined tuberculation of the elytra, and lack of additional puncture types on abdominal ventrite V. See diagnoses of other species for additional details.

Redescription: Length 14–18 mm; width 8–9 mm. Head: Coarsely punctate, punctures closely spaced, separated by ≤1 puncture diameter to confluent. Mentum with apical notch. Eye with impressed sulcus around margin. Prothorax: Pronotum coarsely punctate, punctures separated by ≤1 puncture diameter to confluent. Hypomeron rugose, with large and shallow punctures. Pterothorax: Elytron not costate, with macrotubercles on disc. Microtubercles absent from elytral

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disc and epipleura. Abdomen: Punctate. Abdominal ventrite V punctures separated by ≥1 puncture diameter without larger, setigerous punctures intermixed. Females without median apical notch. Legs: Male and Female legs unmodified. Tarsi with black setae. Males: Pro/meso tarsi robust with large, ventral, tomentose pads. Male terminalia: Parameres weakly tapering with tips sharply tapering and directed medially. Female terminalia: Bursa copulatrix without sclerites or accessory pouch.

Material examined: Holotype (TMNH): 'Kuouland(?) Berg Dr. Brauns. Uniondale Cape Colony; Eurynotus norrisi ♂ Muls; Eurynotus (Biolus) omeri C. Koch dete.,195? Koch; omeri Koch; Holotype No. 1840 Eurynotus omeri KOCH'.

(See Supporting Information, Appendix S1 for additional material examined.)

Distribution: South Africa (Fig. 9).

8. *Biolus sauroides* (Koch) comb. nov.

(Figs 2H, 6A, I, 8H)

Eurynotus (*Biolus*) *sauroides* Koch 1955: 420.– Kamiński 2016: 235.

Diagnosis: Biolus sauroides is sharply separable from all other species by the extremely coarse sculpturing dorsally and ventrally (large, knobby tubercles extending to the disc and base of the elytra and large closely spaced punctures on abdominal underside). Koch's (1955) description outlines most of the species morphology sufficiently. Here we provide only additional characters we found in a description below to supplement Koch's description.

Supplementary description (see: Koch 1955): Abdomen: Abdominal ventrite V with setigerous punctures. Females without median apical notch. Legs: Male midtibia with small spurical projection at apex. Male terminalia: Parameres weakly tapering with tips sharply tapering and directed medially. Female Terminalia: Bursa copulatrix without sclerites or accessory pouch.

Material examined: Holotype (TMNH): 'Garies Namaqualand; Museum Staff June 1930; sauroides Koch; Paratypus Eurynotus sauroides C. Koch sp. n.'.

(See Supporting Information, Appendix S1 for additional material examined.)

Distribution: South Africa (Fig. 9).

II. Genus *Eurynotus* Kirby

(Fig. 3A–J)

Eurynotus Kirby, 1819: 418.– Mulsant and Rey 1854a: 13; 1854b: 156; Lacordaire 1859: 238; Gebien 1938: 414; Koch 1954a: 275; 1954b: 2; Koch 1955: 420; 1956: 27; Iwan 2002: 6, 2004: 739; Banaszkiewicz 2006: 65; Ahn and Frank 2015: 529; Kamiński 2016: 234; Bouchard *et al.* 2021: 184; Lumen and Kamiński 2023: 2.

Type species: Eurynotus muricatus Kirby, 1819; designated by monotypy.

Redescription: Length 8–20 mm; width 4.5–8.25 mm. Shining to dull; coloured tenebrous; dark brown to black. Head: Coarsely to finely punctate, punctures widely (≥1 puncture diameter) to closely (≤1 puncture diameter) spaced. Epistoma with well-defined median notch. Mentum with enlarged, ventrally projecting middle portion with apical, median notch present or absent; lateral wings reduced/slightly hidden. Gula with stridulatory file. Eyes constricted in middle and reniform, with impressed sulcus situated around perimeter of dorsal lobe. Antennae 11 segmented, terminal segments forming weak club. Prothorax: scutellum small and transversely triangular. Pronotum strongly bisinuate with basal angles pointed posteriorly; with or without microtuberculation or micropunctation. Lateral depression or flattening along anterior margin weak, strong, or absent. Hypomeron nearly smooth to finely sculptured or wrinkled; with shallow or deep, fine to coarse punctation. Prosternal process rounded at apex, projecting toward midcoxae in lateral view. Pterothorax: Elytral striae deep or shallow with similarly deep or shallow punctation. Intervals punctate, with or without microtuberculation; macrotubercles present on apical declivity in most species (no tuberculation in *E. alticola*). Elytral intervals visible or obscured by epipleuron in ventral view; humeri without large well-defined knob-like tubercles, at most with slightly raised, weak, costae-like structures. Interval X terminating between hind coxae and elytra apex or base. Epipleura with or without microtubercles, broad basally, narrowing slightly toward apex, wider, subequal, or distinctly narrower than elytral intervals 9 + 10. Apterous. Abdomen: Finely to coarsely punctate with punctures closely or sparsely spaced. Abdominal ventrite V with or without additional, larger setigerous punctures intermixed with smaller punctures, females in some species with median apical notch. Legs: Femurs slightly curved and expanded toward apex. Meso and meta tibia straight to slightly curved and dilated toward apex. Tarsi with dark brown, black, or golden setae; males (and rarely females) of some species with expanded pro/meso tarsi with large, ventral, tomentose pads. Hind tibia in males of some species with setose excavations. Male terminalia: Tegmen bipartite and without ancorae; basal portion membranous ventrally; dorsally with small, triangular membranous field at base of apical portion. Parameres fused dorsally at base with variable shape (i.e. tapered, truncate, parameres rounded or parallel-sided, or slightly curved inward before dilating again toward apex in dorsal view). In lateral view, parameres flattened toward apex, with or without slight curvature. Female Terminalia: Bursa copulatrix with or without additional 'accessory pouch' or accessory gland situated near to spermatheca; with or without sclerites (present in *E. asperatus*).

Species included (nine): Eurynotus alticola Koch, *E. asperatus* Mulsant and Rey, *E. barbosai* Koch, *E. capensis* (Fabricius), *E. constrictus* Koch, *E. graniderma* Koch, *E. privisolum* sp.nov., *E. sulcimargo* Koch, *E. thermarum* Koch.

Distribution: Mozambique and South Africa (Fig. 10).

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KEY TO THE SPECIES OF THE GENUS *EURYNOTUS*

1. Tuberculation completely absent on elytra (Fig. 3A) ..... *Eurynotus alticola*
- Elytral tuberculation present on apical declivity 2
2. Tarsal setae in lateral view golden (Fig. 3E) 3
- Tarsal setae in lateral view black or dark (Fig. 2G) 5
3. Larger (13.75–20 mm). Abdominal ventrite V sinuate laterally. Male midtibia without setose patch ..... *Eurynotus capensis*
- Smaller (8–10 mm). Abdominal ventrite V without lateral sinuation. Male midtibia with setose patch (Fig. 3G) 4
4. Elytral cuticle shining and smooth between macrotubercles. Elytra without microtubercles ..... *Eurynotus barbosai*
- Elytral cuticle opaque with microtexturing between macrotubercles. Elytra with microtubercles ..... *Eurynotus graniderma*
5. Abdominal ventrite V punctation including larger, setigerous punctures (Fig. 6K) ..... *Eurynotus sulcimargo*
- Abdominal ventrite V without larger setigerous punctures, micropunctate or not (Fig. 6L) 6
6. Pronotum with deep lateral explanation/groove (Fig. 3F) ..... *Eurynotus constrictus*
- Pronotum with weak lateral explanation or with only narrow emargination 7
7. Pronotum smooth and shining between punctures; elytra smooth and shining between macrotuberculation. Micropunctation present on pronotum and abdominal ventrite V (Figs 3H, 6L) ..... *Eurynotus privisolum* sp. nov.
- Pronotum opaque; elytra opaque and/or microtuberculate between macrotubercles. Micropunctures absent from pronotum and abdominal ventrite V 8
8. Pronotum and elytra microtuberculate ..... *Eurynotus thermarum*
- Pronotum and elytra lacking microtubercles ..... *Eurynotus asperatus*

1. *Eurynotus alticola* Koch (Fig. 3A)

Eurynotus (*Eurynotus*) *alticola* Koch 1955: 424.– Kamiński 2016: 236.

Diagnosis: While no additional specimens outside of Koch's material were found as of this revision, we feel that Koch's (1955) description is sufficient. Here we outline important characteristics from Koch's description/diagnosis and provide some additional characters to supplement his description. *Eurynotus alticola* most resembles Koch's (1955) *Eurynotus rudebecki* (synonymized here with *E. asperatus*). Upon the investigation presented here, an affinity to *E. capensis* is also noted. *Eurynotus alticola* is differentiated by the presence of larger, setigerous punctures on abdominal ventrite V (absent in *E. asperatus*) and dark or black setae on the tarsi (golden in *E. capensis*). Further, *E. capensis* has starkly modified hind tibiae in the males, and a modification to the lateral edges of abdominal ventrite V in both sexes (apparently absent in both *E. asperatus* and *E. alticola*). Finally, *E. alticola* is the only species devoid of tubercles on the elytra (including the apical declivity).

Supplementary description (see: Koch 1955): Head: Punctures widely spaced, separated by ≤1 puncture diameter. Mentum without apical notch. Eye with impressed sulcus around margin. Prothorax: Pronotum finely punctate, punctures separated by ≥1 puncture diameter. Hypomeron mostly smooth (at most with fine wrinkling), finely and shallowly punctate. Pterothorax: Elytra without tuberculation. Elytral interval X terminating between hind coxae and apex of elytra. Epipleuron subequal to width of elytral intervals 9 + 10. Elytral intervals obscured by epipleuron in ventral view. Abdomen: Punctate. Abdominal ventrite V finely punctate, punctures separated by ≥1 puncture diameter with larger, setigerous punctures intermixed; with margination running along distal edge. Legs: Male and female legs unmodified. Tarsi with dark or black setae. Males: Pro/meso tarsi robust with large, ventral, tomentose pads. Terminalia: No specimens were available for dissection (however, for ventral diagram of male aedeagus, see: Koch 1955: fig. 3).

Material examined: Lectotype, here designated (TMNH): '7 Weeks Poort Berg Ladismith, Cape. 5500–7000 ft.; Paratypus EURYNOTUS alticola sp.n. C.Koch; Paratype No:1246 Eurynotus alticola KOCH'.

Note: As the original description lacks information defining a specific specimen as the name-bearing individual, one from the presumed syntype series is here designated as the lectotype to fix the taxonomic status of the species. No additional specimens aside from the type designated here were available for examination.

Distribution: South Africa (Fig. 10).

2. *Eurynotus asperatus* Mulsant and Rey (Figs 3B, C, 6B, 7G, 8I)

Eurynotus (*Eurynotus*) *asperatus* Mulsant and Rey, 1854a: 23. Mulsant and Rey 1854b: 167; Lacordaire 1859: 239; Gebien 1938: 414; Koch 1954a: 283; 1954b: 2; Kamiński 2016: 236.
=*Eurynotus* (*Eurynotus*) *rudebecki* Koch 1955: 423 syn. nov.– Kamiński 2016: 237.

Note: The description provided below supplements Koch's (1954a, 1955) description of *E. rudebecki* to include new characters and variation observed in this revision.

Diagnosis: One of the most commonly collected and identified species in collections observed in this study (alongside *Eurynotus capensis*). Can be separated from *E. capensis* based on size (*E. capensis*: length 14–20mm, width 7–10mm; *E. asperatus* length 9–13.25mm, width 4.5–6.5mm), and characteristics of the males (modified hind tibiae in *E. capensis*) and females (*E. asperatus* bursa copulatrix with sclerites; *E. capensis* with characteristic

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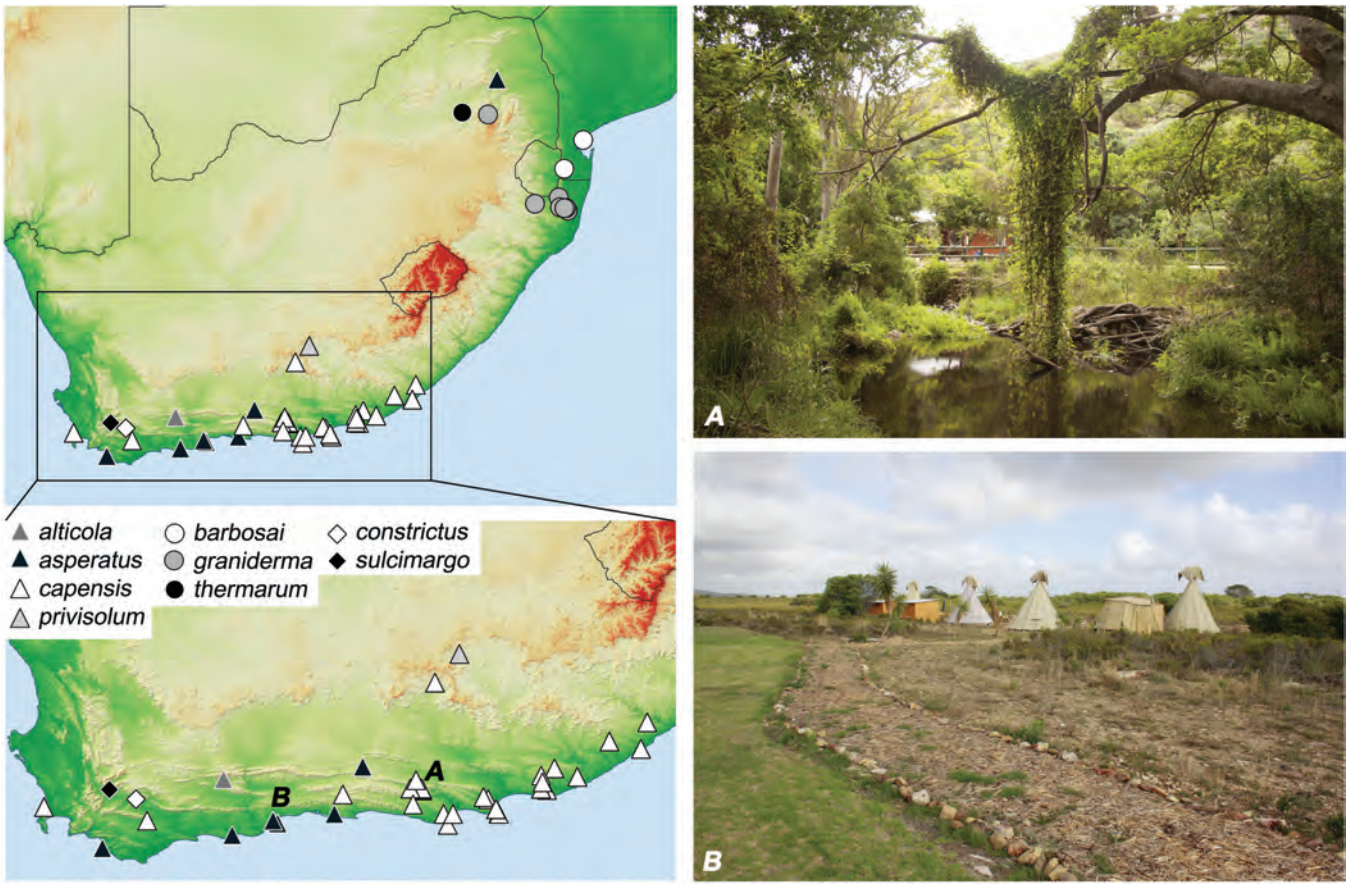


Figure 10. Distribution and selected habits of representatives of the genus *Eurynotus*. Sample photographs of habitat for *Eurynotus* species marked by A and B.

spermatheca and constricted, bilobed bursa copulatrix). From other *Eurynotus*, *E. asperatus* can also be separated by size: *E. graniderma* and *E. barbosai* are smaller (length 8–9.5 mm; width 4.75–5.5 mm); however, *E. thermarum* (while generally smaller) specimens may be similar in size in large specimens (which can then be differentiated based on the width of the epipleura and presence of microtuberculation on the pronotum and elytra). The presence of additional, larger setigerous punctures on abdominal ventrite V (absent in *E. asperatus*) can also be diagnostic. *Eurynotus privisolum*, while similar at first glance, can be differentiated based on the sculpture of the pronotum and head (close, coarse punctation; versus *E. asperatus* with finer, more widely separated punctation). Additional separation of species is possible using the lustre of the cuticle (dull or opaque in *E. asperatus* versus the shinier *E. privisolum*, *E. sulcimargo*, and *E. barbosai*).

Description (to supplement Koch 1954a, 1955): Dorsal surface dull with microgranulation. **Head:** Punctures spaced by ≥1 puncture diameter. Mentum without apical notch. Eye with impressed sulcus around margin. Prothorax: Pronotum finely punctate, punctures separated by >1 puncture diameter. Hypomeron nearly smooth, at most with fine and shallow punctation and light wrinkling. Pterothorax: Elytral interval X terminating between hind coxae and apex of elytra. Epipleuron subequal to width of elytral intervals 9 + 10. Elytral intervals obscured by epipleuron in ventral view. Abdomen: Punctate. Abdominal ventrite V finely punctate, punctures separated by ≥1 puncture diameter without larger, setigerous punctures intermixed. Females without median apical notch. Legs: Male and female legs unmodified. Tarsi with black or dark setae. Males: pro/meso tarsi greatly expanded, with large, ventral, tomentose pads. Male terminalia: Parameres rounded and slightly tapering apically, rounded at apex. Female terminalia: Bursa copulatrix sac-like and with paired sclerites, spermatheca thick and coiled, accessory pouch absent.

Material examined: Eurynotus asperatus: Lectotype, here designated (MNHN): Blue circle label 'Eurynotus asperatus Cap. B. Sp.?; type Mulsant; asperatus' red label with handwritten 'Type'. *Note:* As the original descriptions lack information defining the number or specificity of specimens used, a representative from the presumed syntype series is here designated as lectotype to fix the taxonomic status of the species and genus.

Eurynotus rudebecki Lectotype, here designated (TMNH): Swedish South Africa Expedition 1950–1951 Brunck-Rudebeck/ S. Afr. Cape Prov Mosselbaai. 8–9.1.51. No. 127/ Holotype No: 123? Eurynotus rudebecki KOCH/ rudebecki koch.

(See Supporting Information, Appendix S1 for additional material examined.)

Note: As the original descriptions specify the number of specimens used to over 100, a representative from the syntype series is here designated as lectotype to fix the taxonomic status of the species and genus.

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Distribution: South Africa (Fig. 10).

3. *Eurynotus barbosai* Koch

(Figs 3D, 7A, 8J)

Eurynotus (*Eurynotus*) *barbosai* Koch 1954a: 284.– Koch 1956: 27; Kamiński 2016: 236.

Diagnosis: Eurynotus barbosai is most similar to *E. thermarum* and *E. graniderma*. All three species are differentiable from other congeners by size as they are the smallest (length 8–10 mm; width 4.75–7.5 mm) group within *Eurynotus*. Additionally, these species (along with *E. capensis*) possess distinct modifications to the male mid- and/or hindlegs (small setose excavations on the tibiae). *Eurynotus barbosai* is sharply separable from the most similar species (*E. thermarum* and *E. graniderma*) by the cuticular surface (shining and relatively smooth in *E. barbosai* versus dull and microtuberculated in the other two) and with additional micropunctation in the interstices between punctures (*E. thermarum* and *E. graniderma* instead with microtuberculation, or without additional specific interstitial structures, respectively). Additionally, while all three species are localized around north–north-eastern South Africa, *Eurynotus barbosai* is, as of this revision, the only species with a distribution east of Eswatini and into Mozambique.

Redescription: Length 9–10mm 5–5.5 mm. Head: Punctures separated by ≥1 puncture diameter. Mentum without apical notch. Eye with deeply impressed sulcus around margin. Prothorax: Pronotum smooth, shiny, and finely punctate; larger punctures separated by ≥1 puncture diameter with micropunctures in interstices. Hypomeron shallowly and coarsely punctate; lightly sculptured/wrinkled. Pterothorax: Elytral interval X terminating between hind coxae and elytra apex. Epipleuron wider than width of elytral intervals 9 + 10. Elytral intervals obscured by epipleuron in ventral view. Dorsally shining and without microtuberculation. Abdomen: Punctate. Abdominal ventrite V finely punctate, punctures separated by ≥1 puncture diameter without larger, setigerous punctures intermixed and without micropunctation. Females without median apical notch. Legs: Male mid- and hindlegs with setose patch or groove on tibiae. Female legs unmodified. Tarsi with golden setae. Males: pro/meso tarsi expanded with large, ventral, tomentose pads. Male terminalia: Parameres broad and parallel, truncate at apex with small divot made by medially inflexed parameres. Female terminalia: Bursa copulatrix sac-like and without sclerites, spermatheca thick and coiled, accessory gland and accessory pouch present.

Material examined: Holotype (TMNH): 'Lour, Marques Jan. Rev. H.A, Junod; 3864; Eurynotus sp ign.; Holotype No: 1849 Eurynotus barbosai KOCH'.

Additional Material: TMNH: 'Marracuene', 'SOUTH AFRICA, NATAL Ndumu Game Reserve 26.54S 32.15E, 05–07.xi.1984. R. Oberprieler'.

Distribution: Mozambique and South Africa (Fig. 10).

4. *Eurynotus capensis* (Fabricius)

(Figs 3E, 5E, 7D, 8K)

Helops capensis Fabricius 1794: 440.– Fabricius 1801: 161; Thunberg 1827: 16.

Eurynotus capensis (Fabricius 1794).– Gebien 1938: 414; Koch 1954a: 283; 1954b: 2; 1956: 26; Tschinkel 1978: 315; Iwan 2002: 12; Banaszkiewicz 2006: 63; Kamiński 2016: 236; Bouchard *et al.* 2021: 184.

=*Eurynotus muricatus* Kirby 1819: 419.– Mulsant and Rey, 1854a: 21, 1854b: 165; Lacordaire 1859: 239; Gebien 1938: 414 (syn.); Koch 1954a: 2831954b: 2.

=*Tenebrio caffer* Thunberg 1821: 163.– Ferrer 2009: 118 (syn.).

Diagnosis: Eurynotus capensis is one of the most widely distributed (and well-identified) species in collections. Male specimens are particularly easily identified by the modifications to the hindlegs (tibia with large, setose patches or grooves). Additionally, both males and females share a sinuation of abdominal ventrite V, which is absent in all other species. The closest species morphologically might be *E. thermarum*, *E. barbosai*, and *E. graniderma* (Fig. 3D, G, J); however, all three are sharply separable by size (length 8–13.5mm; width 4.75–7.5mm vs. *E. capensis* length 13.75–20 mm; width 7–10 mm) and males possess an additional patch of setae on the midtibia (absent in *E. capensis*). Furthermore, *E. thermarum* has a more strongly narrowing epipleura and simple punctation of abdominal ventrite V (wider and with additional large setigerous punctures in *E. capensis*, respectively). *Eurynotus graniderma* and *E. thermarum* both additionally have additional microtuberculation of the elytra and/or pronotum.

Redescription: Length 13.75–20 mm; width 7–10 mm. Head: Finely punctate, punctures spaced closely (≤1 puncture diameter) to moderately (~1 puncture diameter). Mentum with apical notch. Eye with weakly impressed circumocular depression. Prothorax: Pronotum finely punctate, punctures separated by ≥1 puncture diameter. Hypomeron nearly smooth, shallowly and finely punctate with, at most, light wrinkling. Pterothorax: Elytral interval X terminates between hind coxae and elytral apex. Epipleuron subequal to elytral intervals 9 + 10. Elytral intervals not obscured by epipleuron in ventral view. Abdomen: Punctate. Abdominal ventrite V finely punctate, punctures separated by ≥1 puncture diameter with larger, setigerous punctures intermixed. Females with median apical notch. Legs: Male hind tibiae modified with large tomentose patch. Male pro- and mesotarsi robust with large, ventral, tomentose pads. Females with fore/meso tarsi dilated or not. With wide, uninterrupted pads on undersides of pro- and mesotarsus when dilated. Undilated female tarsi with glabrous 'lane' running between two rows of setae. Male terminalia: Parameres weakly tapered and rounded apically. Female terminalia: Bursa copulatrix conspicuously constricted in the middle (bilobate) and without sclerites, sac-shaped spermatheca with finger-like projections.

Material examined: Lectotype, here designated (ZMUK): 'Cap: bon: sp Paykull Mus: S:?t; L Helops capensis. F.; red label: TYPE; green square label; ZMUC 00508792; QR code label: 001340'.

(See Supporting Information, Appendix S1 for additional material examined.)

Note: As the original descriptions lack information defining the number or specificity of specimens used, a specimen from the

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presumed syntype series is here designated as lectotype to fix the taxonomic status of the species.

Distribution: South Africa (Fig. 10).

5. *Eurynotus constrictus* Koch

(Fig. 3F)

Eurynotus (*Biolus*) *constrictus* Koch 1955: 421.– Kamiński 2016: 235.

Diagnosis: Eurynotus constrictus (along with *E. sulcimargo*) is distinct within *Eurynotus* for their large, well-defined lateral explanation and/or sulci of their pronota. Some representatives of *Biolus* possess lateral depressions; but even these are not as dramatic, and *Biolus* are sharply separable using other characters (see *Biolus* descriptions). *Eurynotus constrictus* is duller in texture (versus shiny/smooth in *E. sulcimargo*) and has simple punctation of abdominal ventrite V (with larger, intermixed, setigerous punctation in *E. sulcimargo*). Further, the elytral striae punctation in *E. sulcimargo* is distinctively large within *Eurynotus*. *Eurynotus constrictus* is also unique in that some representatives have weakly-raised tuberculation on the elytral humeri (similar to *Biolus*); however, these structures are never as strong, nor raised as in *Biolus*. Further separating the species is the epipleura; which is wider than in representatives of *Biolus*.

Note: For this revision only a single (female) specimen was available for physical examination in addition to photographs of a paratype from TMNH. As such, the following description should be considered as a supplement to Koch's original (1955) description.

Description [supplementary to Koch (1955)]: Head: Coarsely punctate, punctures closely spaced, separated by ≤1 puncture diameter. Mentum without apical notch. Eye with well-defined circumocular depression. Prothorax: Pronotum finely punctate, punctures separated by ≤1 puncture diameter. Hypomeron shallowly and finely punctate with light sculpturing/wrinkling. Pterothorax: Elytral interval X terminating between hind coxae and elytra apex. Epipleuron subequal to width of elytral intervals 9 + 10. Elytral intervals not obscured by epipleuron in ventral view. Abdomen: Punctate. Abdominal ventrite V finely punctate, punctures separated by ≤1 puncture diameter without larger, setigerous punctures intermixed. Females without median apical notch. Female terminalia: Bursa copulatrix sac-like and without sclerites, spermatheca coiled, accessory gland present, accessory pouch absent.

Material examined: Lectotype, here designated (TMNH): 'Oudebosch R. zondereind; museum staff Sept 1933; Paratypus EURYNOTUS constrictus C. Koch sp.n.'.

Additional material: TMNH: 'Robertson South Africa Julie 1944 S.H.Beneke'.

Note: As the original description lacked information defining the specific name-bearing specimen, one from the presumed syntype series is here designated as lectotype to fix the taxonomic status of the species.

Distribution: South Africa (Fig. 10).

6. *Eurynotus graniderma* Koch

(Figs 3G, 6E, 8L)

Eurynotus (*Eurynotus*) *graniderma* Koch 1955: 426.– Kamiński 2016: 236.

Diagnosis: Most similar to *E. barbosai* and *E. thermarum*. Most easily differentiated from *E. barbosai* by the presence of microtuberculation and rugosity of the elytra (absent in *E. barbosai*). *Eurynotus thermarum*, while also possessing microtubercles on the elytra, lacks the same level of rugosity, and has microtubercles on the pronotum (absent in *E. graniderma*). All other species of *Eurynotus* are easily separable using male characteristics: hind tibial setae absent in all species save for *E. capensis*, which lacks them on the midtibia, is larger (length 14–20; width 7–10mm), and lacks the same microtuberculation of *E. graniderma*.

Redescription: Length 8–9.5 mm; width 4.75–5.5 mm. Head: Coarsely punctate, punctures closely spaced, separated by ≤1 puncture diameter. Mentum without apical notch. Eye with circumocular depression. Prothorax: Pronotum finely punctate, punctures separated by ≤1 puncture diameter. Relatively smooth between punctures. Hypomeron shallowly and finely punctate and lightly sculptured/wrinkled. Pterothorax: Elytral interval X terminating between hind coxae and elytral apex. Elytra with microtubercles. Epipleuron subequal to width of elytral intervals 9 + 10. Elytral intervals obscured by epipleuron in ventral view. Abdomen: Punctate. Abdominal ventrite V punctures separated by ~1 puncture diameter with larger, setigerous punctures intermixed. Females without median apical notch. Legs: Male mid- and hind tibiae with setose groove. Male pro/meso tarsi expanded, with ventral tomentose pads. Tarsal setae golden. Male terminalia: Parameres broad and parallel, truncate at apex with small divot made by medially inflexed parameres. Female terminalia: Bursa copulatrix sac-like and without sclerites, spermatheca thick and coiled, accessory pouch absent.

Material examined: Holotype TMNH: 'ngxwala hill Zululand 10-7-15 L. Bevis; Durban Museum'.

(See Supporting Information, Appendix S1 for additional material examined.)

Distribution: South Africa (Fig. 10).

7. ***Eurynotus privisolum*** **sp.nov.**

(Figs 3H, 6H, L)

urn:lsid:zoobank.org:act:C521E6C6-C49C-4A79-9576-1376C196277D.

Diagnosis: This species is, at first glance, similar to *E. asperatus*. However, it is easily separable using the texture/lustre of the cuticle (dull/microreticulate in *E. asperatus*; shining/smooth in *E. privisolum*). Other characteristics separating this species from other *Eurynotus* are: the shape of the pronotum; the presence of micropunctation on the pronotum and abdominal ventrite V; the absence of larger, setigerous punctures on abdominal ventrite V.

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Description: Length 12 mm; width 6 mm. Head: Coarsely punctate, punctures closely spaced, separated by ≤1 puncture diameter. Mentum without apical notch. Eye with weak circumocular depression. Prothorax: Pronotum coarsely punctate, punctures separated by ≤1 puncture diameter, with micropunctation in interstices. Hypomeron shallowly and coarsely punctate with light sculpturing and wrinkling. Pterothorax: Elytral interval X terminating between hind coxae and elytral apex. Epipleuron narrower than width of elytral intervals 9 + 10. Elytral intervals not obscured by epipleuron in ventral view. Abdomen: Punctate. Abdominal ventrite V punctures separated by ≥1 puncture diameter with micropunctation in interstices; without larger, setigerous punctures intermixed. Legs: Tarsal setae black/dark. Male pro/meso tarsi robust with large, ventral, tomentose pads. Male terminalia: Parameres missing. Aedeagus sclerotized dorsally, with small membranous field at base of parameres. Ventrally membranous in basal portion.

Material examined: Holotype, male (TMNH), 'Middelberg div'. reverse side of label 'mus?/nov. 1935', 'Transvaal'.

Note: species is based on a single, damaged specimen; which, for the purposes of this and future studies was disarticulated and subsequently card mounted.

Etymology: Derived from the Latin *privi* (=separate or single) and *solum* (= alone, single, or lonely) in reference to the single lone specimen representing the species.

Distribution: South Africa (Fig. 10).

8. *Eurynotus sulcimargo* Koch

(Fig. 3I)

Eurynotus (*Biolus*) *sulcimargo* Koch 1955: 422.– Kamiński 2016: 236.

Diagnosis: Most similar to *E. constrictus* (see above diagnosis for more details). This species is most easily discernible using the shape of the pronotum (e.g. pronotal explanation), shining cuticle with smooth interstices between punctures, elytral punctation (large strial punctures), and puncture arrangement of abdominal ventrite V (with large setigerous punctures intermixed).

Description: Head: Coarsely punctate, punctures closely spaced, separated by ≤1 puncture diameter. Mentum without apical notch. Eye with weak circumocular groove. Prothorax: Pronotum finely punctate, punctures separated by ≥1 puncture diameter. Hypomeron deeply and sparsely punctate with some light sculpture/wrinkling. Pterothorax: Elytral interval X terminates between hind coxae and elytral apex. Epipleuron wider than width of elytral intervals 9 + 10 and clearly punctate. Elytral intervals obscured by epipleuron in ventral view. Abdomen: Punctate. Abdominal ventrite V coarsely punctate, punctures separated by ≥1 puncture diameter with larger, setigerous punctures intermixed. Females without median apical notch. Legs: Tarsi with black or dark setae. Female terminalia: Bursa copulatrix sac-like and without sclerites, spermatheca thick and coiled, accessory gland present, accessory pouch absent.

Material examined: Lectotype, here designated (TMNH): 'Top of Skurweberge Cold Bokkeveld Ceres Dist.; M. Versfeld 15–30 Oct 1934; Paratypus EURYNOTUS sulcimargo C. Koch sp.n.; Paratype No: 1235 Eurynotus sulcimargo KOCH'.

Additional material: TMNH: 'Fonteintiesberg Worcester C.P. 6000 ft. (K.H. Barnard Mar.1929. on rear side)'.

Note: As the original description lacked information defining the specific name-bearing specimen, one from the presumed syntype series is here designated as lectotype to fix the taxonomic status of the species.

Distribution: South Africa (Fig. 10).

9. Eurynotus thermarum Koch

(Fig. 3J)

Eurynotus (*Biolus*) *thermarum* Koch 1954a: 282.– Koch 1955: 423; Kamiński 2016: 236.

Diagnosis: Similar to *E. barbosai* and *E. graniderma*, can be separated from other species using size, microtuberculation, and male hind tibia structure (see respective diagnoses for separating this species from *E. barbosai* and *E. graniderma*).

Redescription: Length 10–13.25 mm; width 5.25–7.5 mm. Head: Finely punctate, punctures closely spaced, separated by ≤1 puncture diameter. Mentum without apical notch. Eye with circumocular groove. Prothorax: Pronotum finely punctate, punctures separated by ≥1 puncture diameter; interstices with microtubercles. Hypomeron shallowly and finely punctate and lightly sculptured/wrinkled. Pterothorax: Elytral interval X terminating between hind coxae and elytral base. Elytra with microtubercles. Epipleuron narrower than width of elytral intervals 9 + 10. Elytral intervals not obscured by epipleuron in ventral view. Abdomen: Punctate. Abdominal ventrite V finely punctate, punctures separated by ≥1 puncture diameter without larger, setigerous punctures intermixed. Females without median apical notch. Legs: Tarsi with black or dark setae. Female terminalia: Bursa copulatrix sac-like and without sclerites, spermatheca thick and coiled, accessory pouch present.

Material examined: Holotype (TMNH): 'Warmb. 20.2.04 5308; A. spec. Nov. 5308; Holotype No: 1847 Eurynotus thermarum KOCH; thermarum Koch'.

Additional Material (N = 2): TMNH: 'Marble Hall V.1962, TV. RORKE', 'Marble Hall V.1962, TV. RORKE'.

Distribution: South Africa (Fig. 10).

SUPPLEMENTARY DATA

Supplementary data are available at *Zoological Journal of the Linnean Society* online.

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CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY

All data are incorporated into the article and its online supplementary material.

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Redefining generic boundaries in subtribe Eurynotina (Coleoptera: Tenebrionidae): taxonomy of the *Schyzoschelus* generic group

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Abstract

The genus *Heteropsectropus* Kaszab, 1941 (Tenebrionidae: Blaptinae: Platynotini) is revised to include the following three species: *H. aenescens* Kaszab, 1941 (type species); *H. difficilis* Koch, 1954; *H. longantennatus* Koch, 1954. Four synonymies are proposed: *H. difficilis* (= *H. amaroides* Koch, 1954 **syn. nov**., = *H. natalensis* Koch, 1954 **syn. nov**., = *H. transvaalensis* Koch, 1954 **syn. nov**.) and *H. longantennatus* Koch, 1954 (= *H. montisdraconis* Koch, 1954 **syn. nov**.). A new genus, *Muelleropsectropus* **gen. nov.,** is introduced to accommodate *Schyzoschelus malaisei* Koch, 1954. Additionally, the following synonomies are introduced within *Schyzoschelus* Koch, 1954: *Schyzoschelus dumosicola* (= *Schyzoschelus dumosicola* var. *diversipenis* Koch, 1954 **syn. nov**.) and *Schyzoschelus simplicipes* (= *Schyzoschelus simplicipes willowmorensis* Koch, 1954 **syn. nov**.). Diagnostic features and relations between the genera of the *Schyzoschelus* generic group are discussed and an identification key to the genera and the species of *Heteropsectropus* is provided. Ovovivipary is reported for *H. difficilis* and represents the 15th known case of this mode of reproduction for darkling beetles. The first description of pupal morphology for the subtribe Eurynotina is provided as well as that of the first- and later instar larvae.

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Keywords: *Ovovivipary*, *female terminalia*, *larva*, *pupa*, *new taxa*, *synonymy*, *South Africa*

Introduction

Darkling beetles are well known for their ability to thrive in arid environments (Koch 1962; Matthews et al. 2010; Cheli et al. 2022; Pinto et al. 2022; Raś et al. 2022; Ragionieri et al. 2023). Several groups are widely recognized and have received recent taxonomic and phylogenetic attention (e.g. Lumen et al. 2020; Kamiński et al. 2021, 2022; Johnston et al. 2022; Swichtenberg et al. 2023). However, there remain lineages that have not been treated since their initial designation, such as Eurynotina Mulsant and Rey, 1854 (Blaptinae: Platynotini) (Koch 1954a, 1954b, 1955). Consisting of 17 genera and 97 species and subspecies, this subtribe has eluded modern scrutiny until recently (Kamiński 2016; Kamiński et al. 2021; Lumen & Kamiński 2023a, 2023b). Representatives of Eurynotina inhabit different ecosystems across southern Africa (Kamiński 2016), and some (e.g. species of *Eurynotus* and *Biolus*) are ovoviviparous (Lumen & Kamiński 2023a). Despite the extreme rarity of this mode of reproduction among darkling beetles in general (only 14 examples are known), Eurynotina has not received the taxonomic and phylogenetic attention necessary for comprehensive investigation of the evolution of ovovivipary.

The lack of recent investigations concerning Eurynotina is likely driven by a deficit of reliable resources for species and genus identifications. Nearly three-quarters of currently distinguished species are known from relatively small type series, have extremely

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specific diagnostic features, and include very little information on variability (Koch 1954a, 1954b; Kamiński 2016). Furthermore, the available taxonomic resources are insufficiently illustrated, necessitating reliable comparative materials for identification – on both species and generic levels. We have gathered an extensive collection of Eurynotina specimens from several major natural history museums of the world, and are consecutively processing them as a part of the first author's PhD thesis (see Lumen & Kamiński 2023a, 2023b).

This paper is focused on the *Schyzoschelus* generic group. In particular, we treat the taxonomy of the genus *Heteropsectropus* Kaszab, 1941 (Figure 1a–c) and some outstanding examples within *Schyzoschelus* Koch, 1954 as well as outline their generic boundaries (Figures 1e,f and 2). Previously, the only two papers concerning these taxa described seven species of *Heteropsectropus* based on a total of 27 specimens (Kaszab 1941; Koch 1954a). Many of these (12 specimens) represented the type species *Heteropsectropus aenescens* Kaszab, 1941, while the following taxa were based on single specimens: *H. difficilis* Koch, 1954, *H. longantennatus* Koch, 1954, *H. montisdraconis* Koch, 1954, and *H. transvaalensis* Koch, 1954. Since its designation, *Heteropsectropus* was believed to be closely allied to the genus *Schyzoschelus* Koch, 1954 (Kaszab 1941; Koch 1954a), and their relation appears well grounded in several morphological features, e.g. straight clypeal apex (Figure 3e), slender protibiae (Figures 1 and 2), rounded posterior angles of pronotum (Figure 3d), bordered 5th abdominal ventrite (in females), and merged parameres. Furthermore, a sister relation between



Figure 1. Habitus photographs of *Heteropsectropus*, *Muelleropsectropus*, and synonymized *Schyzoschelus* species. (a) *H. longantennatus* (**holotype**), (b) *H. aenescens* (specimen compared with **holotype** by Koch (1954a)), (c) *H. difficilis (H. natalensis* **paratype**), (d) *M. malaisei. Schyzoschelus* habitus, (e) *S. simplicipes* inset with striated abdominal ventrites (*S. simplicipes willowmorensis* **holotype** (left) and **paratype** (right)), (f) *S. dumosicola* inset without striated abdominal ventrites (*S. dumosicola diversipennis* **holotype** (left) and **paratype** (right)).

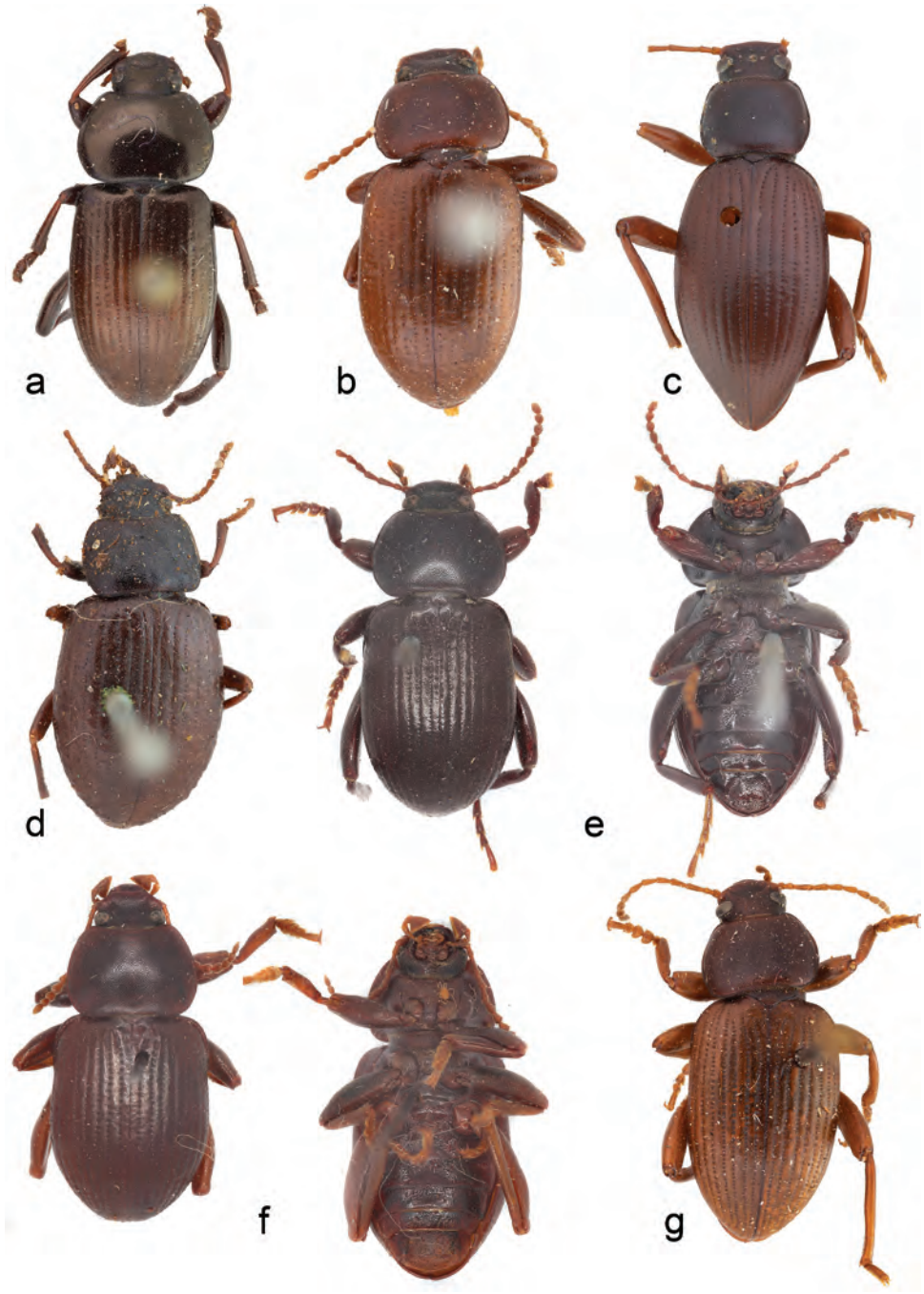


Figure 2. Type materials for representatives of *Schyzoschelus* (*for *S. simplicipes* and *S. dumosicola* see Figure 1(e,f) respectively). (a) *S. aeneomicans* (**holotype**), (b) *S. braunsi* (**holotype**), (c) *S. jenkinsae* (**holotype**), (d) *S. karooensis* (**holotype**), (e) *S. kaszabi* (left, dorsal and right, ventral) (**paratype**), (f) *S. ladini* (left, dorsal and right, ventral) (**paratype**) (g) *S. sympatrius* (**holotype**).

Heteropsectropus amaroides Koch, 1954 and *Schyzoschelus africanus* (Kaszab 1941) was recovered in a recent cladistic analysis (Lumen & Kamiński 2023a). Due to their morphological distinctiveness from other Eurynotina, *Heteropsectropus* and *Schyzoschelus* were recognized as one of the three main lineages of the subtribe, and were informally referred to as the "*Schyzoschelus* generic group" by Koch (1954a). Delimitation between the two genera is based on the bordering of the 5th abdominal ventrite (*Heteropsectropus*: widely bordered in both sexes (Figure 3c); *Schyzoschelus*: bordered in females, where the groove is situated on the extreme apex of ventrite (Figure 3f)), the shape of epipleura (*Heteropsectropus*: epipleuron evenly narrowing toward apex; *Schyzoschelus*: epipleuron

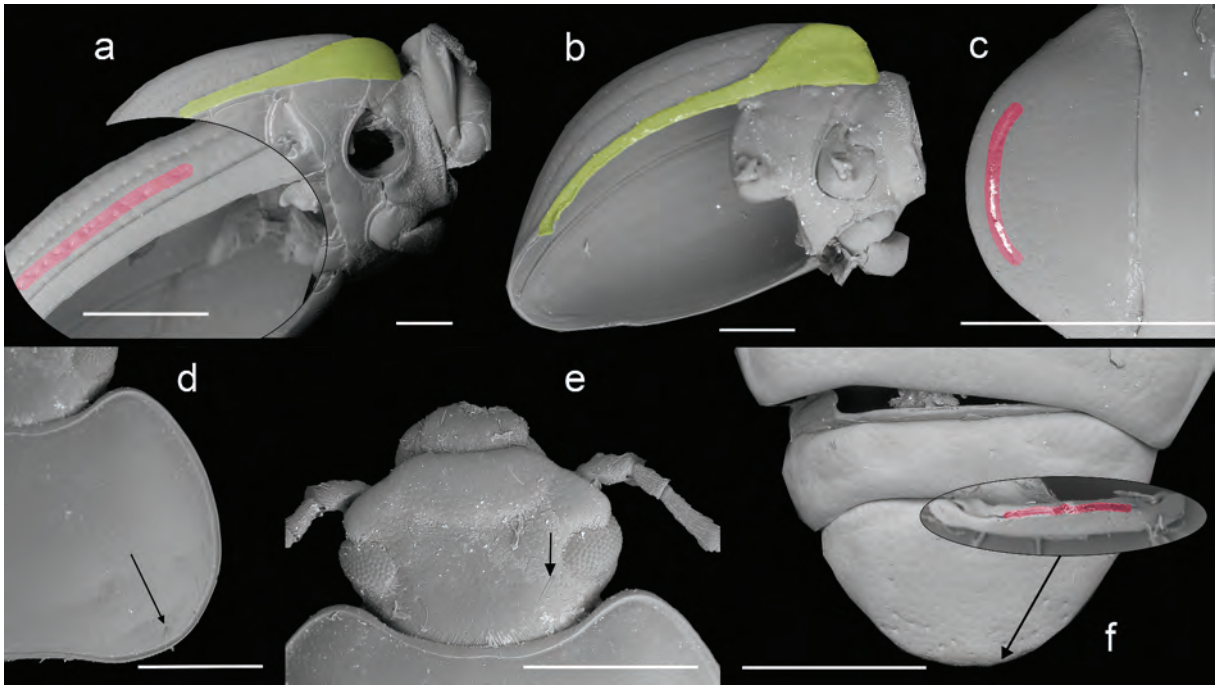


Figure 3. Scanning electron microscope photographs of *Schyzoschelus kaszabi*, *Heteropsectropus difficilis*, and *Muelleropsectropus*. (a) *Schyzoschelus kazsabi* – elytron (epipleura highlighted yellow, elytral stria between intervals ten and 11 highlighted red). (b and c) Heteropsectropus difficilis – elytron (epipleuron highlighted yellow), abdominal ventrite V (subapical sulcus highlighted red). (d, e, and f) Muelleropsectropus malaisei – right half of pronotum (large setae-bearing punctures indicated by arrow), head (large setae-bearing punctures indicated by arrow), and abdominal ventrite V (inset extreme apical sulcus highlighted red). Scale bars = 1 mm.

suddenly narrowed at the level of 5th abdominal ventrite), and degree of sexual dimorphism (strongly highlighted by leg modifications in *Schyzoschelus* (Figure 4e)) (Koch 1954a).

To begin, a revision of *Heteropsectropus* was necessary to address problems with the identification of voucher specimens originating from a breeding experiment conducted by workers of the Ditsong Museum in Pretoria (Schulze 1969). We associated adult specimens of an unidentified *Heteropsectropus* species from the pinned collection with pupae and larvae preserved in ethanol. Data on larval morphology is extremely scarce for Eurynotina (Kamiński et al. 2019b; Lumen & Kamiński 2023a), and no previous contributions provide details on pupal morphology of the group (Kamiński et al. 2018). Reliable identification required revision of the definitions of all species of *Heteropsectropus*. Reevaluation was conducted with reference to type materials concerning the genus, and included the first investigation of female terminalia and the application of scanning electron microscopy. Furthermore, to fully test the generic limits of *Heteropsectropus*, we also broadly investigated *Schyzoschelus*. Materials examined here imposed the need to revisit diagnostic features for both genera within the *Schyzoschelus* lineage.

Methods

Pinned material for the morphological examination of *Heteropsectropus* and *Schyzoschelus* presented here was acquired from the following institutional insect collections: **MIIZPAN** – Muzeum i Instytut Zoologii, Polskiej Akademii Nauk, Warsaw, Poland; **MNHN** – Muséum National d'Histoire Naturelle, Paris, France; **BMNH** – Natural History Museum, London, United Kingdom; **SANC** – South African National Collection of Insects, Pretoria, South Africa; **TMNH** – Ditsong National Museum of Natural History, Pretoria, South Africa. Pupae and larvae preserved in ethanol originating from breeding experiments were loaned from TMNH, and were associated with adult specimens by unique label codes. Original label data for studied specimens are provided in their respective taxonomic sections, and are condensed into single entries after their repositories (in bold). Different institutions' holdings are separated by a period, and different records are enclosed in quotation marks and separated by commas and spaces (e.g.

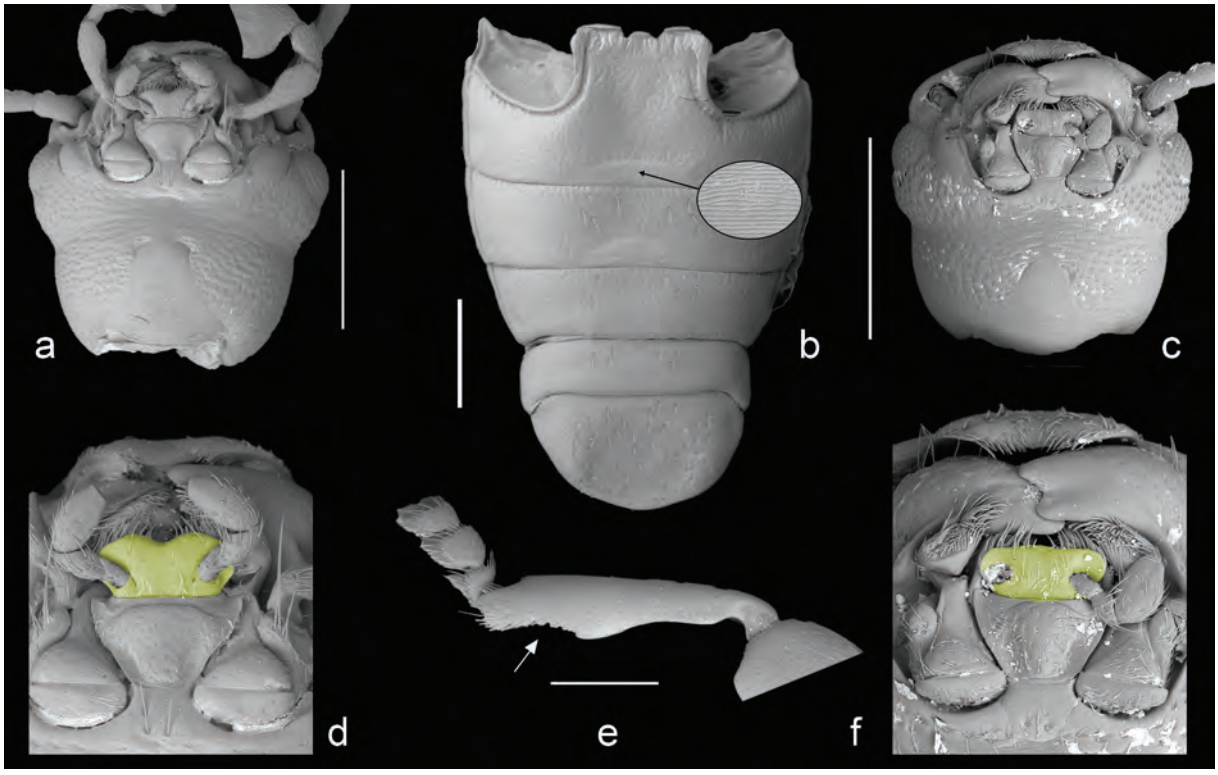


Figure 4. Scanning electron microscope photographs of *Schyzoschelus kaszabi* and *Heteropsectropus difficilis*. (a, b, d, and e) *Schyzoschelus kaszabi* – head (ventral), abdomen (ventral, inset close-up of striations of ventrites), close-up of mentum (prementum highlighted), and right male foreleg (arrow indicating hollowed out area). (c and f) *Heteropsectropus difficilis* – head (ventral), and close-up of mentum (prementum highlighted). Scale bars = 1 mm.

SANC: "specimen record 1", "specimen record 2". **MIIZPAN**: "specimen record 1"). Label data represents individual specimens unless otherwise noted.

The abdomens of adult specimens were dissected after brief incubation in 10% potassium hydroxide (KOH) solution for male and female termialia examination. Female genital tubes were stained with chlorazol black following methods of Kamiński (2021). Morphological nomenclature for larval skeletal structures follows that of Lawrence et al. (2011) and Beutel and Friedrich (2005), while terminology concerning adults has been additionally adopted after Matthews et al. (2010), with specialized terms for female terminalia following Kamiński et al. (2022). Description style follows that of Lumen and Kamiński (2023a) for imagines, Kamiński et al. (2019a) for larvae, and Kamiński et al. (2018) for pupae.

Specimens were photographed using a Canon 1000D body with extension rings and a Canon EF 100 mm macro lens, and a Nikon D3500 body with adapter for a Nikon SMZ800N microscope. Adults and larvae were further imaged using a Hitachi S3400N scanning electron microscope in the Museum and Institute of Zoology, Polish Academy of Sciences (MIIZPAN). The species distribution map was produced based on specimen label data using QGIS v. 3.16, with vector layers downloaded from the Natural Earth web page (www.naturalearthdata.com). The geographic range for the genus *Schyzoschelus* was projected based on distributional records (Kaszab 1941; Koch 1954a). All plates were prepared and edited in Photoshop v. 23.5.1.

Results

Based on type material and additional specimens, we propose the following synonymies within *Hete-ropsectropus*: *H. longantennatus* (= *H. montisdraconis* **syn. nov**.), *H. difficilis* (= *H. amaroides* Koch, 1954 **syn. nov**., = *H. natalensis* Koch, 1954 **syn. nov**.). The total species list for *Heteropsectropus* is thus: *H. aenescens*, *H. difficilis*, and *H. longantennatus*. Based on newly discovered male specimens, we describe a new genus (*Muelleropsectropus* **gen. nov**.) for *Schyzoschelus malaisei* Koch, 1954, which Koch (1954a) described based only on female specimens. We also propose the following synonymies within *Schyzoschelus*: *S. dumosicola* Koch, 1954 (= *S. dumosicola diversipenis* Koch, 1954 **syn. nov**.), *S. simplicipes* Koch, 1954 (= *S. simplicipes willowmorensis* Koch, 1954 **syn. nov**.). Finally,

ovoviviparity is reported for the fifth time for Eurynotina and pupae from the subtribe are photographed and described for the first time along with first- and later instar larvae.

Key to the genera of the *Schyzoschelus generic group*

1. Epipleural base evenly narrowed beyond humeral angle (Figure 3a). Elytron with additional stria terminating before shoulder, resulting in 11 intervals posteriorly (Figure 3a). Ovipositor long (ratio of length of coxites 1–4 to paraprocts < 1:1) (Figure 5c). Bursa copulatrix with terminal "bulb" (Figure 5e). ..... ***Schyzoschelus***
-. Epipleural base abruptly narrowed beyond the humeral angle (Figure 3b). Elytra without prematurely terminating striae – with 10 intervals. Ovipositor short (ratio of length of coxites 1–4 to paraprocts ≈ 1) (Figures 5b and 6c). Bursa copulatrix without terminal "bulb" (Figures 5d and 6a). **2**

2. Prementum without median emargination (Figure 4f). Subapical sulcus on abdominal ventrite V present (Figure 3c). Abdominal ventrite V not concave (Figure 3c). Female without furrow running along extreme apical edge of abdominal ventrite V, and without median notch. Bursa copulatrix without additional pouches (Figure 5d) ..... ***Heteropsectropus***
-. Prementum with median emargination (Figure 4d). Subapical sulcus on abdominal ventrite V absent (Figure 3f). Abdominal ventrite V slightly concave (Figure 3f). Female with furrow running along extreme apical edge of abdominal ventrite V, and with median notch (Figure 3f). Bursa copulatrix with two additional pouches on base (Figure 6a). ..... ***Muelleropsectropus* gen. nov**.

Genus ***Heteropsectropus*** Kaszab, 1941

Heteropsectropus Kaszab, 1941: 34. Koch 1954a: 71; 1956: 27; Lumen and Kamiński 2023.

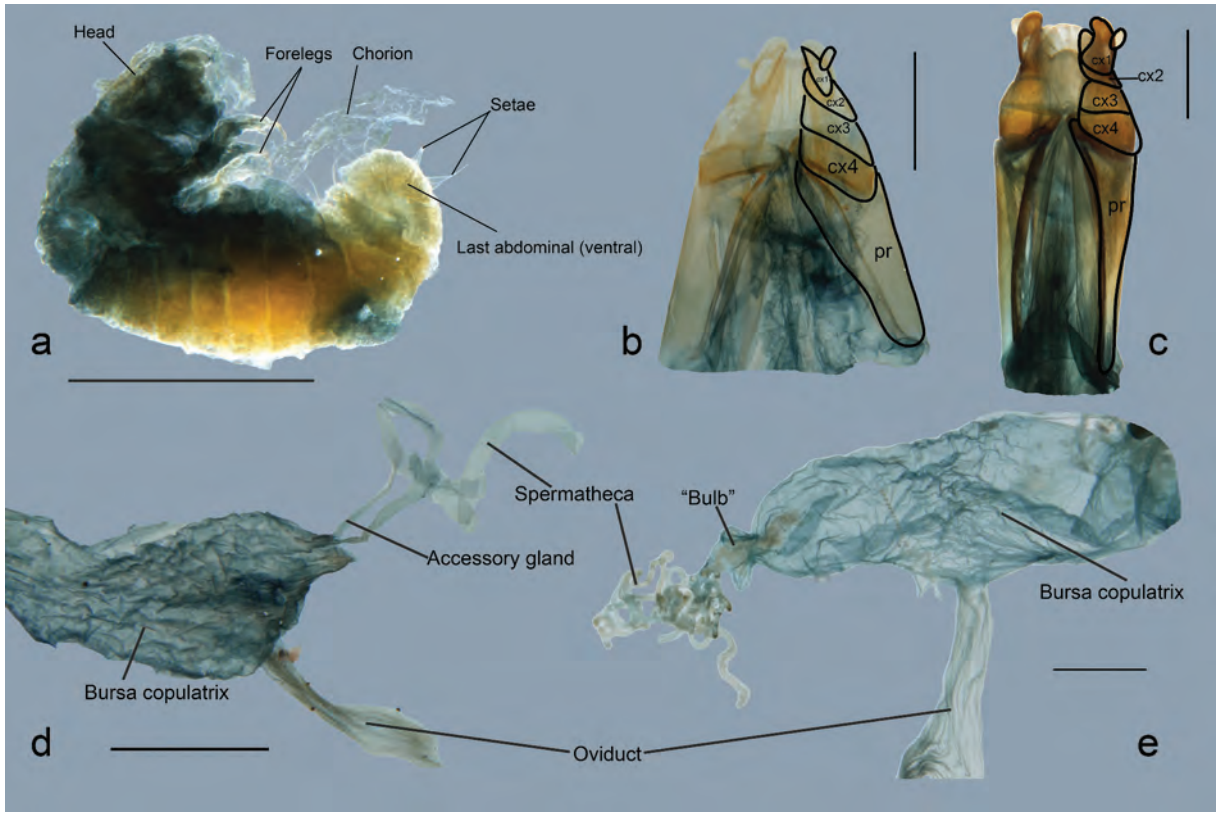


Figure 5. *Heteropsectropus* first-instar larva with female genitalia of *Heteropsectropus difficilis* and *Schyzoschelus kaszabi*. (a, b, and d) *Heteropsectropus difficilis* – first-instar larva, ovipositor (coxites and paraproct outlined), and internal genitalic structures. (c and e) *Schyzoschelus kaszabi* – ovipositor (coxites and paraproct outlined) and bursa copulatrix. Abbreviations: cx1–4, coxites; pr, paraproct. Scale bars = 0.5 mm.

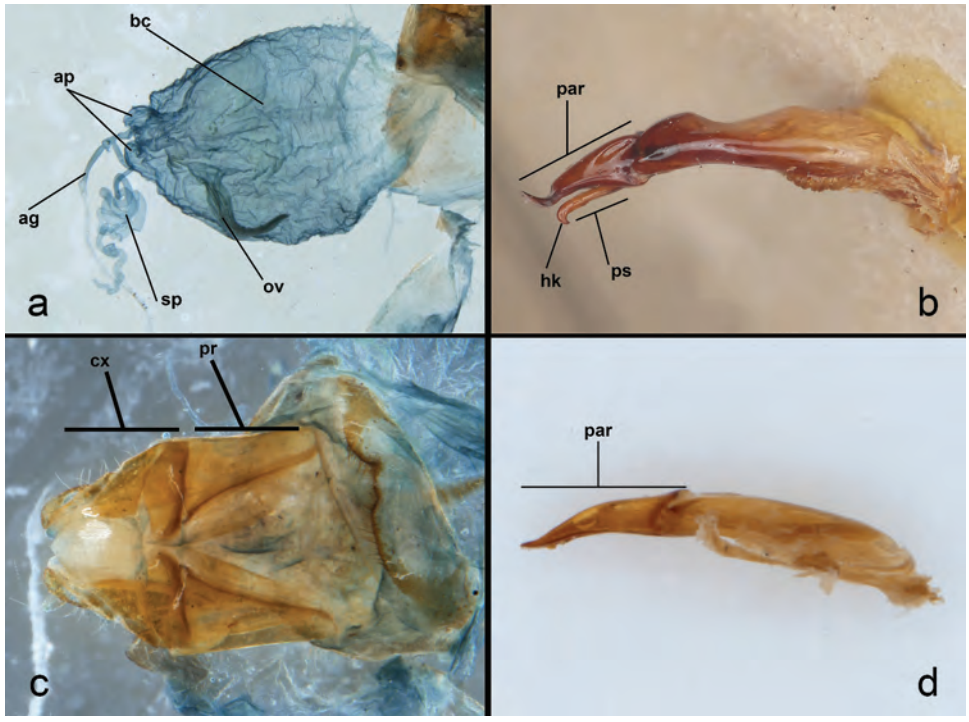


Figure 6. Genitalia of *Heteropsectropus* and *Muelleropsectropus*. (a and c) *M. malaisei* – bursa copulatrix and ovipositor. (b) *H. aenescens* aedeagus. (d) *H. difficilis* aedeagus. Abbreviations: ag, accessory gland; ap, accessory pouch; bc, bursa copulatrix; cx, coxae; hk, hook; ov, oviduct; par, parameres; pr, paraproct; ps, penis; sp, spermatheca.

Type species. *Heteropsectropus aenescens* Kaszab 1941; by original designation.

Diagnosis. *Heteropsectropus* is well defined within the *Schyzoschelus* generic group of Eurynotina by the straight apical margin of the clypeus (Figure 3e), straight/unexpanded foretibiae (Figure 1), rounded basal angles of the pronotum (Figure 3d), abdominal ventrite V with a subapical sulcus (Figure 3c), and parameres with a longitudinal groove running from the apex down to the base (Figure 7c). The genus is further distinguished from other genera within the group by the following suite of characters: epipleura abruptly narrowing at the humeral region (Figure 3b) (gradually narrowing in *Schyzoschelus* (Figure 3a)), with a subapical sulcus on abdominal ventrite V in both males and females (Figure 3c) (present on

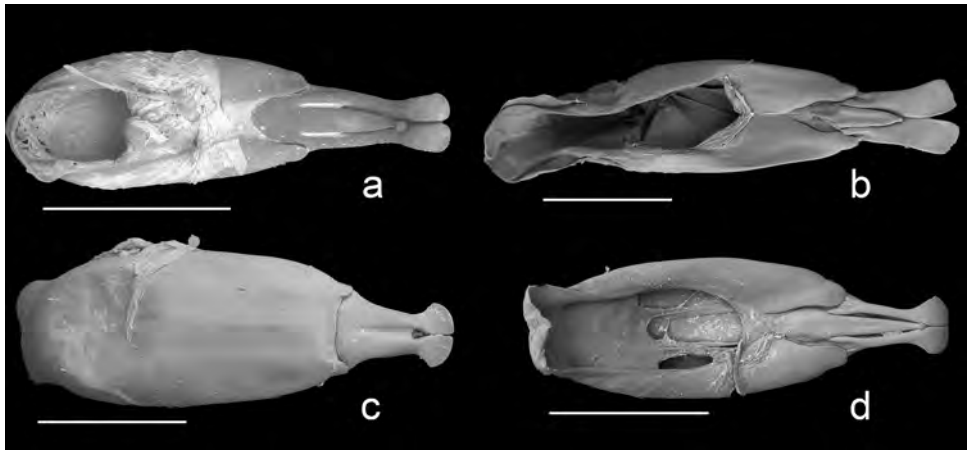


Figure 7. Aedeagi of *Heteropsectropus*, *Muelleropsectropus*, and *Schyzoschelus*. (a) *H. aenescens* (ventral). (b) *Schyzoschelus kaszabi* (ventral). (c and d) *Muelleropsectropus malaisei* (dorsal and ventral respectively). Scale bars = 1 mm.

extreme apex in females of *Schyzoschelus* and *Muelleropsectropus* (Figure 3f)), with a single large puncture bearing a strong seta above each eye (Figure 3e) (absent in *Schyzoschelus* except for *S. ladini*), flat or convex abdominal ventrite V (Figure 3c) (concave in male *Schyzoschelus* and *Muelleropsectropus* (Figures 3f and 4b)), female abdominal ventrite V without apical emargination or notch (present in *Schyzoschelus*, though species described based only on males require future confirmation, and in *Muelleropsectropus* (Figure 3f)), males with straight, unmodified tibiae – except for a patch of dense setae running down apex of hind tibiae (curved or strongly modified tibiae with setal patches in both *Schyzoschelus* and *Muelleropsectropus* (Figure 4e)), larger punctures bearing strong setae on abdominal ventrite V restricted largely to outer edge (Figure 3f) (throughout center in *Schyzoschelus* (Figure 4b), and present on other abdominal ventrites in *Muelleropsectropus* and *Schyzoschelus* (Figures 3f and 4b)). *Heteropsectropus* males also have a relatively long penis (>half the length of the parameres) and a more pronounced curvature, or hook, at the end of the penis (Figures 6b,d and 7a,c,d) (also present in *Muelleropsectropus*, but at most weakly pronounced in *Schyzoschelus* – except for *S. aeneomicans*, which has a long penis and pronounced hook).

Description. Length 6.25–10 mm, width 3–4.75 mm. Color tenebrous; dark brown to black, sometimes with aeneous and/or cupreous luster. **Head**: Coarsely puncate, punctures closely (≤1 feature diameter) spaced; with single larger punctures bearing large setae above each eye. Epistoma apex straight, without well-defined median notch; with two large punctures bearing large setae on apical margin. Prementum without median emargination. Mentum with small ventrally projecting middle portion; lateral wings exposed. Gula with stridulatory file. Eyes constricted in middle and reniform, with impressed sulcus situated around perimeter of dorsal lobe. Antennae 11 segmented, terminal segments forming weak club; either short (extending just beyond pronotal base) or long (extending much farther); males with longer antennae than females. **Prothorax**: scutellum small and transversely triangular. Pronotum with broadly rounded basal angles; dorsally with few to many large, widely spaced setae and punctures situated on lateral edges. Lateral margin well defined with border running along perimeter. Hypomeron nearly smooth to finely wrinkled; with light to absent punctation. Prosternal process round without posterior projection. **Pterothorax**: Elytra with 10 intervals, disc relatively flat to convex. Elytral striae strongly or weakly impressed and punctate. Intervals punctate, few to no bumps or tubercles present on apical declivity. Elytral intervals visible in ventral view. Laterally reflected elytral intervals 2–4× wider than epipleura width. Epipleura broad basally, narrowing abruptly after humeral region. Apterous. **Abdomen**: Punctate. Punctures separated by ≥ 1 diameter. Abdominal ventrite V with subapical sulcus; males with additional, larger setigerous punctures intermixed with smaller punctures, females without median apical notch. **Legs**: femora laterally compressed, slightly curved and thickened. Tibiae straight and only very slightly dilated toward apex; males with strip of tomentose setae running down to apex. Tarsi with golden setae; males with weakly or strongly expanded pro/meso tarsi with ventral, tomentose pads. **Male terminalia**: Tegmen bipartite and without ancorae; basal portion membranous ventrally; dorsally with small, triangular membranous field at base of apical portion. In lateral view, parameres flattened toward apex, with or without slight upward curvature. Penis strongly to weakly sclerotized and with pronounced apical hook. Spiculum gastrale symmetrical and unfused along apex. **Female terminalia** ovipositor short; (~1:1 paraprocts to coxae ratio). Bursa copulatrix without additional pouches. One species (*H. difficilis*) ovoviviparous.

Distribution. South Africa: Eastern Cape, Free State, KwaZulu-Natal, and Gauteng (Figure 8).

Species included (3): *H. aenescens* Kaszab, 1941; *H. difficilis* Koch, 1954; *H. longantennatus* Koch, 1954.

Key to the species of the genus *Heteropsectropus*

1. Antennae short (at most just exceeding the base of the pronotum). Elytral striae not deeply impressed **2**

-. Antennae long (far exceeding the base of the pronotum); Elytral striae deeply impressed (Figure 1a)..... ***Heteropsectropus longantennatus* Koch, 1954**

2. Most lateral (ventrally reflected) elytral intervals narrow (~2–3× epipleural width); parameres upturned and widened apically, penis with strong apical hook (Figue 6b)..... ***Heteropsectropus aenescens* Kaszab, 1941**

-. Most lateral (ventrally reflected) elytral intervals wide (~3–5× epipleural width); parameres flat and narrowed apically, penis with weak apical hook (Figure 6d) ..... ***Heteropsectropus difficilis* Koch, 1954**

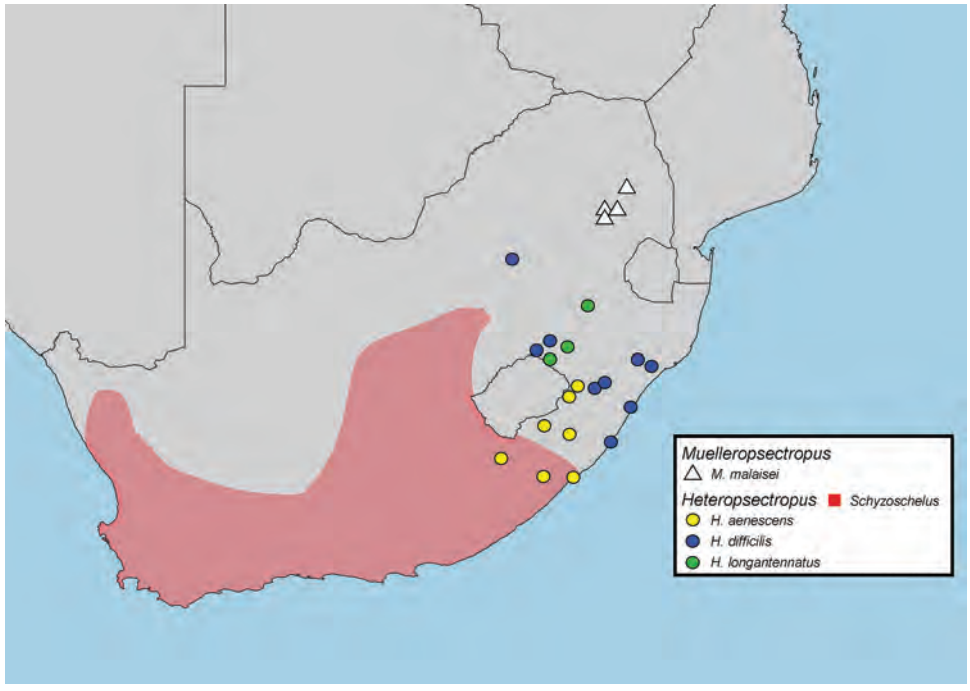


Figure 8. Distributional map of *Heteropsectropus*, *Muelleropsectropus*, and *Schyzoschelus*. Range of *Schyzoschelus* determined using type localities (Kaszab 1941; Koch 1954a) and specimens gathered during this study and by Kamiński (2016).

Heteropsectropus aenescens Kaszab, 1941
(Figures 1b, 6 b, and 7a)
Heteropsectropus aenescens Kaszab, 1941: 34. Koch 1954a: 73.

Material examined

(**BMNH**): "Umtata Caffraria C. Greaves, Heteropsectropus aenescens Kaszab C. Koch det. 1956, Brit. Mus. 1951–55" (with yellow circle PARATYPE label and white QR-code label with code NHMUK014663109). (**TMNH**): "Umtata Caffraria C. Greaves Menederes det. Peringuey" (three specimens). "15 m SE Barkley east. C.P. II.67. L.SCHULZE", "SA KZN Kamberg 13 29.37331°S 29.62798°E 1814 m Grassland Ground Search 08-Nov-2005 III-UKZN" (two specimens, bearing two different codes: MDTP 55,645 and MDTP 1100). (**TMNH**): "TB#26351–29.65, 29.44, Heteropsectropus".

Note: Though we were unable to examine the holotype described by Kaszab (1941), Koch (1954a) directly compared the "Umtata" specimens we examined with that of Kaszab and positively identified them. Additionally, comparisons of our material with both Kaszab's and Koch's illustrations confirmed the unique morphology of the *H. aenescens* aedeagus (upturned apically with a strongly sclerotized hook on the apex of the penis) (Figure 6b). Koch (1954a) also noted that the type of *H. aenescens* was from Gebien's personal collection, which should be in Naturhistorisches Museum Basel (Switzerland).

Diagnosis. Heteropsectropus aenescens is often distinguished within the genus by its coppery shine. While other species also display a similar lustre, it is most commonly pronounced in *H. aenescens*. This species is separable from *H. longantennatus* by the degree of impression of the elytral striae, which are shallowly to unimpressed. *Heteropsectropus aenescens* has more convex elytrae than its congeners, which have an overall flatter elytral disc. The lateral edges of the pronotum can also be used to distinguish *H. aenescens* (with numerous large, well-defined punctures bearing large setae; few such punctures and setae in other species). The lateral-most elytral intervals reflected ventrally are also narrower in *H. aenescens* (~2–3× width of epipleura) compared to *H. longantennatus* and *H. difficilis* (~>3× width of epipleura). Other species are also generally wider (3–4.25 mm *H. aenescens*; 3.25 mm–4.75 mm *H. difficilis*; 3–4.5 mm *H. longantennatus*). The humeri of the elytra in the dorsal view are more rounded in *H. aenescens* compared to the other species (which are generally broader or

square-shaped). The aedeagus is strongly sclerotized, with apically upturned parameres and a pronounced hook on the apex of the penis (Figure 6b) (less sclerotized, absent, and weak, respectively, in *H. difficilisi* (Figure 6d); parameres less strongly upturned and hook on apex of penis less pronounced in *H. longantennatus*). *Heteropsectropus aenescens*, as of this revision, is restricted to the South East region of South Africa (Eastern Cape and KwaZulu-Natal), whereas *H. longantennatus* and *H. difficilis* are distributed more northward (Figure 8).

Description. Length 6.75–9 mm, width 3–4.25 mm. Color tenebrous; dark brown to black often with aeneous and/or cupreous luster. **Head**: Antennae short, extending just beyond pronotal base. **Prothorax**: dorsally with many large, widely spaced setae and punctures situated on lateral edges. **Pterothorax**: Elytral striae weakly impressed; apical declivity with few to no bumps or tubercles. Laterally reflected elytral intervals ~ 2–3× wider than epipleura width. **Legs**: males with strongly expanded pro/meso tarsi with ventral, tomentose pads. **Male terminalia**: parameres narrowing from base before widening and flattening toward apex, curving upward in lateral view. Penis strongly sclerotized with pronounced apical hook.

Distribution. South Africa: Eastern Cape and KwaZulu-Natal (Figure 8).

***Heteropsectropus difficilis* Koch, 1954** (Figures 1c, 4 c,f, 5 a,b,d, 6 d, 9 a–k, and 10a–d).
Heteropsectropus difficilis Koch, 1954a: 76.
= *Heteropsectropus amaroides* Koch, 1954a: 75 **syn. nov.**
= *Heteropsectropus natalensis* Koch, 1954a: 75 **syn. nov.**
= *Heteropsectropus transvaalensis* Koch, 1954a: 74 **syn. nov**.

Material examined

Heteropsectropus difficilis Koch, 1954: **Holotype** (**TMNH**): "Christiana Transvaal Dr. Brauns. Holotype No: 1782 Heteropsectropus difficilis KOCH difficilis Koch".

Heteropsectropus amaroides Koch, 1954: **Paratypes** (**TMNH**): "'N' Kandhla Forest Zululand R.F. Lawrence Jan 1937. Paratype No: 1781 Heteropsectropus amaroides KOCH". (BMNH): "Malvern Natal 7.97 8477? Marshall Coll. 1911–263. Heteropsectropus amaroides C. Koch Det, Koch 1954" (also with yellow circle "Paratype" label and QR code label with code NHMUK014663128).

Heteropsectropus natalensis Koch, 1954: **Holotype** (**TMNH**): "Karkloof Natal 2.97 Marshall Coll. 1911–263. Heteropsectropus natalensis C. Koch det., 1954" (also with red circle "Type" label, Red square "HOLOTYPE natalensis Koch" label, and QR code label with code NHMUK014663129.) **Paratype** (TMNH): same data as holotype with additional labels (Paratype No: 1779 Heteropsectropus natalensis KOCH).

Heteropsectropus transvaalensis Koch, 1954: **Holotype** (**TMNH**): "Highlands J'burg T Sept 1901 under stones Heteropsectropus transvaalensis Koch C. Koch det., 195 transvaalensis Koch".

Additional material examined

(**SANC**): "Johannesberg Mondeor TVL 27-9-1959 C. H. Draper" (two specimens; one with year 1960). "Natal RT Lawrence Feb 1938", "Nr. Balgowan Natal Jan 1953 D.W. Rorke", (**TMNH**): "S.Afr., Ntl-Drakensb Cathedral Peak for. 28.57S–29.12 E 15.3.1976; E-Y: 1088 from under stones leg. Endrödy-Younga", "Golden Gate Nat. Park I.1968. R. Jones Heteropsectropus sp. FROM INSECTARIUM NO. 807" (four adult specimens, 2 pupae, several larvae). "Golden Gate Southern O. F.S. 1.3.67. L. SCHULZE".

Diagnosis. Heteropsectropus difficilis is the most widespread species of the genus – with its range extending from the eastern coast of KwaZulu-Natal to Johannesberg in Gauteng province. Formerly represented by four species, *H. difficilis* is relatively variable compared to *H. aenescens* and *H. longantennatus*. This species is most easily separable via elimination of the other two. Otherwise, *H. difficilis* is sharply separable by aedeagal morphology (less sclerotized and without upturned paramere apex and with weak apical hook of the penis; compared with the other species with more sclerotized aedeagi and more pronounced hooks and upturned parameres) (compare Figure 6b,d). Superficially, *H. difficilis* resembles *H. longantennatus* more in body shape (more squared elytral humeri, less metallic than *H. aenescens*, wider reflected elytral intervals, etc.). However, *H. difficilis* differs from *H. longantennatus* by the length of the antennae (short – at most only slightly surpassing base of pronotum; rather than long – distinctly surpassing the base of the pronotum) (compare Figure 1a–c).

Description. **Imagines**: Length 6.75–10.0 mm, width 3.25–4.75 mm. Color tenebrous; dark brown to black less commonly with aeneous and/or

cupreous luster. **Head**: antennae short, extending just beyond pronotal base **Prothorax**: dorsally with few large, widely spaced setae and punctures situated on lateral edges. **Pterothorax**: elytral striae weakly impressed; apical declivity with few to no bumps or tubercles. Laterally reflected elytral intervals ~ 3–5× wider than epipleura width. **Legs**: males with weakly expanded pro/meso tarsi with ventral, tomentose pads. **Male terminalia**: parameres narrowing from base, in lateral view flattening toward apex and straight, without upward curvature. Penis weakly sclerotized with weakly pronounced apical hook.

Larval stages

First instar (*extracted from bursa copulatrix*) (Figure 5a). Length ≈1.5 mm. Body overall weakly sclerotized. Enclosed within thin, transparent membrane. **Head**: prognathous; dorsoventrally flattened; width nearly equal to prothorax. Stemmata present. **Thorax**: prolegs notably longer and thicker than meso- and metathoracic legs; pretarsus sclerotized. Last abdominal segment with long, thin setae on dorsal side, without row of four socketed setae along apex.

Later instars (Figure 9a–k). Length up to 13 mm, width up to 1.5 mm. **Head**: prognathous, distinctly retracted into prothorax; dorsoventrally flattened; width nearly equal to prothorax; sides rounded; strongly constricted before occipital foramen; yellow in apical part, strongly sclerotized basally; punctation extremely fine. Epicranial stem length approximately one-third of head capsule length; frontal sutures curved, fading in two-thirds of head length. Frons faintly punctured, with microsculpture. Epicranial plates weakly smooth, without microsculpture; each plate with two deep setose points; lateral portions moderately setose (11–13 setae present). Stemmata present. Clypeus rounded, slightly darker medially, with two deep setose points. Labrum transverse, weakly emarginate, with apical row of eight elongated setae. Epipharynx as in Figure 9g. Mandibles asymmetrical, with strongly sclerotized apices, base white and dark; left mandible with triangular premolar tooth and two distinct apical teeth; right mola reduced, with single apical tooth. Labium with distinct prementum, mentum and submentum; gula well developed, elongated and rectangular; rectangular prementum bears pair of setae in center, ligula twice shorter and subequal in width to first labial segment, labial palps 2-segmented; mentum elongated, with pair of setae at base and two pairs of longer setae lateromedially; trapezoidal submentum bears pair of setae basally. Hypopharyngeal sclerome pentagonal; bicuspidate, with apical denticle elongated; with deep depression in middle. Maxillary palpi 3-segmented. Antennae 3-segmented, second antennomere 2× longer than wide and subequal to first one. **Thorax**: thoracic tergites yellow, first and second segments covered with brown spots. Prothoracic tergum subquadrate, about 1.5× length of meso- or metaterga; dorsally covered with single brown spot. Meso- and metathoracic tergites wider than long. Thoracic tergites sparsely setose on dorsal surfaces. Mesothoracic spiracle simple, ovate, approximately 2.0× size of abdominal spiracles; reduced metathoracic spiracle visible. Prothoracic leg noticeably longer, thicker than meso- and metathoracic legs; prothoracic pretarsus sclerotized; tibiotarsus with two long spines on the inner side, femur with row of two spines, prothoracic trochanter with two stout spines ventroapically; prothoracic coxa without spines, laterally setose. Prothoracic pretarsus and tibiotarsus combined about 2.0× length of femur; about 1.8× length of trochanter. Meso- and metalegs not modified. **Abdomen**: Abdominal tergites yellow, faintly rugose, with sparse elongate seate laterally. Abdominal laterotergites with lateral margins indistinctly pigmented. Abdominal segment VIII with row of four setae basally. Pygidium rounded apically; urogomphi absent; marginal row of four socketed spines present. Pygopods short, subconical.

Pupa (Figure 10a–d). Length (from anterior edge of pronotum to tips of urogomphi) 9–10 mm, width ~4.5 mm; body color yellow with extremely sparse brownish setae. Lateral processes of middle abdominal segments well developed, bearing posterior grinding edges. Grinding surfaces of all lateral processes situated in sagittal plane. **Head**: hypognathous; surface flat and glabrous; projection above antennal insertion rounded; antennae 11 segmented, terminal segments forming weak club; extending beyond pronotal base; labrum and mandibles without setation; clypeus not emarginate; last segment of maxillary palpi wide. **Thorax**: pronotum with broadly rounded basal angles; not setose; weakly punctured. Lateral margin well defined with border running along perimeter. Hypomeron finely wrinkled; with light to absent punctation. Prosternal process round without posterior projection. Elytral sheath glabrous; not costate; meso- and metaventrite smooth. Legs glabrous. **Abdomen**: all surfaces

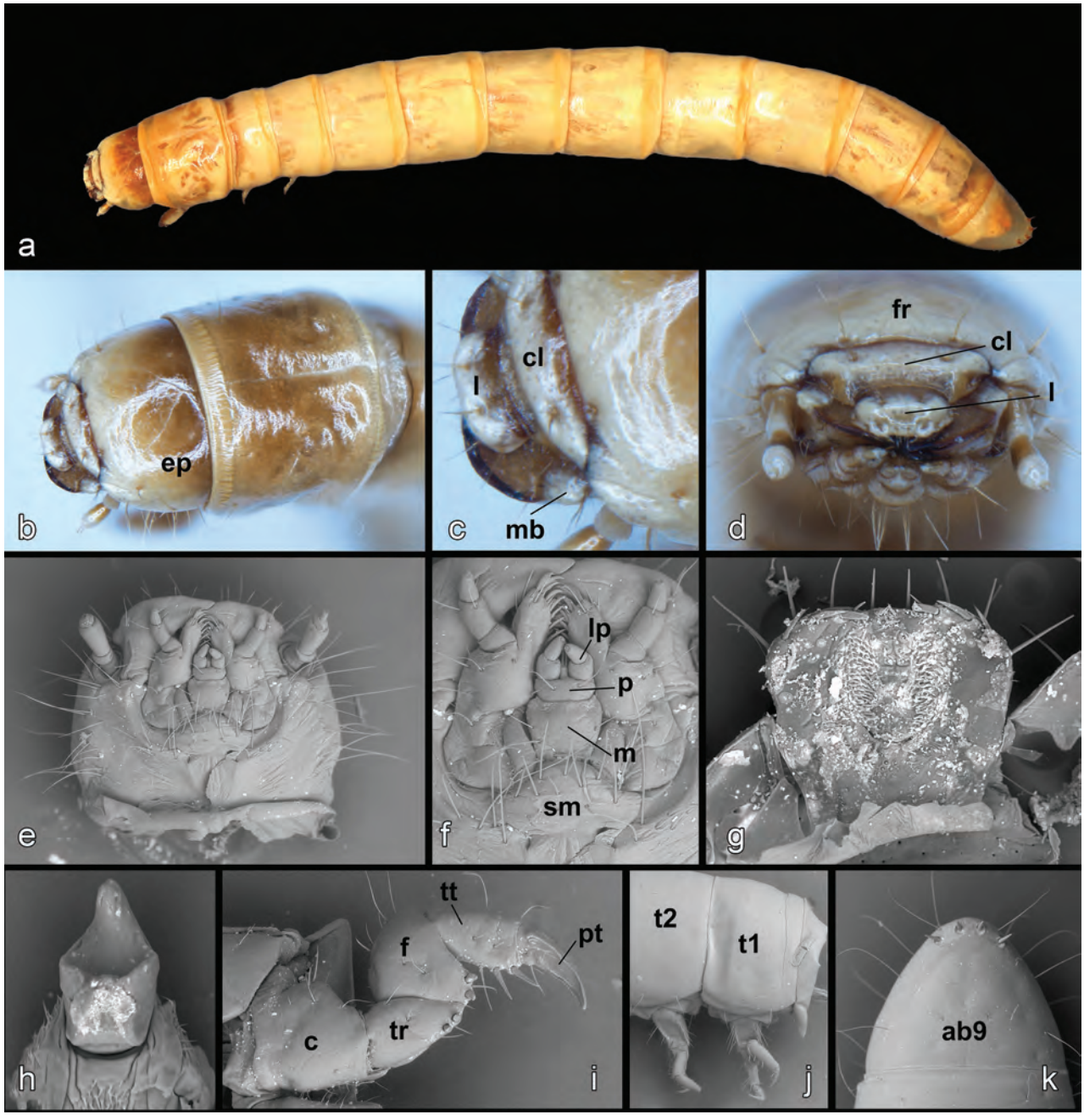


Figure 9. Larva of *Heteropsectropus difficilis*. (a) Dorsal habitus. (b) head (dorsal). (c) labrum/clypeus (dorsal). (d) anterior view. (e) head (ventral). (f) mentum (close up). (g) epipharynx. (h) hypopharyngeal sclerome. (i) left foreleg. (j) meso- and metathoracic section (lateral view). (k) last abdominal segment (dorsal). Abbreviations: ab9, abdominal segment 9; c, coxa; cl, clypeus; ep, epicranial plates; f, femora; fr, frons; l, labrum; lp, labial palpus; m, mentum; mb, mandibular base; *p*, prementum; pt, pretarsus; sm, submentum; t1, thoracic segment 1; t2, thoracic segment 2; tr, trochanter; tt, tibiotarsus.

covered by extremely sparse setae; spiracles annular, vertically ovate to reniform, pigmented. Tergites 1–4 widened. Tergite 5 with subapical sulcus; 1.5× longer than tergite 4. Tergites 1–5 with grinding processes (Figure 10c). Remaining tergites without grinding surfaces. Tergite 9 short, bearing relatively short divergent urogomphi, each gradually tapered and more sclerotized toward upturned, sharp apices; cleft between urogomphi V-shaped.

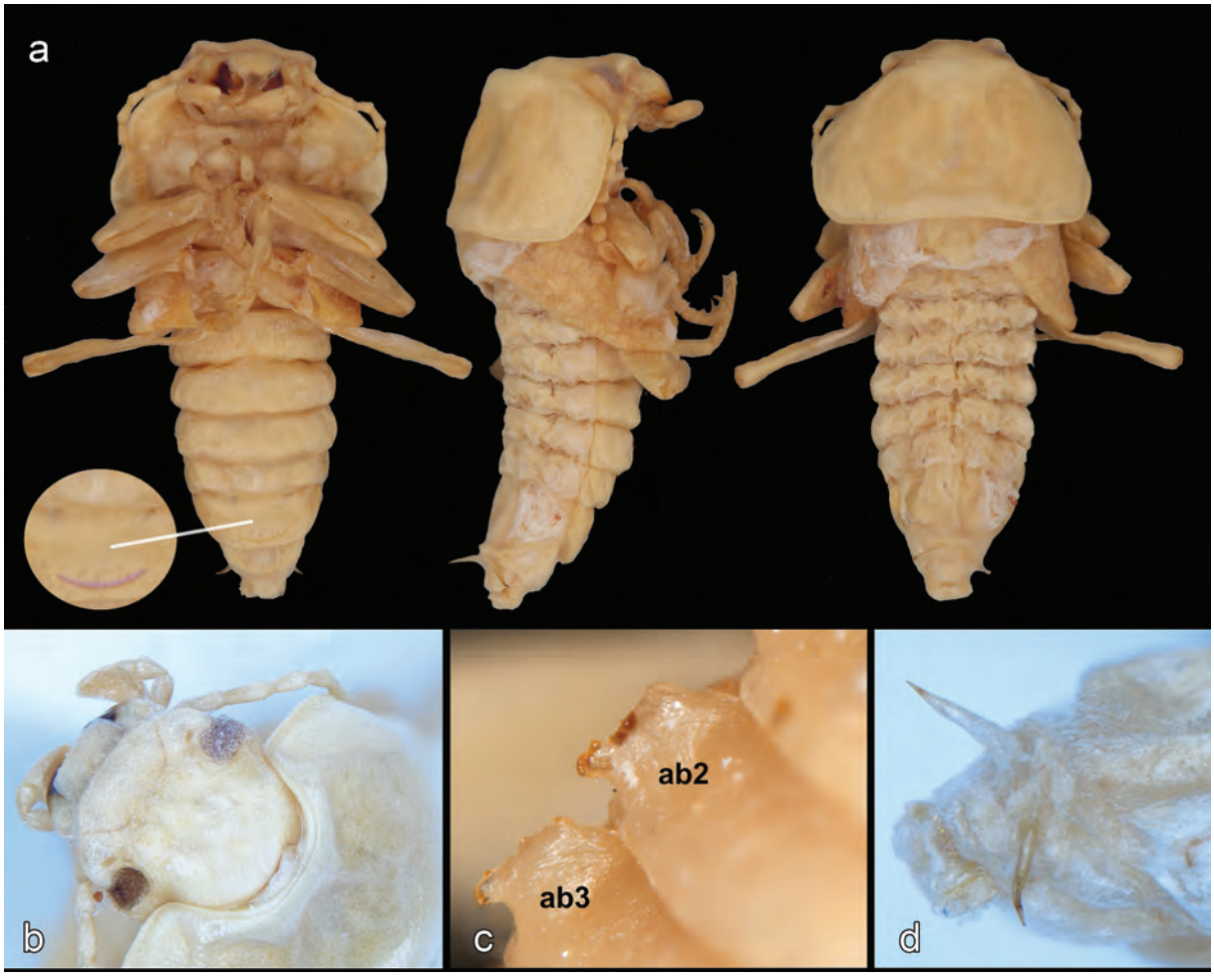


Figure 10. Pupa of *Heteropsectropus difficilis*. (a, left to right) ventral, lateral, and dorsal views. (b) dorsal head (close up). (c) abdominal gin traps (close up). (d) urogomphi (dorsal). Abbreviations: ab2, 3, abdominal segments 2, 3.

Distribution. South Africa: Gauteng, KwaZulu-Natal, and Free State (Figure 8).

Heteropsectropus longantennatus Koch, 1954 (Figure 1a).
Heteropsectropus longantennatus Koch, 1954a: 76.
= *Heteropsectropus montisdraconis* Koch, 1954a: 77 **syn. nov.**

Material examined

Heteropsectropus longantennatus **Holotype** (**TMNH**): "Volksrust 1.1922.A.Rob.9 G.V.Dam. Holotype No: 1783 heteropsectropus longantennatus KOCH Heteropsectropus longantennatus Koch C. Koch Det., 195 Longantennatus Koch".

Heteropsectropus montisdraconis **Holotype** (**BMNH**): "S.Africa R.E. Turner. Brit.Mus.1927–25. Natal: Van Beenen Drakensberg Dec.1926 HoloTYPE montis-draconis Koch unique holotype! Heteropsectropus montis-draconis Koch C. Koch Det., 195" (also bearing white QR label with code NHMUK 014663130 and red, circled "Type" label).

Additional material examined

(**MIIZPAN**): "−28.68741, 28.947903, 18/1/18, leg. MJ. Kaminski" (also bearing blue Tenebrionidbase QR label with ID# 26352).

Diagnosis. Heteropsectropus longantennatus is sharply separable from all other species by its geographic location (largely restricted to the Drakensberg mountain range and extending northward along the borders of KwaZulu-Natal and Free State), antennae (long – extending distinctly beyond pronotum base; short – barely exceeding the pronotum base in

other species), and elytra (with strongly impressed striae; weakly impressed in other species).

Description. Length 6.25–8.25 mm, width 3–4.5 mm. Color tenebrous; dark brown to black, less commonly with aeneous and/or cupreous luster. **Head**: antennae long, extending beyond pronotal base. **Prothorax**: dorsally with few large, widely spaced setae and punctures situated on lateral edges. **Pterothorax**: elytral striae weakly impressed; apical declivity with few to no bumps or tubercles. Laterally reflected elytral intervals ~ 3–5× wider than epipleura width. **Legs**: males with weakly expanded pro/meso tarsi with ventral, tomentose pads. **Male terminalia**: parameres narrowing from base before widening and flattening toward apex, weakly lying flat in lateral view. Penis strongly sclerotized with weakly pronounced apical hook.

Distribution. South Africa: KwaZulu-Natal and Free State (Figure 8).

Genus ***Muelleropsectropus* gen. nov.**

Type species. Schyzoschelus malaisei Koch, 1954; here designated.

Diagnosis. Muelleropsectropus is well defined within the *Schyzoschelus* generic group of Eurynotina by the straight apical margin of the clypeus (Figure 3e), straight/unexpanded foretibiae, rounded basal angles of the pronotum (Figure 3d), abdominal ventrite V with a sulcus (Figure 3f), and parameres with a longitudinal groove running from the apex down to the base (Figure 7c). The genus is further distinguished from other genera within the group by the following suite of characters: epipleura abruptly narrowing at the humeral region (Figure 3b) (gradually narrowing in *Schyzoschelus* (Figure 3a)), sulcus present on extreme apex in females (Figure 3f) (*Heteropsectropus* with a subapical sulcus on abdominal ventrite V in both males and females (Figure 3c)), with a single large puncture bearing a strong seta above each eye (Figure 3e) (absent in *Schyzoschelus*, except for *S. ladini*), flat or concave abdominal ventrite V (Figure 3f) (flat to convex in *Heteropsectropus* (Figure 3c)), female abdominal ventrite V with apical emargination or notch (Figure 3f) (absent in some *Schyzoschelus* and in *Heteropsectropus*), males with curved or strongly modified tibiae with setal patches (straight, unmodified tibiae – except for a patch of dense setae running down apex of hind tibiae in *Heteropsectropus*), larger punctures bearing strong setae on abdominal ventrites with those on ventrite V restricted largely to outer edge (Figure 3f) (throughout center in *Schyzoschelus* (Figure 4b), and absent on other abdominal ventrites in *Heteropsectropus*). Aedeagus similar to *Heteropsectropus* (long penis with sclerotized hook at apex).

Description. Length 8.5–10 mm, width 4–5 mm. Color tenebrous; dark brown to black, sometimes with aeneous and/or cupreous luster. **Head**: coarsely puncate, punctures closely (≤1 feature diameter) spaced; with single larger punctures bearing large setae above each eye. Epistoma apex straight, without well-defined median notch; with two large punctures bearing large setae on apical margin. Prementum with median emargination. Mentum with small ventrally projecting middle portion; lateral wings exposed. Gula with stridulatory file. Eyes constricted in middle and reniform, with impressed sulcus situated around perimeter of dorsal lobe. Antennae 11-segmented, terminal segments forming weak club; long, extending beyond pronotal base; males with longer antennae than females. **Prothorax**: scutellum small and transversely triangular. Pronotum with broadly rounded basal angles; dorsally with few to many large, widely spaced setae and punctures situated on lateral edges. Lateral margin well defined with border running along perimeter. Hypomeron nearly smooth to finely wrinkled; with light to absent punctation. Prosternal process round without posterior projection. **Pterothorax**: elytra with 10 intervals, disc relatively flat to convex. Elytral striae strongly impressed and punctate. Intervals punctate, with few to no bumps or tubercles present on apical declivity. Elytral intervals visible in ventral view. Laterally reflected elytral intervals ~3× wider than epipleura width. Epipleura broad basally, narrowing abruptly after humeral region. Apterous. **Abdomen**: punctate. Punctures separated by > 1 diameter. Abdominal ventrite V without subapical sulcus; males convex with additional, larger setigerous punctures intermixed with smaller punctures, females with extreme apical groove running along edge and median apical notch. **Legs**: femora laterally compressed, slightly curved and strongly thickened. Tibiae slightly curved; males with apical grooves or ridges with tomentose pockets. Tarsi with golden setae and strongly expanded pro/meso tarsi with ventral, tomentose pads in males. **Male terminalia**: tegmen bipartite and without ancorae; basal portion membranous ventrally; dorsally with small, triangular membranous field at base of apical portion. Parameres narrowing from base before widening and flattening toward apex, curving upward in lateral view. Penis strongly sclerotized with small pronounced apical hook. Spiculum

gastrale symmetrical and unfused along apex. **Female terminalia:** ovipositor short; (~1:1 paraprocts to coxae ratio). Bursa copulatrix with two additional pouches.

Distribution. South Africa: Mpumalanga (Figure 8). **Species included (1)**. *M. malaisei* (Koch, 1954).

Muelleropsectropus malaisei (Koch, 1954) (Figures 1d, 3 d–f, 6 a,c, and 7c,d).
Schyzoschelus malaisei Koch, 1954a: 78.

Material examined

Holotype (**TMNH**): "Marieps Mnt. IV: 1932 G. van Son. HOLOTYPE No: 1784 Schyzoschelus malaisei KOCH Malisei Koch".

Additional material examined

(**TMNH**): "S.Afr., E.Transvaal Berlin; Karst plat. 25.31S–30.46E 4.2.1987; E-Y:2414 under fungous logs leg. Endrody-Younga", "S.Afr; E.Tvl.Uitsoek high alt. grassveld 25.15 S – 30.34 E 12.12.1986; E-Y:2381 grassnetting leg. Endrody-Younga", "Transvaal Mt. Anderson 29.1.1955 I.Rudebeck" (two specimens). "E.Y.Western Coll. B.M. 1924–176 Transvaal".

Diagnosis. See diagnosis of *Muelleropsectropus* **gen. nov.**

Distribution. See distribution of *Muelleropsectropus* **gen. nov.**

Genus ***Schyzoschelus*** **Koch, 1954**
Schyzoschelus Koch, 1954a: 72; Koch 1956: 27; Lumen and Kamiński 2023.

Type species. *Schyzoschelus kaszabi* Koch, 1954; by original designation.

Species included (13): *S. aeneomicans* Koch, 1954; *S. africanus* (Kaszab 1941); *S. bispinosus* (Kaszab 1941); *S. braunsi* Koch, 1954; *S. capensis* (Kaszab 1941); *S. dumosicola* Koch, 1954; *S. jenkinsae* Koch, 1954; *S. kaszabi* Koch, 1954; *S. ladini* Koch, 1954; *S. karrooensis* Koch, 1954; *S. simplicipes* Koch, 1954; *S. sympatrius* Koch, 1954; *S. validus* (Fairmaire 1894).

Schyzoschelus aeneomicans Koch, 1954 (Figure 2a).
Schyzoschelus aeneomicans Koch, 1954a: 90.

Material examined

Holotype (**TMNH**): "'Nutwoods' Arminel-Alic C. P.-Walker leg. Holotype No: 1818 Schyzoschelusd aeneomicans KOCH Paracharactes aeneomicans Koch C. Koch det.,195 aeneomicans Koch".

Schyzoschelus africanus (Kaszab, 1941).
Psectropus africanus Kaszab, 1941: 36.
Schyzoschelus africanus (Kaszab, 1941). Koch 1954a: 82.

Material examined

(**TMNH**): "Willowmore Capland Dr. Brauns (4 specimens)" and another specimen with the same data and two additional labels: "S.A.M. Psectropus africanus Kasz. C. Koch det. 1957".

Schyzoschelus bispinosus Kaszab, 1941.
Psectropus bispinosus (Kaszab, 1941). Kaszab 1941: 38; Koch 1954a: 77.

Material examined

(**TMNH**): "CAPE col. Dumbrody. J. A. O'niel 1901 bispinosus (Kaszab)".

Schyzoschelus braunsi Koch, 1954 (Figure 2b).
Schyzoschelus braunsi Koch, 1954a: 83.

Material examined

Holotype (**TMNH**): "Willowmore Capland Dr. Brauns. Holotype No: 1786 Schyzoschelus braunsi KOCH Braunsi Koch".

Schyzoschelus capensis (Kaszab, 1941).
Psectropus capensis Kaszab, 1941: 37.
Schyoschelus capensis (Kaszab, 1941). Koch 1954a: 80.

Material examined

(**TMNH**): "Triangle 83, 2:20"".

Schyzoschelus jenkinsae Koch, 1954 (Figure 2c).
Schyzoschelus jenkinsae Koch, 1954a: 88.

Material examined

Holotype (**TMNH**): "Zwartberg C.P. nr. Avondrust Vii.1950.E.A.Pienaar Jenkinsae Koch HOLOTYPE No: 1815 Schyzoschelus jenkinsae KOCH".

Schyzoschelus karrooensis Koch, 1954 (fig. D).
Schyzoschelus karrooensis Koch, 1954a: 79.

Material examined

Paratype (**TMNH**): "Oudtshoorn 7 06 PARATYPE No: 1785 Schyzoschelus Karooensis KOCH Paratypus Schyzoschelus Karrooensis C. Koch sp.n".

Schyzoschelus kaszabi Koch, 1954 (fig. E).
Schyzoschelus kaszabi Koch, 1954a: 85.

Material examined

Holotype (**TMNH**): "Naauwpoort, C.P. 27-x-1948 Koch & van Son Kaszabi koch HOLOTYPE No: 1795 Schyzoschelus kaszabi KOCH".

Additional material

(**TMNH**): "Bloemfontein, O.R.C. 2-9-05 G. A. K. Marshall. 1908–213", "S.Afr.,Cape-Karoo Welwood farm 31.58 S − 24.28E 14.9.1983; E–Y:2007 groundtraps, 98 days leg. Penrith groundtrap with meat bait (2 specimens)", "S.Afr.,Cape-Karoo Vanwykafontein farm 30.38S–25.23E 22.9.1983; E–Y:2019 groundtraps,90 days leg. Penrith groundtrap with meat bait", "S.Afr., Cape-Karoo woodcliff farm 31.57S–24.38E 13.9.1983; E–Y:2004 singled day leg. Penrith". (**SANC**): "South Africa CP Middelburg 31.3.S 25.0 E 25/viii/1989 M de Jager AcLG1151 ex unbaited pitfalls near *Pentzia* spp NATIONAL COLL. OF INSECTS Pretoria.S.Afr (4 specimens, 5 additional specimens with different date: 7/IX/1989)", "S. Africa, O.F.S. Krugersdrift Dam BLOEMFONTEIN SE 2926 Aa NATIONAL COLL. OF INSECTS Pretoria.S.Afr (2 specimens)".

***Schyzoschelus ladini* Koch**, 1954 (fig. F).
Schyzoschelus ladini Koch, 1954a: 88.

Material examined

Holotype (**TMNH**): "Resolution Albany Distr VI 1928 A. Walton. Ladini Koch HOLOTYPE No: 1805 Schyzoschelus ladini KOCH" **Paratype** (**TMNH**): same data as holotype.

Additional material

(**SANC**): "SOUTH AFRICA: ECape Asante Sana Game Reserve *ca* 41 km E Graaf-Reinett 32° 15.934'S 24°58.801E 1400 m T1S1d 23.x.2010 J. M. Midgley NATIONAL COLL. OF INSECTS Pretoria.S.Afr Midgley donation 2021", "SOUTH AFRICA: ECape Asante Sana Game Reserve *ca* 43.5 km E Graaf-Reinett 32°17.092'S 24°00.521E 1024 m T2S1c 23.x.2010 J.M. Midgley NATIONAL COLL. OF INSECTS Pretoria.S.Afr Midgley donation 2021", "SOUTH AFRICA: ECape Asante Sana Game Reserve *ca* 38 km E Graaf-Reinett 32°15.689'S 24°57.099E 1419 m T3S1c 23.x.2010 J.M. Midgley NATIONAL COLL. OF INSECTS Pretoria.S.Afr Midgley donation 2021", "SOUTH AFRICA: ECape Asante Sana Game Reserve *ca* 41 km E Graaf-Reinett 32° 15.894'S 24°58.962E 2004 m T1S4a 15.iv.2010 J. M. Midgley NATIONAL COLL. OF INSECTS Pretoria.S.Afr Midgley donation 2021", "SOUTH AFRICA: ECape Asante Sana Game Reserve *ca* 43 km E Graaf-Reinett 32°15.128'S 24°00.418E 2011 m T2S5d 25.xi.2009 J.M. Midgley NATIONAL COLL. OF INSECTS Pretoria.S.Afr Midgley donation 2021".

Schyzoschelus sympatrius Koch, 1954 (Figure 2g).
Schyzoschelus sympatrius Koch, 1954a: 84.

Material examined

Holotype (**TMNH**): "Willowmore cape of g. Hope Dr. Brauns. HOLOTYPE No:1789 Schyzoschelus sumpatrius KOCH synpatrius Koch".

Schyzoschelus validus (Fairmaire, 1894).

Psectropus validus Fairmaire, 1894: 661. Gebien 1938: 391: Kaszab 1941: 35.

Schyzoschelus validus (Fairmaire, 1894). Koch 1954a: 87.

Material examined

(**TMNH**): "Resolution Albany Distr. VI 1928 A. Walton", "Port Eliz. 90.49. Psectropus validus Fairm Schyzoschelus Validus (Fairm) C. Koch det., 1954". (**SANC**): "Grahamstown, CP. 26-2-1955 G. A. Gill. AcC. 2992. NATIONAL COLL. OF INSECTS Pretoria.S.Afr" (**MNHM**): "Mars 1875 Baltrasna highl ds GRAHAMSTOWN Afrique du Sud Museum Paris Coll. P. Ardoin 1978".

Schyzoschelus dumosicola Koch, 1954a (Figure 1f).

Schyzoischelus dumosicola Koch, 1954a: 91.

= *Schyzoschelus dumosicola* var. *diversipenis* Koch, 1954a: 91 **syn. nov.**

Material examined

Schyzoschelus dumosicola dumosicola **Holotype** (**TMNH**): "Algoa Bay Capland Dr. Brauns 30.8.96, Dumosicola Koch, HOLOTYPE No: 1819 *Schyzoschelus dumosicola* KOCH". **Paratype** (**NRS**): same data as holotype.

Schyzoschelus dumosicola var. *diversipenis* **Holotype** (**TMNH**): "Algoa Bay Capland. Dr. Brauns. V. diversipenis HT Koch". **Paratype** (**TMNH**): "Addo Bush, Juli 1919, leg. J. Drury".

Note: In 1954b, Koch described a sympatric variation of *Schyzoschelus dumosicola* that slightly differed in the morphology of aedeagi from the nominal form. The name was considered subspecific under art. 45.6.4 (ICZN 1999) by subsequent authors. Kamiński (2016) elevated *S. d. diversipenis* to specific rank based on sympatry of the two subspecies, as his catalog could only make nomenclatural acts based on the original publication rather than specimens. Upon comparison of the type material and Koch's (1954a) figures, we conclude that these two entities are indeed variants of the same species co-occuring in the same locality (Willowmore). We propose synonymizing the two entities.

Schyzoschelus simplicipes Koch, 1954 (Figure 1e).

Schyzoischelus simplicipes Koch, 1954a: 84.

= *Schyzoschelus simplicipes willowmorensis* Koch, 1954a: 85 **syn. nov.**

Material examined

Schyzoschelus simplicipes simplicipes **Paratype** (**TMNH**): "George dist. C.P., C. Thorne Aug. 193? Paratypus SCHYZOSCHELUS simplicipes C. Koch sp.n. (two specimens)".

Schyzoschelus simplicipes willowmorensis **Holotype** (**TMNH**): "Willowmore, C.P. 1-XI-1948 Koch & van Son Paracharactes simplicipes ssp. willowmorensis C. Koch det., 195 KOCH ssp. willowmorensis HT Koch". **Paratype** (**TMNH**): same data as holotype.

Note: In 1954b, Koch described the above-mentioned subspecies of *Schyzoschelus simplicipes* based on subtle morphological differences (i.e. width of male tarsi and density of puncatation of the head and pronotum). Upon comparison of the type specimens and Koch's (1954a) figures, we conclude that these two entities are indeed variants of the same species co-occuring in the same locality (Willowmore). We propose synonymizing the two entities.

Discussion

Redefining taxonomic boundaries in the Schyzoschelus *generic group*

Many of the genera within Eurynotina are enigmatic, and are rarely collected/found in collections (Lumen & Kamiński 2023a, 2023b). In particular, the *Schyzoschelus* generic group has gone untreated since it was established nearly 70 years ago (Koch 1954a). This paper is the most comprehensive treatment of the group since its original designation. Despite sampling collections around the world, some taxa covered in this paper are known only from small collecting series – or singletons. As a result, taxonomic definitions are relatively "rigid", as almost no data on their morphological variability exists. For example, the *Schyzoschelus africanus* species group is made up of six species centered around Willowmore, South Africa, and represents a cluster of closely related species. Koch (1954a) noted that some of them may represent recent, closely related, endemic forms. While some species have characteristics that appear to be clearly diagnosable or stable (e.g. shape of hind tibiae/femora in *S. africanus* and tooth of the foretibiae in *S. capensis*), other species are more subtle or represent variation addressed in this publication (i.e. subspecies of *S. simplicipes*, *S. dumosicola*, and *S. diversipenis*). We hope the results here might offer a scaffold from which additional, more comprehensive revisions can be built.

Our observations largely support characters put forth by Koch (1954a) to demarcate the *Schyzoschelus* generic group from other Eurynotina, i.e. straight clypeal apex (Figure 3e), slender protibiae (Figures 1, 2 , and 4), rounded posterior angles of pronotum (Figure 3d). However, other characteristics were in need of revision. Namely, the merging of parameres used by Koch (1954a) to contrast *Heteropsectropus* and *Schyzoschelus* from the *Oncotus* generic group is in fact a characteristic found in all Eurynotina (Lumen & Kamiński 2023a). Instead, representatives of the *Schyzoschelus* generic group bear a unique groove running the length of the parameres through the fused basal portion (Figure 7c). Furthermore, the bordering of abdominal ventrite V used as a key feature is varied and present in some form in genera throughout all three generic groupings of Eurynotina, i.e. *Eurynotus* group: *Phylacastus* Fairmaire, 1897; *Oncotus* group: *Isoncophallus* Koch, 1954, *Menederes* Solier, 1848, *Stridigula* Koch, 1954, *Psectropus* Solier, 1848; *Schyzoschelus* group: *Schyzoschelus*, *Heteropsectropus*, and *Muelleropsectropus*) (Koch 1954a, 1954b, 1955; Kamiński 2016; present paper).

Within the *Schyzoschelus* generic group, Koch (1954a) defined *Schyzoschelus* via their stronger sexual dimorphism (male modifications to legs, striae on abdominal ventrites (Figures 1e, 4b,e) and abdominal ventrite V modifications (concavity in males, extreme apical grooves in females (Figures 3f and 4b), while attributing weaker sexual dimorphism and a subapical groove on abdominal ventrite V to *Heteropsectropus* (Figures 1a–c and 3c). However, Koch (1954a) had misgivings about two species in particular, as they display somewhat intermediate features – *Schyzoschelus malaisei* (Figure 1d) and *S. aeneomicans* (Figure 2a). Both were described by Koch (1954a) based on a single female and male specimen, respectively. During our investigation we found new male and female specimens of *S. malaisei*, which enabled us to establish a firmer taxonomic position for this species and reevaluate the taxonomic boundaries between the genera of the *Schyzoschelus* generic group. While some of the following features have a male bias due to a shortage of specimens, they proved reliable for distinguishing relatively large species groupings: strong modification of male tibiae (curved, hollowed-out, setose, etc.) (Figure 4e), abdominal segments (I and II with striated basal border (absent (Figure 1f) or present (Figures 1e and 4b)), abdominal ventrite V concavity (absent (Figure 3c) or present (Figure 4b)), abdominal ventrite V with large punctures and strong setae on apical/outside margin only (Figure 3) (or in middle/concavity (Figure 4)), large punctures with strong setae on abdominal ventrites other than V (Figure 4) (present/absent), number of elytral intervals (10 or 11) determined by a prematurely terminating stria (Figure 3a vs. Figure 3b), size of the epipleura at the humerus (large or small, narrowing abruptly or gradually, respectively (Figure 1a,b)). Using our new suite of characters and additional specimens, it was possible to reassess diagnostic features provided for *S. malaisei*. Unfortunately, we did not obtain additional material outside the type for *S. aeneomicans*; however, while it does have setation, lustre, and aedeagal characteristics similar to *Heteropsectropus*, the more consistent characteristics (i.e. number of elytral rows and epipleural width) are most in line with *Schyzoschelus*. Since we cannot presently confidently reassess its affiliation, we chose to leave it within *Schyzoschelus*. Alternatively, *S. malaisei* showed an even stronger affinity with *Heteropsectropus*, so we designate a new genus (*Muelleropsectropus* **gen. nov**.) to accommodate it. Similar to *S. aeneomicans*, *Muelleropsectropus* has *Heteropsectropus*-like traits (i.e. head/pronotal setae and aedeagal qualities); however, *Muelleropsectropus* has 10 elytral intervals (vs. 11), and a wide epipleural humerus (vs. narrow). Further, female specimens made it possible to compare internal morphology between *Schyzoschelus*, *Heteropsectropus*, and *Muelleropsectropus*. Contrastingly, the morphology of the bursa copulatrix differs between all three: *Schyzoschelus* with a terminal "bulb-like" pouch (Figure 5e), *Muelleropsectropus* with two additional pouches (Figure 6a), and *Heteropsectropus* without any additional pouches (Figure 5d). It is still possible that further examination within *Schyzoschelus* could reveal more divisions or subsequent lumping of taxa; however, without more specimens, representatives of both sexes, etc., more action will remain impeded. The divisions and characteristics we present here (see key and diagnoses) provide clear, well-defined groupings based on the most comprehensive set of material available for future workers to use.

Variability within Heteropsectropus

Most of the diversity within *Heteropsectropus* (four of seven species) was based on singletons (Koch 1954a), i.e. *H. difficilis*, *H. longantennatus*, *H. montisdraconis*, and *H. transvaalensis*. Through comparison with additional material obtained as a result of this study, the variation within these taxa is easily encapsulated within fewer, more easily diagnosed, species concepts. For instance, *H. montisdraconis* and *H. longantennatus* were both described from single (male) specimens collected from localities within 160 km of one another (Koch 1954a; Kamiński 2016). Comparison of type material also revealed very little difference between the original specimens externally and internally. The case of *H. difficilis*, *H. amaroides*, *H. natalensis*, and *H. transvaalensis* proved to be more challenging. Namely, while the individual type specimens do indeed appear different, extremes concerning characters such as the "flatness" or "squareness" of the elytra described by Koch (1954a) fall well within a continuum more easily explained by variation over geographic space (Figure 8). Despite these findings, the first two groupings designated in the identification key provided by Koch (1954a) proved to be sharply and reliably separable based on some of his original characteristics, i.e. *H. longantennatus* + *H. montisdraconis*, and *H. aenescens*. *Heteropsectropus longantennatus* (= *H. montisdraconis* **syn. nov**.) is the only species of the genus with deeply impressed elytral striae and elongate antennae (Figure 1a). In the case of *H. aenescens*, the shape of the elytra is helpful in diagnostics, especially in conjunction with the intensity of setation on

the pronotum (see *Muelleropsectropus* in Figure 3d) (though Koch (1954a) made no mention of this feature). The rest of the species then fell into a set of difficult-to-interpret concepts that likely suffered from diagnosing individuals. The new classification we present provides clearer concepts, and the remaining species are well diagnosable (i.e. *H. aenescens*, *H. difficilis*, *H. longantennatus*).

Immature stages and ovoviviparity

The limits of the generic groupings with Eurynotina are important – not only for diagnostic and taxonomic purposes, but also for behavioral and ecological studies. To date, there are only 15 recorded species of Tenebrionidae that are ovoviviparous (Lumen & Kamiński 2023a; present paper). Such a rare reproductive strategy likely has interesting evolutionary origins and implications, and may be useful in phylogeny-based classification (Evangelista et al. 2019; Djernæs et al. 2020; Li 2022). As a result of our investigation here, an additional species of Eurynotina is now recorded as ovoviviparous. This discovery seems especially interesting as it concerns the second lineage within the subtribe – the other consists of closely related sister genera *Biolus* and *Eurynotus* (Lumen & Kamiński 2023a). *Heteropsectropus* is a more distantly related taxon, so while the evolutionary pattern and phylogenetic context of ovoviviparity in Eurynotina remains uncertain, it may be more widespread in the subtribe.

Though Schulze L (1969) included a picture of an identified *Heteropsectropus* larva in her paper, she did not provide any detailed comments or descriptions of it. Despite an overall scarcity of materials in entomological collections for examination, Eurynotina (specifically *Heteropsectropus difficilis*) now represents one of the best-described examples of African darkling beetles, as the first- and later instar larvae, pupae, and adults of both sexes are now described here. Interestingly, the spikes on the last abdominal segment of the larvae are not visible in the cast of the first-instar larva, and appear in later instars during development (Figures 5a and 9k). Modifications to the abdominal segment are diagnostic for many tribes within Blaptinae (Kamiński et al. 2019a, 2021); therefore, changes to these structures throughout development may be of further diagnostic or evolutionary import. Additionally, a pale extension on the base of the mandibles may be diagnostic for the subtribe (Figure 9b,c), as it has also been observed in *Eurynotus asperatus* (Kamiński et al. 2019b). To date, all larvae in Eurynotina possess a wide ligula and four spikes on the last abdominal segment in later instars (Kamiński et al. 2019b). The pupa of *Heteropsectropus* is identifiable by morphology congruent with adults: pronotal shape strongly resembling adults, straight clypeus, and sulcus on abdominal ventrite V (Figure 10a,b).

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ORIGINAL ARTICLE

Systematic Entomology

Complementary genomic and morphological data elucidate the phylogeny of obscure darkling beetles (Blaptinae: Platynotini: Eurynotina)

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Abstract

Enigmatic and elusive, the darkling beetle subtribe Eurynotina Koch (Tenebrionidae: Blaptinae) is a southern African endemic composed of nearly 100 species, which prior to this study were classified within 18 genera. Over 75% of the currently recognized species are known exclusively from their small descriptive series, sometimes only by holotypes. The shortage of individual specimens makes the challenges presented by damaged material more problematic for genetic recovery, while also further hindering comprehensive morphological treatment. These shortcomings have led to this group becoming one of the least studied subtribes within the subfamily Blaptinae. To bridge data gaps caused by the scarcity of the material and produce a robust phylogeny of Eurynotina, a combination of different datasets is used: nuclear targeted enrichment (499 loci spanning 155,172 amino acids), mitochondrial (12 loci/2395 amino acids) and morphology (91 characters). All datasets were analysed separately as well as combined, which offered detailed and taxonomically comprehensive phylogenetic topologies including representatives of all known genera. As a result, the following taxonomic changes are proposed to reflect the phylogenetic topologies and introduce stability to the subtribe: *Colophonexsula* Lumen & Kamiński **gen. nov**. is erected to receive *C. puerilis* (Koch) **comb. nov**.—a species formerly classified within *Colophonesthes*. Subgenera *Anamenederes* Koch **stat. nov**., *Menoncotus* Koch **stat. nov**. and *Quadroncotus* **Koch stat. nov**. are elevated to generic level. The following generic synonyms are introduced: *Stridigula* Koch (=*Cilioncotus* Koch **syn. nov**.); *Eurynotus* Kirby (=*Biolus* Mulsant & Rey **syn. nov**. =*Neosolenopistoma* Bouchard & Bousquet **syn. nov**.). The concept of the genus *Oncotus* Solier **sens. nov**. is revised. Additionally, the following new species are described: *Psectrapus byki* Lumen & Kamiński **sp. nov**., *P. simplicimentulum* Lumen & Kamiński **sp. nov**., *Ograbies calumnus* Lumen & Kamiński **sp. nov**. Two new synonyms are introduced at the species level: *Oncotus capensis* Solier (=*Oncotus capicola* Koch **syn. nov**.); *Stridigula arguta* Koch (=*O. humerisetosus* Koch **syn. nov**.). Neotypes are designated for *Oncotus farctus* Solier,

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Psectrapus bipartitus Solier and *Oncotus capensis* Solier to fix the status of *Oncotus*, *Psectrapus* and *Ograbies*, respectively. The following new combinations are introduced as a result of the aforementioned taxonomic decisions: *Eurynotus brunoi* (Lumen & Kamiński) **comb. nov.**, *Menoncotus chaetotaxicus* (Koch) **comb. nov.**, *M. jokli* (Koch) **comb. nov.**, *M. sinuatipes* (Koch) **comb. nov.**, *Quadroncotus irrepertus* (Koch) **comb. nov**. and *Stridigula namaquanus* Koch **comb. nov**. The new concept of Eurynotina comprises 21 genera.

KEYWORDS
Africa, classification, Museomics, new species discovery, Tenebrionidae

INTRODUCTION

Despite a growing number of phylogenetic contributions, the systematics of darkling beetles (Coleoptera: Tenebrionidae) remain insufficiently studied (Kamiński et al., 2021). Recent studies still rely on dated morphological concepts (e.g. Doyen & Tschinkel, 1982; Watt, 1974), and focus on resolving relationships at the subfamily level using molecular data. While such efforts offer valuable reference points for targeted taxonomic work (Aalbu et al., 2023; Kamiński et al., 2024; Kergoat et al., 2014; Ragionieri et al., 2023), numerous lineages of Tenebrionidae remain unassessed within a robust phylogenetic framework. A key limitation in studying some lineages of Tenebrionidae is the scarcity of freshly collected, ethanol-preserved material suitable for molecular work. Advancements in sequencing technologies have begun to mitigate these challenges, particularly through museomics, the extraction of DNA from historical specimens (Dabney et al., 2013; Hagemann et al., 2024; Smith et al., 2021). Museomics has enabled molecular insights even from beetles long preserved in collections (e.g., Jin et al., 2020; Johnston et al., 2022; Kim & Farrell, 2024). However, for some of the most taxonomically obscure and elusive groups, museomics data remain insufficient for resolving phylogenetic relationships.

One such lineage is Eurynotina Koch (Blaptinae: Platynotini: Tenebrionidae), a subtribe confined to southern Africa, comprised of 18 genera and 92 valid species and subspecies, only known from several 100 specimens distributed in a handful of museum collections (Koch, 1954a; Koch, 1954b; Koch, 1955; Lumen & Kaminski, 2024; Lumen & Kamiński, 2023; Lumen & Kamiński, 2024). While some species are relatively common, the majority (>75%) are known only from their small descriptive series (Kamiński, 2016). Further, in many cases, the specimens are damaged or hollow (missing extractable tissue), reducing the likelihood of genetic capture/recovery for sequencing and subsequent phylogenetic analyses. Morphological investigation is also hampered by a lack of data in cases where specimens are badly damaged (i.e. missing body parts), or are represented only by male or female specimens, preventing full codification into morphology matrices, for example, *Schyzoschelus aeneomicans* Koch known only by the male holotype, or *Oncotus irrepertus* Koch known only by the type series of seven females (Kamiński, 2016). As a result, the systematic revision of the group has largely been stalled.

Contrastingly, the sister subtribe Platynotina Mulsant & Rey has received extensive treatment (e.g., Banaszkiewicz, 2007; Endrody-Younga, 1988; Endrody-Younga, 2000; Ferrer, 1983; Ivie et al., 2021; Iwan, 1990; Iwan, 1995; Iwan, 2002; Iwan et al., 2012; Iwan & Kamiński, 2014; Kamiński, 2012; Kamiński, 2013; Kamiński, 2014; Kamiński, 2015; Kamiński, 2017; Kamiński & Iwan, 2013; Kamiński & Schoeman, 2018; Kaszab, 1941; Koch, 1956; Schimrosczyk, 2010), while Eurynotina has only recently attracted focused attention (e.g., Banaszkiewicz, 2006; Kamiński, 2016; Kamiński et al., 2019; Kamiński & Schawaller, 2019; Koch, 1954a; Koch, 1954b; Koch, 1955; Lumen & Kaminski, 2024; Lumen & Kamiński, 2023; Lumen & Kamiński, 2024). The imbalance of taxonomic work between the two subtribes of Platynotini not only limits our understanding of Eurynotina itself but also constrains broader evolutionary and biogeographic interpretations within the subfamily Blaptinae. Furthermore, given its endemic distribution and ecological specificity (ovoviviparity), Eurynotina represents a potentially valuable model for understanding patterns of arid-adapted diversification in southern African Coleoptera (Lumen & Kamiński, 2024), which remains difficult to assess and study due to outdated classification.

Representatives of Eurynotina are morphologically defined within Blaptinae by the presence of a stridulatory gula and lack of aedeagal ancorae (Koch, 1956; Lumen & Kamiński, 2024). Present classification places the subtribe as sister to Platynotina, where both entities form Platynotini (Kamiński et al., 2021). The monophyly of Eurynotina, with regard to Platynotina, has not been fully tested. Both subtribes contain taxa violating their current morphological tribal definitions (Kamiński, 2015; Lumen & Kamiński, 2023), and the most comprehensive phylogenetic study included only a fraction of the taxonomic diversity of Eurynotina (i.e., four species) (Kamiński et al., 2021). Furthermore, relations within Eurynotina remain uninvestigated, and the tentative subdivision of the subtribe proposed by Koch (1954a, 1954b, 1955) into the three following morphological generic groups remains untested: (i) *Eurynotus* group (clypeal apex deeply emarginated: genera *Eurynotus* Kirby and *Phylacastus* Fairmaire); (ii) *Schyzoschelus* group (clypeal apex straight: *Heteropsectropus* Kaszab and *Schyzoschelus* Koch); (iii) *Oncotus* group (clypeal apex shallowly, but clearly emarginate: *Byrrhoncus* Koch, *Capidium* Koch, *Colophonesthes* Koch, *Hirtograbies* Koch, *Isoncophallus* Koch, *Menederopsis* Koch, *Menederes* Solier, *Ograbies* Péringuey, *Oncotus* Solier, *Phaleriderma* Koch, *Psectrapus* Solier and *Stridigula* Koch). Subsequently, Lumen and Kamiński (2024), Lumen and Kaminski (2024) added *Muelleropsectropus* Lumen & Kamiński and *Biolus* Mulsant & Rey into the *Schyzoschelus* and *Eurynotus* lineages respectively Lumen and Kamiński (2024), Lumen and Kaminski (2024).

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The present study aims to test the monophyly of subtribe Eurynotina and investigate the coherence and phylogenetic relations between its genera. To overcome limitations of traditional datasets, a triad of complementary approaches is employed: (i) targeted enrichment (TE) sequencing of 499 nuclear loci from ethanol-preserved specimens (following Kanda, 2017; Swichtenberg et al., 2023; Kamiński et al., 2024), (ii) mitochondrial DNA recovery from both fresh and historical specimens and (iii) morphological cladistic analysis. Each dataset is analysed independently and in combination to maximize phylogenetic resolution. This integrative approach, combining high-throughput museomics with fresh tissue sequencing and morphological systematics, is one of the first comprehensive efforts of its kind within Tenebrionidae. Finally, a new classification of the subtribe is introduced based on the acquired topologies.

MATERIALS AND METHODS

Taxon sampling

Operational taxonomic units (OTUs) for phylogenetic analyses were defined in a preliminary taxonomic study, which included verification of type material, morphology, and testing diagnostic features for all previously described species (see: Kamiński, 2016, Lumen & Kamiński, 2023; Lumen & Kamiński, 2024; Lumen & Kaminski, 2024, Table S1). As such, in the case of morphology-based analyses, representatives of all morphologically coherent genera and subgenera of Eurynotina were scored, with additional sampling made for incongruent species to more densely cover the morphological diversity of the subtribe. Similarly, molecular investigations aimed to cover the preestablished subtribial diversity by combining ethanol-preserved and pinned, dried specimens (Table S2). Morphological features were scored for all Eurynotina species included in the molecular analyses to ensure the compatibility of OTUs from each dataset.

A wide array of outgroup taxa was included to test the monophyly of Eurynotina using ethanol-preserved specimens. Namely, representatives of all major lineages of the sister subtribe Platynotina (Iwan, 2002; Kamiński, 2015; Koch, 1956): *trigonopoid* (*Atrocrates* Koch, *Melanopterus* Mulsant and Rey, *Schelodontes* Koch, *Trigonopus* Mulsant and Rey), *melanocratoid* (*Sebastianus* Iwan, *Styphacus* Fairmaire), *platynotioid* (*Asiopus* Sharp, *Anchophthalmus* Gerstaecker) and *gonopoid* (*Anomalipus* Latreille, *Gonopus* Latreille) lineages. Additionally, two *Stenolamus* Gebien species representing the closely related tribe Opatrini Brullé, and *Blaps mucronata* Latreille of the distantly affiliated Blaptini (Kamiński et al., 2023; Kamiński et al., 2024) were included. This set of outgroup taxa was later trimmed to increase the parsimoniousness of morphological runs, leaving only *Gonopus deplanatus* Fåhraeus (Platynotina) as an outgroup reference for remaining analyses.

Pinned material for morphological examination was acquired from the following institutional insect collections: BPBM, Bernice P. Bishop Museum (Honolulu, Hawaii, USA); HNHM, Magyar Természettudományi Múzeum (Budapest, Hungary); MIZPAN, Muzeum i Instytut Zoologii, Polska Akademia Nauk (Warsaw, Poland); NHMB, Natural History Museum Basel (Basel, Switzerland); MNHN, Museum d'Histoire Naturelle (Paris, France); NHMUK, Natural History Museum (London, United Kingdom); NMNW, Windhoek National Museum of Namibia (Windhoek, Namibia); PERC, Purdue Entomological Research Collection (West Lafayette, Indiana, USA); RBINS, Royal Belgian Institute of Natural Sciences (Brussels, Belgium); RMCA, Royal Museum for Central Africa (Tervuren, Belgium); SANC, South African National Collection of Insects (Pretoria, South Africa); SMNS, Staatliches Museum für Naturkunde (Karlsruhe, Germany); TMNH, Ditsong National Museum of Natural History (Pretoria, South Africa); ZMHB, Museum für Naturkunde (Berlin, Germany); ZMUK, Zoologisches Museum, Universität Kiel (Kiel, Germany).

Ethanol-preserved specimens used for extractions were collected by the authors (permit numbers in acknowledgments) or acquired from the wet collections of MIZPAN and PERC. Additional pinned specimens originating from MIZPAN were processed to extend the taxonomic coverage of molecular-based analyses (Table S2).

Morphological dataset

Morphological terminology follows Matthews et al. (2010), with additional specialized terms for terminalia following Banaszkiewicz (2006), Iwan and Kamiński (2016) and Lumen and Kamiński (2023), Lumen and Kamiński (2024), Lumen and Kaminski (2024). Dissections followed the methodology outlined in Kamiński et al. (2021): specimens were relaxed in 10% KOH solution prior to dissection, and genital tubes were stained with chlorazol black. Images were taken using a Canon 1000D body with extension rings and a Canon EF 100 mm macro lens, a Nikon D3500 body with an adapter for a Nikon SMZ800N microscope, and with a Hitachi S3400N SEM in MIZPAN. Figures were assembled using Photoshop v.23.5.1.

Morphology of adult specimens was evaluated and scored in a morphological matrix in MESQUITE v.3.61 (Maddison & Maddison, 2019). Characters were largely derived from Lumen and Kamiński (2024) and further modified as a result of the aforementioned preliminary taxonomic study with new characters presented in the results section (also see Figures 3–5). Characters from previous studies are available in Table S3. Morphology was determined and scored based on the synthesis of multiple specimens in an effort to capture the average state(s) for each OTU (Table S2). The full morphological matrix is available for this publication (Table S4). Larval features were excluded as data on preimaginal stages within Eurynotina are scarce (Kamiński et al., 2019; Lumen & Kaminski, 2024; Lumen & Kamiński, 2023; Lumen & Kamiński, 2024).

Targeted enrichment (TE) dataset

DNA was extracted from the head capsules and pronota of specimens using QIAamp DNA Micro Kit following the manufacturer's protocols. Grinding of the cuticle was also avoided to preserve specimens for morphological examination. Extractions were performed in a sterilized

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laminar flow hood to minimize contamination from non-target DNA (see Kanda et al., 2015). Extraction voucher specimens were rearticulated and card-mounted. Additionally, unique identifiers (TB or MEL#s) were assigned to each specimen for referencing records uploaded to the Sequence Read Archive (BioProject: PRJNA1016168). All voucher specimens are preserved in the Purdue Entomological Research Collection (PERC) and MIZPAN (Table S2).

Extracts were sent to Daicel Arbor Biosciences for library preparation, targeted enrichment and sequencing on a NovaSeq 6000 system using 150 bp paired-end runs. Targeted enrichment was performed using MyBaits probe kits for 620 nuclear loci spanning ~820 kb. Loci were chosen from an existing set of protein coding loci used in Pimeliinae (Kanda, 2017; Swichtenberg et al., 2023) with baits modified based on transcriptomic data from *Eleodes delicatus* (Blaptinae), *Eulabis bicarinatus* (Tenebrioninae), *Tenebrio molitor* (Tenebrioninae) and *Clamoris americanum* (Phrenapatinae) and checked using BLAST filtration against the *Tribolium castaneum* Herbst, *T. confusum* Jacquelin du Val and *T. madens* Charpentier genomes. Final probes (80 bp each) were double tiled for fresh material and triple tiled for museum specimens.

Sequence assemblies were performed on Purdue University's Bell community cluster, within the Rosen Center for Advanced Computing (McCartney et al., 2014). Read quality was assessed with FastQC v.0.11.9 (Andrews, 2010). Reads with an average sequence quality across any 4 bases below 20 were removed with Trimmomatic (Bolger et al., 2014). The HybPiper v. 2.0 pipeline (Johnson et al., 2016), operating in DIAMOND mode (Buchfink et al., 2015), was used to assemble reads using the set of orthologues designed by Kanda (2017).

The resulting nucleotide sequences were translated to amino acids and then aligned in MAFFT with the L-INS-I algorithm (Katoh et al., 2005). Low-quality amino acid sequence sites were masked, while sequences with over 50% gaps per locus were trimmed in trimAl (Capella-Gutiérrez et al. 2009). Surviving sequences were concatenated using FASConCAT (Kück & Meusemann, 2010) into a partitioned dataset including a total of 499 loci spanning 155,172 amino acids (Kamiński & Lumen, 2025).

Mitochondrial dataset

Due to poor recovery of targeted nuclear protein coding genes for pinned historical specimens, bycatch mitochondrial data were harvested for all specimens included in sequencing (Figure S1). The mitochondrial genomes for selected fresh samples representing Eurynotina (*Byrrhoncus* sp. MEL127, *Eurynotus asperatus* Muslant & Rey TB23375) and Platynotina (*Anomalipus elephas* Fåhraeus TB26363, *Asiopus aciculatus* LeConte MEL147) were assembled de novo using the multicell mode in SPAdes v.3.13.035 (Bankevich et al., 2012). Prior to this process, raw data were checked for quality and trimmed as described above. Assembled mitochondrial scaffolds were identified using BLAST searches against the published mitochondrial genome from *Asbolus verrucosus* LeConte (NC_027256). Resulting sequences of 13 protein coding genes were used in HybPiper v. 2.0 to recover mitochondrial loci from all remaining samples. The SendSketch script, as implemented in BBMap/36.92 (Bushnell, 2014), was used to characterize the metagenomic profile of assembled contigs and check for contamination. Similar to the TE dataset, obtained nucleotide sequences were translated to amino acids, aligned with MAFFT and trimmed in trimAl. Data were concatenated in FASConCAT into a partitioned dataset comprising a final total of 12 loci spanning 2395 amino acids (Kamiński & Lumen, 2025).

Data analysis

All phylogenetic analyses were performed on Purdue University's Bell community cluster, within the Rosen Center for Advanced Computing. Resulting trees were visualized in FigTree 1.4.4 (Rambaut, 2009) and Winclada 1.61 (Nixon, 2002).

Monophyly of Eurynotina

Targeted enrichment data from fresh, ethanol-preserved specimens was used to test the monophyly of the subtribe. Maximum likelihood (ML) analyses were run in IQ-TREE 2 (Minh et al., 2020) using an edge-unlinked partition model (−Q), with the dataset partitioned by loci and the best-fit models for each locus selected via ModelFinder (Kalyaanamoorthy et al., 2017). Support for the resulting topology was assessed using 10,000 UltraFast Bootstrap (UFB) (Hoang et al., 2018) iterations. The molecular matrix was also analysed using ExaBayes 1.5.1 (Aberer et al., 2014). Two independent runs, each with 1 cold chain and 3 heated chains, were performed. Analyses were run for 500,000 generations with a burn-in fraction of 0.25, and convergence was determined by the average standard deviation of the split frequencies (ASDSF); runs were considered to have converged at ASDSF <0.01.

Generic relationships of Eurynotina

Morphology

The morphological dataset (Table S4) was imported into TNT v.1.5 (Goloboff & Catalano, 2016) for phylogenetic inference using maximum parsimony. A setk script, developed by Salvador Arias, was used to identify the most appropriate K value through the formula proposed by Goloboff et al. (2008). The resulting k value was then used in the implied weighting scheme for implicit enumeration search. Nodes were evaluated for Bremer support with the Bremer.run script within TNT (Bremer, 1994). Performance of characters in parsimony analysis was verified by calculating the consistency (ci) and retention indices (ri) in TNT with *wstats.run* script, whereas the values of CI and retention RI indices for the whole matrix were obtained in the same software with *stats.run* script. Additionally, ML analyses were run in IQ-TREE 2 (Minh et al., 2020) as specified above. UFB values were then mapped onto the cladogram from the parsimony analyses.

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Museomics

ML (IQ-TREE 2) and Bayesian (ExaBayes) analyses were performed on the concatenated TE and mitochondrial datasets (see *Monophyly of Eurynotina*). The concatenated dataset consisted of 510 loci spanning 157,567 amino acids (Kamiński & Lumen, 2025).

Combined analysis

A concatenated dataset of TE, mitochondrial and morphological data was analysed both in IQ-TREE 2 and MrBayes v.3.2.7a (Kamiński & Lumen, 2025). Data partitions and models of sequence evolution were assessed with IQ-TREE 2. The ML run was performed under the same specifications as stated above (see *Monophyly of Eurynotina*). MrBayes analysis was conducted with models inferred from IQ-TREE 2. Two independent runs, each with one cold and three heated chains, were performed. Analyses were run for 1 million generations, while parameters were sampled every 1000 generations. A burn-in fraction of 25% was used on the resulting data, and convergence was determined by the ASDSF; runs were considered to have converged at ASDSF <0.05.

RESULTS

Monophyly of Eurynotina

Analysis of the TE dataset included 11 of the 18 currently recognized genera representing all previously designated lineages among Eurynotina, that is, *Eurynotus*, *Oncotus* and *Schyzoschelus* generic groups. Topologies obtained in ML and ExaBayes runs are fully convergent (Figure 1 and Figure S2). The monophyly of the Eurynotina was highly supported (UFB = 100; PP = 1.0) regardless of the inference method (Figure 1). The subtribe was always recovered sister to Platynotina. Within Eurynotina, the distinctiveness of the *Eurynotus* lineage (sensu Koch, 1954a; Koch, 1954b) was not supported by the analysis as *Phylacastus* was projected as an independent lineage (Figure 1). On the other hand, the *Oncotus* and *Psectrapus* lineages were rendered monophyletic with high support. Representation of the *Schyzoschelus* lineage was too scarce to properly test its phylogenetic status with this dataset, as only *Heteropsectropus* was sampled (Figure 1).

The monophyly of the majority of the genera representing Eurynotina was not challenged; however, the data suggest that the taxonomic concepts of *Eurynotus* and *Menederes* should be revisited (Figure 1). In the first case, *Eurynotus* was rendered paraphyletic in regard to *Biolus*. In the case of *Menederes*, its subgeneric components (i.e., *Anamenederes* and *Menederes*) were recovered as independent phylogenetic lineages (Figure 1).

Generic relationships of Eurynotina

Molecular analysis

Including museum specimens greatly increased the number of genera for study. Namely, 15 out of 18 genera were included in the analysis (Figure 2, Table S1). Despite exhaustive efforts, no molecular data were recovered for *Schyzoschelus*, while *Menederopsis and Muellerop-sectropus* were not sampled due to the scarcity of available specimens. Museum samples are mostly represented on the phylogenetic tree based on mitochondrial data, as the recovery of targeted nuclear loci was poor (Figure S1). Branch support for the majority of clades was relatively high – especially in the ExaBayes run. Exabayes and IQ-TREE topologies were largely congruent and both returned weakly supported topologies within the *Oncotus* lineage (Figure 2 and Figure S3). The two analyses differed in the recovered position of the genus *Stridigula*; specifically, its placement as either sister to a clade of the rest of the *Oncotus* lineage (ExaBayes: Figure 2), or within and sister to subgenus *Menederes* (IQ-TREE: Figure S3).

Similarly, as in the TE-based analysis, the subtribe Eurynotina was divisible into four major phylogenetic lineages, that is, *Eurynotus*, *Phylacastus*, *Schyzoschelus* and *Oncotus*. All were fully supported by both analyses (Figure 2 and Figure S3).

Analysis revealed taxonomic inconsistencies within the *Eurynotus* lineage and the genus *Menederes*. In the former, the data falsify the distinction between the genera *Biolus* and *Eurynotus* (Figure 2). In the latter, the topology suggests the independent nature of the subgenera *Anamenederes* and *Menederes*. On the other hand, the monophyly of the following genera was supported (Figure 2): *Byrrhoncus*, *Heteropsectropus*, *Isoncophallus*, *Ograbies*, *Oncotus*, *Phylacastus* and *Psectrapus*.

Morphological matrix

A total of 91 characters (numbered 0–90 in keeping with the morphological phylogeny depiction) were scored for 61 Eurynotina species representing all genera and coherent species groups, including 17 type species (Tables S1 and S3). The total dataset is composed of 14 characters of the head, 20 of the prothorax, 22 of the pterothorax, 19 of the legs and 16 of the abdomen and genitalia. The matrix is modified from previous studies (Lumen & Kamiński, 2024; Iwan, 2002, Table S3). Parsimony-uninformative and/or single-species diagnostic characters were determined and pruned during matrix construction. The consistency (ci) and retention indices (ri) are provided for each character. Figures are provided for characters newly investigated as of this publication (see Figures 3–5); previously examined characters are better outlined in Lumen and Kamiński (2024) and Iwan (2002). Below are the newly generated characters (for the full list and matrix see Tables S3 and S4 respectively). Character occurrence is reported using taxon names reflecting new classification here for diagnostic purposes (see Figures 6 and 7).

Head characters

Demarcation between frons and clypeus reduced (Character #4): (0) Absent; (1) Present. In most taxa, the epistoma has some form of visible division between the clypeus and frons. The demarcation can

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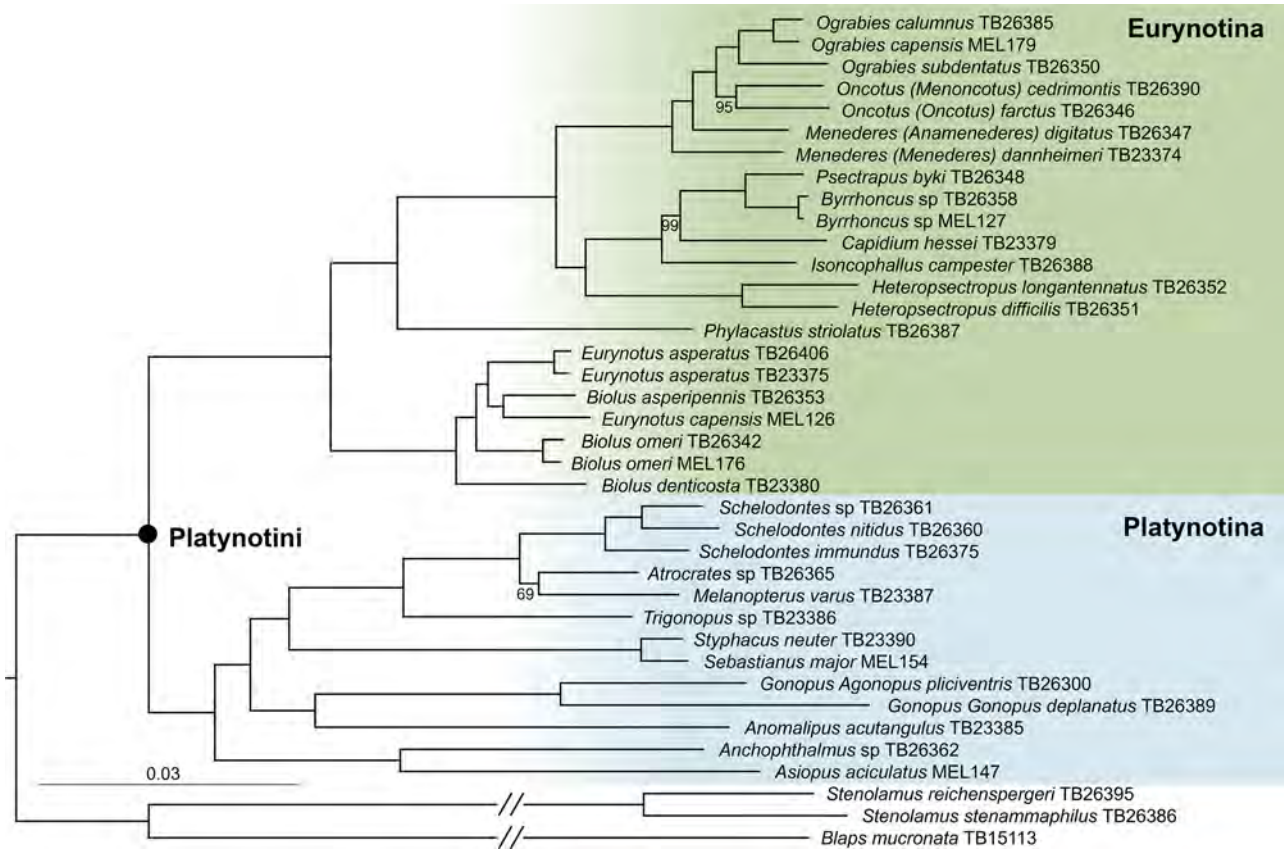


FIGURE 1 Phylogeny of the tribe Platynotini inferred from a targeted enrichment dataset using fresh, ethanol-preserved specimens. Topology is the Majority Rule consensus from a Bayesian analysis (ExaBayes) of the concatenated matrix covering 499 nuclear loci (151,172 aligned amino acid positions). All depicted nodes received full Bayesian support (posterior probability = 1.0). Ultrafast bootstrap values (below nodes) from IQ-TREE 2 (see Figure S2) and posterior probabilities (above nodes).

take the form of a small suture or sulcus running longitudinally across the width of the head or depression, or be reduced such that there is little to no demarcation visible. Demarcation is reduced (1) (Figure 3a) in *Byrrhoncus*, *Capidium*, *Colophonesthes*, *Colophonexsula* **gen. nov.**, *Isoncophallus*, *Phylacastus*, *Psectrapus*. [ci = 0.333, ri = 0.846].

Epistoma and clypeus **(Character #5):** (0) Fused and undifferentiated; (1) Fused and differentiated. In most taxa the epistoma and clypeus are fully fused (0); however, in *Phaleriderma* the clypeus is pronounced in structure and offset from the epistoma (1) (Figure 3b). [ci = 1.00, ri = 1.00].

Epistomal margin with raised carina **(Character #6):** (0) Absent; (1) Present. The anterior edge of the epistoma with a raised carina running along the border. Present (1) (Figure 3f) in *Anamenederes* **stat. nov.**, *Menederes* **sens. nov.**, *Menederopsis*, *Menoncotus* **stat. nov.**, *Ograbies*, *Oncotus* and *Quadroncotus* **stat. nov.** [ci = 1.00, ri = 1.00].

Epistomal carina complete **(Character #7):** (0) Absent; (1) Complete; (2) Interrupted medially or restricted to lateral margins. The epistomal carina (see Character #6), when present, is complete along the entire border of the epistoma (1) in *Menederopsis* and *Ograbies*. The carina is interrupted in the middle and restricted to the lateral edges of the epistoma (2) (Figure 3c) in *Anamenederes* **stat. nov.**, *Menederes* **sens. nov.**, *Menoncotus* **stat. nov.**, *Oncotus*, *Quadroncotus* **stat. nov.** [ci = 1.00, ri = 1.00].

Prementum cordiform **(Character #8):** (0) Absent; (1) Present. Prementum either with straight anterior edge (0) (Figure 3e) or with curvature, bend or median notch, giving a slight cordiform shape (1) (Figure 3d). The prementum was cordiform (1) in *Anamenederes* **stat. nov.**, *Eurynotus asperatus*, *E. privisolum*, *Hirtograbies* (except *H. gariepinus*), *Menederopsis*, *Ograbies* (except *O. campi*), *Oncotus*, *Phaleriderma*, *Psectrapus*, *Quadroncotus* **stat. nov.**, *Schyzoschelus* and *Stridigula namaquanus*. [ci = 0.111, ri = 0.636].

Prothorax characters

Pronotal setae on dorsal surface, excluding extreme margin **(Character #15):** (0) Absent; (1) Present (restricted to isolated setae on edges and/or corners); (2) Present and abundant. Most taxa (*Byrrhoncus*, *Capidium*, *Colophonesthes*, *Colophonexsula* **gen. nov.**, *Eurynotus*, *Gonopus*, most *Hirtograbies*, *Isoncophallus*, *Menoncotus* **stat. nov.**, *Oncotus*, *Phylacastus* and *Psectrapus*) lack strong setation of the pronotum (0). Some (*Anamenederes* **stat. nov.**, *Heteropsectropus*, *Menederes* **sens. nov.**, *Menederopsis*,

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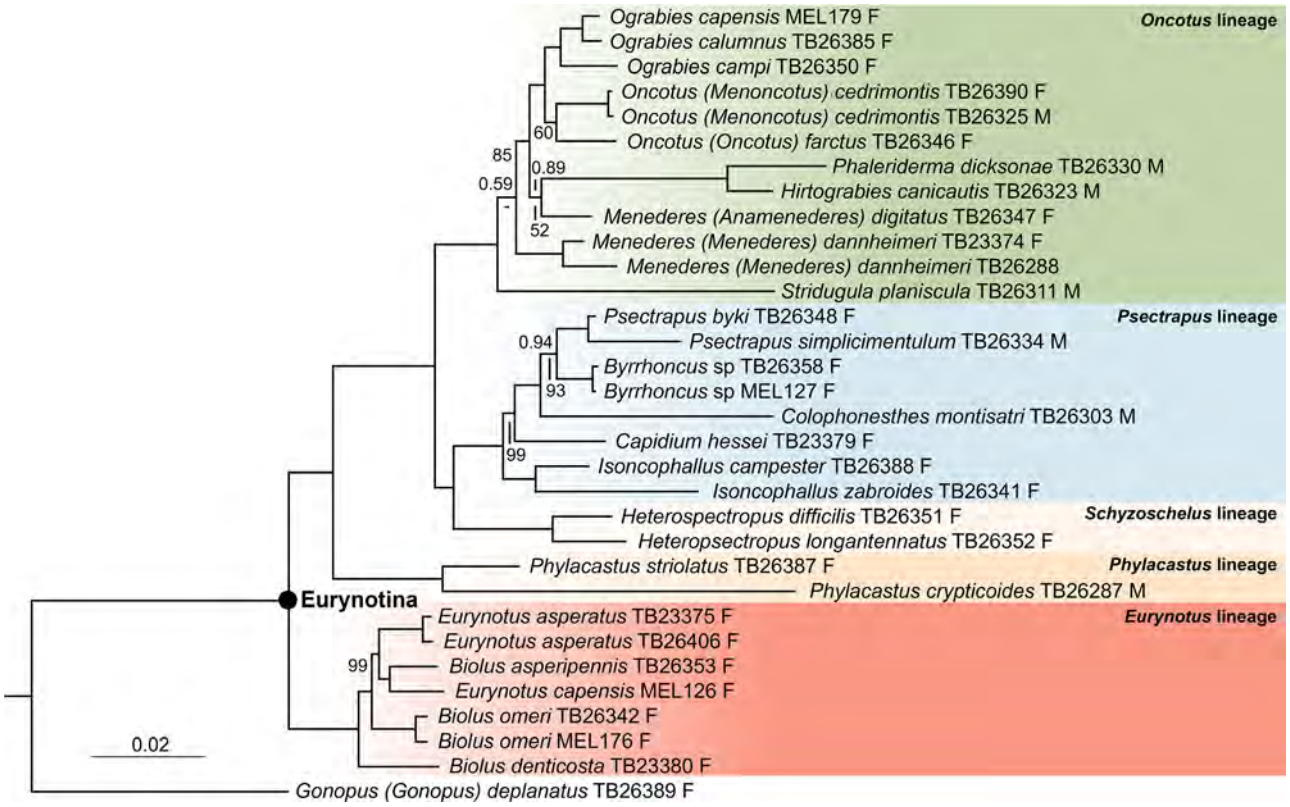


FIGURE 2 Phylogeny of the subtribe Eurynotina inferred from nuclear targeted enrichment and mitochondrial datasets. Topology is the Majority Rule consensus from Bayesian analysis (ExaBayes) of the concatenated matrix covering 510 loci (157,567 aligned amino acid positions). Branch support is indicated as Ultrafast bootstrap values (below nodes) from IQ-TREE 2 (see Figure S3) and posterior probabilities (above nodes). Missing values denote full branch support. Specimens labelled "M" indicate data derived from pinned museum material; "F" denotes fresh, ethanol-preserved specimens.

Muelleropsectropus, *Ograbies*, *Phaleriderma*), *Quadroncotus* **stat. nov.**, *Schyzoschelus* (*except S. africanus* (0), *and Stridigula*) have setation restricted to the lateral edges or basal angles (1) (Figure 3g), and only *Hirtograbies canicautis* had abundant setation of the dorsum of the pronotum (2) (Figure 3h). [ci = 0.286, ri = 0.762].

***Pronotal lateral margin sulcus* (Character #21):** (0) Absent; (1) Present. Along the lateral edge of the pronotum there is often a small (or wide) sulcus or groove (see Character #22) (1) (Figure 3g,j). Absent in *Capidium* (0) (Figure 3i), where the 'bead' of the lateral edge is more tightly adhered to the pronotum with a reduced sulcus. [ci = 1.00, ri = 1.00].

***Pronotal lateral margin sulcus* (Character #22):** (0) Wide, ill-defined, and/or pronotum explanate; (1) Relatively narrow, well-defined running along the border. Lateral margin sulcus either narrow and well defined (1) (Figure 3g), or without well-defined borders (pronotal margin appearing explanate or drawn-out with broad depression along lateral edges) (0) (Figure 3j). Most taxa were relatively well defined (1). *Capidium*, *Oncotus*, *Menoncotus* **stat. nov.** and *Quadroncotus* **stat. nov.** had explanate, wider or poorly defined sulci on the pronotum (0), while *Eurynotus* and *Phaleriderma* had both states (0, 1) represented among the species. [ci = 0.143, ri = 0.700].

Lateral margins of pronotum explanately overhanging hypomeron (Character #23): (0) Absent; (1) Present. In some taxa the dorsal surface of the pronotum hangs over the 'sides' of the pronotum (hypomeron) in an eave-like fashion (1) (Figure 3k); otherwise, the edge of the pronotum is gradually or abruptly rounded into the hypomeron (0). Present (1) in *Stridigula*, *Oncotus* and *Quadroncotus* **stat. nov.** [ci = 0.500, ri = 0.833].

***Hypomeron setation* (Character #28):** (0) Absent; (1) Present. Hypomeron either without setae or, at most, with short appressed setation (0) (Figure 3k), or with long, free setae (1) (Figure 3l). Only *Hirtograbies*, *Ograbies* and *Phaleriderma* had long setation of the hypomeron (1). [ci = 0.500, ri = 0.900].

Hypomeron posterio-basal margin carina meeting with basolateral angle forming a triangle (Character #29): (0) Absent; (1) Present. Present (1) (Figure 3m) in *Eurynotus*, *Gonopus* and *Phylacastus*. Absent (0) (Figure 3n) in all other taxa. [ci = 1.00, ri = 1.00].

Hypomeron posterio-basal margin carina running to the **posterior of** the **pronotum not meeting** the **dorsal margins (Character #30):** (0) Absent; (1) Present. Present in almost all taxa. Absent in *Eurynotus*, *Gonopus* and *Phylacastus*. [ci = 1.00, ri = 1.00].

Pterothorax characters

Hyaline elytra (Character #34): (0) Absent; (1) Present. Nearly all Eurynotina are dark and well sclerotized (0) (Figure 4e).

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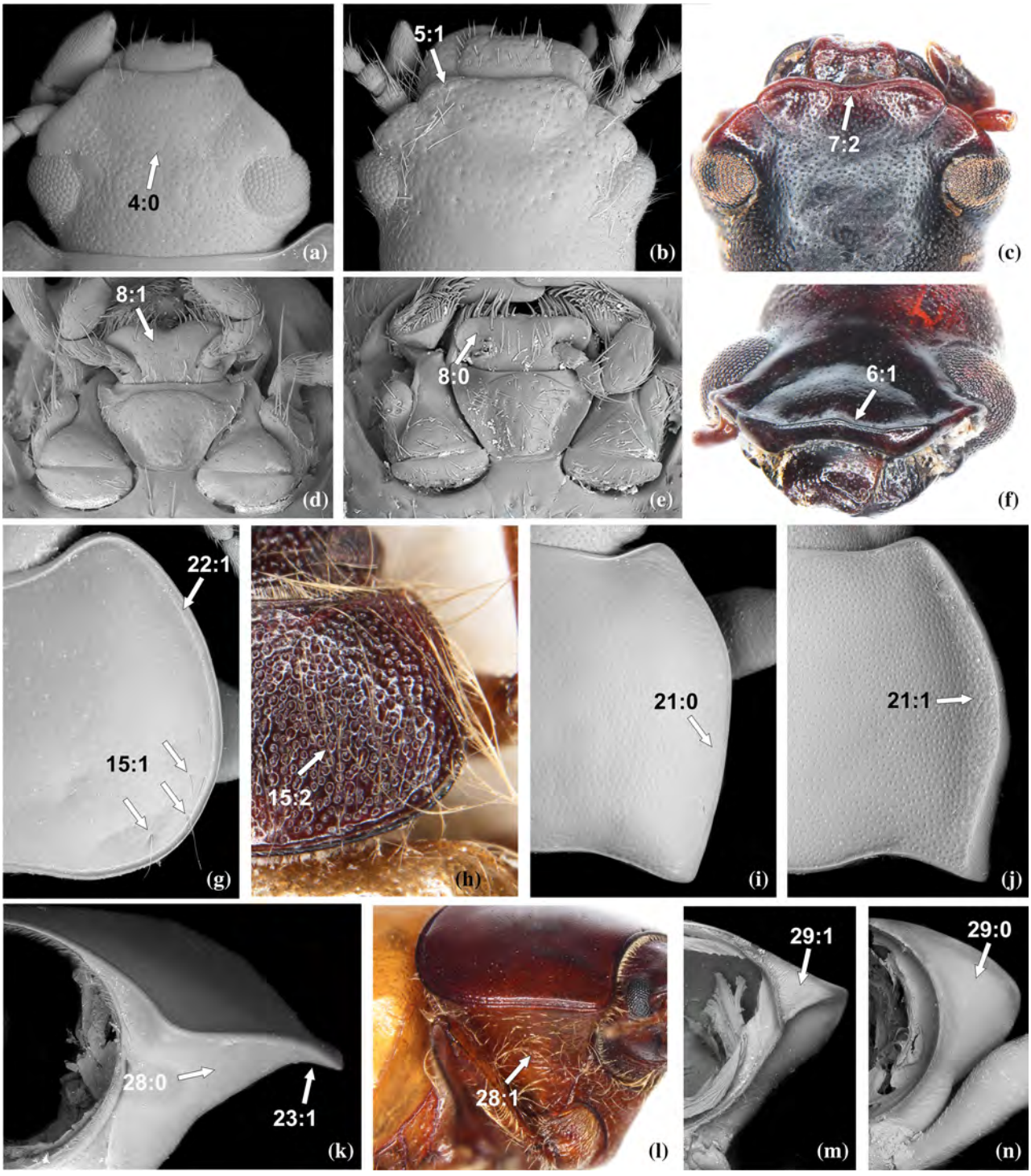


FIGURE 3 New characters used in the cladistic analysis of Eurynotina. (a) *Capidium hessei* (Head, dorsal). (b) *Phaleriderma husserli* (Head, dorsal). (c) *Oncotus farctus* (Head, dorsal). (d) *Schyzoschelus kaszabi* (Prementum). (e) *Heteropsectropus difficilis* (Prementum). (f) *Menederopsis constrictus* (Head, anterior). (g) *Muelleropsectropus malaisei* (Pronotum, dorsal). (h) *Hirtograbies canicautis* (Pronotum, dorsal). (i) *Capidium hessei* (Pronotum, dorsal). (j) *Eurynotus sulcimargo* (Pronotum, dorsal). (k) *Oncotus farctus* (Pronotum, anterior). (l) *Ograbies testaceus* (Pronotum/Hypomeron, lateral). (m) *Eurynotus capensis* (Pronotum, posterior). (n) *Schyzoschelus ladini* (Pronotum, posterior). For full description of all features used in cladistic analysis, see Table S3.

Ograbies have elytra that are exceptionally fragile and often yellowish or slightly transparent (1) (Figure 4a). [ci = 1.00, ri = 1.00].

***Dorsal elytral setae* (Character #35):** (0) Absent; (1) Present. Most taxa lack setae on the elytra (0). Only *Phaleriderma* and *Hirtograbies* possess setation of the elytra (Figure 4b); however, *P. dicksonae* and

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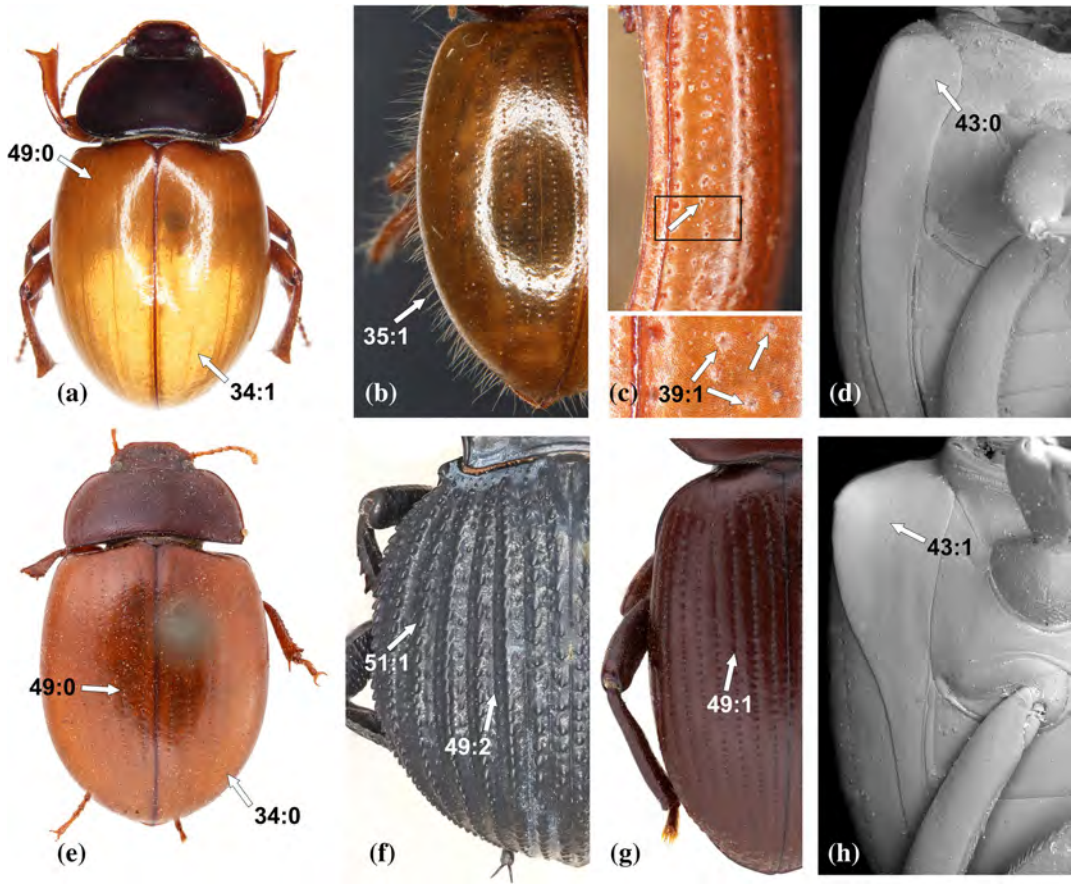


FIGURE 4 New characters used in the cladistic analysis of Eurynotina. (a) *Ograbies testaceus* (Habitus, dorsal). (b) *Hirtograbies nanus* (Elytra, dorsal). (c) *Menederes dannheimeri* (Elytra, lateral). (d) *Eurynotus capensis* (Epipleura, ventrolateral). (e) *Quadroncotus irrepertus* (Habitus, dorsal). (f) *Gonopus deplanatus* (Elytra, dorsal). (g) *Menederes dannheimeri* (Elytra, dorsal). (h) *Oncotus farctus* (Epipleura, ventrolateral). For full description of all features used in cladistic analysis, see Table S3.

H. gariepinus are exceptions that lack dorsal setae (0). [ci = 0.500, ri = 0.667].

Last lateral-most elytral interval with scattered punctation **(Character #39):** (0) Absent; (1) Present. In *Menederes* and *Menoncotus*, the last elytral interval has scattered punctation or texturing that does not form a well-defined stria (1) (Figure 4c); in contrast, in other taxa, the last interval is uninterrupted, "smooth", and/or otherwise striopunctate (0). [ci = 0.500, ri = 0.667].

Base of epipleura **(Character 43):** (0) Rounded – gradually narrowing; (1) Angular – sharply narrowing. The contour of the epipleura can gradually taper from the base to the apex (0) (Figure 4d), or sharply constrict near the base or midpoint (1) (Figure 4h). Angular (1) in *Anamenederes* **stat. nov.**, *Capidium*, *Colophonexsula* **gen. nov.**, *Gonopus*, *Oncotus* and *Quadroncotus* **stat. nov**. [ci = 0.250, ri = 0.625].

Base of elytra **(Character #48):** (0) simple; (1) with setose pit. Only present (1) (Figure 8l) in *Stridigula* (though reduced in *S. namaquensis*). [ci = 1.00, ri = 1.00].

Elytral striae **(Character #49):** (0) Not impressed; (1) Weakly impressed; (2) Strongly impressed. The elytral striae can present as: Not impressed (0) (Figure 4a,e); with no impressions visible, with or without obvious strial punctures. Weakly impressed (1) (Figure 4g); close examination showing some depression(s). Strongly impressed (2) (Figure 4f); conspicuous punctate impressions. The impression of the elytral striae varies within genera and is useful for species determinations. However, some genera have an overall trend of weaker impression (0 or 1) (e.g. *Ograbies*). [ci = 0.143, ri = 0.294].

Elytral interval punctation **(Character #52):** (0) Present (faint); (1) Present (strong). Elytrae in most taxa are puncto-striate; however, the punctation can either be faint (0) (smaller, sometimes difficult to observe even under magnification), or strong (1) (large, conspicuous and often readily observable with little to no magnification). Some groups are variable in their punctation e.g. *Psectrapus* lineage with strong (1) punctation (except for *Colophonexsula* **gen. nov**. and *Capidium hessei*), or *Eurynotus* with faint (0) punctation (except for *E. constrictus*). *Hirtograbies* displayed strong (1) punctation. *Anamenederes* **stat. nov.**, *Menederes* **sens. nov.**, *Menederopsis*, *Menoncotus* **stat. nov.**, *Ograbies*, *Oncotus*, *Quadroncotus* **stat. nov**. and *Stridigula* all displayed weak (0) punctation. [ci = 0.100, ri = 0.526].

Tubercles of apical decline of elytra **(Character #53):** (0) Absent; (1) Present. Many Eurynotina have some level of tuberculation of the elytral apex, which can be useful for determining species-level differences. All but one species of *Eurynotus* (*E. alticola*) has tubercles on

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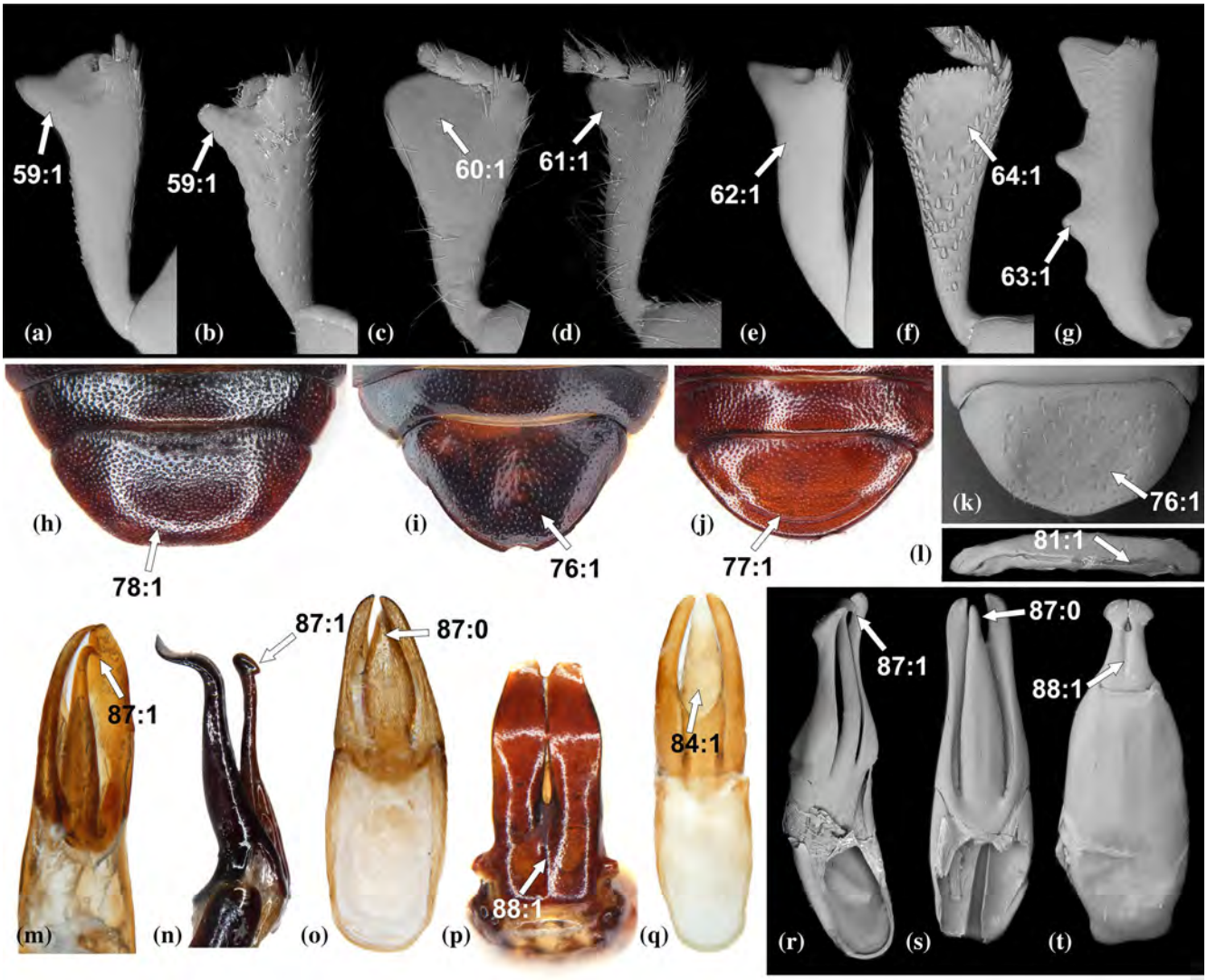


FIGURE 5 New characters used in the cladistic analysis of Eurynotina. (a) *Oncotus farctus* (Foreleg, anterior). (b) *Quadroncotus irrepertus* (Foreleg, anterior). (c) *Phaleriderma husserli* (Foreleg, anterior). (d) *Hirtograbies canicautis* (Foreleg, anterior). (e) *Ograbies capensis* (Foreleg, anterior). (f) *Psectrapus byki* (Foreleg, posterior). (g) *Gonopus deplanatus* (Foreleg, anterior). (h) *Psectrapus bipartitus* (Abdominal ventrite V). (i) *Muelleropsectropus malaisei* (Abdominal ventrite V). (j) *Isoncophallus campester* (Abdominal ventrite V). (k) *Schyzoschelus kaszabi* (Abdominal ventrite V). (l) *Muelleropsectropus malaisei* (Abdominal ventrite V, posterolateral). (m) *Colophonesthes montisatri* (Aedeagus, ventral). (n) *Menederes dannheimeri* (Aedeagus, lateral). (o) *Phaleriderma husserli* (Aedeagus, ventral). (p) *Schyzoschelus ladini* (Aedeagal parameres, dorsal). (q) *Capidium bipunctatum* (Aedeagus, dorsal). (r) *Oncotus farctus* (Aedeagus, ventrolateral). (s) *Oncotus cedrimontis* (Aedeagus, ventral). (t) *Muelleropsectropus malaisei* (Aedeagus, dorsal). For a full description of all features used in cladistic analysis, see Table S3.

the apical decline (1). Additionally, *Anamenederes* **stat. nov.**, *Capidium*, *Colophonesthes*, *Gonopus*, *Heteropsectropus*, *Isoncophallus*, *Menederes* **sens. nov.**, *Menoncotus* **stat. nov.**, *Phylacastus* (except *P. ancoralium*), *Psectrapus* and *Muelleropsectropus* have tuberculation of the apical decline (1). [ci = 0.125, ri = 0.759].

Leg characters

***Foretibiae slender* (Character #58):** (0) Absent; (1) Present. Foretibiae without expanding modifications as in following characters (see Characters #59–64). *Capidium*, *Eurynotus*, *Heteropsectropus*, *Muelleropsectropus* and *Schyzoschelus* all have relatively slender, cylindrical foretibiae (1). [ci = 0.333, ri = 0.920].

***Foretibiae Oncotus type* (Character #59):** (0) Absent; (1) Present. Tibiae expanding apically, with apices of the foretibiae bearing a lateral tooth-like projection which may vary in shape and specific characterization; however, this character merely records the presence of the protuberance in terms of absence and presence. Present (1) (Figure 5a,b) in *Anamenederes* **stat. nov.**, *Oncotus* **sens. nov.**, *Menederes rufilabris*, *Menoncotus* **stat. nov.** and *Quadroncotus* **stat. nov.** [ci = 0.500, ri = 0.833].

***Foretibiae Phaleriderma type* (Character #60):** (0) Absent; (1) Present. Broad triangularly expanded foretibiae with rounded corners (1) Present in *Phaleriderma* (Figure 5c). [ci = 1.00, ri = 1.00].

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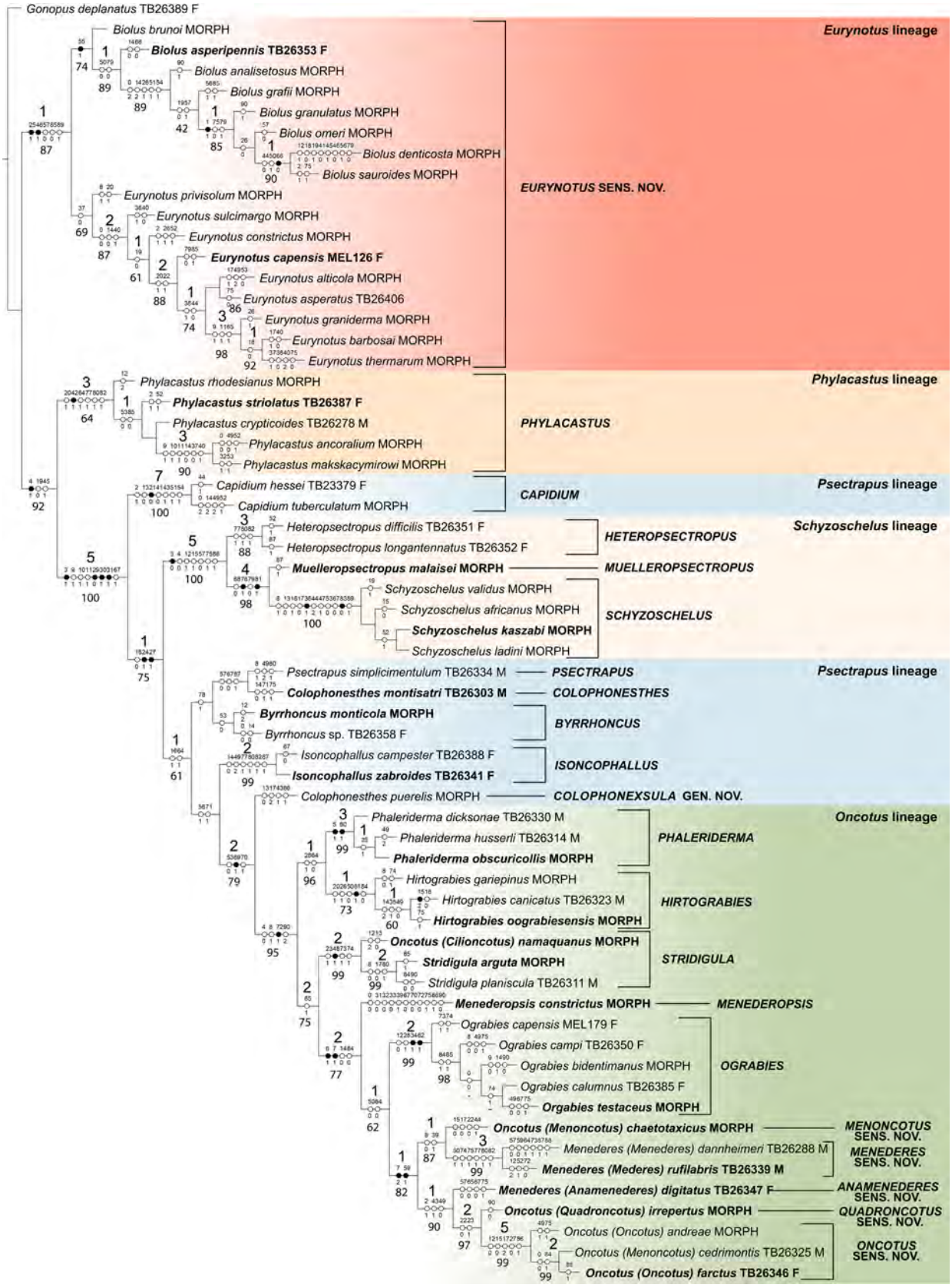


FIGURE 6 Phylogeny of Eurynotina based solely on morphological data. The most parsimonious cladogram recovered from a weighted TNT analysis is shown. Support values indicate Bremer support (above nodes) and IQTree Ultrafast bootstrap values (below nodes). Non-homoplastic character state changes are indicated by black circles, and homoplastic changes by white circles. Character numbers and states correspond directly to the list provided Table S3. Specimens labelled "M" are derived from pinned museum material; "F" denotes fresh specimens; "MORPH" indicates taxa included only in the morphological dataset; bold taxon names indicate type species.

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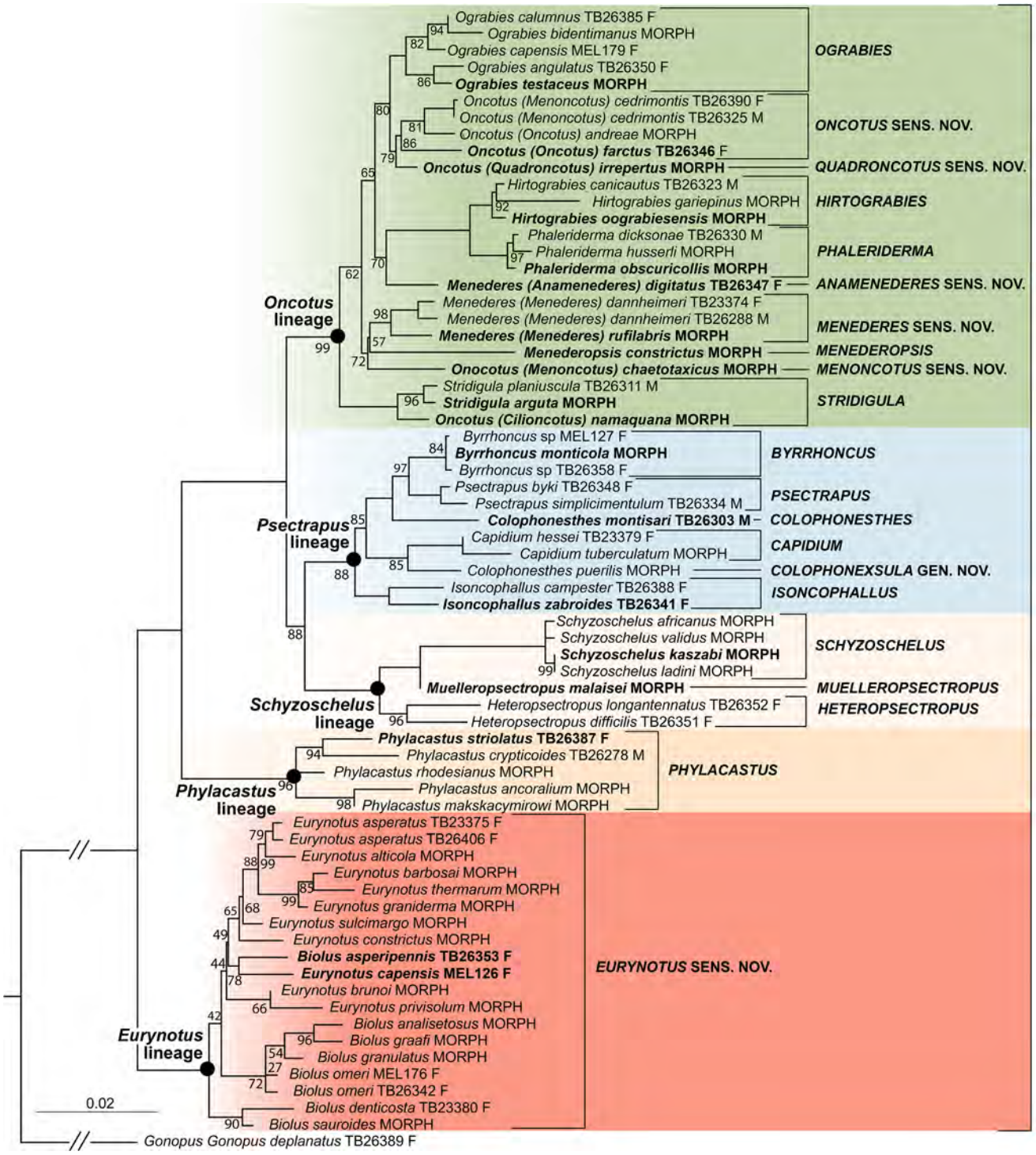


FIGURE 7 Phylogeny and new classification of the subtribe Eurynotina. The tree shown is the maximum likelihood topology obtained with IQ-TREE from the concatenated matrix comprising 510 loci (157,567 aligned amino acid positions) and 91 morphological characters. Branch support is indicated as ultrafast bootstrap values (below nodes); missing values denote full branch support. Specimens labelled "M" indicate data derived from pinned museum material; "F" denotes fresh specimens; "MORPH" indicates taxa included based solely on morphological data; bold taxon names indicate type species.

***Foretibiae Hirtograbies type* (Character #61):** (0) Absent; (1) Present. Similar to (Character #60), broadly expanded, triangular foretibiae; however, less expanded, more pointed and less rounded in the corners (1) Present in *Hirtograbies* (Figure 5d). [ci = 1.00, ri = 1.00].

***Foretibiae Ograbies type* (Character #62):** (0) Absent; (1) Present. Foretibiae with characteristically chamfered foretibiae that are broadly flattened and expanded, with or without broad emargination along the lateral edge that may give rise to toothed or edge-like

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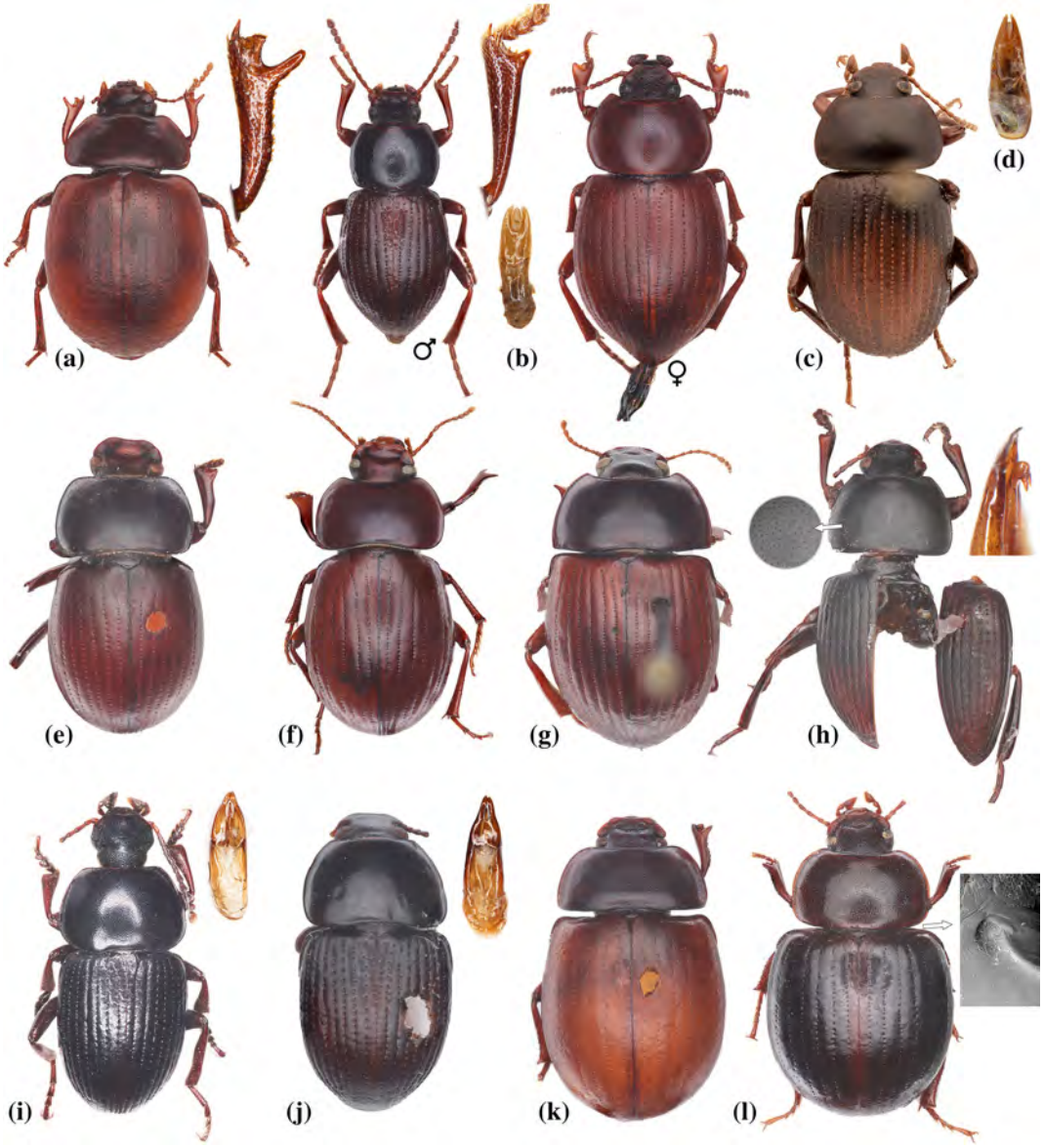


FIGURE 8 Habitus and diagnostic features of taxa representing Eurynotina. (a) *Anamenederes digitatus* comb. nov. (b) *Colophonexsula puerilis* comb. nov. (left male, right female). (c) *Menoncotus chaetotaxicus* comb. nov. (d) *Menoncotus sinuatipes* comb. nov. (aedeagus). (e) *Ograbies capensis*. (f) *Ograbies calumnus* Lumen & Kamiński sp. nov. (g) *Oncotus farctus*. (h) *Psectrapus bipartitus*. (i) *Psectrapus byki* Lumen & Kamiński sp. nov. (j) *Psectrapus simplicimentulum* Lumen & Kamiński sp. nov. (k) *Quadroncotus irrepertus* comb. nov. (l) *Stridigula arguta*.

projections (1) Present in *Ograbies*–Unique within Eurynotina (Figure 5e). [ci = 1.00, ri = 1.00].

***Foretibiae Gonopus type* (Character #63):** (0) Absent; (1) Present. In these analyses, *Gonopus* has a unique foretibiae in this study, bearing multiple armaments (1) (Figure 5g). [ci = –, ri = –].

***Foretibiae flattened, with posterior excavation* (Character #64):** (0) Absent; (1) Present. Taxa without slender or the aforementioned shape of foretibiae. Apically expanded foretibiae with a slight excavation or concavity on the ventral side. Taxa displaying this trait (1) (Figure 5f) were: *Menederes dannheimeri*, *Phylacastus*, *Psectrapus* lineage (except for *Capidium*) and *Stridigula*. [ci = 0.200, ri = 0.750].

***Miditibia laterally compressed* (Character #69):** (0) Absent (not flattened); (1) Present (flattened). Flattened (1) in *Colophonexsula* **gen. nov**. and the *Oncotus* lineage. [ci = 1.00, ri = 1.00].

***Miditibia apical shape* (Character #70):** (0) Unflared apically; (1) Flared apically. Flared (1) in *Gonopus*, *Phylacastus* and the *Oncotus* lineage (except *Menederopsis*). [ci = 0.250, ri = 0.893].

***Hindtibiae laterally compressed* (Character #71):** (0) Absent (not flattened); (1) Present (flattened). Flattened (1) in *Colophonesthes*, *Colophonexsula* **gen. nov.**, *Isoncophallus*, the *Oncotus* lineage, *Phylacastus ancoralium* and *P. crypticoides*. [ci = 0.250, ri = 0.893].

***Hindtibiae apical shape* (Character #72):** (0) Unflared apically; (1) Flared apically. Flared (1) in the *Oncotus* lineage (except for *Menederes rufilabris* and *Menederopsis*). [ci = 0.333, ri = 0.900].

***Male midfemoral setal patch* (Character #73):** (0) Absent; (1) Present. Present (1) in *Menederes dannheimeri*, *Ograbies capensis* and *Stridigula*. Taxa unexamined (?) due to missing specimens or body parts for evaluation of this trait were: *Byrrhoncus* sp. (TB26358),

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Hirtograbies oograbiensis, *Oncotus andreae* and *Quadroncotus* **stat. nov**. [ci = 0.333, ri = 0.500].

Male hindfemoral setal patch **(Character #74):** (0) Absent; (1) Present. Present (1) in *Hirtograbies gariepinus*, *Menederes*, *Oncotus* **sens. nov.**, *Stridigula* and some *Ograbies* (*O. calumnus*, *O. testaceus*, *O. capensis*). Taxa unexamined due to missing specimens or body parts for evaluation of this trait were: *Byrrhoncus* sp. (TB26358), *Hirtograbies oograbiensis*, *Oncotus andreae* and *Quadroncotus* **stat. nov**. [ci = 0.167, ri = 0.500].

Abdomen and genitalia characters

Abdominal ventrite V shape **(Character #76):** (0) Convex; (1) Concave. Abdominal ventrite V is either conspicuously concave or convex/flattened. See Lumen & Kaminski, 2024. Concave (1) (Figure 5i,k) in *Muelleropsectropus* and *Schyzoschelus*. [ci = 1.00, ri = 1.00].

Abdominal ventrite V subapical sulcus **(Character #77):** (0) Absent in one or both sexes; (1) Present in both males and females. Small sulcus or groove situated before the apical edge of the last visible abdominal ventrite. Depending on the taxa, it may be absent (0) in males, females or both. Alternatively, the sulcus may be present in both males and females (1). Abdominal ventrite V sulcus present in males and females (1) (Figure 5j) in *Heteropsectropus*, *Isoncophallus*, *Menederes* **sens. nov**. and *Phylacastus*. [ci = 0.250, ri = 0.700].

Fifth abdominal ventrite short **(Character #78):** (0) No (quadrate or elongate); (1) Yes (broader than long). Abdominal ventrite V "short" (1) (Figure 5h) in *Byrrhoncus*, *Colophonesthes*, *Gonopus* and *Psectrapus*. [ci = 0.500, ri = 0.750].

F*emale abdominal ventrite V subapical sulcus* **(Character #80):** (0) Absent; (1) Present. Small sulcus or groove situated before the apical edge of the last visible abdominal ventrite. Present (1) in *Heteropsectropus*, *Isoncophallus*, *Menederes* **sens. nov**., *Phylacastus*, *Psectrapus* and *Stridigula* (except *S. namaquanus*). [ci = 0.167, ri = 0.615].

"*Schyzoschelus-type*" *female-emargination of abdominal ventrite V* **(Character #81):** (0) Absent; (1) Present. See Lumen and Kaminski (2024). Present (1) (Figure 5l) in *Muelleropsectropus* and *Schyzoschelus*. [ci = 1.00, ri = 1.00].

Male abdominal ventrite V subapical sulcus **(Character #82):** (0) Absent; (1) Present. Small sulcus or groove situated before the apical edge of the last visible abdominal ventrite. Present (1) in *Isoncophallus*, *Heteropsectropus*, *Menederes* **sens. nov**. *and Phylacastus*. [ci = 0.250, ri = 0.700].

Strongly sclerotized penis with apical hook **(Character #87):** (0) Absent; (1) Present. Hook is present (1) (Figure 5m,n,r) in *Anamenederes* **stat. nov**., *Colophonesthes*, *Heteropsectropus longantennatus*, *Isoncophallus*, *Menederes dannheimeri*, *Muelleropsectropus*, *Oncotus farctus* and *Psectrapus*. Absent (0) (Figure 5o,s) in all other examined taxa. Taxa unexamined due to missing specimens or body parts for evaluation of this trait were: *Byrrhoncus* sp. (TB26358), *Hirtograbies oograbiensis*, *Oncotus andreae* and *Quadroncotus* **stat. nov**. [ci = 0.143, ri = 0.250].

Parameres in dorsal view with longitudinal depression or groove (Character #88): (0) Absent; (1) Present. Though the parameres of eurynotines are fused at the base, there may be a small, longitudinal furrow or groove running from the base to the apical opening (1) (Figure 5p), giving the impression of two separate parameres. Present (1) (Figure 5p,t) in *Menederes dannheimeri* and the *Schyzoschelus lineage*. [ci = 0.500, ri = 0.857].

Cladistic analysis

All previously recognized genera and subgenera of Eurynotina were sampled and included in a cladogram (Figure 6). A heuristic search with characters equally weighted yielded 17 most parsimonious trees of 385 steps, with a CI of 0.275 and a RI of 0.776. Topological differences between the maximum parsimony trees mostly concerned shallow nodes and members of the *Psectrapus* lineage (Figure 6). Analysis of the morphological matrix with a weighted strategy (k = 9.272) returned a single topology with a score of 18.47861 after 89,126,092 rearrangements. Bremer support values are shown in Figure 6. Branch support for the majority of recovered nodes was low. ML topology (IQ-TREE2) is largely convergent with the MP cladogram obtained in the weighted analysis (Figure S4).

From the five generic lineages recognized by molecular analysis, the following four were recovered (Figure 6, Figure S4): *Eurynotus* lineage (*Eurynotus* **stat. nov**. = *Biolus* **syn. nov**.), *Phylacastus* lineage (monogeneric), *Schyzoschelus* lineage (*Heteropsectropus*, *Muelleropsectropus*, *Schyzoschelus*) and *Oncotus* lineage (*Anamenederes* **stat. nov**., *Hirtograbies*, *Menederes* **stat. nov**., *Menederopsis*, *Menoncotus* **stat. nov**., *Ograbies*, *Oncotus* **stat. nov**., *Phaleriderma*, *Stridugula*, *Quadroncotus* **stat. nov**.). Members of the *Psectrapus* lineage are dispersed throughout the cladogram, forming four separate lineages: *Capidium*; *Byrrhoncus*, *Colophonesthes* and *Psectrapus*; *Colophonexsula* **gen. nov**.; *Isoncophallus* (Figure 6). Furthermore, the ML analysis rendered *Byrrhoncus* non-monophyletic (Figure S4). Overall, the phylogenetic relation of the recovered generic lineages is highly convergent with molecular-based topologies, e.g., the basal placement of *Eurynotus* and its relation with *Phylacastus*, *Schyzoschelus* and *Oncotus* lineages.

Distinctiveness of the genus *Eurynotus* **sens. nov**. is supported by the following synapomorphies: basal angles of pronotum produced posteriorly (Table S3–25:1), elytral base arcuately concave between humeri (Table S3–46:1). Unlike in the molecular analyses (Figures 1 and 2), the previously recognized genus *Biolus* was recovered as sister to *Eurynotus* (Figure 6). Similarly, as in the case of molecular data, morphological analysis does not support a sister relation between *Eurynotus* and *Phylacastus* lineages (Figures 1 and 2).

The genus *Phylacastus* was recovered as monophyletic (Figure 6). The distinctiveness of this taxon is based on the following features: pronotum lateral shape straight (Table S3–20:1), base of epipleura forming a slight border parallel to the base of elytra (Table S3–42:1 synapomorphy), foretibiae flattened, with posterior excavation (64:1), abdominal ventrite V subapical sulcus present in males and females

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(77:1), female abdominal ventrite V subapical sulcus present (80:1), male abdominal ventrite V subapical sulcus present (82:1).

The cladistic analysis clustered *Heteropsectropus*, *Muelleropsectropus* and *Schyzoschelus* (Figure 6). This grouping is supported by the following synapomorphies and symplesiomorphies: clypeus emargination absent/straight (Table S3–3:0 synapomorphy), demarcation between frons and clypeus not reduced (4:0), Submentum pentagonal (Table S3–12:1), pronotal setae present on dorsal surface restricted to isolated setae on edges and/or corners (15:1), male midtarsus expanded (Table S3–57:0), abdominal ventrite V with two punctation types (Table S3–75:1), parameres in dorsal view with longitudinal depression or groove (88:1).

Within the members of the *Psectrapus* group, cladistic analysis revealed a close relation between *Byrrhoncus* and *Colophonesthes* + *Psectrapus* (Figure 6). This clade is supported by a shortened abdominal ventrite V (78:1). Both *Isoncophallus* and *Colophonsexsula* **gen. nov**. are distinct for having unexpanded male tarsi (Table S3–56:1) and laterally compressed hind tibiae (71:1). The latter genus was affiliated with the *Oncotus* lineage through the synapomorphic structure of laterally compressed midtibiae (69:1). Distinctiveness of *Capidium* is grounded in the following features: lateral depression at frons/clypeal suture (Table S3–2:1), elongate submentum (Table S3–13:0), reduced pronotal lateral margin sulcus (21:0 synapomorphy), produced epipleural shoulder (Table S3–41:0), angular/sharply narrowing epipleural base (43:1), elytral intervals with large, sparse tubercles (Table S3–51:1) and tubercles on the elytral disc (Table S3–54:1).

Distinctiveness of the *Oncotus* lineage is supported by the following features (Figure 6): visible demarcation between frons and clypeus (4:0), cordiform prementum (8:1), hind tibiae flared apically (72:1 synapomorphy), bursa copulatrix with paired sclerites (Table S3–90:2).

Similar to molecular data, the morphological analysis does not support the monophyly of the genus *Menederes*, as both its subgenera were recovered as separate lineages (Figure 6). Namely, *Anamenederes digitatus* Koch was projected onto a clade containing *Oncotus and Quadroncotus* species. On the other hand, both species of the subgenus *Menederes* – *M. dannheimeri* Koch, *M. rufilabris* Solier – were rendered sister to *Menoncotus chaetotaxicus* Koch. The clade is supported by the following features: prementum not cordiform (8:0) and lateralmost elytral interval with scattered punctation (39:1).

As implemented above, the cladistic analysis revealed inconsistencies within the subgeneric classification of the genus *Oncotus* (Figure 6). Besides the already described affiliation of some of the species towards species previously classified within *Menederes*, *O. namaquanus* Koch was rendered sister to the genus *Stridigula* (Figure 6). This relation is supported by: lateral margins of pronotum explanately overhanging hypomeron (23:1), base of elytra with setose pit (48:1 synapomorphy), males with midfemoral setal patch (73:1), males with hindfemoral setal patch (74:1).

The analysis supported the monophyly of *Hirtograbies*, *Ograbies* and *Phaleriderma* (Figure 6). The following synapomorphies were recovered: *Hirtograbies* – foretibiae *Hirtograbies* type (61:1); *Ograbies* – hyaline elytra (34:1), foretibiae *Ograbies* type (62:1); *Phaleriderma* – epistoma and clypeus fused and differentiated (5:1), foretibiae *Phalerideram* type (60:1).

Combined analysis

Integration of morphological and molecular data enabled a comprehensive analysis of Eurynotina, which included representatives of all 18 previously designated genera (Figure 7 and Figure S5). All five major phylogenetic lineages recognized in molecular-only analysis were recovered: *Eurynotus* (UFB = 100, PP = 0.99), *Phylacastus* (UFB = 96, PP = 1.00), *Schyzoschelus* (UFB = 100, PP = 1.00), *Psectrapus* (UFB = 88, PP = 0.78) and *Oncotus* (UFB = 99, PP = 0.97). The lowest support and highest topological inconsistencies between ML and MrBayes runs were reported within the *Eurynotus* and *Oncotus* lineages (Figure 7, Figure S5), which were both highly saturated with data extracted from museum and morphology-only specimens.

The following genera were rendered non-monophyletic in the ML analysis: *Eurynotus* paraphyletic in regard to *Biolus*; *Colophonesthes* with two sampled species (*montisatri* and *puerilis*) recovered as independent lineages; *Oncotus* with representatives of different subgenera dispersed throughout the *Oncotus* lineage; *Menoncotus* with representatives divided over three separate lineages (*cedrimontis*, *chaetotaxicus*, *capicola*); and *Menederes* with subgenus *Anamenederes* projected within a clade composed of *Hitrograbies* + *Phaleriderma*. On the other hand, the monophyly of all other genera was highly supported (Figure 7).

The analysis in MrBayes highlighted inconsistencies in weakly supported clades from the ML run (Figure S5). For example, subgenus *Quadroncotus* was recovered far outside *Oncotus*, while the relationship of *Menoncotus*, *Menederopsis* and *Stridigula* with other members of the *Oncotus* lineage was unresolved. On the other hand, both analyses were fully convergent in the cases of internal relations within the *Psectrapus* lineage and the following genera: *Ograbies*, *Oncotus* sens. nov., *Menederes* sens. nov., *Stridigula* (Figure S5).

DISCUSSION

The analyses presented here demonstrate the targeted enrichment approach proposed by Kanda (2017) as a powerful tool for investigating phylogenetic relationships among Tenebrionidae (see also Kamiński et al., 2024; Swichtenberg et al., 2023). Fresh ethanol-preserved specimens yielded large amounts of high-quality data (499 loci spanning 151,172 nuclear amino acids), which resulted in a well-resolved phylogenetic topology (Figure 1). This dataset enabled thorough verification of the monophyly of Eurynotina in regard to the sister subtribe Platynotina. However, unlike in the case of ultraconserved elements—the commonly used alternative to the probe set implemented here (e.g., Baca et al., 2017; Bradford et al., 2022; Gustafson et al., 2023; Sota et al., 2022)—the recovery of targeted loci in historical specimens was low and random (Figure S1). Fortunately, data for 12 mitochondrial loci were obtained as bycatch for both fresh

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and historical specimens which, after combination with the aforementioned nuclear dataset, significantly increased the number of species and genera for phylogenetic analyses (Figure 2). The combined targeted and mitochondrial dataset provided more detailed insight into the relationships within Eurynotina, enabling verification of monophyly for some genera. Despite the overall success of the combined molecular analyses, clades with more historical specimen data were characterized by lower branch supports (e.g., *Oncotus* lineage). To verify the performance of the combined dataset, taxa with both fresh and historical specimens were included (e.g., *Oncotus cedrimontis* TB26390F, TB26325M; *Menederes dannheimeri* TB233374F, TB26288M; see Figure 7). The recovered sister relationships between fresh and museum representatives of the same taxa demonstrate the reliability of the sequencing strategies implemented here.

Morphological analysis included all genera and about 2/3rds (61 of 92) of the total species diversity of Eurynotina (Figure 6). While there are some gaps in the morphological matrix related to the elusive character of the subtribe (i.e., species with unknown males/females or damaged specimens lacking body parts for scoring), the overall amount of missing data is surprisingly low (1.5%). Although the constructed dataset is characterized by high levels of homoplasy (CI = 0.275), there are many features retaining phylogenetic signal (RI = 0.776). Nearly 45% of the features implemented in the cladistic analysis were new as of this study, highlighting a shortage of detailed morphological studies within the group. This tendency resonates well with a general pattern within Tenebrionidae, where despite recent phylogenetic efforts, some morphology from previous broader studies has largely been recycled and remain untested (e.g., Doyen & Tschinkel, 1982; Tschinkel & Doyen, 1980; Watt, 1974).

Combining genomic and morphological data yielded a comprehensive phylogenetic hypothesis for Eurynotina, which included representatives of all genera and major species groups (Figure 7). Despite what appears to be a huge disproportion (157,567 amino acids vs. 91 morphological features), morphology enabled the inclusion of many species for which sequencing efforts were unsuccessful or impossible. Thus, the number of operational taxonomic units was greatly increased, enabling a deeper verification of the monophyly of all genera. In the majority of cases, taxa included solely based on morphology were projected to be closely related to their congeners (e.g., *Ograbies testaceus*, *Oncotus adreae*, *Hirtograbies oograbiensis* in Figure 7), supporting the reliability of the combined approach. The topology obtained in the combined analysis of genomic and morphological data was then usable to inform changes in the classification of Eurynotina (Figure 7).

Although the monophyly of Eurynotina was tested only with the targeted enrichment dataset (Figure 1), the broad range of included outgroup taxa allowed for a thorough investigation. Notably, all major generic groups within Platynotina, designated based on molecular and morphological methods, were sampled (Iwan, 2002; Kamiński, 2015; Kamiński et al., 2019, 2021; Koch, 1956). The results support Koch's (1954a), Koch's (1954b), Koch's (1955) concept of Eurynotina and confirm the applicability of the following morphological definition: presence of a stridulatory gula (a feature shared with Platynotina), presence of elytral tubercles (a feature independently shared by *Anomalipus*, *Gonopus* and *Phymatoplata* Koch within Platynotina), and the absence or extreme reduction of aedeagal ancorae. Given that Platynotina represents one of the most intensively studied groups of darkling beetles, with both molecular and morphological phylogenies available, the monophyly and the hereby presented composition of Eurynotina appear to be well supported.

Morphological and molecular datasets resulted in largely convergent topologies, highlighting issues with Koch's (1954a), Koch's (1954b), Koch's (1955) informal subdivision of Eurynotina. Notably, in all analyses, the genus *Phylacastus* was recovered as a distinct lineage within the subtribe (Figures 1, 2, 6 and 7), rather than as sister to the genus *Eurynotus*, as hypothesized by Koch (1954a). Furthermore, all datasets indicate that Koch's *Oncotus* lineage is not monophyletic (Figures 1, 2, 6 and 7). According to molecular data, the following genera constitute a previously overlooked taxonomic cluster that should be excluded from the *Oncotus* lineage (Figures 1, 2 and 7): *Byrrhoncus*, *Capidium*, *Colophonesthes*, *Colophonexsula* gen. nov., *Isoncophallus* and *Psectrapus* (here referred to as the *Psectrapus* lineage). However, the monophyly of this grouping of genera was not recovered by the cladistic analysis, likely due to the distinctive morphology of some representatives (e.g., *Capidium*, *Colophonexsula* gen. nov.; see Figure 6) and convergent or divergent traits such as the structure of abdominal ventrite V (e.g. Characters 77, 78, 80 and 82). Nevertheless, the existence of the *Psectrapus* lineage appears to be well supported genetically by the targeted enrichment and targeted enrichment + mitochondrial datasets. The *Schyzoschelus* lineage, designated to accommodate *Heteropsectropus* and *Schyzoschelus* (Lumen & Kaminski, 2024), is the only group from Koch's (1954a), Koch's (1954b), Koch's (1955) designations which proved to be monophyletic in our analyses (Figures 1, 2, 6 and 7). Based on critical evaluation of the topologies presented here, Eurynotina is divisible into the *Eurynotus*, *Phylacastus*, *Psectrapus*, *Schyzoschelus* and *Oncotus* lineages.

While morphological data support the taxonomic distinctiveness of *Eurynotus* and *Biolus* as proposed by Lumen and Kamiński (2024), the molecular phylogenetic topologies do not. Instead, molecular data indicate a paraphyletic *Eurynotus* in regard to *Biolus* (Figures 1 and 2). Re-evaluation of morphological data in this study did not provide any reliable features for adopting the molecular topologies that would sustain a separate, monophyletic *Biolus* and *Eurynotus*. Taking into consideration the high molecular and morphological support of the "*Biolus* + *Eurynotus*" clade (Figures 1, 2, 6 and 7), and its diagnosability, the following synonymy is proposed: *Eurynotus* (=*Biolus*). The identification key provided by Lumen and Kamiński (2024) can still reliably be used to identify all species. The divergence of morphological and molecular data for *Eurynotus* remains puzzling and will likely require further investigation based on a more comprehensive representation of the species in molecular phylogenies.

Within the *Psectrapus* lineage, the performed analyses supported the monophyly of most genera (Figures 1, 2, 6 and 7), that is, *Byrrhoncus*, *Capidium*, *Isoncophallus* and *Psectrapus*. The only taxonomic issue concerned the placement of *C. puerilis*, which prior to this paper was interpreted as a member of the genus *Colophonesthes*

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(Kamiński, 2016; Koch, 1954b). Likely due to its unique morphology (Figure 8b and Taxonomy section), *C. puerilis* was rendered sister to the *Oncotus lineage* in the cladistic analysis, while the combined analysis recovered it as sister to *Capidium* within the *Psectrapus* lineage (Figure 7). Regardless, the results convergently highlight the autonomous status of *C. puerilis* in regard to remaining *Colophonesthes*. Additionally, some morphology of C. *puerilis* was erroneously overlooked by Koch (1954b), who stated that all members of *Colophonesthes* lack teeth on the foretibia (present in *C. puerilis*). However, he did record that this species significantly differs from other congeners by having more widely spaced parameres (versus more closely converging in *Colophonesthes montisatri* and *C. barnardi*). As a result, a new genus *Colophonexsula* is hereby erected to accommodate *C. puerilis*. The new taxon is easily diagnosable by the autapomorphic structure of protibiae (equipped with apical projection – Figure 8b), highly marked sexual dimorphism and overall aedeagal morphology (Figure 8b).

The most severe taxonomic inconsistencies revealed here concern the genera representing the *Oncotus* lineage (Figure 7), which is not surprising given their "bin-group" status in Koch's (1954a), Koch's (1954b), Koch's (1955) treatments. In particular, the subgenera of *Oncotus* (i.e., *Cilioncotus*, *Menoncotus*, *Oncotus*, *Quadroncotus*) appear to have been either prematurely erected and/or had certain characteristics overlooked. Namely, Koch's (1954a) definition for subgenus *Menoncotus*, on closer inspection, was based purely on the position of the 9th stria of the elytra, with all *Oncotus* united by modified tibiae and with additional setae on the pronotum and/or elytra and abdominal ventrite V. Those characteristics were found to be highly variable in this investigation. Revisionary work towards the designation of the OTUs implemented in the cladistic analysis revealed the divergent morphology of *O. cedrimontis* and *O. capicola* from the *Menoncotus* bauplan in respect to the shape of the pronotum, elytra and aedeagi, while the rest of *Menoncotus* (*M. jokli*, *M. sinuatipes*, *M. chaetotaxicus*) are largely consistent. Koch used these differences to distinguish *O. capicola* and *O. cedrimontis*, while seeming to ignore their strong affinities to *Ograbies* and *Oncotus s. str*., respectively. Upon investigation, *O. capicola* not only morphologically aligns with *Ograbies* (especially in the shape of the forelegs) but was also recovered well within the genus in molecular topologies. The type material of *Ograbies capensis* further exactly matched Koch's (1954b) type of *O. capicola*. As such, the two species are hereby synonymized under *Ograbies capensis* (see taxonomy section for further details). In the case of *O. cedrimontis*, the more right-angled bases of the pronotum, dimpling of the basal angles and shape of the aedeagus better align with *O. farctus*, which was recovered as sister in all analyses (Figures 1, 2, 6 and 7). While only the small type series was available for the rest of *Menoncotus*, morphological examinations and analyses recover the group as distinct from both *Ograbies* and *Oncotus*. As such, we elevate *Menoncotus* to generic rank (see Taxonomy).

Taxonomic investigation of *Cilioncotus*—the third subgenus of *Oncotus*—revealed a close similarity to the genus *Stridigula* (Figures 6 and 8l). Namely, *O. humerisetosus*, one of two members of this subgenus, was found to be synonymous with *Stridigula arguta*—the type species of *Stridigula*. Furthermore, as revealed here, *Stridigula* and the remaining species of *Cilioncotus* (*O. namaquanus*) are united by a unique structure of elytra, which bears a setose pit at the base (Figure 8l). As a result, the close affiliation of both taxa was highly supported by the conducted cladistic analysis (Figure 6), while the distinctiveness of *Cilioncotus* in the context of other former *Oncotus* was underpinned by molecular data (Figures 1 and 2). Furthermore, both *Cilioncotus* and *Stridigula* inhabit the Succulent Karoo ecosystem near the border between Namibia and South Africa (Kamiński, 2016). The setose pit uniting *Cilioncotus* and *Stridigula* was fully overlooked by Koch (1954b), who only briefly reported the presence of humeral setation for *O. humerisetosus*. In order to accommodate the phylogenetic data in the classification of Eurynotina, the following synonymy is proposed: *Stridigula* (=*Cilioncotus*) (for more details see Taxonomy).

Although the monotypic *Quadroncotus* was recovered as sister to the newly defined *Oncotus* in both the cladistic and combined analyses (Figures 6 and 7), the taxon remains enigmatic. Notably, no new specimens were identified during the course of this study, and *Quadroncotus* continues to be represented in global collections by only seven partially damaged female specimens (Kamiński, 2016; Koch, 1954b). This lack of material precludes the examination of male terminalia, which are essential for assessing the status of this species under the newly adopted concept of *Oncotus* **sensu nov**. Moreover, the external morphology of *O. andreae*, *O. cedrimontis* and *O. farctus*, members of *Oncotus* **sensu nov**., is relatively invariant, a pattern not observed when compared to *Quadroncotus*. Specifically, *Q. irrepertus* **comb. nov**. differs in several key morphological traits: (1) protibiae with a well-developed apical tooth and irregularly sculptured/toothed lateral margins; (2) short antennae, approximately equal to the width of the head; and (3) pronotum lacking depressions along the laterobasal margins. Given these differences, *Quadroncotus* is herein elevated to the rank of genus. Nevertheless, the status of this taxon should be revisited pending the discovery of additional material, particularly males.

All types of data convergently revealed the polyphyletic nature of the genus *Menederes* by rendering the monotypic subgenus *Anamenederes* as a separate entity among *Oncotus* lineage (Figures 1, 2, 6 and 7). While describing *Anamenederes*, Koch (1954b) noticed its divergent morphology and highlighted, inter alia, a diverging placement of the 9th elytral interval and bent meso- and metatibiae. Nevertheless, based on similarly structured male terminalia, he decided to affiliate *Anamenederes* and *Menederes* together while outlining a close similarity to *Schyzoschelus* (none of the data here supported such a relation). Furthermore, the investigation of male terminalia among all abovementioned taxa revealed great variability of structure among the members of the former subgenus *Menederes*, falsifying Koch's (1954b) hypothesis. To reflect the topologies presented here, the subgenus *Anamenederes* is elevated to genus status.

In summary, the integrative approach adopted here enabled a comprehensive phylogenetic treatment of a long-neglected group of darkling beetles (Figure 7). As a result, a new classification is introduced to better reflect relationships within Eurynotina. The taxonomic and phylogenetic framework established here may serve to support other non-taxonomic studies (e.g. evolution of ovovivipary and desert

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adaptations). However, some questions remain due to a shortage of suitable specimens. For example, monotypic taxa such as *Quadroncotus* and *Menederopsis* were not possible to include in molecular analyses at this time. Future efforts in locating extractable specimens of these taxa may assist in clarifying their phylogenetic positions (i.e. the most closely related genera to *Menederopsis* and the placement of *Quadroncotus* relative to *Oncotus*). Broader taxon sampling in future molecular analyses will likely provide greater resolution and shed light on the evolutionary history of this morphologically challenging group.

TAXONOMY

The taxonomic acts presented below are intended to establish and stabilize generic/species concepts as a result of phylogenetic analyses presented above and are based on the combined phylogenetic topology (Figure 7).

Subtribe Eurynotina Muslant and Rey.

Genera included (21). *Anamenederes* Koch **stat. nov.**, *Byrrhoncus* Koch, *Capidium* Koch, *Colophonesthes* Koch, *Colophonexsula* Lumen & Kamiński **gen. nov.**, *Eurynotus* Kirby (=*Biolus* Mulsant & Rey **syn. nov.**, =*Neosolenopistoma* Mulsant & Rey **syn. nov.**), *Heteropsectropus* Kaszab, *Hirtograbies* Koch, *Isoncophallus* Koch, *Menederes* Solier, *Menederopsis* Koch, *Menoncotus* Koch **stat. nov.**, *Muelleropsectropus* Lumen & Kamiński, *Ograbies* Péringuey, *Oncotus* Solier **stat. nov.**, *Phalerideroma* Koch, *Phylacastus* Fairmaire, *Psectropus* Solier, *Quadroncotus* Koch **stat. nov.**, *Schyzoschelus* Koch, *Stridigula* Koch **sens. nov.** (=*Cilioncotus* Koch **syn. nov.**).

Genus *Anamenederes* Koch stat. nov. (Figure 8a).

Menederes (*Anamenederes*) Koch, 1954b: 68.

Type species. *Menederes* (*Anamenederes*) *digitatus* Koch, by original designation.

Status. Formerly a subgenus of *Menederes*. In all phylogenetic analyses presented here, *Anamenederes* forms a separate lineage within Eurynotina (Figures 1, 2, 6 and 7). To restore the monophyly of *Menederes*, *Anamenederes* is hereby elevated to generic level.

Diagnosis. Member of *Oncotus* lineage (Figure 7). This genus is slightly globose, similar to *Quadroncotus* **sens. nov.**, *Oncotus* **sens. nov**. and *Ograbies* (Figure 8). *Anamenederes* is unique within Eurynotina for the morphology of the foretibia, which bears an elongate projection near the tarsus insertion point (Figure 8a). Aside from this, *Ograbies* differs by the lack of setation of hypomeron (long and free setae in *Ograbies*). *Oncotus* **sens. nov**. and *Quadroncotus* **sens. nov**. possess the lateral margins of pronotum explanately overhanging hypomeron (23:1). Internally, females have paired sclerites in the bursa copulatrix.

Species included (monotypic). *A. digitatus* (Koch) **comb. nov**.

Genus *Colophonexsula* Lumen and Kamiński gen. nov. (Figure 8b). http://zoobank.org/urn:lsid:zoobank.org:act:8B85CAC4-DEAB-4FB6-BC78-FAB3AEC54C7D.

Type species. *Colophonesthes puerilis* Koch; here designated.

Status. In all conducted phylogenetic analyses, *C. puerilis* was recovered separately from *Colophonesthes* – represented here by its type species *C. montisatri* (Figures 1, 2, 6 and 7). To restore the monophyly of *Colophonesthes*, the new genus *Colophonexsula* is erected.

Diagnosis. Within the *Psectrapus* lineage, *Colophonexsula* is easily diagnosed by its unique foretibiae, which possess a small apical projection (Figure 8b). Furthermore, *Colophonexsula* displays strong sexual dimorphism, with larger females that have wider pronota, as well as differing in the texturing (punctation/lustre) in the elytra (males shiny with larger punctation; females dull with finer punctation) (Figure 8b).

The habitus of *Colophonexsula* greatly resembles *Psectrapus* or *Colophonesthes*. However, they differ by the structure of female fifth abdominal ventrites (with sulcus in *Psectrapus*, absent in *Colophonexsula*); the same character differentiates *Colophonexsula* from *Isoncophallus*, of which members possess a sulcus in both sexes. From *Capidium*, *Colophonexsula* differs by having rounded basal angles of the pronotum and a lack of strong tuberculation on elytra. From *Byrrhoncus* and *Colophonesthes*, it can be separated based on aedeagal morphology (Figure 8b): long, thin parameres, which diverge medially before converging apically, giving a pincer- or scythe-like appearance in *Byrrhoncus*; parameres situated closer together in *Colophonesthes* (Koch, 1954b).

Etymology. This genus is named for *Colophonesthes* with the added suffix "*exsula*" for stranger or exile, in reference to the phylogenetic placement of this new genus.

Species included (monotypic). *C. puerilis* (Koch) **comb. nov**.

Genus *Eurynotus* Kirby sens. nov.

Eurynotus Kirby, 1819: 418.

= *Biolus* Mulsant & Rey, 1854: 25. **syn. nov**.

= *Neosolenopistoma* Bouchard et al., 2021: 265 **syn. nov**.

Type species. *Eurynotus muricatus* Kirby, designated by monotypy.

Status. Lumen and Kamiński (2024) proposed a new classification of *Eurynotus* by redefining and elevating the subgenus *Biolus* to generic rank. Results presented here based on molecular data are highly incongruent with those based solely on morphology (Figures 1 and 2 vs. 6). Re-evaluation of morphological data did not provide any reliable features for adopting molecular topologies that would sustain separate, monophyletic *Biolus* and *Eurynotus*. Taking into consideration the monophyly of *Biolus* + *Eurynotus* and its diagnosability, the following synonymy is proposed: *Eurynotus* (=*Biolus*). The identification key provided by Lumen and Kamiński (2024) can still reliably be used to identify all species.

Diagnosis. *Eurynotus* is one of the most easily recognized, collected and identified groups within Eurynotina and represents one of the largest (both in body size and number of taxa) genera within the subtribe (9–22 mm in length; 17 species). Morphologically, the genus is easily separable from other genera by the shape of the pronotum (bisinuate, with basal angles strong/acute/rectangular and produced backward towards the elytra), the structure of the prosternum (projecting between forecoxae) and, in most species, the presence of strong elytral tuberculation on the elytrae.

Species included (17). *E. alticola* Koch, *E. analisetosus* Koch, *E. asperatus* Mulsant & Rey, *E. asperipennis* Mulsant & Rey, *E. barbosai* Koch, *E. brunoi* (Lumen & Kamiński) **comb. nov.**, *E. capensis* (Fabricius),

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E. constrictus Koch, *E. denticosta* Mulsant and Rey, *E. graafi* Koch, *E. graniderma* Koch, *E. granulatus* (Fabricius), *E. omeri* Koch, *E. privisolum* Lumen & Kamiński, *E. sauroides* Koch, *E. sulcimargo* Koch, *E. thermarum* Koch.

Genus *Menoncotus* Koch stat. & sens. nov. (Figure 8c,d).

Oncotus (*Menoncotus*) Koch, 1954b: 34.

Type Species. *Menoncotus chaetotaxicus* Koch, by original designation.

Status. Koch (1954b) originally designated four following subgenera within *Oncotus*: *Cilioncotus*, *Menoncotus*, *Oncotus* and *Quadroncotus*. *Menoncotus* superficially appeared to be the least consistent or well defined of the groups (i.e. a 'bin taxon'). Some of its representatives display a general external affinity also matched by general male reproductive morphology (e.g. *O. chaetotaxicus* Koch, *O. jokli* Koch, *O. sinuatipes* Koch) (Figure 8d), while others diverge (*O. cedrimontis* Koch, *O. capicola* Koch) (Figure 7). Those assumptions were supported by phylogenetic analyses conducted here as representatives of this subgenus were projected in three separate clades rendering *Menoncotus* paraphyletic (Figure 7).

To restore the monophyly of *Oncotus*, *Menoncotus* is hereby elevated to generic level. Furthermore, in the reorganization proposed here, *O. capicola* **syn. nov**. is synonymized with *Ograbies capensis* and *O.* (*Menoncotus*) *cedrimontis* is moved into *Oncotus s. str*. (see relevant sections for more information). *Menoncotus* remains a difficult case with few specimens (22) available for defining the group.

Diagnosis. *Menoncotus* **sens. nov**. has foretibiae with lateral projections and hypomeron without long, free setae (similar to *Oncotus*), setting it apart from *Ograbies*, *Hirtograbies* and *Phaleriderma*; however, the simple, tapering parameres of the aedeagus (separating the genus from many eurynotines that have characteristic parameres, Figure 8d) and pronotum with rounded basal angles lacking depressions (Figure 8c) separate the genus from *Oncotus* **sens. nov**. Additionally, *Menoncotus* is separable from *Menederes* **sens. nov**. based on their body shape (shorter/rotund rather than overall more elongate) and the structure of abdominal ventrite V (without a sulcus near to the apex).

Species included (3). *M. chaetotaxicus* (Koch) **comb. nov**., *M. jokli* (Koch) **comb. nov**., *M. sinuatipes* (Koch) **comb. nov**.

Genus *Ograbies* Péringuey.

Ograbies Péringuey, 1899: 293.

***Ograbies capensis* (Solier)**.

Oncotus capensis Solier, 1848: 220.

=*Oncotus capicola* Koch, 1954b: 36 **syn. nov**.

Status. When originally outlining his concepts, Koch (1954b) mentioned that his newly described *Oncotus* (*Menoncotus*) *capicola* shared similar features with *Ograbies*. Examination of his material, descriptions and comparison with material from other collections (i.e. MNHN) leads us to conclude that *Oncotus capicola* is identical to *Ograbies capensis*. The foretibiae are unmistakably of the *Ograbies* type (62:1). Further, specimens included in phylogenetic analyses (molecular, morphological and combined) were always deeply nested in a well-supported, monophyletic *Ograbies* (Figures 1, 2, 6 and 7). *Ograbies capensis* is divergent from the rest of *Ograbies* in a couple of ways: reduction in setation of the hypomeron and different shape of the aedeagus; however, a new species described here is morphologically very similar (see *O. calumnus*). *Ograbies capensis* is separable from *O. calumnus* based on internal (presence of paired sclerites in the bursa copulatrix, absent in *O. calumnus*) and external (finer punctation of the hind tibiae, coarse punctation on the outer surface in *O. calumnus*) morphology. While several specimens fitting our diagnostic criterion were located in different collections, a search for the original type material was undertaken at the MNHN where Solier's material is housed to ensure taxonomic clarity and stabilize the nomenclature of *Ograbies*. Despite extensive efforts, the original holotype could not be located. Therefore, under the provisions of Article 75.3 of the ICZN (1999), the designation of a neotype is warranted. The hereby selected specimen from MNHN (Figure 8e) directly matches the type locality stated in the original description ("Cap Bonne Esperance") and constitutes a form of *Ograbies* fully aligning with original diagnostic features, that is, reddish coloration and reduced punctation of the pronotum and head, and reduced striation of the elytra (Solier, 1848).

Type material. *Oncotus capensis* **Neotype** Here designated **MNHN:** "Oncotus/capensis/Sol. C.B.Esp./Coll. R. Oberthur/ex coll Deyrolle/Cap. b. Sp" (Figure 8e).

Ograbies capicola **Holotype NRS:** "De Vylder"/"Cap. b. Sp."/"Victorin und Kinb". **Paratype TMNH:** "De Vylder"/"Cap. b. Sp."/"PARATYPE No: 1658"/"Oncotus"/"capicola KOCH". Paratype.

***Ograbies calumnus* Lumen and Kamiński sp. nov**.

http://zoobank.org/urn:lsid:zoobank.org:act:F9F02503-A639-4E23-92FC-905658AEF185.

Status. Koch (1954b) when giving his diagnoses and descriptions of species for *Ograbies* used Solier's (1848) description to associate specimens with *O. capensis*. After re-evaluating *Ograbies capensis*, two female *Ograbies* specimens in need of description remained on hand, which loosely matched Koch's concept of *O. capensis*.

Diagnosis. This species is most similar to *O. capensis*, *O. campi* and *O. angulatus*. *Ograbies calumnus* is separable by the sculpturing of the head capsule (dense and fine) with a velvety/matte finish, and hind tibiae with coarse punctation on the outer surface. Other species are separable by coloration (most species are bicolored), the structure of the basal border of the pronotum (complete in this species; incomplete in *O. frigidus* and *O. subdentatus*), and bursa copulatrix sclerites (absent in this species, present in others).

***Description*:** Length 10–11 mm, width 4–6 mm. Coloured tenebrous; reddish-brown, dark brown to black. **Head**: Finely punctate, punctures crowded and spaced (≤1 puncture diameter apart) in distribution. Prementum with median emargination. Mentum with broad, ventrally projecting middle portion; lateral wings exposed. **Prothorax**: Finely punctate, punctures widely spaced (≥1 puncture diameter apart) in distribution; matte and lightly textured. Without middle emargination of basal margin. **Pterothorax**: Elytra matte and lightly textured, punctatostriate. With very lightly to impunctate intervals. **Abdomen**: Ventrite V without larger setigerous punctures intermixed among smaller punctures. **Legs**: femurs laterally compressed, slightly curved and thickened. Hind tibiae with coarse punctation on outer

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surface. **Male** unknown. **Females**: Ovipositor short (coxites 1–4 combined length ≤ paraprocts). Bursa copulatrix sac-like, without sclerites.

Etymology. Named from the Latin *calumn* (=to trick), based on Koch's (1954b) erroneous diagnosis of *Ograbies capensis*, into which this species fits.

Type data. Holotype (female) **MIZPAN**: "Blue Tenebrionidbase label, Catalog # 26385, POI 45 (South Africa, −34.244125, 18.410154), 9 Oct 2019, Red label Holotype *Ograbies calumnus*." **Paratype** (female) **SANC**: "L'Agulas 19.XII.1995, S. Africa Cape Prov. G Minet, Yellow label Paratype *Ograbies calumnus*" (Figure 8f).

Note: The holotype was extracted, sequenced and included in analyses.

Genus *Oncotus* Solier sens. nov.

Oncotus Solier, 1848: 218.

Type species. *Oncotus farctus* Solier, by subsequent designation.

Status. In order to restore the monophyly of *Oncotus*, a new taxonomic interpretation of this taxon is hereby proposed. The new genus is based on the subgenus *Oncotus* (*O. andreae* Koch, *O. farctus* Solier) with the addition of *O. cedrimontis* Koch – formerly classified within *Menocotus*.

Diagnosis. Member of the *Oncotus* lineage. *Oncotus* **sens. nov**. is defined by its relative oblong/short and slightly dorsoventrally flattened habitus, epistomal canthus interrupted in the middle (restricted to lateral corners/edges), relatively square/angular basal angles of the pronotum with slight depressions, pronotal lateral edge "eave-like" (overhanging the hypomeron), foretibiae with lateral projections on the apex. *Oncotus farctus* and *O. andreae* are nearly indistinguishable externally; however, *O. andreae* has truncate and apically rounded parameres versus *O. farctus* and *O. cedrimontis*, which both have more similar aedeagal morphology (parameres slightly sinuate apically) that is unique within Eurynotina.

Species included (3). *O. andreae* Koch, *O. cedrimontis* Koch, *O. farctus* Solier.

***Oncotus farctus* Solier**.

Oncotus farctus solier, 1848: 218.

Status. While revising the Eurynotina, Koch (1954a), Koch (1954b), Koch (1955) lacked access to a significant portion of historical type materials. To overcome this limitation, he sought to interpret taxonomically relevant information from the original description by Solier (1848). As a result of the investigation of museum material and comparison with Solier (1848) description, Koch's (1954b) interpretation appears to have been accurate and is sustained here; however, his species *Oncotus andreae* is externally almost identical. The presumed type material for *Oncotus farctus* was not located at the time of this study despite an exhaustive search of the institution presumably housing Solier's specimens (MNHN). Here, we designate a neotype from MNHN from a locality within the locus typicus ("Cap. bon Esperance") and overlaps morphologically with Solier's (1848) and Koch's (1954b) descriptions, illustrations and photographs to stabilize the genus and species concept for *Oncotus* and *Oncotus farctus* respectively. Additionally, the newly selected neotype has relevant anatomy exposed (male genitalia) to provide a basis by which the species can be reliably separated from *Oncotus andreae* (see diagnosis).

Diagnosis. Within the genus *O. farctus* has a diagnostic aedeagus with widely diverging parameres and a well-defined and sclerotized penis with hook (Figure 5r). *Oncotus andreae* is extremely similar in external appearance, but is separable by aedeagus: *Oncotus andreae* with truncate aedeagus and smaller opening between parameres and without hook on penis (see figures 10A and B from Koch, 1954b). From *O. cedrimontis* the species is again differentiable by the aedeagus, which have more dramatically divergent parameres and a hook on the penis. Additionally, *O. cedrimontis* is differentiable by the width of the elytral interval 9, which is relatively narrow in *O. farctus* and *O. andreae* (interval 8 subequal to interval 9; rather than 9th interval nearly twice width of interval 8 as in *O. cedrimontis*).

Material examined: Neotype, here designated **MNHN**: "MUSEUM PARIS/ENV. DE/CAPETOWN/A. RAFFRAY 1899" (Figure 8g).

Genus *Psectrapus* Solier.

Psectrapus Solier, 1848: 213.

***Psectrapus bipartitus* Solier (**Figure 8h).

Psectrapus bipartitus Solier, 1848: 215.

Status. While revising the Eurynotina, Koch (1954a), Koch (1954b), Koch (1955) did not have access to a significant portion of historical type materials concerning the group. To overcome this limitation, he sought to interpret taxonomically relevant information from original descriptions (in this case by Solier (1848)). However, the restricted material available to him at the time led to inaccuracies, particularly concerning *Psectrapus bipartitus* Solier, the type species of *Psectrapus*. Koch's (1954b) interpretation emphasized the expansion of the pro- and mesotarsus in males as a unique feature, while overlooking other important diagnostic features, such as the fine punctuation of the head and pronotum, and disregarding the original type locality, "Cap de Bonne Espérance." Specimens from relatively distant localities (Mossel Bay, Bredasdorp, Montagu) were incorrectly attributed to *P. bipartitus*. Recent examination of newly available material has revealed that the broadening of the pro- and mesotarsi is not unique to *P. bipartitus*, but shared with at least two other species (*P. byki* Lumen & Kamiński **sp. nov**., *P. simplicimentulum* Lumen & Kamiński **sp. nov**.), which differ in pronotal punctuation, aedeagal morphology and geographical distribution. To ensure taxonomic clarity and stabilize the nomenclature of *Psectrapus*, a search for the original type material was undertaken at the MNHN, where Solier's materials are housed. Despite extensive efforts, the original holotype could not be located. Therefore, under the provisions of Article 75.3 of the ICZN (1999), the designation of a neotype is necessary. The hereby selected specimen (Figure 8h) directly matches the type locality stated in the description and constitutes the only form of *Psectrapus* fully aligning with original diagnostic features (widened tarsi and fine punctuation of head and pronotum).

Diagnosis*: *Psectrapus bipartitus has a uniquely matte or silky habitus. Compared to the rest of the genus, *P. bipartitus* has less-strongly defined punctation of both the elytra and pronotum. Other species have shinier elytra and pronota (*P. nitens*), and/or more well-defined punctation. Additionally, *P. bipartitus* is the only species with a bifurcated hook (i.e. two hooks) on the penis in males.

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***Redescription*:** Length 7–8 mm, width 4–5 mm. Coloured tenebrous; reddish-brown, dark brown to black. **Head**: Finely punctate, punctures widely spaced (≥1 puncture diameter apart) in distribution. Prementum with median emargination. Mentum with large, broad, ventrally projecting middle portion; lateral wings concealed. **Prothorax**: Finely punctate, punctures widely spaced (≥1 puncture diameter apart) in distribution; matte and lightly textured. Without middle emargination of basal margin. **Pterothorax**: Elytra matte and lightly textured, with finely punctate intervals and striae. **Abdomen**: Ventrite V without larger setigerous punctures intermixed among smaller punctures; apical sulcus present in females. **Legs**: Femurs laterally compressed, slightly curved and thickened. Males with large apical setal patches on foretibiae and strip of setae on hind tibiae, pro/meso tarsi strongly expanded with ventral, tomentose pads. **Male terminalia**: Parameres narrowly separate and strongly narrowing apically. Penis strongly sclerotized with small and pronounced bifurcate hook(s) at apex.

***Material examined*: Neotype**, here designated, male **MNHN**: Blue circle label "Oncotus obtusus Cap. Bon Esp.", White label "Museum Paris Coll. DE MARSEUL 1890" Red label "Psectrapus bipartitus LECTOTYPE" (Figure 8h).

***Psectrapus byki* Lumen and Kamiński sp. nov. (**Figure 8i).

http://zoobank.org/urn:lsid:zoobank.org:act:5907BFB9-60D9-4971-AB14-5BE08253FA9D.

***Diagnosis*:** *Psectrapus byki* is unique for the strong medial narrowing of the aedeagal parameres before expanding again towards the apex; giving rise to a uniquely shaped window exposing the penis (Figure 8i). Additionally, this species has a more pronounced medial indentation of the pronotal base compared to other species. Furthermore, males can be separated from *P. bipartitus* by a lessened degree of protarsal widening: preapical protarsomere in males of *P. bipartitus* less than half than that of the second tarsomere, in *P. byki* this relation is ca. 1.5.

***Description*:** Length 6.5–8 mm, width 3.0–3.8 mm. **Head:** finely punctate, punctures closely spaced, separated by ≤1 feature diameter. Mentum with prominent median portion and exposed wigs. Eye only slightly impressed by genal canthus, well developed. **Prothorax**: Pronotum finely punctate, punctures separated by 1–2 feature diameters. **Pterothorax**: Striae punctato-sulcate with punctures separated by 1–2 feature diameters. Intervals finely punctate. **Abdomen**: Finely punctate. Abdominal ventrite V punctures separated by ~1 feature diameter. Females with apical sulcus situated at tip of ventrite V. **Legs**: Male hind tibiae very slightly flattened/twisted, appearing bent. Female legs unmodified. Male pro/meso tarsi enlarged, with ventral, tomentose pads. **Male terminalia**: Parameres strongly narrowing medially before expanding towards apex, forming uniquely shaped oval opening for penis. **Female terminalia:** Bursa copulatrix sac-like and without sclerites, spermatheca thick and coiled, accessory pouch absent.

***Material examined*:** Holotype, male **TMNH**: "S. Afr: Little Karroo Gamkaberg 1000m, 33.43 S –21.57 E", "15.5.1995: E-Y 3082, groundtraps. 30 days, leg. Tom Berry.". Paratypes, female **MIZ**: same data as holotype; male **MIZ**: "S. Afr: LittleKarroo Gamkaberg 1000m 33.44 S – 21.57 E", "15.5.1994: E-Y: 3074 groundtraps 30 days, leg. Tom Berry"; male **TMNH**: "S. Afr: Little Karroo Gamka tourist camp, 33.42 S – 21.34 E", "25.10.1993: E-Y: 2903 window trap, leg. Endrödy-Younga"; female **TMNH**: "S. Afr: W Cape Prov. Gamkaberg Nat. Res. 33.42 S – 21.57 E", "1.7.1998: E-Y: 3240 groundtraps, leg. Tom Berry".

***Etymology*:** Named after Dr. Adam Byk (Institute of Forest Sciences; Warsaw University of Life Sciences), a Polish entomologist specializing in Scarabaeoidea.

Note: A specimen from the type series was affixed with a label "TB# 26348" and extracted, sequenced, for inclusion in molecular analyses.

***Psectrapus simplicimentulum* Lumen and Kamiński sp. nov. (**Figure 8j).

http://zoobank.org/urn:lsid:zoobank.org:act:9C3363E1-4589-4315-974C-388A22E5ADFA.

***Note*:** The specimens of this species were incorrectly interpreted by Koch (1954b), who did not see Solier's type material for *P. bipartitus*.

***Diagnosis*:** Superficially most similar to *P. bipartitus* (Figure 8h,j); however, it can be differentiated from it by the penis with a single, unbifurcated hook (bifurcated in *P. bipartitus*) and denser punctation (widely spaced in *P. bipartitus*).

***Description*:** Length 7–7.5 mm, width 3–3.5 mm. **Head:** finely punctate, punctures closely spaced, separated by ≤1 feature diameter. Prementum without median emargination. Mentum with relatively narrow, ventrally projecting middle portion; lateral wings exposed. **Prothorax**: Pronotum without middle emargination of basal margin; dorsally without large, widely spaced setae and punctures situated on lateral edges; finely punctate, punctures separated by ≤1 feature diameter. **Pterothorax**: Elytral striae strongly impressed and punctate. Intervals punctate, with few bumps or tubercles present on apical declivity. Punctate. Punctures separated by ≤1 diameter. Abdominal ventrite V broad (wider than long) with larger setigerous punctures intermixed among smaller punctures. **Legs**: Tibiae straight to slightly curved; without apical setal patches or strips running apical 1–2/3rds. Tarsi with golden setae and expanded pro/meso tarsi with ventral, tomentose pads in males. **Male terminalia**: Parameres narrowly separate and strongly narrowing apically. Penis strongly sclerotized with unbifrucated apical hook.

***Material examined*: Holotype MIZPAN**: S. Africa. R. E. Turner Brit. Mus. 1921–248., Mossel Bay, Cape Province, May 1921, Psectrapubs bipartitus Sol., Psectrapus bipartitus C. Koch det., 1952, Blue label: Tenebrionid Base Aaron D. Smith Catalogue # 26334, Red Holotype Label. **Paratypes NHMUK**: "Same data as Holotype, additional labels: Psectropus bipartitus Sol. det.? G. Blair, Oncotus? sp. M.J.D.Brendell det. 1975, Yellow Holotype Label", "S. Afr. Cape Prov. 20 miles SE Swellendam 3.I.51, Swedish South Africa Expedition 1950–1951 Brinck – Rudebeck, yellow "paratype" Label." **MNHN**: "blue-green label CAFR, coll. R. Oberthur ex Coll. Deyrolle", "Caffraria R. Oberthur ex Coll. Deyrolle".

Etymology: Named for the relative simple form of the aedeagus–penis without bifurcated hook and uniformly narrow window between the parameres.

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Note: The holotype was extracted, sequenced and included in molecular analyses.

Genus *Quadroncotus* Koch stat. & sens. nov. (Figure 8k).

Oncotus (*Quadroncotus*) Koch, 1954b: 40.

Type species. *Oncotus irrepertus* Koch, by original designation.

Status. Formerly a subgenus of *Oncotus*, *Quadroncotus* is here elevated to generic rank based on the phylogenetic topologies presented here as well as its unique morphology.

Diagnosis. Morphologically and phylogenetically closest to *Oncotus* **sens. nov**. (Figures 6 and 7). Both share the following features: pronotal lateral margin with sulcus (22:0), lateral margins of pronotum overhanging hypomeron (23:1), body relatively round/ovoid and foretibiae expanded. However, the expansion of the tibiae differs in *Quadroncotus* **stat. nov**. in that it has a less well-defined apical tooth and more irregularly sculptured/toothed lateral edges of the tibiae, which are distinct for the genus (Figure 8k). Further, *Oncotus* **sens. nov**. has depressions on the latero-basal edges of the pronotum (absent in *Quadroncotus*). As of these analyses, the genus is well diagnoseable from *Oncotus* and other groups; however, to date, only seven specimens are known (all female), so future studies may reveal more characteristics (i.e., males) to better define this taxa or affiliate it with other groups.

Species Included (1). *Q. irrepertus* (Koch) **comb. nov**.

Genus *Stridigula* Koch sens. nov. (Figure 8l).

Stridigula Koch, 1954b: 60; 1956: 27.

= *Cilioncotus* Koch, 1954b: 41 **syn. nov**.

Type species. *Stridigula arguta* Koch; by original designation.

Status. Preliminary observation showed a superficial resemblance between *Stridugula* and *Cilioncotus* (a former subgenus within *Oncotus*), which was further supported by the phylogenies presented here (Figures 6 and 7). The features formerly proposed to distinguish those two taxa were inconsistent. Furthermore, closer morphological examination revealed that *Oncotus* (*Cilioncotus*) *humerisetosus* is synonymous with *Stridugula arguta*. As such, a synonymy between Stridugula and Cilioncotus is proposed here.

Diagnosis. Member of *Oncotus* lineage. Easily distinguishable from other Eurynotina based on the presence of a setose pit at the base of the elytra (Figure 8l).

***Species included* (3):** *S. arguta* Koch (=O. *humerisetosus* Koch **syn. nov**.), *S. namaquanus* Koch **comb. nov**., *S. planiuscula* (Fairmaire).

AUTHOR CONTRIBUTIONS

Ryan Lumen: Writing—original draft; review and editing; conceptualization; data acquisition; data curation; formal analysis; investigation; methodology; sampling; software; study design; visualization. **Adam M. Rork**: Writing—review; software. **Aaron D. Smith**: Writing—review; data acquisition; funding acquisition; sampling. **Marcin J. Kamiński**: Writing—review and editing; conceptualization; data acquisition; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; sampling; software; study design; visualization.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

The sequencing data in FASTQ format have been deposited in the NCBI SRA (https://www.ncbi.nlm.nih.gov/) under BioProject PRJNA1016168 (BioSamples: 45730786–45,730,816). All phylogenetic matrices, supplementary trees in editable formats, and partition files are available via Harvard Dataverse at: https://doi.org/10.7910/DVN/CTUUX6.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Label data and deposition of the specimens used in the morphological investigation.

Table S2. Metadata of sequenced specimens of Platynotini.

Table S3. Description of morphological characters used in the phylogenetic analyses of Eurynotina.

Table S4. Morphological matrix used in TNT format for phylogenetic analysis of Eurynotina.

Figure S1. Heat maps showing recovery efficiency obtained with the HybPiper v2.0 pipeline for museum specimens representing Eurynotina. A total of 620 nuclear genes were targeted, and 12 mitochondrial loci were recovered as bycatch. Each column corresponds to a gene, and each row represents a sample. The shading of each box indicates the proportion of the target length recovered; darker colors represent a higher percentage of gene recovery.

Figure S2. Phylogeny of the tribe Platynotini inferred from a targeted enrichment dataset. Only fresh, ethanol-preserved specimens were included. The tree shown is the majority-rule consensus from an IQ-TREE2 analysis of the concatenated matrix comprising 499 loci and 155,172 aligned amino acid positions. Ultrafast bootstrap values from IQ-TREE2 are indicated above branches.

Figure S3. Phylogeny of the subtribe Eurynotina inferred from targeted enrichment and mitochondrial datasets. The tree shown is the majority-rule consensus from an IQ-TREE2 analysis of the concatenated matrix comprising 510 loci and 157,567 aligned amino acid positions. Branch support is indicated by ultrafast bootstrap values. Specimens labeled "M" represent data derived from pinned museum material, whereas "F" denotes fresh specimens.

Figure S4. Phylogeny of the subtribe Eurynotina inferred from morphological data. The tree shown is the majority-rule consensus from an IQ-TREE2 analysis of 91 characters (see Table S1). Branch support is indicated by ultrafast bootstrap values. Specimens labeled "M" represent data derived from pinned museum material, "F" denotes fresh specimens, and "MORPH" indicates specimens not included in the molecular analysis (see Figure S3).

Figure S5. Phylogeny of the subtribe Eurynotina, inferred from a concatenated dataset of 510 loci (157,567 aligned amino acid positions) and 91 morphological characters. The depicted topology represents the majority-rule consensus of post-burn-in trees from Bayesian analysis. Branch support is shown as posterior probabilities; absence of values indicates full support. Specimens labeled "M" are derived from pinned museum material, "F" from fresh specimens, and "MORPH" from morphological data only.

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#05

Natural History Monographs
of the Upper Silesian Museum

2025

Ryan Lumen
Marcin J. Kamiński

Revision Of Subtribe Eurynotina (Coleoptera: Tenebrionidae: Blaptinae)



Muzeum Górnośląskie w Bytomiu

DEPARTMENT OF NATURAL HISTORY
UPPER SILESIAN MUSEUM

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— **Ryan Lumen**

For *Marysia* and *Zosia*, with all my love.
— **Marcin Jan Kamiński**

Ryan Lumen & Marcin Jan Kamiński

Revision of subtribe Eurynotina (Coleoptera: Tenebrionidae: Blaptinae)

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Abstract: Revision of subtribe Eurynotina (Coleoptera: Tenebrionidae: Blaptinae). This monograph is the most comprehensive taxonomic treatment and first revision of the entire darkling beetle subtribe Eurynotina (Coleoptera: Tenebriondae). The classification adopted here is based on recent phylogenetic contributions to the subtribe. As such, the taxonomic part of this monograph is subdivided into five sections representing distinct phylogenetic lineages based on morphological and molecular data within Eurynotina, i.e. *Eurynotus* (monogeneric), *Phylacastus* (monogeneric), *Schyzoschelus* (*Heteropsectropus* Kaszab, *Muelleropsectropus* Lumen & Kamiński, *Schyzoschelus* Koch), *Psectrapus* (*Byrrhoncus* Koch, *Capidium* Koch, *Colophonexsula* Lumen & Kamiński, *Isoncophallus* Koch, *Psectrapus* Solier), and *Oncotus* (*Anamenederes* Koch, *Hirtograbies* Koch, *Menederes* Solier **stat. nov.**, *Ograbies* Péringuey, *Oncotus* Solier, *Phalerіderma* Koch, *Quadroncotus* Koch, and *Stridigula* Koch) lineages. Sections detail the taxonomic history for each genus and species, and further include morphological and geographical distribution data, along with label information for the material examined. Specifically, each lineage section includes an illustrated key to the genera, while the particular genus sections include keys to all species. New synonomies are proposed for *Capidum* (*Blaps bipunctata* Thunberg (=*Blaps striatula* Thunberg **syn. nov.**)), *Hirtograbies* (*H. longipilis* Koch (=*H. brevicornis* Koch **syn. nov.**, =*H. namibensis* Koch **syn. nov.**), and *Menederes* (=*Menoncotus* Koch **syn. nov.**, =*Menederopsis* Koch **syn. nov.**). New combinations are as follows: *Menederes chaetotaxicus* (Koch) **comb. nov.**, *Menederes constrictus* (Koch) **comb. nov.**, *Menederes jokli* (Koch) **comb. nov.**, *Colophonexsula enisa* (Koch) **comb. nov.**, *Colophonexsula nitens* (Koch) **comb. nov**. The following new species are described: *Isoncophallus crispiformus* **sp. nov.**, *Isoncophallus ovanullum* **sp. nov.**, *Phalerіderma iwani* **sp. nov.**, *Psectrapus distaticum* **sp. nov.**, *Psectrapus latimentulum* **sp. nov.**, and *Schyzoschelus aetheculus* **sp. nov**. Neotypes are designated for *Menederes rufilabris* Solier, *Ograbies singularis* Péringuey, *Ograbies testaceus* (Solier), and *Schyzoschelus validus* (Fairmaire) to formally fix their taxonomic and species concepts. Finally, the status of *Capidium hessei* Koch **stat. res.** is restored. Habitus photographs, diagnostic features, and distributional maps are provided for current and future workers to direct research and collecting efforts for all 94 species and 19 genera representing Eurynotina.

Key words: Africa, darkling beetles, identification keys, species discovery, type specimens.

I. Introduction

Originally established in 1854, Eurynotina Mulsant & Rey did not receive much taxonomic attention for the first century of its existence (Kamiński 2016). The first major treatment was by Koch (1954a, b, 1955), who performed a comprehensive morphological revision establishing 95 southern African species and subspecies in 16 genera. He further designated three generic complexes based primarily on the shape of the clypeus: I. *Eurynotus* complex (genera with clypeal apex deeply emarginated: *Eurynotus* Kirby and *Phylacastus* Fairmaire) (Fig. 1A), II. *Schyzoschelus* complex (clypeal apex straight: *Heteropsectropus* Kaszab and *Schyzoschelus* Koch), and III. *Oncotus* complex (clypeal apex shallowly, but clearly emarginate: *Byrrhoncus* Koch, *Capidium* Koch, *Colophonesthes* Koch, *Hirtograbies* Koch, *Isoncophallus* Koch, *Menederopsis* Koch, *Menederes* Solier, *Ograbies* Péringuey, *Oncotus* Solier, *Phaleriderma* Koch, *Psectrapus* Solier, and *Stridigula* Koch).

The phylogenetic placement of Eurynotina within Blaptinae Leach and its monophyly is supported by molecular and morphological data (Lumen *et al*. 2025). All members of this tribe in their adult forms possess relatively simple, clavate antennae (lacking compound/stellate sensoria), externally and internally closed procoxal cavities, visible intersternal membrane of abdominal ventrites 3–5, and paired, elongate defensive reservoirs that are not annulated (Kamiński *et al*. 2021). Larval forms are characterised by enlarged prolegs (adapted for digging, Fig. 1B) and ninth tergite without urogomphi (Kamiński *et al*. 2019, 2021, Raś *et al*. 2022, Lumen *et al*. 2024a, b, 2025). Additionally, all members of this subtribe possess a stridulatory surface on the gular region of the head (Fig. 1C) a synapomorphy that unites Eurynotina with Platynotina Mulsant & Rey. Though we have observed hand collected specimens performing stridulatory behaviors, the purpose of this stridulatory surface in Platynotini remains unknown, and no other Blaptinae displays a similar structure (Koch 1956). Eurynotina differs from Platynotina by the lack of aedeagal ancorae (Fig. 1D) (Koch 1956, Iwan 2001, 2004); however, a single species, *Phylacastus ancoralium* Lumen & Kamiński, was observed to possess relatively short ancorae on its adeagus (Lumen & Kamiński 2023). On the other hand, *Anomalipus heraldicus* Gerstaecker of Platynotina lacks visible ancorae (Iwan 2004) making subtribal definitions at times problematic. A supporting feature to distinguish most representatives of the both subtribes is the presence (Eurynotina, Fig. 1A) or absence (Platynotina) of tubercles on the elytral surface (Koch 1955, 1956, Iwan 2002). However, there are exceptions here as well, e.g., *Phymatoplata* Koch of Platynotina has tubercles, while some Eurynotina lack them (Iwan 2002, Lumen & Kamiński 2023, 2024a).

Through the efforts leading towards this monograph, the entomological materials of some of the largest and most relevant natural history collections on the planet were sampled. However, the world's holdings concerning the subtribe were revealed to be extremely scarce compared to closely related lineages of darkling beetles (e.g., Platynotina or Opatrini). Additionally, in many cases, available specimens were damaged and/or labeled with vague data, precluding detailed morphological and biogeographic studies (Fig. 1E). Although some representatives of Eurynotina are relatively common, most species and subspecies (over 75%) are known only from holotypes or relatively small type series (Koch 1954a, b, 1955, Kamiński 2016). The paucity of diverse material concerning the subtribe has resulted in very narrow taxonomic concepts for many species and genera, making identifications challenging or impossible without reference to type specimens (Koch 1954a, b, 1955, Kamiński 2016).

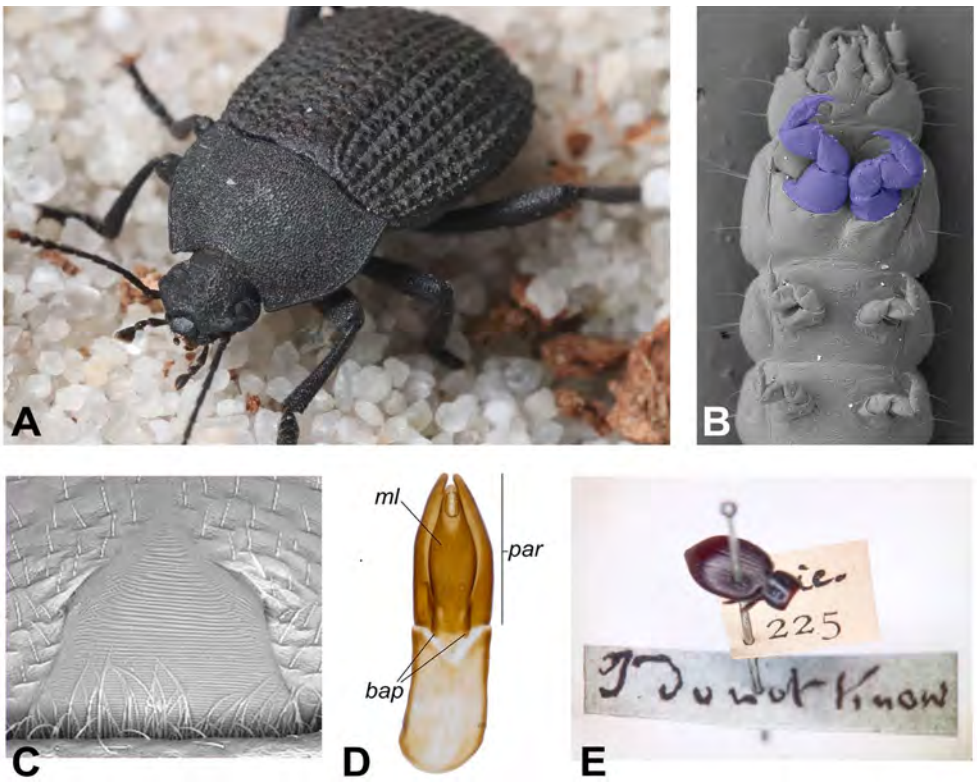


Fig. 1. Diagnostic characters of the subtribe Eurynotina. *Eurynotus granulatus* with coarse tubercles on elytra (**A**), larva of *Eurynotus asperatus* with enlarged prolegs – in blue (**B**), stridulatory gula of *Eurynotus capensis* (**C**), aedeagus of *Phylacastus crypticoides* lacking ancorae (**D**), unidentified damaged specimen of Eurynotina (**E**). **Abbreviations**: ml = Median lobe, par = Parameres, bap = basal apophyses.

Contrastingly, the sister subtribe Platynotina Mulsant & Rey is represented by a large amount of material in the majority of natural history museums worldwide (e.g., *Upembarus wittei wittei* Koch with 8,267 syntype specimens, see Koch 1956), and has received much more attention from taxonomists over the past 70 years (e.g., Iwan 1995, 1998, 2002, 2003, 2004, 2005, 2006, Endrödy-Younga 2000, Iwan & Kamiński 2012, Kamiński 2012, 2013a, b, c, 2014, 2015, 2017, Kamiński & Iwan 2013, Kamiński & Ras 2011, Kamiński & Schoeman 2018, Ivie *et al.* 2021).

The lack of stable classification, reliable identification resources, and phylogenetic hypotheses further contributes to the negligence of this enigmatic darkling beetle group. For example, multiple species are ovoviviparous. With only ten cases known outside the subtribe, ovoviviparity is extremely rarely observed among darkling beetles (Schulze 1969, Tschinkel 1978, Iwan 2000). To date, ovoviviparity has been reported for representatives of all of Koch's (1954a, b, 1955, present data) generic complexes, and may be more prevalent within the subtribe than initially assumed (Lumen & Kamiński 2024a, b). Experimental observations of Eurynotina are extremely scarce (see Lumen & Kamiński 2024a), and the majority of known ovoviviparous species have been discovered in preserved specimens. Specifically, first instar larvae have been observed in the bursae copulatrices of pinned specimens (Tschinkel 1978, Iwan 2000, Lumen & Kamiński 2024a, b). Despite their interesting life histories and potential

for ecological study, there is a dearth of ethological and ecological data for Eurynotina, leaving the drivers for traits such as ovovivipary unknown. The most up to date record on the phenomenon of ovovivipary in Eurynotina was summarized by Lumen & Kamiński (2024a). Though the habitat requirements for most species remain to be investigated in depth, none of the factors Lumen & Kamiński (2024a) included had strong correlations with the ovovivipary.

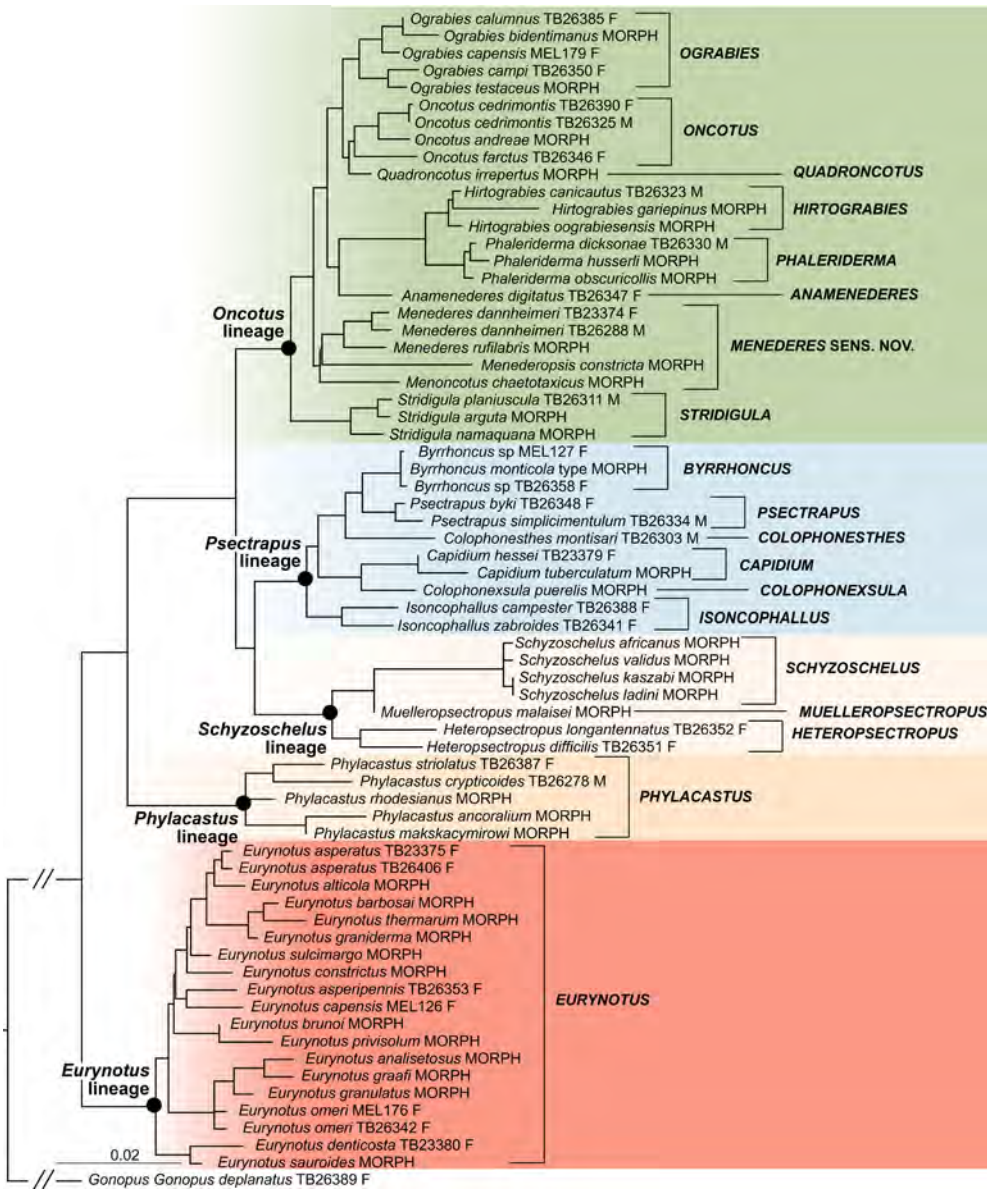


Fig. 2. Summary of phylogenetic relations and classification among the subtribe Eurynotina. Topology based on combined analysis of molecular and genomic data (see Lumen *et al*. 2025) with operational taxonomic units and classification updated to reflect the work presented here.

Mainly restricted to southern Africa, the majority of Eurynotina occurs in the country of South Africa (Fig. 6). To date, the northernmost records reach into Zimbabwe (*Phylacastus rhodesianus* Koch). Many taxa have small individual ranges over a wide variety of southern African habitat types encompassing different geological and climatic regimes (Kamiński 2016), making them potentially valuable for ecological or conservation studies. For instance, some are restricted to arid landscapes (e.g., *Phaleriderma*); while other species, such as some *Eurynotus*, can be abundant in riparian habitat. Occurrence records are provided within this manuscript to facilitate future investigations.

Recent systematic work on Eurynotina (Lumen *et al*. 2025) has provided invaluable phylogenetic context for the revisionary work presented here, and was based on a wide representation of materials and taxa, including type specimens of all known species. While designating operational taxonomic units for their phylogenetic studies, Lumen *et al*. (2025) tested the morphological coherence of preexisting genera and, based on the analysis of combined morphological and molecular (targeted enrichment and mitogenomic) datasets, proposed a robust phylogenetic hypothesis for the subtribe. The resulting topologies allowed for the division of Eurynotina into five evolutionary lineages: *Eurynotus*, *Phylacastus*, *Schyzoschelus*, *Psectrapus*, and *Oncotus* (Fig. 2-5). The monograph presented here is intended as a comprehensive study aimed towards revising all species-level concepts within Eurynotina, and to propose a stable classification of the entirety of this historically neglected subtribe of darkling beetles all contained within a single, centralized work.

Ovovivipary

To date, ovovivipary is an extremely rare reproductive strategy among darkling beetles (Iwan 2010, Lumen & Kamiński 2024a), with only 16 ovoviviparous species recorded (Lumen & Kaminski 2024a) out of the over 30,000 species in the family Tenebrionidae (Bouchard *et al*. 2021). With a single exception of *Alegoria castelnaui* Fleutiaux & Sallé (tribe Ulomini Blanchard) (Dutrillaux *et al.* 2010), all remaining cases concern the tribe Platynotini. Within the tribe, ovovivipary appears to be restricted to the Malagasy and South African taxa, as no cases have been recorded outside these regions despite extensive efforts (e.g., Iwan 1998, 2000, 2002, 2010, Kamiński 2015). Though Eurynotina specimens are often scarce, efforts here and previously (see Lumen & Kamiński 2024a, b) found seven species from among the *Eurynotus*, *Psectrapus* and *Schyzoschelus* lineages to be ovoviviparous (Table 1). Ovoviviparous species were identified based on dissections of female museum specimens, in which fully developed first instar larvae were found (see Lumen & Kamiński 2024a, b).

Recent attempts to tie ovovivipary with specific morphological and climatic traits were unsuccessful (Lumen & Kamiński 2024a). As such, it is possible that there are independent origins for this mode of reproduction for Malagasy Platynotina and for Eurynotina (Lumen & Kamiński 2024a). Despite the great morphological diversity of female genital tubes (e.g., presence of various types of sclerites or additional pouches on the bursa copulatrix) there appears to be no relation to ovovivipary, as it has been reported both for species with modified bursae copulatrices and those with simple, plesiomorphic ducts (Lumen & Kamiński 2024a, b). Currently, a scarcity of materials concerning Eurynotina inhibits more detailed evolutionary studies of ovovivipary in a phylogenetic context. In particular, the number of dissections is often insufficient to satisfactorily evaluate presence of ovovivipary, leaving lineages where it is difficult to confidently confirm or reject the phenomenon (e.g., *Quadroncotus* where only the seven pinned specimens from the type series are known). In summary, it is currently impossible to firmly state if ovovivipary has a single or multiple origins within Eurynotina, or how widespread it is phylogenetically.

Previous claims that reductions in clutch size and increased egg size could be preadaptations for ovovivipary within Platynotini (Iwan 2000, 2010) are supported by the materials examined here. When present, gravid females of Eurynotina were carrying single, large eggs within their bursa copulatrix, and no examples with multiple eggs were found. Nevertheless, more morphological studies are needed to fully investigate the evolutionary origins of ovovivipary within Eurynotina, which in turn requires more material (see Table 1 for presently known ovoviviparous species of Eurynotina).

Tab. 1. List of known ovoviviparous Eurynotina species.

Taxon	References
***Eurynotus* lineage**	
Eurynotus barbosai	Lumen & Kamiński 2024a
Eurynotus brunoi	Lumen & Kamiński 2024a
Eurynotus capensis	Tschinkel 1978, Lumen & Kamiński 2024a
Eurynotus granulatus	Lumen & Kamiński 2024a
***Schyzoschelus* lineage**	
Heteropsectropus difficilus	Lumen & Kamiński 2024a
***Psectrapus* lineage**	
Isoncophallus ovanullum	Current treatment (see taxonomy section)
Psectrapus sp. *	Current treatment

* The specimen remains unidentifiable based on characters used here, as it is female and association with other specimens was impossible based on label data. Label data: **MNHN** blue circle label "Oncotus obtusus ?? Cap ??", Museum Paris Coll De Marseul 1890".

Immature stages

The morphology of larvae within Eurynotina has been described for only the following species (Kamiński *et al*. 2019, Lumen & Kamiński 2024a, b): *Eurynotus analisetosus* Koch, *Eurynotus asperatus* Mulsant & Rey, *Eurynotus granulatus* (Fabricius), and *Heteropsectropus difficilis* Koch. To date, all known larvae of Eurynotina are characterized by a convergent morphology which includes the presence of four spines on the edge of abdominal segment 9 (absent in first instar larvae, which possess setae instead), enlarged front legs, and laterally expanded bases of mandibles (see Fig. 9C in Lumen & Kamiński 2024b). However, most of these features except the expanded mandibles are likely plesiomorphic for the Dendarini+Pedinini+Platynotini clade within Blaptinae, and are also present in tribes Pedinini Eschscholtz and Dendarini Mulsant & Rey (Kamiński *et al*. 2019). As such, at this point only the presence of a lateral expansion of mandibles can be viewed as a potential autapomorphy for Eurynotina when considering larval morphology. Pupal morphology has been described for a single Eurynotina species – *Heteropsectropus difficilis* (Lumen & Kamiński 2024b). The paucity of pupal descriptions is characteristic for the whole tribe

Platynotini, as of the ~590 species only eight have described pupae (Steiner 1995, Iwan 2002, Kamiński *et al.* 2018).

How to use this monograph

Each species account consists of the literary & taxonomic record of all previous names, a diagnosis to separate the taxon from similar species, habitat information in the form of a range map, and material examined for this study (including repository and type information). New species as of this publication are further provided with formal descriptions to fulfill the requirements of the ICZN (1999).

The taxonomy section is first organized by phylogenetic lineage (B. *Eurynotus*, C. *Phylacastus*, D. *Schyzoschelus*, E. *Psectrapus*, and F. *Oncotus* lineages), with their constituent genera organized alphabetically in their respective sections. The taxonomy section(s) each begin with a dichotomous key. The first key to the generic lineages provides characteristics to identify specimens to the genus level, while also providing the generic lineage to which it belongs. Additionally, each generic lineage section includes an additional key to its genera, and each genus section includes a key to its species. While some of these keys may seem redundant at first, they offer the opportunity to contrast specimens against other taxa with slightly different characteristics, as well as to sort out typical and atypical forms within each genus. Each section's dichotomous key has a coordinating plate of figures for reference to morphology used to identify specimens (e.g., "Plate E1, 2, 3, etc…" for E. *Psectrapus* lineage generic key, and "Plate vi.1, 2, 3, etc…" for vi. *Byrrhoncus* species key.).

Images representing the diveristy of male reproductive morphology are presented in figures 7-65, as they can come in useful for generic or species level determinations as supplements to the diagnoses and dichotomous keys/figures. Finally, a series of photographs representing type material examined for all species and names treated in subtribe Eurynotina is provided (Figures T1-122).

It is our hope that this monograph will serve as a resource for future studies by giving workers and entomologists better access to this group.

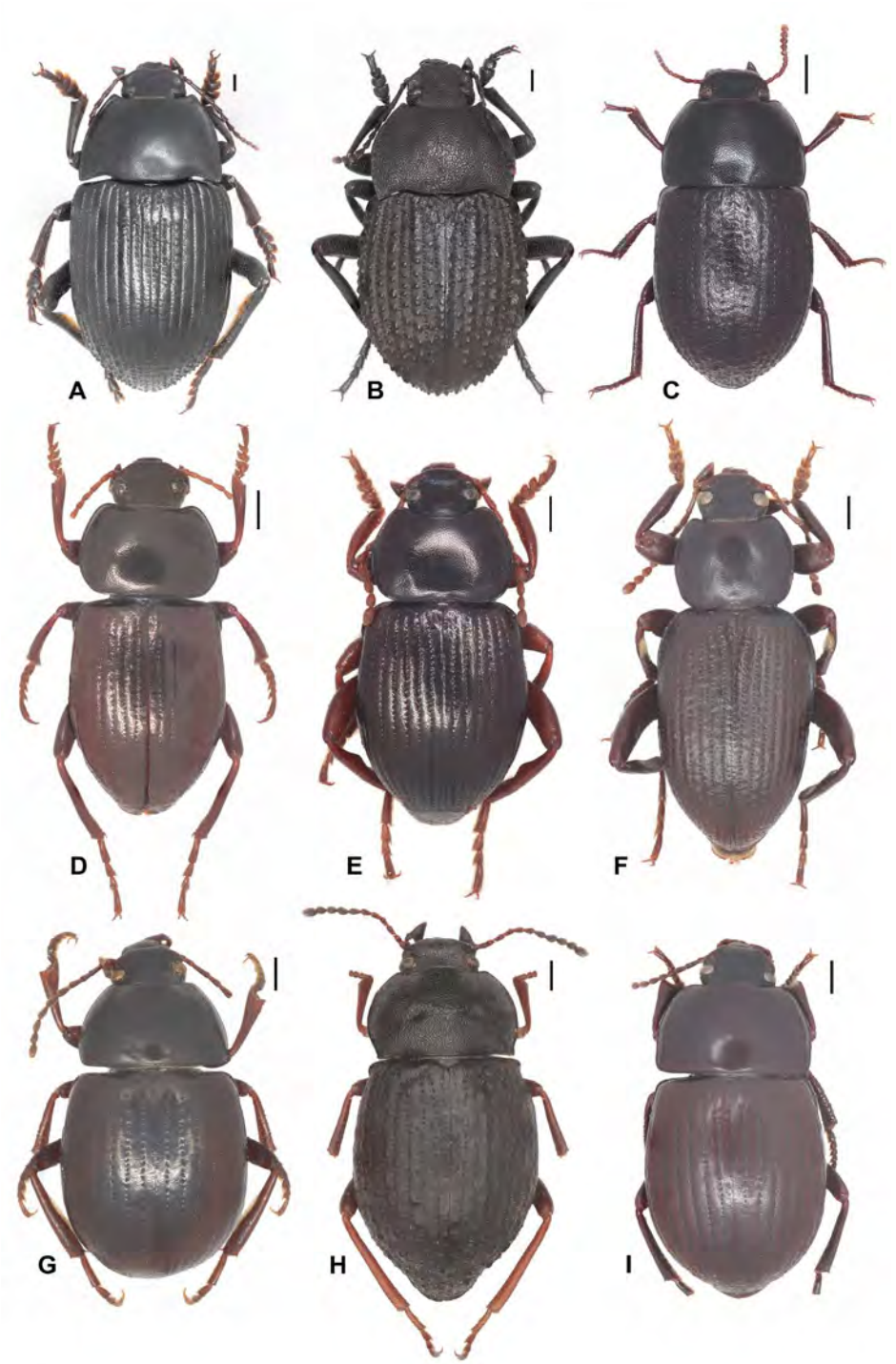


Fig. 3. Representative diversity of the subtribe Eurynotina. *Eurynotus capensis* (**A**), *Eurynotus omeri* (**B**), *Phylacastus rhodesianus* (**C**), *Heteropsectropus aenescens* (**D**), *Muelleropsectropus malaisei* (**E**), *Schyzoschelus ladini* (**F**), *Byrrhoncus monticola* (**G**), *Capidium tuberculatum* (**H**), *Colophonesthes montisatri* (**I**). Scale bar = 1mm.

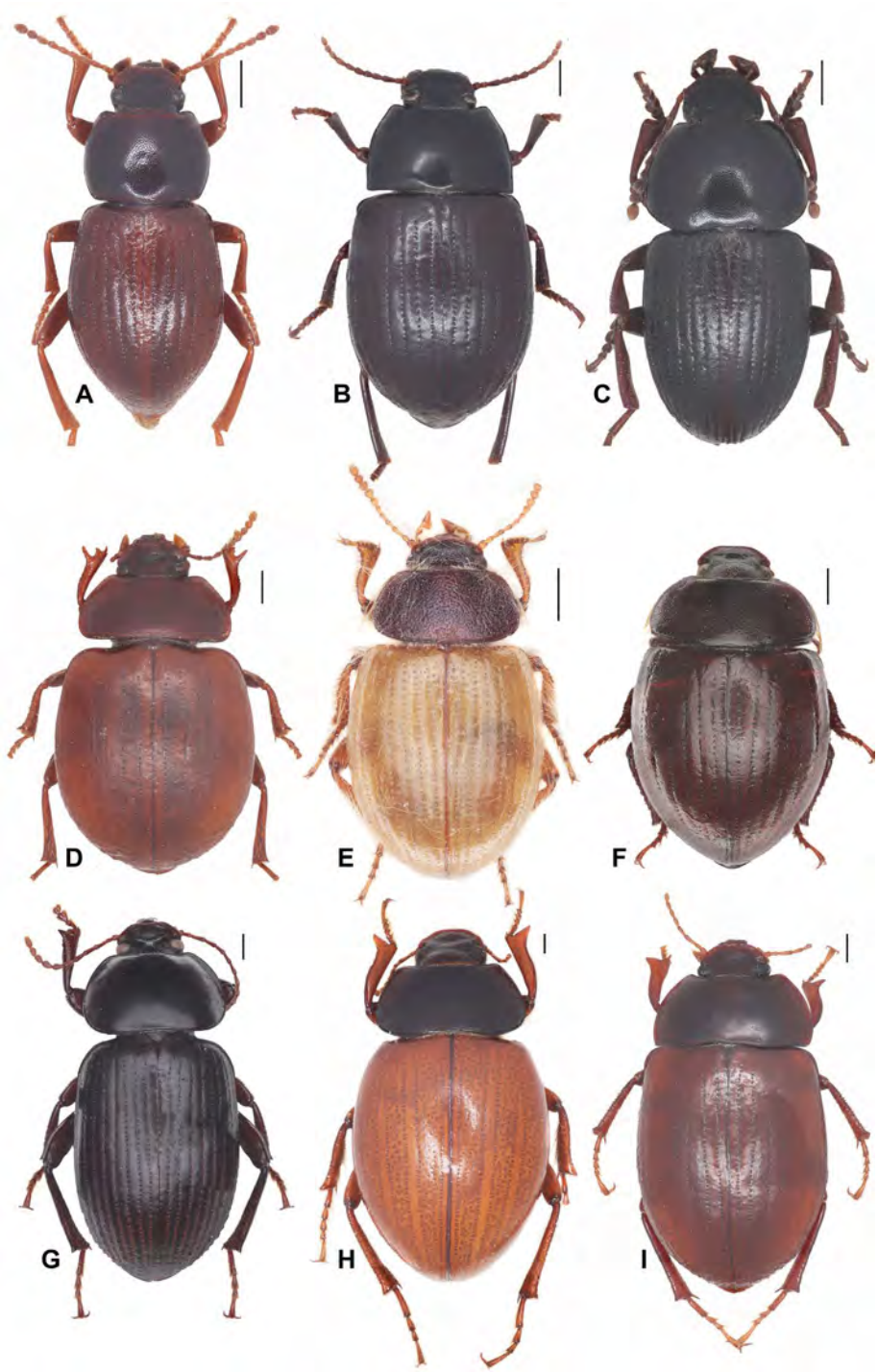


Fig. 4. Representative diversity of the subtribe Eurynotina. *Colophonexsula puerilis* (**A**), *Isoncophallus angulicollis* (**B**), *Psectrapus byki* (**C**), *Anamenederes digitatus* (**D**), *Hirtograbies canicautis* (**E**), *Hirtograbies gariepinus* (**F**), *Menederes dannheimeri* (**G**), *Ograbies testaceus* (**H**), *Oncotus cedrimontis* (**I**). Scale bar = 1mm.



Fig. 5. Representative diversity of the subtribe Eurynotina. *Phaleriderma iwani* (**A**), *Quadroncotus irrepertus* (**B**), *Stridigula arguta* (**C**). Scale bar = 1mm.

II. Material and Methods

Pinned material for morphological examination was acquired from the following institutional insect collections:

BPBM – Bernice P. Bishop museum; Honolulu, Hawaii, United States;

CASC – California Academy of Sciences; San Francisco, California, United States;

HNHM – Hungarian Natural History Museum; Budapest, Hungary;

IMSA – Iziko South African Museum; Cape Town, South Africa;

MIZPAN – Muzeum i Instytut Zoologii, Polska Akademia Nauk; Warsaw, Poland;

MNHN – Muséum National d'Histoire Naturelle; Paris, France;

NHMB – Naturhistorisches Museum; Basel, Switzerland;

NHMUK – Natural History Museum; London, United Kingdom;

NHRS – Swedish Museum of Natural History; Stockholm, Sweden;

NMNW – Windhoek National Museum of Namibia; Windhoek, Namibia;

NRS – Naturhistoriska Riksmuseum; Stockholm, Sweden;

RBINS – Royal Belgian institute of Natural Sciences; Brussels, Belgium;

RMCA – Royal Museum for Central Africa; Tervuren, Belgium;

SANC – South African National Collection of Insects; Pretoria, South Africa;

SMNS – Staatliches Museum für Naturkunde; Karlsruhe, Germany;

SU – Stellenbosch University; Stellenbosch, South Africa;

TMNH – Ditsong National Museum of Natural History; Pretoria, South Africa;

UUZM – Uppsala University Museum of Evolution; Uppsala, Sweden;

ZMHB – Museum für Naturkunde; Berlin, Germany;

ZMUK – Zoologisches Museum, Universität Kiel; Kiel, Germany.

Private collections are indicated without codons.

Original label data for studied specimens are condensed into single entries after their repositories (in bold), and records are isolated within quotations and separated by a comma outside the quotations with each collection's holdings ending in a period (e.g., **SANC**: "specimen record 1", "specimen record 2". **MIZPAN**: "specimen record 1".). Cases with multiple specimens from the same collecting event are indicated by the number of specimens within the quotes with label data (e.g. **RMCA**: "Specimen record (three specimens".). Types are indicated in bold and additional non-type material follow in an indented paragraph.

Adult morphological terminology follows Matthews *et al.* (2010), with additional specialized terms for male and female terminalia following Banaszkiewicz (2006), Iwan & Kamiński (2016), Lumen & Kamiński (2023). Dissections followed methodology outlined in Kamiński (2021). Specimens were soaked in 10% KOH solution before dissection of genitalia which were then stained with chlorazol black.

Images were taken using a Canon 1000D body with extension rings and a Canon EF 100 mm macro lens, a Nikon D3500 body with adapter for a Nikon SMZ800N microscope, and with a Hitachi S3400N SEM in MIZPAN. Species distribution maps were produced based on specimen label data using QGIS v. 3.16, with vector layers downloaded from the Natural Earth web page (www.naturalearthdata.com). Photographs, as well as distribution maps, were edited in Photoshop v. 23.5.1.

III. Taxonomy

A. Subtribe Eurynotina Mulsant & Rey

Eurynotaires Mulsant & Rey, 1854a: 13.– Mulsant & Rey 1854b: 156; Bouchard *et al*. 2005: 510, 2011: 422.

Eurynotina Mulsant & Rey, 1854.– Koch 1956: 25; Iwan 2001: 352, 2002: 5, 2004: 739; Bouchard *et al*. 2005: 510; 2011: 422, 2021: 51; Kamiński 2016: 229; Lumen & Kamiński 2023: 2; 2024a: 1; 2024b: 122; Lumen *et al*. 2025: 1.

=Psectropini Kaszab, 1941: 33.– Koch 1954b: 1 (syn.); Iwan 2001: 352; Bouchard *et al*. 2005: 510, 2011: 422. Type genus. *Psectropus* Solier, 1848.

=Oncotini Koch, 1954a: 274.– Iwan 2001: 352, 2002: 7; Koch 1954b: 3, 1955: 419, 1956: 25; Bouchard *et al*. 2005: 510 (syn.), 2011: 422. Type genus. *Oncotus* Solier, 1848.

=Schyzoschelina Koch, 1956: 25. Iwan 2001: 352; Bouchard *et al*. 2005: 510 (syn.), 2011: 422. Type genus. *Schyzoschelus* Koch, 1954.

Type genus. *Eurynotus* Kirby.

Diagnosis

As a subtribe within Blaptinae, all representatives of Eurynotina fall within the following diversity: adult antennae lack compound/stellate sensoria; procoxal cavities externally and internally closed; intersternal membrane of abdominal ventrites 3–5 visible; paired abdominal defensive reservoirs present, elongate, not annulated. Larvae: prolegs enlarged (adapted for digging); ninth tergite lacking urogomphi (Kamiński *et al*. 2021).

Together with Platynotina, Eurynotina constitutes the tribe Platynotini (Kamiński *et al*. 2021). Members of this tribe can be easily distinguished from other Blaptinae by having a gular region covered with a stridulatory surface. The monophyly of Eurynotina is strongly supported by molecular data (Lumen *et al*. 2025). Morphologically, representatives of this subtribe are distinguishable from Platynotina by lack of ancorae (except *Phylacastus anocralium* which possesses a reduced form of this feature; Lumen & Kamiński 2023, Figs 7-65) and the presence of elytral tubercles in the majority of species.

Genera included (19)

Anamenederes Koch, *Byrrhoncus* Koch, *Capidium* Koch, *Colophonesthes* Koch, *Colophonexsula* Koch, *Eurynotus* Kirby, *Heteropsectropus* Kaszab, *Hirtograbies* Koch, *Isoncophallus* Koch, *Menederes* Solier **stat. nov.**, *Muelleropsectropus* Lumen & Kamiński, *Ograbies* Peringuey, *Oncotus* Solier, *Phaleriderma* Koch, *Phylacastus* Fairmaire, *Psectrapus* Solier, *Quadroncotus* Koch, *Schyzoschelus* Koch, *Stridigula* Koch.

Distribution

Lesotho, Mozambique, Namibia, South Africa, Zimbabwe (Fig. 6). Although extralimital records in Kenya based on specimen data are included here, whether they represent real, established populations is questionable (see *Eurynotus asperatus*).

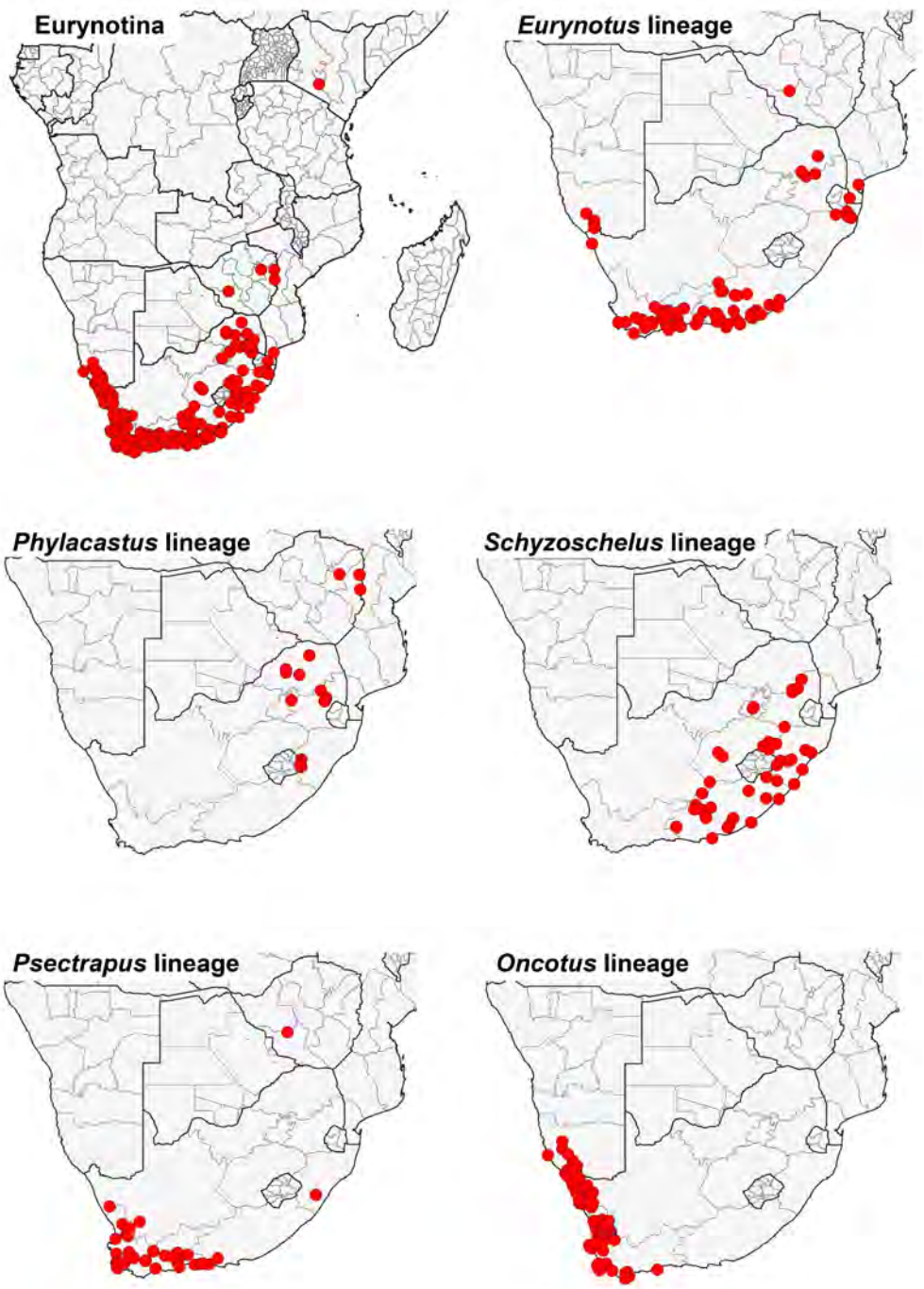


Fig. 6. Distribution of the subtribe Eurynotina and its major phylogenetic lineages.

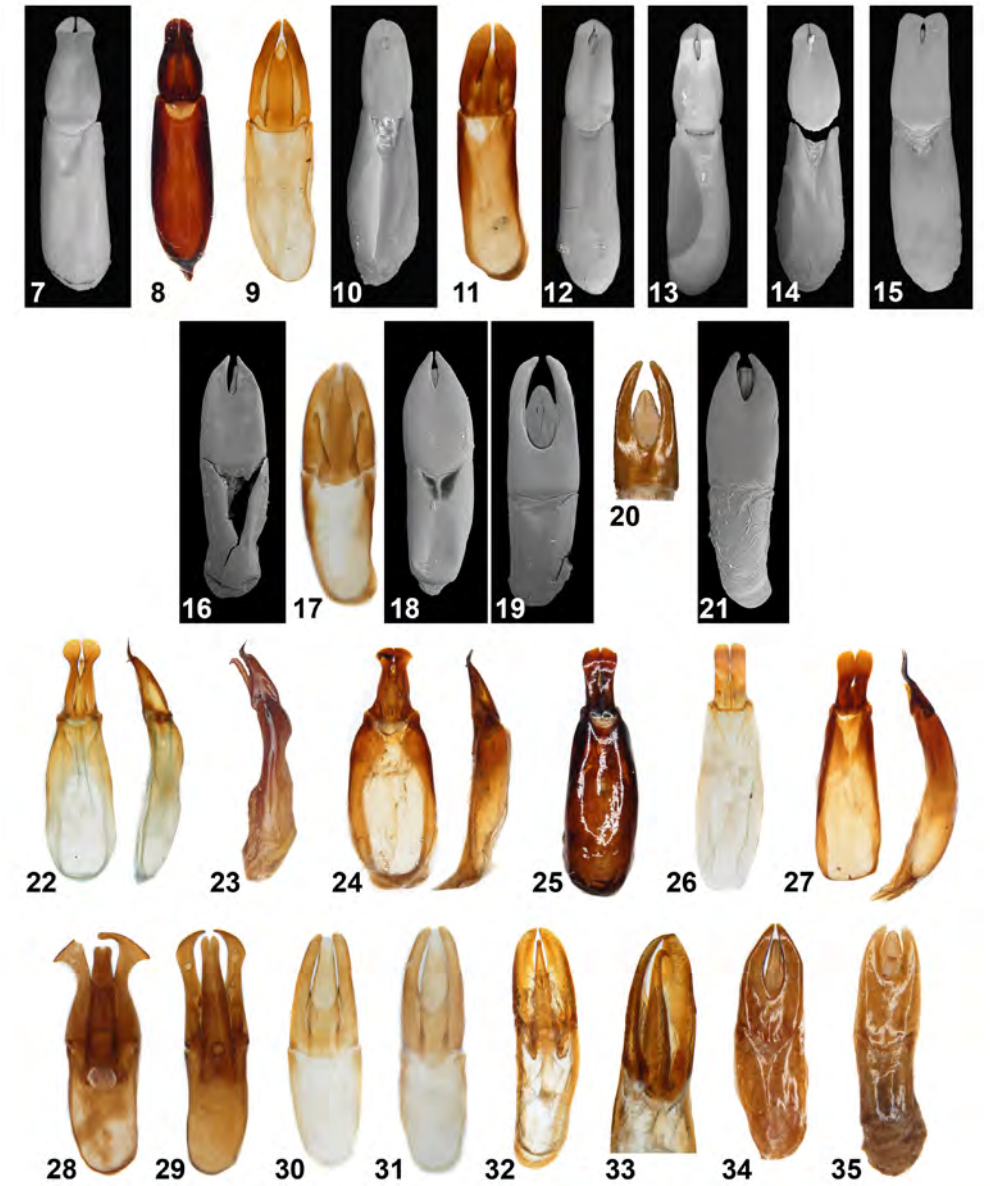


Fig. 7-35. Morphology of male terminalia within the subtribe Eurynotina. ***Eurynotus* lineage**: *Eurynotus analisetosus* (7), *Eurynotus asperipennis* (8), *Eurynotus brunoi* (9), *Eurynotus denticosta* (10), *Eurynotus graafi* (11), *Eurynotus granulatus* (12), *Eurynotus omeri* (13), *Eurynotus sauroides* (14), *Eurynotus barbosai* (15). ***Phylacastus* lineage**: *Phylacastus ancoralium* (16, 17), *Phylacastus makskacymirowi* (18), *Phylacastus rhodesianus* (19, 20), *Phylacastus striolatus* (21). ***Schyzoschelus* lineage**: *Heteropsectropus aenescens* (22), *Heteropsectropus difficilis* (23), *Muelleropsectropus malaisei* (24), *Schyzoschelus aetheculus* (25), *Schyzoschelus validus* (26), *Schyzoschelus kaszabi* (27). ***Psectrapus* lineage**: *Byrrhonchus monticola* (28), *Byrrhonchus parvithorax* (29),*Capidium bipunctatum* (30), *Capidium tuberculatum* (31), *Colophonesthes montisatri* (32, 33), *Colophonexsula enisa* (34), *Colophonexsula puerilis* (35).



Fig. 36-65. Morphology of male terminalia within the subtribe Eurynotina. ***Psectrapus* lineage**: *Isoncophallus crispiformus* (36), *Isoncophallus campester* (37), *Isoncophallus ornatipes* (38), *Isoncophallus zabroides* (39), *Psectrapus byki* (40), *Psectrapus distaticum* (41), *Psectrapus latimentulum* (42), *Psectrapus simplicimentulum* (43). ***Oncotus* lineage**: *Anamenederes digitatus* (44-46), *Hirtograbies gariepinus* (47), *Hirtograbies canicautis* (48), *Menederes chaetotaxicus* (49), *Menederes constrictus* (50), *Menederes dannheimeri* (51), *Menederes jokli* (52), *Menederes rufilabris* (53), *Ograbies angulatus* (54), *Ograbies capensis* (55), *Ograbies frigidus* (56), *Ograbies subdentatus* (57), *Ograbies testaceus* (5), *Oncotus andreae* (60), *Oncotus cedrimontis* (61), *Oncotus farctus* (62), *Phaleriderma husserli* (63), *Stridigula arguta* (64), *Stridigula planiuscula* (65).

Key to genera of Eurynotina (See Plate A parts 1-4 for figures):

1. Epistomal emargination deep and relatively narrow (Figs 1–3) **2**

— Epistomal emargination shallow, relatively wide, or absent (epistoma straight) (Figs 4–6; see also 19–21, 34–36) **3**

2. Basal pronotal angles not produced posteriorly (Fig. 7) ..... ***Phylacastus* lineage**

— Basal pronotal angles produced posteriorly (Fig. 8) ..... ***Eurynotus* lineage**

3. Epistoma without emargination (straight) (Figs 4–5) ..... (***Schyzoschelus* lineage**) **4**

— Epistoma with weak or shallow emargination (Fig. 6; see also 19–21, 34–36) ... **6**

4. Epipleural base evenly narrowing toward apex (Fig. 9). Elytra with 11 intervals between the suture and epipleuron. Ovipositor elongate (paraprocts longer than coxites) (Fig. 11) .... ***Schyzoschelus***

— Epipleural base sharply or abruptly narrowing toward apex (Fig. 10). Elytra with 10 intervals. Ovipositor short (paraprocts roughly equal to coxites) (Fig. 12) ... **5**

5. Prementum not emarginate (Fig. 13). Subapical sulcus on ventrite V present (male & female). Abdominal ventrite V without concavity or notch (Fig. 15). Bursa copulatrix without additional pouches ..... ***Heteropsectropus***

— Prementum emarginate (Fig. 14). Abdominal ventrite V without subapical sulcus. Abdominal ventrite V slightly concave, female with furrow running along extreme apical edge, and with median notch (Fig. 16). Bursa copulatrix with two additional pouches ..... ***Muelleropsectropus***

6. Elytral base with small, setose pit (Fig. 17) ..... (***Oncotus* lineage**) ***Stridigula***

— Elytral base without setose pit **7**

7. Hypomeron with long setae (Fig. 18); sometimes reduced or difficult to see (e.g. *Ograbies capensis*, *Hirtograbies gariepinus*, and *Hirtograbies longipennis*) .... (***Oncotus* lineage in part**) **8**

— Hypomeron never with long setae; glabrous or at most only with short, appressed setae **10**

8. Epistoma apex with raised carina (Fig. 19). Elytra never with setae (glabrous). Foretibiae broad, often with slight emargination/narrowing in the middle, giving a "boot" shape, or with strong lateral emargination leaving two projections along lateral edge (Figs 22–23) .... ***Ograbies***

— Epistoma without raised carina (Figs 20–21). Elytra setose (exception: *Hirtograbies gariepinus*; see Fig. T87). Foretibiae without emargination or narrowing in the middle, instead gradually or more abruptly widening to the apex **9**

9. Epistoma and clypeus with clear delineation (Fig. 20). Anterior border of pronotum incomplete ..... ***Phaleriderma***

— Epistoma and clypeus without delineation (fully fused) (Fig. 21). Anterior border of pronotum complete (Figs 24–25) ..... ***Hirtograbies***

10. Basal angles of pronotum produced (Figs 26–27). Foretibiae slender and round in cross section (not flattened or expanded) (Fig. 29) ..... (***Psectrapus* lineage**) ***Capidium***

— Basal angles of pronotum rounded, or triangular but never strongly produced (Fig. 28; see also Figs 17, 55, and 57). Foretibiae flattened and expanded apically (Figs 30–33) **11**

11. Epistomal margin without raised carina (Fig. 34) ..... (***Psectrapus* lineage**) **12**

— Epistomal margin with raised carina (Figs 35–36) ..... (***Oncotus* lineage**) **16**

12. Abdominal ventrite V relatively broad ('short' in length and 'wide') (Figs 39–41). Males never with subapical sulcus, females with or without subapical sulcus **13**

— Abdominal ventrite V more-or-less quadrate to elongate, relatively flat, without or with weak convexity. Subapical sulcus present in males and females (Figs 42–44), or absent in both **14**

13. Males with greatly expanded fore- and midtarsus (Fig. 37). Abdominal ventrite V convex or bulbous (Fig. 39). Females with sulcus on abdominal ventrite V (e.g., Fig. 40). Aedeagus with relatively narrow paramere window and parameres overall parallel and evenly tapered apically (Fig. 47). Sclerotized penis with apical hook (sometimes bifurcated) (Fig. 48) .... ***Psectrapus***

— Males with weakly expanded fore- and midtarsus (Fig. 38). Females without subapical sulcus on abdominal ventrite V. Abdominal ventrite V weakly to not-convex nor bulbous. Aedeagus with extremely wide paramere window and greatly inwardly curved apical tips that are not tapered apically. Penis without apical hook (Figs 45–46) ... ***Byrrhoncus***

14. Abdominal ventrite V in both males and females with subapical sulcus (Figs 42–44) .... ***Isoncophallus***

— Abdominal ventrite V without sulcus **15**

15. Aedeagus not tapered, rounded apically, with narrow opening, with or without apical hook on penis (Fig 49) ..... ***Colophonesthes***

— Aedeagus slightly tapered, not rounded apically, with wide opening exposing penis, never with apical hook (Figs 50–51) ..... ***Colophonexsula***

16. Last elytral interval with many large scattered punctures (Figs 52–53) ..... ***Menederes***

— Last elytral interval without large scattered punctures **17**

17. Foretibiae with long, finger-like projection off lateral edge of apex (Fig. 54) .... ***Anamenederes***

— Foretibiae with tooth or projection on apex not long and finger-like (Figs 56 & 58) ... **18**

18. Outer margin of foretibiae irregular, bumpy and/or cragged (Fig. 58). Basal angles of pronotum more rounded, and without depression or dimple (Fig. 57) ... ***Quadroncotus***

— Outer margin of foretibiae smooth, without irregular bumps or cragginess (Fig. 56). Basal angles of pronotum relatively angular, with slight depression or dimple (Fig. 55) ... ***Oncotus***

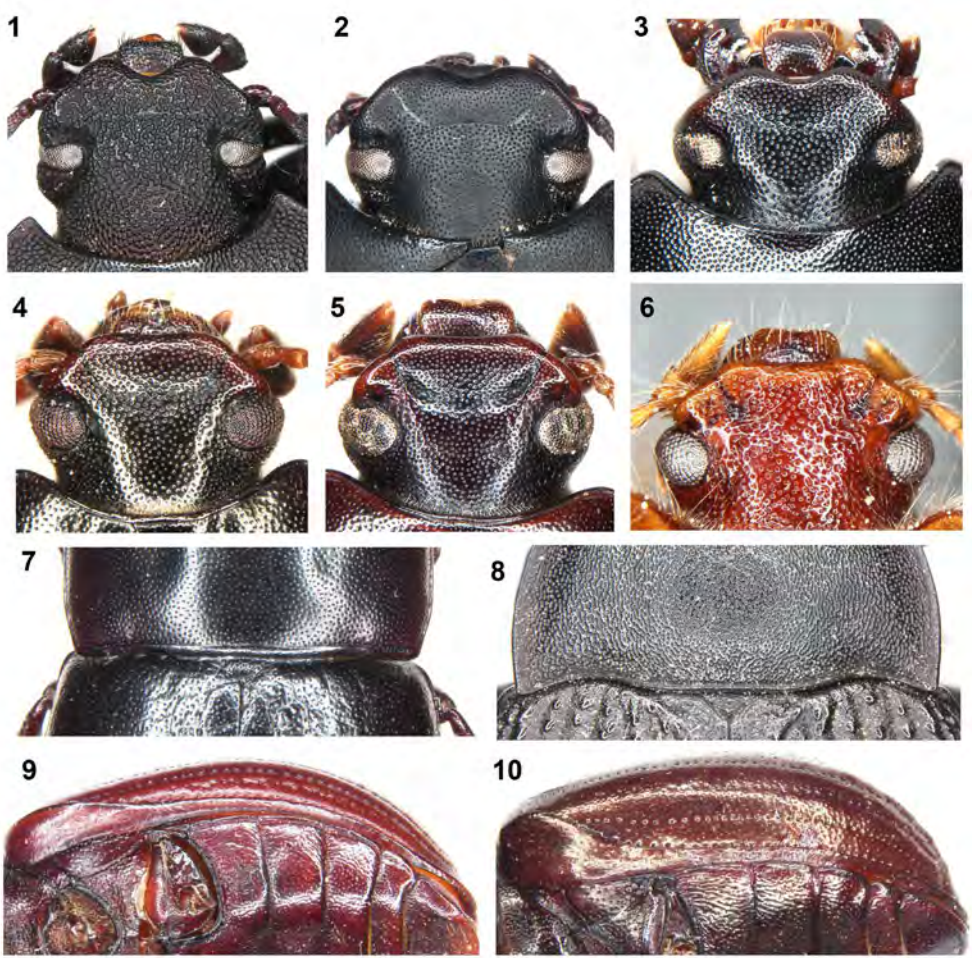


Plate A. Part 1. Subtribe Eurynotina lineages and generic diagnostic features. **Anatomic features**: Head (1–6). Pronotum (7–8). Elytra (Lateral) (9–10). **Taxa depicted**: *Eurynotus analisetosus* (8). *Eurynotus asperatus* (2). *Eurynotus omeri* (1). *Heteropsectropus aenescens* (4, 10). *Hirtograbies longipilis* (6). *Phylacastus makskacymirowi* (7). *Phylacastus rhodesianus* (3). *Schyzoschelus karrooensis* (5). *Schyzoschelus ladini* (9).

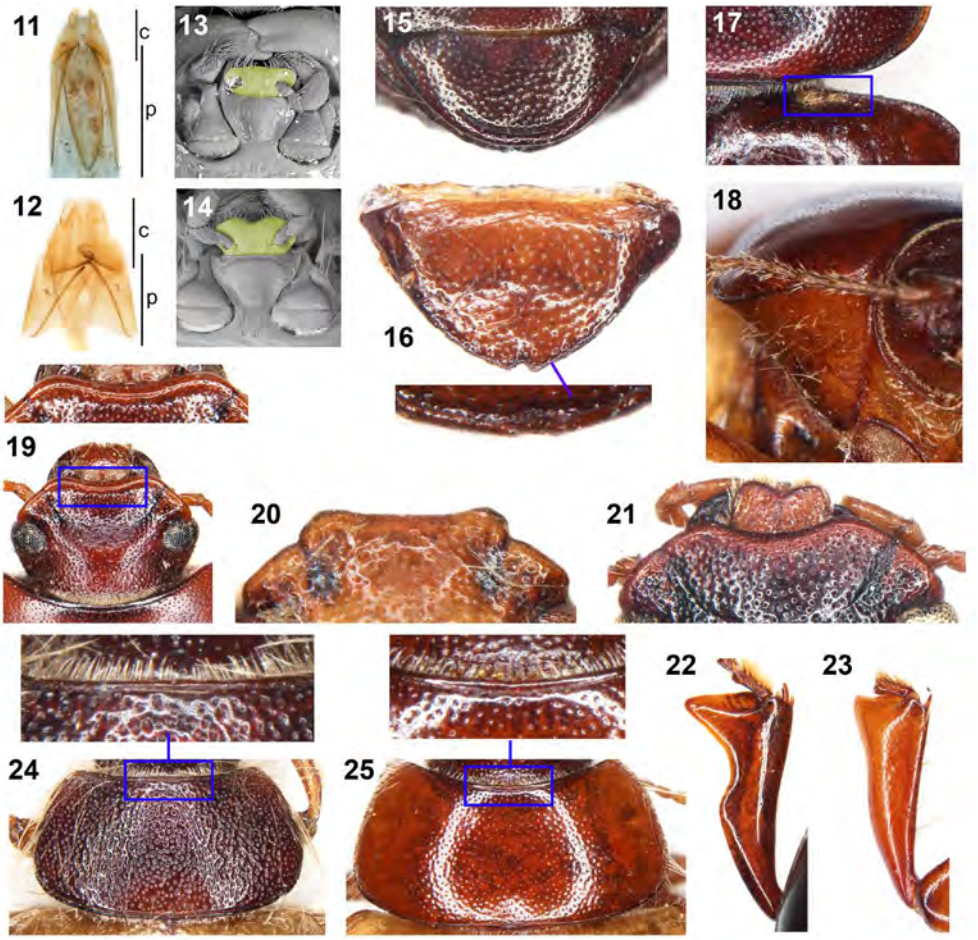


Plate A. Part 2. Subtribe Eurynotina lineages and generic diagnostic features. **Anatomic features**: Ovipositor (11–12). Prementum (highlighted) (13–14). Abdominal Ventrite V (15–16). Elytral humeral setal pocket (17). Hypomeron (18). Head (19). Epistoma (20–21). Foretibia (22–23). Pronotum (24–25). **Taxa depicted**: *Heteropsectropus difficilis* (12, 13, 15). *Hirtograbies canicautis* (24). *Hirtograbies gariepinus* (21). *Hirtograbies nanus* (25). *Muelleropsectropus malaisei* (16). *Ograbies angulatus* (18). *Ograbies campi* (19). *Ograbies frigidus* (23). *Ograbies subdentatus* (22). *Phaleriderma husserli* (20). *Schyzoschelus africanus* (11). *Schyzoschelus kaszabi* (14). *Stridigula arguta* (17). **Abbreviations**: c = coxites; p = paraprocts.

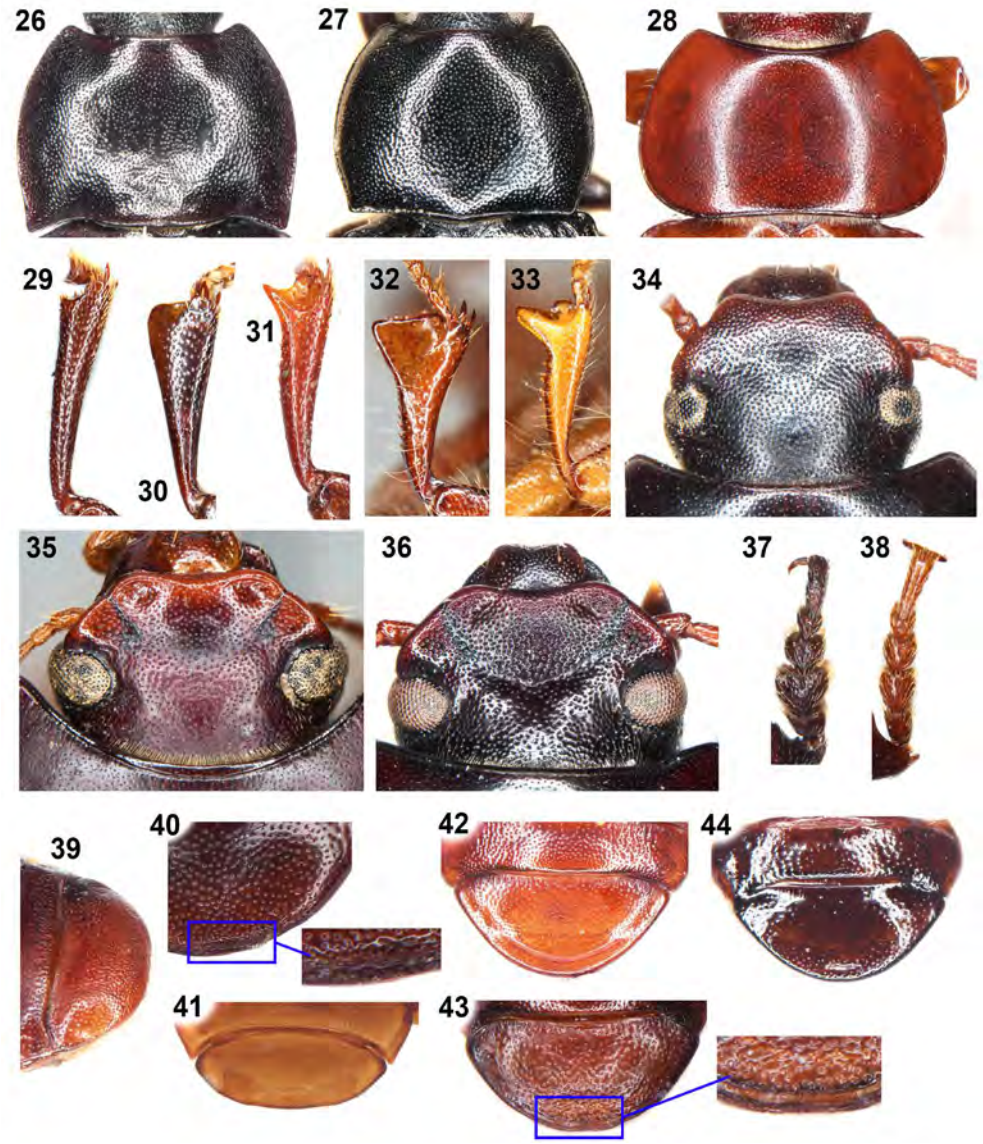


Plate A. Part 3. Subtribe Eurynotina lineages and generic diagnostic features. **Anatomic features**: Pronotum (26–28). Foretibiae (29–33). Head (34–36). Foretarsus (37–38). Abdominal Ventrite V (39–44). **Taxa depicted**: *Byrrhoncus monticola* (38, 41). *Capidium bipunctatum* (27, 29). *Capidium hessei* (26). *Colophonesthes montisatri* (34). *Hirtograbies longipilis* (33). *Hirtograbies oograbiensis* (32). *Isoncophallus campester* (42). *Isoncophallus ornatipes* (43). *Isoncophallus ovanullum* (30, 44). *Menederes dannheimeri* (36). *Menederes jokli* (31). *Ograbies campi* (28). *Oncotus farctus* (35). *Psectrapus byki* (37, 40). *Psectrapus latimentulum* (39).

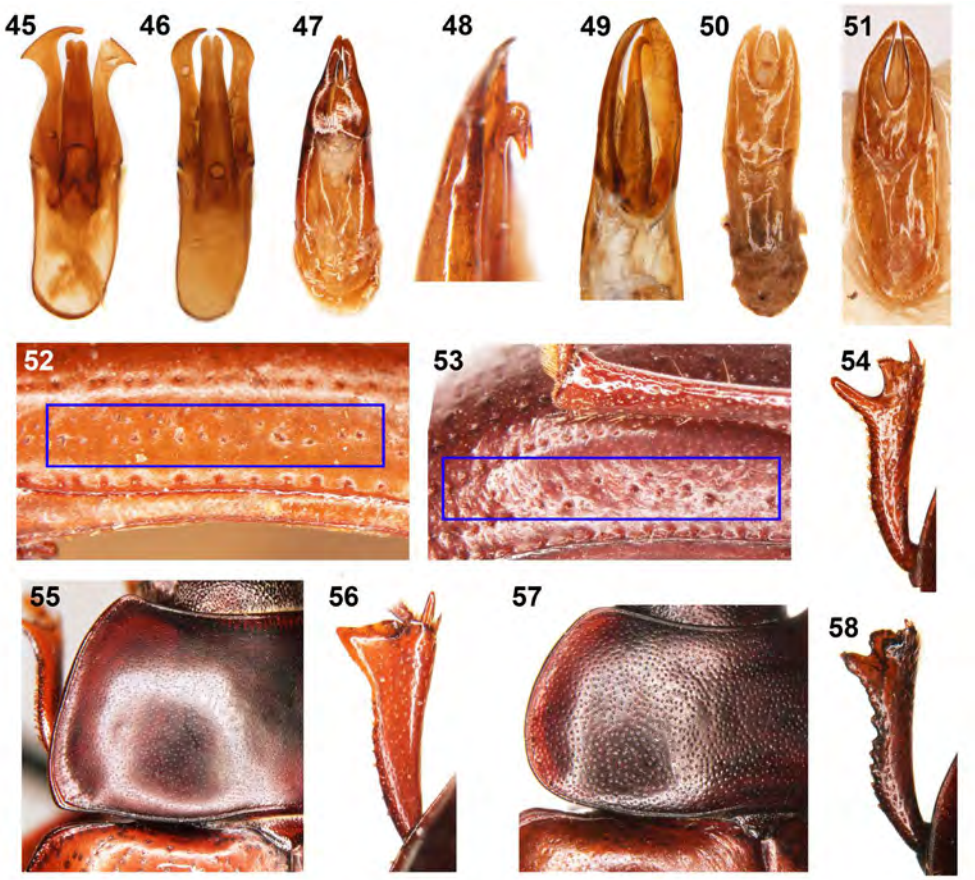


Plate A. Part 4. Subtribe Eurynotina lineages and generic diagnostic features. **Anatomic features**: Aedeagus (45–51). Last (lateral) elytral interval (52–53). Foretbia (54, 56, 58). Pronotum (55, 57). **Taxa depicted**: *Anamenederes digitatus* (54). *Byrrhoncus monticola* (45). *Byrrhoncus parvithorax* (46). *Colophonesthes montisatri* (49). *Colophonexsula enisa* (51). *Colophonexsula puerilis* (50). *Menederes dannheimeri* (52, 53). *Oncotus cedrimontis* (55, 56). *Psectrapus bipartitus* (48). *Psectrapus simplicimentulum* (47). *Quadroncotus irrepertus* (57, 58).

B. *Eurynotus* lineage

Genera included (1)

Eurynotus Kirby

i. Genus *Eurynotus* Kirby

Eurynotus Kirby, 1819: 418.– Mulsant & Rey 1854a: 13, 1854b: 156; Lacordaire 1859: 238; Gebien 1938: 414; Koch 1954a: 275; 1954b: 2; 1955: 420, 1956: 27; Iwan 2001: 352, 2002: 6, 2004: 739; Banaszkiewicz 2006: 65; Ahn & Frank 2015: 529; Kamiński 2016: 234; Bouchard *et al*. 2021: 184; Kamiński *et al*. 2019: 92, 2021: 152; Lumen & Kamiński 2023: 2, 2024a: 1, 2024b: 122; Lumen et al. 2025: 2

= *Biolus* Mulsant & Rey, 1854a: 25.– Mulsant & Rey 1854b: 169; Lacordaire 1859: 239; Koch 1954a: 276, 1954b: 2; Kamiński 2016: 234; Lumen & Kamiński 2024a: 1; Lumen *et al*. 2025: 2 (syn.). Type species. *Eurynotus asperipennis* Mulsant & Rey, 1854; designated by Koch (1954b).

= *Neosolenopistoma* Bouchard & Bousquet, 2021: 265 (in: Bouchard *et al*. 2021).– Lumen & Kamiński 2024a: 14; Lumen *et al*. 2025: 18 (syn). Type species. *Eurynotus denticosta* Mulsant & Rey, 1854; original designation.

Type species. *Eurynotus muricatus* Kirby; designated by monotypy.

Diagnosis

One of the most easily recognized, collected, and identified taxa within Eurynotina. It represents one of the largest, both in body size and number of taxa, genera within the subtribe (8–22mm in length; 17 species). Morphologically *Eurynotus* is easily separable from other genera by the shape of the pronotum (bisinuate, with basal angles strong/acute/rectangular and produced backward toward the elytra), the structure of the prosternum (projecting between forecoxae), and, in most species, presence of strong elytral tuberculation on the elytrae.

Species included (17)

E. alticola Koch, *E. analisetosus* Koch, *E. asperatus* Mulsant & Rey, *E. asperipennis* Mulsant & Rey, *E. barbosai* Koch, *E. brunoi* (Lumen & Kamiński), *E. capensis* (Fabricius), *E. constrictus* Koch, *E. denticosta* Mulsant & Rey, *E. graafi* Koch, *E. granicerma* Koch, *E. granulatus* (Fabricius), *E. omeri* Koch, *E. privisolum* Lumen & Kamiński, *E. sauroides* Koch, *E. sulcimargo* Koch, *E. thermarum* Koch.

Key to species of *Eurynotus* after Lumen & Kamiński (2024a) (See Plate i parts 1-2 for figures):

1. Humeri of elytra with large and raised, well-defined knob-like tubercles, callosities, or costae. Epipleura narrower than elytral intervals 9+10 (Fig. 1). Macrotubercles present (Fig. 3) or absent on elytral disc. Prosternal process in lateral view with or without well-defined protuberance and/or depression on descending surface between forecoxae, giving a 'pinched' appearance to prosternal process apex (Fig. 4). Lateral elytral intervals visible ventrally **2**

— Humeri of elytra without well-defined large knob-like tubercles (some weakly raised tubercles in *E. constrictus*). Epipleura wider or subequal to elytral intervals 9+10 (Fig. 2). Elytral macrotubercles absent from disc. Prosternal process in lateral view with weak or absent protuberance, lacking well-defined depression on descending surface between forecoxae (Fig. 5). Lateral elytral intervals visible ventrally or not **9**

2. Elytra costate (Fig. 6), or elytral disc with distinct macrotubercles (Fig. 7) or with shining bumps/callosities (Fig. 3) **3**

— Elytral disc lacking obvious macrotubercles or callosities **8**

3. Tarsal setae (excluding male pads on pro- and mesotarsi) black or dark (Fig. 8) **4**

— Tarsal setae (excluding male pads on pro- and mesotarsi) golden (Fig. 9) **6**

4. Elytra costate, with large punctures giving lattice-like appearance (Fig. 6) ..... ***Eurynotus denticosta***

— Elytra not costate, without large punctures giving lattice-like appearance **5**

5. Elytral tubercles not reaching base; tubercles subdentate. Male midtibia unmodified ..... ***Eurynotus omeri***

— Elytral tubercles reaching base; tubercles large and knob-like (Fig. 7). Male midtibia with apical spur-like projection (as in Fig. 10) ..... ***Eurynotus sauroides***

6. Abdominal ventrite V without large, setigerous punctation or micropunctation. Bursa copulatrix with axe-sphaped sclerite (Fig. 11) ..... ***Eurynotus granulatus***

— Abdominal ventrite V with large, setigerous punctation interspersed with smaller punctures (as in Fig. 12); with or without micropunctation (Fig. 13). Bursa copulatrix without sclerites, or sclerite not axe-shaped **7**

7. Pronotum (Fig. 14) and abdominal ventrite V with micropunctation interspersed between larger punctation. Elytra and epipleura intensely microtuberculate (Fig. 15). Males without expanded tarsi. Bursa copulatrix without sclerite ..... ***Eurynotus graafi***

— Pronotum and abdominal ventrite V without micropunctation. Elytra and epipleura less intensely microtuberculate. Males with expanded pro- and mesotarsi. Bursa copulatrix with chevron-shaped sclerite (Fig. 16) ..... ***Eurynotus analisetosus***

8. Prosternal process with distinct protuberance. Pronotal punctation widely spaced (>1 puncture diameter). Male hind tibiae usually curved (Fig. 18). Tarsal setae golden in lateral view (as in Fig. 9). Circumocular depression weak. Female abdominal ventrite V with notch (as in Fig. 12). Male parameres truncate at tip (Fig. 19) ..... ***Eurynotus asperipennis***

— Prosternal process with at most weakly produced protuberance. Pronotal punctation closely spaced (<= 1 puncture diameter). Male hindtibiae mostly straight (Fig. 17). Tarsal setae black or dark in lateral view (as in Fig. 8). Circumocular depression present. Female abdominal ventrite V without notch (as in Fig. 13). Male parameres tapered to point at tip (Fig. 20) ..... ***Eurynotus brunoi***

9. Tuberculation completely absent on elytra ..... ***Eurynotus alticola***

— Elytral tuberculation present on apical declivity **10**

10. Tarsal setae golden in lateral view (Fig. 9) **11**

— Tarsal setae black or dark in lateral view (as in Fig. 8) **13**

11. Larger (13.75–20mm). Abdominal ventrite V sinuate laterally (Fig. 21). Male midtibia without setose patch ..... ***Eurynotus capensis***

— Smaller (8–10mm). Abdominal ventrite V without lateral sinuation. Male miditiba with setose patch (Fig. 22) **12**

12. Elytral cuticle shining and smooth between macrotubercles. Elytra without microtubercles ..... ***Eurynotus barbosai***

— Elytral cuticle opaque with microtexturing between macrotubercles. Elytra with microtubercles (Fig. 23) ..... ***Eurynotus graniderma***

13. Abdominal ventrite V punctuation including larger, setigerous punctures (as in Fig. 12) .... ***Eurynotus sulcimargo***

— Abdominal ventrite V without larger setigerous punctures, micropunctate (as in Fig. 13) or not **14**

14. Pronotum laterally explanate and with deep lateral groove (Fig. 24) ... ***Eurynotus constrictus***

— Pronotum at most weakly explanate laterally and/or with only narrow emargination (as in Figs 25–26) **15**

15. Pronotum and elytra smooth and shining between punctures/macrotuberculation (Fig. 25). Micropunctation present on pronotum and abdominal ventrite V .... ***Eurynotus privisolum***

— Pronotum and elytra opaque (Fig. 26) and/or microtuberculate between macrotubercles. Micropunctures absent from pronotum and abdominal ventrite V **16**

16. Pronotum and elytra microtuberculate (Figs 27–28) ..... ***Eurynotus thermarum***

— Pronotum and elytra lacking microtubercles ..... ***Eurynotus asperatus***



Plate i part 1. *Eurynotus* species diagnostic features. **Anatomic features**: Elytra (Lat: 1–2; Dors: 3; Base: 6–7). Prosternum (4–5). Tarsus (8–9). **Taxa depicted**: *Eurynotus analisetosus* (3), *Eurynotus capensis* (2, 5, 9), *Eurynotus denticosta* (6), *Eurynotus omeri* (1, 4, 8), *Eurynotus sauroides* (7).



Plate i part 2. Eurynotus species diagnostic features. **Anatomic features**: Male midtibia (10). Male midtibia (10). Bursa copulatrix (11, 16). Abdominal ventrite V (12–13). Pronotal disc (14). Elytra (Tubercles: 15). Hind tibia (17–18), Aedeagus (19–20), Abdominal Ventrite V (21), Male midtibia (22), Elytron microtubercles (23, 28), Pronotum (lateral margin: 24–26; Microsculpture: 27). **Taxa depicted**: *Eurynotus analisetosus* (16), *Eurynotus asperatus* (26), *Eurynotus asperipennis* (17, 19), *Eurynotus barbosai* (22), *Eurynotus brunoi* (18, 20), *Eurynotus capensis* (21), *Eurynotus constrictus* (24), *Eurynotus denticosta* (10), *Eurynotus graafi* (12, 14–15), *Eurynotus graniderma* (23), *Eurynotus granulatus* (11), *Eurynotus privisolum* (13, 25), *Eurynotus thermarum* (27–28). **Abbreviation**: acc. = accessory.

1. *Eurynotus alticola* Koch

Eurynotus (*Eurynotus*) *alticola* Koch, 1955: 424.– Kamiński 2016: 236; Lumen & Kamiński 2024a: 23; Lumen *et al*. 2025: 18.

Diagnosis

Eurynotus alticola most resembles *E. asperatus* and *E. capensis*. *Eurynotus alticola* is differentiated by the presence of larger, setigerous punctures on abdominal ventrite V (absent in *E. asperatus*) and dark or black setae on the tarsi (golden in *E. capensis*). Further, *E. capensis* has starkly modified hind tibiae in the males, and a modification to the lateral edges of abdominal ventrite V in both sexes (apparently absent in both *E. asperatus* and *E. alticola*). Finally, *E. alticola* is the only species devoid of tubercles on the elytra (including the apical declivity).

Material examined

Lectotype, designated by Lumen & Kamiński (2024a) **TMNH** (Fig. T1): "7 Weeks Poort Berg Ladismith, Cape. 5500–7000 ft.; Paratypus EURYNOTUS alticola sp.n. C.Koch; Paratype No:1246 *Eurynotus alticola* KOCH".

Distribution

South Africa: Western Cape (Map 1).



Map 1. Distribution of *Eurynotus alticola* Koch.

2. *Eurynotus analisetosus* Koch

Eurynotus (*Biolus*) *analisetosus* Koch, 1954a: 278.– Kamiński 2016: 235.

Biolus analisetosus (Koch, 1954).– Lumen & Kamiński 2024a: 19.

Eurynotus analisetosus Koch, 1954.– Lumen *et al*. 2025: 18.

Diagnosis

Eurynotus analisetosus is most similar to other species with tubercles on the elytral disc (e.g. *E. granulatus*, *E. graafi*, *E. omeri*, *E. denticosta*, and *E. sauroides*). External features

to separate them include the color of the tarsal setae (*E. analisetosus* - golden; *E. omeri*, *E. denticosta*, and *E. sauroides* - black or brown/dark), sculpturing of abdominal ventrite V (with two puncture types and apical median notch in females; simple and without female notch in *E. granulatus* & *E. omeri*), microtuberculation (more intense in *E. graafi*), elytral costae (present only in *E. denticosta*). Internally, the female bursa copulatrix of *E. analisetosus* has a sclerite situated near to the apex (all species except for *E. granulatus* lack sclerites) and an 'accessory' pouch (present in *E. analisetosus*, *E. graafi*, and *E. granulatus*; absent in, *E. omeri*, *E. sauroides*, *E. denticosta*, *E. asperipennis*). *Eurynotus graafi* can be differentiated by the surface sculpturing (much more intense microtuberculation than in *E. analisetosus*). Other species with bursa copulatrix sclerites (*Eurynotus granulatus*) can be further separated by the shape of the sclerite (chevron-shaped, versus axe-like in *E. granulatus*).

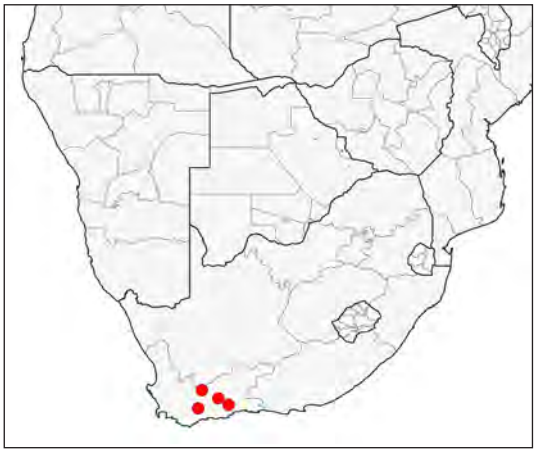
Material examined

Holotype, male **TMNH** (Fig. T2): "7 weeks Poort C.P, 17-XI-1940 G van Son; Eurynotus (Biolus) analisetosus C. Koch det., 195? Koch; analisetosus Koch; Holotype No: 1843 Eurynotus analisetosus KOCH".

TMNH: "Seven Weeks Poort XII.1968, Potgieter & Jones; Eurynotus ex aff. granulatus (F.); From Insectarium No.904; 904", "S. Afr.; Cape Gamkaberg Nat. Res. Feb. - March 1994 leg. Tom Berry". **SMNS**: "Südafrika RSA, Kl. Karoo, zwischen Montagu u. Barrydale, 18.4.2000 leg. Burmeister; coll. Grimm (three specimens)". **MIZPAN**: "Republic of South Africa Anysberg Nature Reserve 17/11/2015 -33.463; 20.588; under stone leg. Marcin Jan Kamiński". **SANC**: "South Africa: W. Cape Trap 5-5, Mimosa Grove Farm (S of Herbertsdale) 34°04'23"S 21°46'24"E 25.xii.2005-03.i.2006 M Burger P Groenewald S. Stoffberg, K. Tolle, Caught in pitfall and funnel traps Trap 5-5, NATIONAL COLL. OF INSECTS Pretoria, South Africa", "South Africa: W. Cape Trap 5-2, Mimosa Grove Farm (S of Herbertsdale) 34°05'32"S 21°47'38"E 25.xii.2005-03.i.2006 M Burger P Groenewald S. Stoffberg, K. Tolle, Caught in pitfall and funnel traps Trap 5-2, NATIONAL COLL. OF INSECTS Pretoria, South Africa".

Distribution

South Africa: Western Cape (Map 2).



Map 2. Distribution of *Eurynotus analisetosus* Koch.

3. *Eurynotus asperatus* Mulsant & Rey

Eurynotus (*Eurynotus*) *asperatus* Mulsant & Rey, 1854a: 23.– Mulsant & Rey 1854b: 167; Lacordaire 1859: 239; Gebien 1938: 414; Koch 1954a: 283, 1954b: 2; Kamiński 2016: 236; Lumen & Kamiński 2024a: 23; Lumen *et al*. 2025: 18.

= *Eurynotus* (*Eurynotus*) *rudebecki* Koch, 1955: 423.– Kamiński 2016: 237; Lumen & Kamiński 2024a: 23 (syn.).

Diagnosis

One of the most commonly collected and identified species in collections alongside *Eurynotus capensis*. Can be separated from *E. capensis* based on size (*E. capensis*: length 14–20mm, width 7–10mm; *E. asperatus* length 9–13.25mm, width 4.5–6.5mm), and characteristics of the males (modified hind tibiae in *E. capensis*) and females (*E. asperatus* bursa copulatrix with sclerites; *E. capenses* with characteristic spermatheca and constricted, bilobed bursa copulatrix). From other *Eurynotus*, *E. asperatus* can also be separated by size: *E. graniderma* and *E. barbosai* are smaller (length 8–9.5mm, width 4.75–5.5mm); however, *E. thermarum* (while generally smaller) specimens may be similar in size in large specimens (which can then be differentiated based on the width of the epipleura and presence of microtuberculation on the pronotum and elytra). The presence of additional, larger setigerous punctures on abdominal ventrite V (absent in *E. asperatus*) can also be diagnostic. *Eurynotus privisolum*, while similar at first glance, can be differentiated based on the sculpture of the pronotum and head (close, coarse punctation; versus *E. asperatus* with finer, more widely separated punctation). Additional separation of species is possible using the luster of the cuticle (dull or opaque in *E. asperatus* versus the shinier *E. privisolum*, *E. sulcimargo*, and *E. barbosai*).

Material examined

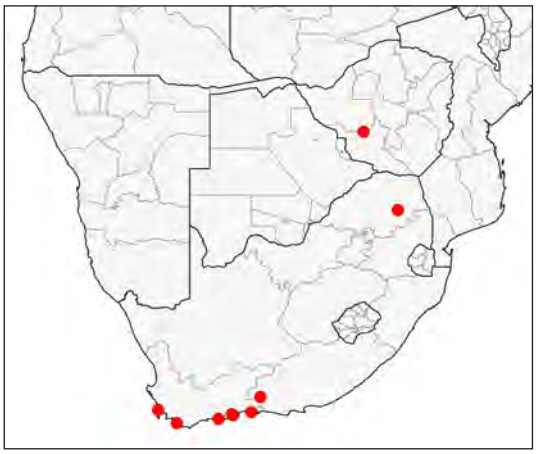
Eurynotus asperatus: **Lectotype**, male, designated by Lumen & Kamiński (2024a) **MNHN** (Fig. T3): Blue circle label "Eurynotus apseratus caff? ?; type Mulsant; asperatus" red label with handwritten "Type".

Eurynotus rudebecki: **Lectotype**, male, designated by Lumen & Kamiński (2024a) **TMNH** (Fig. T17): "Swedish South Africa Expedition 1950–1951 Brunck -Rudebeck / S. Afr. Cape Prov Mosselbaai. 8–9.1.51. No. 127 / Holotype No: 123? Eurynotus rudebecki KOCH / rudebecki koch".

TMNH: "S. Afr. Cape Prov. Mosselbaai 8– 9.I.51. No.127 Swedish South Africa Expedition 1950-1951 Brinck — Rudebeck (three specimens)", "J. H. Brady Cape Town (five specimens)". **MIZPAN**: "South Afr. -34.14/22.06, 9.1.2017 TIPI Kamiński Smith (three specimens)". **MNHN**: "Mossel Bay (Cape Colony); G.B. Mal 1913; Museum Paris (nine specimens)", "Caffrerie coll.R. Oberthür ex. Coll. Deyrolle Budapest", "♂ 13.XII.1969 Mossel Bay AFRIQUE DU SUD Cl. Besnard leg. Museum Paris Coll. P. Ardoin (two specimens)", "Selinus Caffreria Museum Paris 1935 coll. M. Sedillot", "Nairobi (B. E. A) Museum Paris 1913 coll. Guy Babault PROBABLY WRONG LABEL", "WILLOWMORE Cape Colony W. G. Kobrow 339", "Stilbaai [Stiro?]. K. Friedl. J[text rubbed off] 31", "Gans Bay Cape. Colony H.Skoog?", "14.XII.1969 Mossel Bay AFRIQUE DU SUD Cl. Besnard leg., Museum Paris 1978 Coll. P. Ardoin", "S.Afr.CapeProv. Knysna? Buffelsbaai, coast funbos 21-26.XII.1981 leg. S&J Peck". **RBINS**: "Coll. Mus. Tervuren Transvaal : Shilowana (H. A. Junod) 1906/1907 ex. Coll. Breuning (two specimens)" – The area of this locality is quite remote from the range of all other specimens we examined.

Distribution

South Africa: Eastern Cape, Western Cape (Map 3).



Map 3. Distribution of *Eurynotus asperatus* Mulsant & Rey.

4. *Eurynotus asperipennis* Mulsant & Rey

Eurynotus asperipennis Mulsant & Rey, 1854a: 23.– Mulsant & Rey 1854b: 169; Lacordaire 1859: 239; Gebien 1938: 414; Koch 1954a: 280, 1954b: 2; Banaszkiewicz 2006: 63; Kamiński 2016: 235; Lumen *et al*. 2025: 18.

Biolus asperipennis (Mulsant & Rey, 1854a).– Lumen & Kamiński 2024a: 19.

Diagnosis

Lacks sclerite in bursa copulatrix (present in *E. analisetosus* and *E. granulatus*). *Eurynotus asperipennis* has two puncture types on ventrite V (single type in *E. omeri* and *E. granulatus*), and golden setae on the tarsi (dark/black in *E. omeri*, *E. sauroides*, and *E. brunoi*). Without close inspection, *E. brunoi* (Length 15–18mm, Width 7.5–10mm) specimens may appear similar to smaller specimens of *E. asperipennis* (Length 19–22mm; Width 8–11mm); however, *E. asperipennis* have golden tarsal setae (black or dark in *E. brunoi*), a weaker circumocular depression, the pronotal process is more pronounced, and the male tibiae are also at most only slightly modified in *E. brunoi*, while in *E. asperipennis* they are more strongly curved. See the diagnosis of *E. brunoi* for more details.

Material examined

Lectotype, male, designated by Lumen & Kamiński (2024a) **MNHN** (Fig. T4): "Eurynotus ?. ?. cap. ?; blue circle label ‘Eurynotus asperipennis cap ? ?" also with a red label with a handwriting: "Type".

MIZPAN: "Port Elizabeth; CNHM 1955 Karl Branssik Col ex Eduard Knirsch", "green label: bay?, Eurynotus asperipennis Muls, Eurynotus asperipennis ?? Gebien det. 1938", "Port Elizabeth, specimen orig. without Labels in colln, but associated with specimen bearing attached data, CNHM 1955 Karl Brancsik Colln ex Eduard Knirsch". **MNHN**: "Eurynotus tuberculatus cap. (?)", "Le Cap, Eurynotus tuberculatus, Museum Paris 1930 coll. A. Sicard",

"Dumbzody (Cap de b esp), Museum Paris 1906 coll. L. Fairmaire, Eurynotus asperipennis Muls.", "Le Cap, Dendarus tuberculatus, Museum Paris 1930 coll. A. Sicard (two specimens)", "Willowmore, Capland. Dr. H. Braun, Museum Paris Coll P. Ardoin, Eurynotus granulatus DET.C.KOCH", "mars 1896 Rockhurst GRAHAMSTOWN Afrique du Sud, Museum Paris Coll. P. Ardoin (four specimens)", "Port Elizabeth Dr Martin, Museum Paris 1906 Coll.L.Fairmaire". **RBINS**: "Coll. Mus. Tervuren S. Afr. : Cape Prov. 15 km N Grahamstown 14 - I - 89 Jocqué 1370 (two specimens, one with extra folded note: SEM13/12/10 NR3)", "Coll. Mus. Tervuren S.Afr. : Cape Prov. Ecca Pass 16-I-89 leg. R. Jocque 1371 (two specimens)". **TMNH**: "S.Afr.; Baviaanskloof Geelhoutbos; 300m 33.38 S - 24.14 E, 10.11.2015; E-Y:3975 under stones & logs leg. Ruth Müller (two specimens)", "Resolution Albany Distr VI 1928 A. Walton (four specimens; 3 bearing additional Eurynotus granulatus DET. C. KOCH label)". **BPBM**: "Cape Province Coll. BISHOP, Hunt Zool Mus TG Bishop Colln Hug Z022". **SANC**: "South Africa, CP Kirkwood, 33.24S 25.27E 28.XI.1988 R.Oberprieler, National Collection of Insects Pretoria", "South Africa: ECape Trap18-8 Farm Matjiesfontein, NWW of Jansenville 32°50'50"S 24°25'12"S 01-09.ii.2007 M.Burger, M. Fabricius, K. Jacobs & A. Pretorius, Caught in pitfall and funnel traps Trap 18-8 NATIONAL COLL. OF INSECTS Pretoria, South Africa", "South Africa: ECape Trap18-4 Farm Suurhoek 20km NWW of Jansenville 32°52'22"S 24°28'04"S 01-09.ii.2007 M.Burger, M. Fabricius, K. Jacobs & A. Pretorius, Caught in pitfall and funnel traps Trap 18-4 NATIONAL COLL. OF INSECTS Pretoria, South Africa".

Distribution

South Africa: Eastern Cape (Map 4).



Map 4. Distribution of *Eurynotus asperipennis* Mulsant & Rey.

5. *Eurynotus barbosai* Koch

Eurynotus (*Eurynotus*) *barbosai* Koch, 1954a: 284.– Koch 1956: 27; Kamiński 2016: 236.

Eurynotus barbosai Koch, 1954.– Lumen & Kamiński 2024a: 25; Lumen *et al*. 2025: 18.

Diagnosis

Eurynotus barbosai is most similar to *E. thermarum* and *E. graniderma*. All three species are differentiable from other congeners by size as they are the smallest (Length: 8–10mm;

Width: 4.75–7.5mm) group within *Eurynotus*. Additionally, these species (along with *E. capensis*) possess distinct modifications to the male mid- and/or hindlegs (small setose excavations on the tibiae). *Eurynotus barbosai* is sharply separable from the most similar species (*E. thermarum* and *E. graniderma*) by the cuticular surface (shining and relatively smooth in *E. barbosai* versus dull and microtuberculated in the other two) and with additional micropunctation in the interstices between punctures (*E. thermarum* and *E. graniderma* instead with microtuberculation, or without additional specific interstitial structures respectively). Additionally, while all three species are localized around north-northeastern South Africa, *Eurynotus barbosai* is the only species with a distribution east of Eswatini and into Mozambique.

Material examined

Holotype, male **TMNH** (Fig. T5): "Lour, Marques Jan. Rev. H.A, Junod; 3864; Eurynotus sp c?n; Holotype No: 1849 Eurynotus barbosai KOCH".

TMNH: "Marracuene", "SOUTH AFRICA, NATAL Ndumu Game Reserve 26.54S 32.15E, 05–07.xi.1984. R. Oberprieler".

Distribution

Mozambique: Maputo. South Africa: KwaZulu-Natal (Map 5).



Map 5. Distribution of *Eurynotus barbosai* Koch.

6. *Eurynotus brunoi* (Lumen & Kamiński)

Biolus brunoi Lumen & Kamiński 2024a: 19.

Eurynotus brunoi (Lumen & Kamiński, 2024).– Lumen *et al*. 2025: 18.

Diagnosis

This taxon is most similar to *Eurynotus asperipennis*. In addition to characteristics provided in the diagnosis of *E. asperipennis*, *E. brunoi* can be separated from other *Eurynotus* species via: tarsal setae dark/black rather than golden; tubercles absent on elytral disc; abdominal ventrite V with large setigerous punctures; head punctation coarse and closely spaced (≤1 feature diameter separation). Additionally, *E. brunoi* aedeagal parameres are distinctly pointed (truncate or apically blunted or rounded in all other species of *Eurynotus*).

Material examined

Holotype, male **TMNH** (Fig. T6): "S. Afr.; E Cape; 1070m 30km NE Somerset East 32.31 S - 25.34 E / 30.11.2007; E-Y:3767 general collecting leg. Ruth Müller. **Paratypes**: **TMNH**: "S. Afr., Cape-Karroo Woodcliff farm 31.57 S - 24.38 E; 13.9.1983;E-Y:2004 singled day leg. Penrith, (two specimens)". "S.Afr.; E Cape 1450m 50km NE Graaf Reinet 32.09 S - 24.51 E; 27.11.2007.E-Y: 3766 under stones leg. Ruth Müller (five specimens)", "S. Afr.; E Cape; 1070m 30km NE Somerset East 32.31 S - 25.34 E / 30.11.2007; E-Y:3767 general collecting leg. Ruth Müller (four specimens)", "S.Afr., E.Cape Prov. Swaershoek Pass 32.17 S - 25.32 E, 10.10.1984; E-Y:2142 ground & vegetation leg. R. Müller", "S.Afr.;E Cape; 1070m 30km N Bedford 32.24 S - 26.05 E, 12.12.2007; E-Y 3768 general collecting leg. Ruth Müller (three specimens)". **MNHN**: "Cap. B. Esp.".

Distribution

South Africa: Eastern Cape (Map 6).



Map 6. Distribution of *Eurynotus brunoi* (Lumen & Kamiński).

7. *Eurynotus capensis* (Fabricius)

Helops capensis Fabricius, 1794: 440.– Fabricius 1801: 161; Thunberg 1827: 16.

Eurynotus capensis (Fabricius, 1794).– Gebien 1938: 414; Koch 1954a: 283, 1954b: 2, 1956: 26; *Tschinkel* 1978: 315; Iwan 2002: 12; Banaszkiewicz 2006: 63; Kamiński 2016: 236; Bouchard *et al*. 2021: 184; Lumen & Kamiński 2024a: 25; Lumen *et al*. 2025: 8.

= *Eurynotus muricatus* Kirby, 1819: 419.– Mulsant & Rey, 1854a: 21, 1854b: 165; Lacordaire 1859: 239; Gebien 1938: 414; Koch 1954a: 283 (syn.), 1954b: 2; Kamiński 2016: 236; Lumen & Kamiński 2024a: 25; Lumen *et al*. 2025: 18.

= *Tenebrio caffer* Thunberg, 1821: 163.– Ferrer 2009: 118 (syn.); Kamiński 2016: 236; Lumen & Kamiński 2024a: 25.

Diagnosis

Eurynotus capensis is one of the most widely distributed (and well-identified) species in collections. Male specimens are particularly easily identified by the modifications to

the hind legs (tibia with large, setose patches or grooves). Additionally, both males and females share a sinuation of abdominal ventrite V, which is absent in all other species. The closest species morphologically might be *E. thermarum*, *E. barbosai*, and *E. graniderma*; however, all three are sharply separable by size (length 8–13.5mm; width 4.75–7.5mm versus *E. capensis* length 13.75–20mm; width 7–10mm) and males possess an additional patch of setae on the mid-tibia (absent in *E. capensis*). Furthermore, *E. thermarum* has a more strongly narrowing epipleura and simple punctation of abdominal ventrite V (wider and with additional large setigerous punctures in *E. capensis* respectively). *Eurynotus graniderma* and *E. thermarum* both have additional microtuberculation of the elytra and/or pronotum.

Material examined

Helops capensis: **Lectotype**, male, designated by Lumen & Kamiński (2024a) **ZMUK** (Fig. T7): "Cap: bon: sp Paykule Mus: S: ?t; L Helops capensis. F.; red label: TYPE; green square label; ZMUC 00508792; QR code label: 001340".

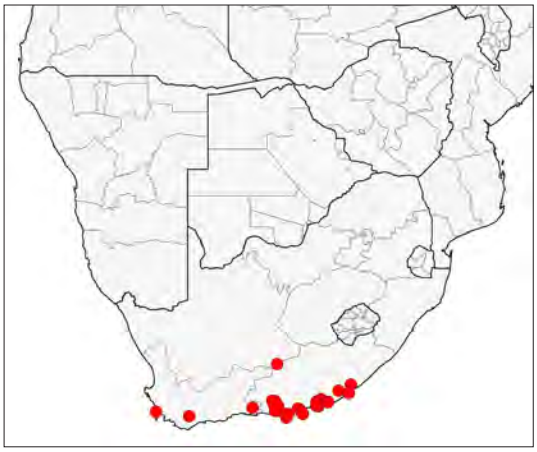
Eurynotus muricatus: **Lectotype**, male **NHMUK** (Fig. T13): "Ent. Club 44.12 NHMUK 016500784 -illegible- africa".

MNHN: "Museum Paris Colonie Du Cap East London R. Ellenberger 1923", "Port Elizabeth, Museum Paris (three specimens)", "S. AFRICA Humandorp 4-XII.1970 S.S, Museum Paris 1978 Coll. P. Ardoin", "Trappes Valley.C.P, Nov. 1924 H.Cronwright -illegible-", "C.B.Esp., Coll.R.Oberthür ex coll.Deyrolle (three specimens)", "Coll DeWalsche Cote S. Est Cap de bon.Esp 11/40", "Grahamstown S.Afr.", "Africa mer. Capetown x.1991 S.??", "nr. Uitenhage,CP. IX. 50 CGC.Dickson (two specimens)", "Museum Paris Colonie Du Cap Port Elisabeth L. Bedel 1898, Port elizabeth Dr. Martin", "Cape Provsa PrtElizabeth, 1957 NLHKrauss (two specimens)", "Newton Park, Port Elizabeth. CP; Aug.50.Rorke", "Trappes Valley.C.P, Feb. 1925 H.Cronwright -illegible-", "Port Elizabeth 2 1896 Jplague?, Museum Paris", "Museum Paris Province du Cap East London V Ellenberger 1919 (two specimens)", "Port Elizabeth Dr. Martin, Museum Paris 1906 Coll. L. Fairmaire (five specimens)", "S. AFRICA Humansdorp 4-XII.1970 S.S, Museum Paris 1978 Coll. P. Ardoin (two specimens)", "Port Elizabeth ?? 1896 ??", "Coll DeWalsche Cote S. Est Capd. Domn.Esp 11.70", "PtEliz 80-66", "Eurynotus capensis H. Gebien det. 1939, Zambesi, Mus. Zool. Polonicum Warszawa 12/45", "Port Elizabeth O. C. Dickson, Eurynotus capensis det. Koch", "Port Elizabeth Dr. Martin, Museum Paris Coll. J. Chatanay 1914", "Transvaal ex coll. Fruhstorfer, Museum Paris 1906 Coll. L. Fairmaire", "East London Dr. Martin, Museum Paris Coll. J. Chatanay 1914", "Zuur Anys Mtns. N. of Karreedouw C.P. IX. '51 C.G.O. Dickson", "Port Elizabeth 10.1896 ??". **BPBM**: "South Africa: 30 km SW Grahamstown 6.XII.1970; J. & J.H. Sedlacek Collectors Bishop (eight specimens)". **TMNH**: "S. Afr., Cape-Karroo Woodcliff farm 31.57 S -24.38 E; 13.9.1983; E-Y:2004 single day leg. Penrith", "S. Afr.: Baviaanskloof Geelhoutbos; 300m 33.38 S - 24.14 E / 10-11.11.2015; E-Y3978 light trap & with touch leg. Ruth Müller (four specimens)", "S. Afr.: Baviaanskloof Doodsklip; 150m 33.39 S - 24.25 E / 11-12.11.2015; E-Y3980 under stones leg. Ruth Müller (three specimens)", "Trappes Valley.C.P, Jan. 1925 H.Cronwright -illegible- (three specimens)", "Trappes Valley.C.P, Feb. 1925 H.Cronwright -illegible-", "Trappes Valley.C.P, Nov. 1924 H.Cronwright -illegible- (three specimens)", "S.Afr.; Baviaanskloof Geelhoutbos; 300m 33.38 S - 24.14 E, 10.11.2015; E-Y:3975 under stones & logs leg. Ruth Müller (three specimens)", "S.Afr.; Baviaanskloof Doodsklip 150m 33.39 S - 24.25 E, 11-12.11.2015;

E-Y3980 under stones leg. Ruth Müller (four specimens)", "Cintes East East London distr. 32.58S-28.00E, IX.1967 L.Schules". **MIZPAN**: "Republic of South Africa Baviaanskloof, Doodsklip 12/11/2015 -33.658; 24.432; under stone Leg. Marcin Jan Kamiński", "Zambesi, Eurynotus capensis H. Gebien det. 1939, Mus. Zool. Polonicum Warszawa 12/45 (two specimens)", "Coll DeWalsche Cote S. Est Capd. Domn.Esp nov 70, Tenebrionide", "South Afr. -34.14/20.06 9.1.2017 Mossel Bay Kamiński SMITH", "SÜDAFRIKA, East. Cape Jeffreys bay I. Puchner XII.97, Collection s. Bečvář", "C.B.Esp., Coll.R.Oberthür ex coll.Deyrolle, Eurynotus muricatus, Kirby", "Port Elizabeth, Museum Paris (two specimens)", "MEL133, red label: VOUCHER, South Africa Doodsklip 12/11/15 -33.66/24.43", "South Afr. Baviaanskloof 19/11/2015 -33.63 / 24.24 Kamiński (three specimens)", "Republic of South Africa Baviaanskloof, Geelhoutbos 10/11/2015 -33.633; 24.244; under stone Leg. Marcin Jan Kamiński". **RBINS**: "Port Elizabeth, CNHM 1955 Karl Branesik Colln ex. Eduard Knirsch", "Trappes Valley -illegible-", "COLL. MUS. TERVUREN Cape Province: East London ex. coll. Breuning (six specimens)", "270, Blue label: Cap von Ludw. 1837, cite sammlung stuttgart". **NMNW**: "Port Elizabeth S. at 34°02'S, 25°39'E. CAPE, R.S.A. 14 Mar 1974, H 17998, Namibian National Insect Collection State Museum P.O. Box 1203 WINDHOEK, Namibia". **SANC**: "Port Elizabeth S. at 34°02'S, 25°39'E. CAPE, R.S.A. 14 Mar 1974, H 17998, Namibian National Insect Collection State MuseumP.O. Box 1203 WINDHOEK, Namibia", "Avontuur k.p xii-1963 E. Holm Dept: of Entomology University of Pretoria, National Collection of Insects Pretoria, South Africa Ex UPSA, May 2002", "Hankey SE 33.24 Dd 8-X.1985 E. Holm National Collection of Insects Pretoria, South Africa", "Alexandria Sep. 1950 A?PE.333, On weeds ??? G.A. Hepburn, C.I.E. Coll. No. 16189, National Collection of Insects Pretoria, South Africa", "South Africa,CP Hankey, 33.50S 24.33E i.1978 S.J.v. Tonder, National Collection of Insects Pretoria, South Africa", "Despatch 27 June 1927, National Collection of Insects Pretoria, South Africa", "Trappes Valley Jan 1921, National Collection of Insects Pretoria, South Africa", "Kingwilliamstown, CP Dec1908 C.W.Mally SN.3271., National Collection of Insects Pretoria, South Africa (two specimens)", "Port Elizabeth Cape Province 5.2 1954, C.I.Coll. No. 17240, National Collection of Insects Pretoria, South Africa (two specimens, one with extra label: ?Selinus punctatostriatus? E.A.J.Duffy det. 1960)", "Seal Point 34 10 S 24 50 E 15 IV.1994 I Kelly Department of Entomology University of Pretoria, This specimen ex undergraduate student collection treat label data with caution, National Collection of Insects Pretoria, South Africa Ex UPSA, May 2002". Bečvář private collection: "R.S.A. Eastern Cape pr. 30 km W Alexandria 27.i.2000 lgt. S. Bečvář, collection S. Bečvář (two specimens)", "Africa mer. ?? Capetown, X.1991 S.J-?, Collection s. Bečvář (two specimens)". **NHMUK**: "P. Elizabeth, Nevinson Coll. 1918-14 (six specimens)", "Cap, Nevinson Coll. 1918-14 (two specimens)", "Distant Coll 1911-383 (four specimens)", "Int S. Africa, Eurynotus muricatus Kirby Int. S. Africa Earl of Derby", "C. Bon. Spei, Fry Coll. 1905.100.", "71'6", "S. Africa. Holab, Sharp Coll 1905-313", "Port Elizabeth 92-10", "Port Eliz. 90-49 (two specimens)", "Port Elizabeth 91-33", "Pt. Eliz. 80-66 (four specimens)", "CAPE Grahams Town., E.Y. Western Coll. B.M. 1924-176 (two specimens)", "Cape Pt. Elizabeth, E.Y. Western Coll. B.M. 1924-176.", "Port Eliz. 90-67., Eurynotus muricatus (three specimens)", "Port Elizabeth 81-33", "Cap b. sp, Nevinson Coll. 1918-14", "P. B. Spei Port Elizabeth, Fry Coll. 1905.100".

Distribution

South Africa: Eastern Cape, Western Cape (Map 7).



Map 7. Distribution of *Eurynotus capensis* (Fabricius).

8. *Eurynotus constrictus* Koch

Eurynotus (*Biolus*) *constrictus* Koch, 1955: 421.– Kamiński 2016: 235.

Eurynotus constrictus Koch, 1955.– Lumen & Kamiński 2024a: 26; Lumen *et al*. 2025: 8.

Diagnosis

Eurynotus constrictus, along with *E. sulcimargo*, are distinct within *Eurynotus* for the shape of their pronota: with explanate lateral margins with more widened sulci compared to their congeners. Some representatives of *Eurynotus* possess lateral depressions; though they are less pronounced, and are sharply separable using other characters. *Eurynotus constrictus* is duller in texture (versus shiny/smooth in *E. sulcimargo*) and has simple punctation of abdominal ventrite V (with larger, intermixed, setigerous punctation in *E. sulcimargo*). Further, the elytral striae punctation in *E. sulcimargo* is distinctively large within *Eurynotus*. *Eurynotus constrictus* is also unique in that some representatives have weakly-raised tuberculation on the elytral humeri.



Map 8. Distribution of *Eurynotus constrictus* Koch.

Material examined

Lectotype, male, designated by Lumen & Kamiński (2024a) **TMNH** (Fig. T8): "Oudebosch R. zondereinde; museum staff Sept 1933; Paratypus EURYNOTUS constrictus C. Koch sp.n.".

TMNH: "Robertson South Africa Julie 1944 S.H.Beneke".

Distribution

South Africa: Western Cape (Map 8).

9. *Eurynotus denticosta* Mulsant & Rey

Eurynotus denticosta Mulsant & Rey, 1854a: 29.– Mulsant & Rey 1854b: 173; Gebien 1938: 414; Koch 1954a: 276, 1954b: 2, 1955: 420; Iwan 2001: 387; Banaszkiewicz 2006: 63; Kamiński 2016: 237; Lumen *et al*. 2025: 19.

Biolus denticosta (Mulsant & Rey, 1854a).– Lumen & Kamiński 2024a: 20.

Diagnosis

Eurynotus denticosta is arguably the most characteristic species of the genus. The structure of the elytra is unique within the genus (with extremely large punctation and costae giving the appearance of a lattice-like structure).

Material examined

Lectotype, male, designated by Lumen & Kamiński (2024a) **HNHM** (Fig. T9): "Budapest / C. B. Esp. Coll. R. Oberthür ex. Coll. Deyrolle / Paratype 1854 Eurynotus denticosta Mulsant / Red LECTOTYPE label". **Paralectotype HNHM**: Same labels as lectotype, with additional yellow "PARALECTOTYPE" label.

MNHN: "Swellendam: S.Afr ("T." on backside of label); F. Bates. 81-19.", "28. XI.1970 Mossel Bay Afrique Du Sud J.& M. Sedlacek Museum Paris Coll. P. Ardoin 1978 (three specimens, 1 male, 1 female, 1 undetermined)", "SAM-COLL 50-30 Riversdale", "Cap Muséum Paris 1906 Coll. L. Fairmaire", "Stilbaal turnoff 34°10'S., 21°19' E, CAPE, R.S.'. 11 Apr. 1975 M.J. & M-L. Penrith H31506 Namibian National Insect Collection State Museum P.O. Box 1203 WINDHOEK, Namibia", "J.H.Brady Cape Town". **RBINS**: "Coll. Mus. Tervuren S. Afr.: Cape Prov. 5 km W Albertinia 12-I-89 Jocqué 1364 (two specimens)", "Turvuren Coll. Mus. Turvuren Cape Province: East London ex. coll. Breuning", "Mus. Roy. Afr. Centr. The Maurice ex. Coll. Dr. Breuning (two specimens)", "Coll. Mus. Tervuren Transvaal: Shilowane (H.A. Junod) 1906/1907 ex. Coll. Breuning (five specimens)" – The area of this locality is quite remote from the range of all other specimens we examined; as a precaution we omitted these specimens from our maps, as they may represent incorrect locality records. **TMNH**: "S. Afr., S. W. Cape Bredasdorp, 15 km N 34.24 S -20.02 E 20.9.1985; E-Y: 2256 from under stones leg. Endrödy-Younga (two specimens)". **SMNS**: "513. [det. label unintelligible] ??? Sammlung Stuttgart Schawaller".

Distribution

South Africa: Eastern Cape, Western Cape (Map 9).



Map 9. Distribution of *Eurynotus denticosta* Mulsant & Rey.

10. *Eurynotus graafi* Koch

Eurynotus (*Biolus*) *graafi* Koch, 1954a: 279.– Kamiński 2016: 235.

Biolus graafi (Koch, 1954).– Lumen & Kamiński 2024a: 20.

Eurynotus graafi Koch, 1954.– Lumen *et al*. 2025: 19.

Diagnosis

Koch (1954a) noted this species' size in his original description, designating it the largest species of the genus. With the reinstatement of *E. asperipennis* (length 19–22mm, width 8–11mm), *E. graafi* can no longer be clearly separated by size. However, *E. graafi* can be separated from other species by the nature of the punctation of the head and pronotum (coarse and confluent); and from similar species using the sculpturing of the elytra and epipleura (both with intense microtuberculation). Additionally, the pronotum and abdominal ventrite V bear small, micropunctures; absent in other species.

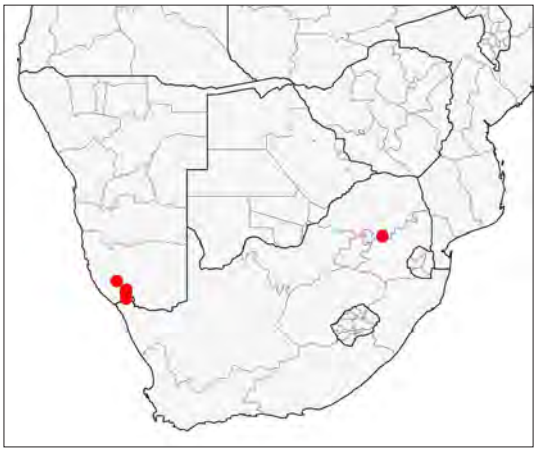
Material examined

Holotype, female **TMNH** (Fig. T10): "Kuboos Richtersveld [.1949.C.Koch; graafi Koc; Eurynotus (Biolus) Graafi Koch C. Koch det., 195?; Holotype No: 1845 Eurynotus graafi KOCH".

TMNH: "S.Afr.; Richtersveld Paradieskloof 28.19S -17.00E; 9.9.2001; E-Y:3416 under stones leg. TMSA staff (two specimens)", "21.9.1973; E-Y:132 from under stones leg. Endrödy-Younga; S. Afr., Namib Rosh- Pinah 28.04 S - 16.59 E", "S. Afr.: Mpumalanga Groblersdal, 1168m 25°15'S 29°34'E 17-20.IX.2002 TMSA Expedition; Blue Ridge West Platinum Mine EMPR SRK Consulting Light trap", "NAMIBIA Upper Boomriver 27.52 S - 17.00 E 4.IV.2002 leg. E. Holm, M. Gebhardt", "Namibia; Namuskluft Zebrafontein 27.45 S - 16.53 E, 2-6.IV.2002 leg.E.Holm, M.Gebhardt".

Distribution

Namibia: ǁKaras. South Africa: Northern Cape (Map 10). Although an extralimital record is included here from Mpumalanga, whether it represents real established population is questionable.



Map 10. Distribution of *Eurynotus graafi* Koch.

11. *Eurynotus graniderma* Koch

Eurynotus (*Eurynotus*) *graniderma* Koch, 1955: 426.– Kamiński 2016: 236; Lumen & Kamiński 2024a: 26; Lumen *et al*. 2025: 19.

Diagnosis

Most similar to *E. barbosai* and *E. thermarum*. Most easily differentiated from *E. barbosai* by the presence of microtuberculation and rugosity of the elytra (absent in *E. barbosai*). *Eurynotus thermarum*, while also possessing microtubercles on the elytra, lacks the same level of rugosity, and has microtubercles on the pronotum (absent in *E. graniderma*). All other species of *Eurynotus* are easily separable using male characteristics: hind tibial setae absent in all species save for *E. capensis*, which lacks them on the midtibia, is larger (length 14–20; width 7–10mm), and lacks the same microtuberculation of *E. graniderma*.



Map 11. Distribution of *Eurynotus graniderma* Koch.

Material examined

Holotype, male **TMNH** (Fig. 11): "Ngxwala hill Zululand 10-7-15 L. Bevis; Durban Museum".

TMNH: "S.Afr., Natal Miguze 17.XII.1976 leg. P.E. Reavel (two specimens)", "S.Afr., Zululand Mkuzi Game Reserve P.E. Reavell 7.1976 (four specimens)", "Gwalaweni Forest II.'57", "Ithombo Zulyland 6-09 Marley / Durban Museum / C. Koch det., 195 bele-marleyi C. Koch det., 195", "1.10.2022;E-Y:3521 under stones leg.TMSA staff, S.Afr.;Mpumalanga Aquarius Platinum mine 25.10 S S - 30.10 E".

Distribution

South Africa: KwaZulu-Natal, Limpopo (Map 11).

12. *Eurynotus granulatus* (Fabricius)

Helops granulatus Fabricius, 1787: 214.

Blaps granulate (Fabricius, 1787).– Fabricius 1792: 107.

Eurynotus granulatus (Fabricius, 1787).– Gebien 1906: 230, 1938: 414; Koch 1954a: 280, 1954b: 2, 1956: 25; Iwan 2001: 384; Banaszkiewicz 2006: 63; Kamiński 2016: 235; Lumen *et al*. 2025: 19.

Biolus granulatus (Fabricius, 1787).– Lumen & Kamiński 2024a: 21.

= *Eurynotus norrisi* Mulsant & Rey 1854a: 27.– Mulsant & Rey 1854b: 171; Lacordaire 1859: 239; Gebien 1938: 414; Koch 1954a: 277, 1954b: 2; Kamiński 2016: 235; Lumen & Kamiński 2024a: 21 (syn.)

Diagnosis

Most similar to *E. omeri* (e.g. both with simple abdominal ventrite V punctation, similar in size, with tubercles/risen callosities on elytral disc). The two can be differentiated based on setation of the tarsi (*E. granulatus* golden; *E. omeri* black/dark brown), the sclerite within the bursa copulatrix (present in *E. granulatus*; absent in *E. omeri*), and characterisation of the dorsal surface (*E. granulatus* blunter/shorter and more crowded tubercles; while *E. omeri* has sharper/taller and more widely spaced tuberculation with a slightly more lustrous surface). In-so-far as other species are concerned, the abdominal ventrite V punctation (simple) separates it from *E. analisetosus*, *E. asperipennis*, *E. graafi*, and *E. sauroides* (with two or more types of punctation). The tubercles/raised callosities present on the elytral disc further separate it from *E. asperipennis* (lacking discal tubercles). The presence of a sclerite in the bursa copulatrix separates this species from all but *E. analisetosus* (which in contrast to *E. granulatus* axe-shaped sclerite, has a flatter, chevron-shaped sclerite).

Material examined

Helops granulatus: **Lectotype**, male, designated by Lumen & Kamiński (2024a) **ZMUK** (Fig. T12): QR code label "ZMUKFabricius 004512".

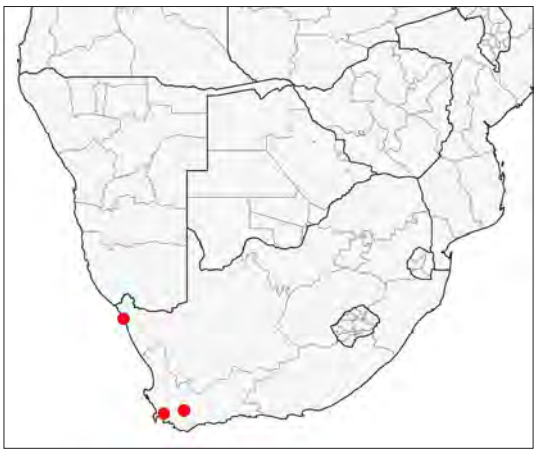
Eurynotus norrisi: **Lectotype**, male, designated by Lumen & Kamiński (2024a) **MNHN** (Fig. T14): "Eurynotus norrisii bug? spinola indiff cap.bon.jp.? / small blue circle label: Eurynotus nori -illegible- / Type Mulsant / Norrisii / Red label: Type".

MNHN: "circle label: C.G. Hope, Eurynotus norrisi Bug? C.G. Hope", "Eurynotus norrisii Bug. Cap.", "small illegible square label, eurynotus norisii", "Le Cap", "Stellenbosch South Africa Julie 1944 B.J.v.D.vyve?", "South Africa Robertson Juli 1944", "South Africa

Robertson 29.6.1942 (two specimens)", "South Africa Robertson 18.6.1927", "Robertson Cape Colony Leg. Hugo?, Eurynotus norrisi Muls", "norrisi!, EX. Musaeo E.Alcard 1899", "Robertson, S.A 18-4-27 J.C. le Roux", "Montagrie? 3.84". **BPBM**: "Hunt Zool Mus TG Bishop Clln Hug Z022, Pt Nolloth Namaqualand".

Distribution

South Africa: Northern Cape, Western Cape (Map 12).



Map 12. Distribution of *Eurynotus granulatus* (Fabricius).

13. *Eurynotus omeri* Koch

Eurynotus (*Biolus*) *omeri* Koch, 1954a: 277.– Kamiński 2016: 235; Lumen *et al*. 2025: 19.

Biolus omeri (Koch, 1954).– Lumen & Kamiński 2024a: 21.

Diagnosis

Eurynotus omeri is most similar to *E. granulatus*. The most glaring differences and distinctive traits of *E. omeri* are the tarsal setae (black), the sharp, well-defined tuberculation of the elytra, and lack of additional puncture types on abdominal ventrite V.

Material examined

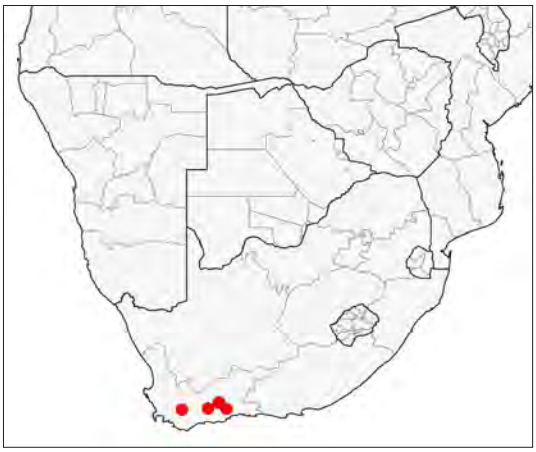
Holotype, male **TMNH** (Fig. T15): "Kuouland(?) Berg Dr. Brauns. Uniondale Cape Colony; Eurynotus norrisi ♂ Muls; Eurynotus (Biolus) omeri C. Koch dete.,195? Koch; omeri Koch; Holotype No. 1840 Eurynotus omeri KOCH".

TMNH: "S. Afr: W Cape Prov. Gamkaberg Nat. Res. 33.44 S - 21.57 E; 1.2.1994: E-Y:3239 groundtraps 28 days leg. Tom Berry (10 specimens)", "S. Afr.: LittleKarroo Gamka Mt. 1000m 33.43 S - 21.56 E 25.10.1993: E-Y:2899 ground and stones leg. Endrödy-Younga EURYNOTUS norrisi Muls. & Rey det W. Schawaller 2005 (five specimens)", "S. Afr: W Cape Prov Gambkaberg Nat. Res. 33.42 S - 21.57 E", "S. Afr: LittleKarroo Gambkabg. deBrug 1000m 33.42 S - 21.57 E 14.1.1994: E-Y:3079 groundtraps 28 days leg. Tom Berry EURYNOTUS norrisi Muls. & Rey det W. Schawaller 2005 (two specimens)", "S. Afr: W Cape Prov Gambkaberg Nat. Res. 33.42 S - 21.57 E / 1.12.1994: E-Y:3245 groundtraps 32 days leg. Tom Berry (three specimens)", "S. Afr: W Cape Prov

Gambkaberg Nat. Res. 33.42 S - 21.57 E / 1.2.1995 : E-Y:3247 groundtraps 28 days leg. Tom Berry (two specimens)", "S. Afr: LittleKarroo Gambkabg. deBrug 1000m 33.44 S - 21.57 E 15.2.1994: E-Y:3071 groundtraps 28 days leg. Tom Berry", "S. Afr: W Cape Prov Gambkaberg Nat. Res. 33.44 S - 21.57 E / 2.1.1994: E-Y:3238 groundtraps 30 days leg. Tom Berry (two specimens)". **MIZPAN**: "(Red voucher label) / 7/1/2017 Gamkaberg p146 Kamiński", "South Afr 2022/25/1 -33.77/19.75 (four specimens)", "South Afr. -33.72/21.03 7.1.2017 Gamkaberg Kamiński Smith", "7.1.2017 Gamkaberg POI46 Kamiński", "South AFR 2022 Jan. Kamiński".

Distribution

South Africa: Western Cape (Map 13).



Map 13. Distribution of *Eurynotus omeri* Koch.

14. *Eurynotus privisolum* Lumen & Kamiński

Eurynotus privisolum Lumen & Kamiński 2024a: 26.– Lumen *et al*. 2025: 19.

Diagnosis

This species is, at first glance, similar to *E. asperatus*. However, it is easily separable using the texture/luster of the cuticle (dull/microreticulate in *E. asperatus*; shining/smooth in *E. privisolum*). Other characteristics separating this species from others are: the shape of the pronotum; the presence of micropunctation on the pronotum and abdominal ventrite V; the absence of larger, setigerous punctures on abdominal ventrite V.

Material examined

Holotype, male **TMNH** (Fig. T16): "Middelberg div." opposite side of label "mus?/nov. 1935", "Transvaal".

Distribution

South Africa: Eastern Cape (Map 14).



Map 14. Distribution of *Eurynotus privisolum* Lumen & Kamiński.

15. *Eurynotus sauroides* Koch

Eurynotus (*Biolus*) *sauroides* Koch, 1955: 420.– Kamiński 2016: 235.

Biolus sauroides (Koch, 1955).– Lumen & Kamiński 2024a: 22.

Eurynotus sauroides Koch, 1955.– Lumen *et al*. 2025: 19.

Diagnosis

Eurynotus sauroides is sharply separable from all other species by the extremely coarse sculpturing dorsally and ventrally (large, knobby tubercles extending to the disc and base of the elytra and large closely spaced punctures on abdominal underside).



Map 15. Distribution of *Eurynotus sauroides* Koch.

Material examined

Holotype, female **TMNH** (Fig. T18): "Garies Namaqualand; Museum Staff June 1930; sauroides Koch; Paratypus Eurynotus sauroides C. Koch sp. N.".

SANC: "South Africa, E. Cape Gamkaskloof Nat. Res., "Die Hel" N Calitzdorp 33.21S 21.37E, 15.v.1995 M. De Jager; collected from under stones AcL01 1400; National Coll of Insects Pretoria S. Afr. (four specimens)", "Willowmore Capland G. Kobrow 9.1904 (four specimens)", "Laingsburg d. VII.1950 E.A.Pienaar", "South Africa ECape Swartberg Nature Res. Nat. Conservation Officer Zannie van der Walt Jan-Feb 2006, National Coll. of Insects Pretoria, South Africa". **TMNH**: "5.9.1979; E-Y:1634 singled leg. Endrödy-Younga, S.Afr., Cape-Karoo Farm Zwartskraal 33.10S - 22.32E", "S.Afr., Cape-Karroo Zwartskraal farm 33.10 S - 22.32 E, X.1983 D. Oosthuizen?", "Willowmore Capland G Kobrow 10.1904".

Distribution

South Africa: Eastern Cape, Western Cape (Map 15).

16. *Eurynotus sulcimargo* Koch

Eurynotus (*Biolus*) *sulcimargo* Koch, 1955: 422.– Kamiński 2016: 236.

Eurynotus sulcimargo Koch, 1955.– Lumen & Kamiński 2024a: 27; Lumen *et al*. 2025: 19.

Diagnosis

Most similar to *E. constrictus* (see diagnosis for more details). This species is most easily discernible using the shape of the pronotum (e.g. pronotum explanate), shining cuticle with smooth interstices between punctures, elytral punctation (large strial punctures), and puncture arrangement of abdominal ventrite V (with large setigerous punctures intermixed).

Material examined

Lectotype, male, designated by Lumen & Kamiński (2024a) **TMNH** (Fig. T19): "Top of Skurweberge Cold Bokkeveld Ceres Dist.; M. Versfeld 15–30 Oct 1934; Paratypus EURYNOTUS sulcimargo C. Koch sp.n.; Paratype No: 1235 Eurynotus sulcimargo KOCH".

TMNH: "Fonteintiesberg Worcester C.P. 6000 ft. (K.H. Barnard Mar.1929. on backside)".

Distribution

South Africa: Western Cape (Map 16).



Map 16. Distribution of *Eurynotus sulcimargo* Koch.

17. *Eurynotus thermarum* Koch

Eurynotus (*Biolus*) *thermarum* Koch, 1954a: 282.– Koch 1955: 423; Kamiński 2016: 236.

Eurynotus thermarum Koch, 1954.– Lumen & Kamiński 2024a: 27; Lumen *et al*. 2025: 19.

Diagnosis

Similar to *E. barbosai* and *E. graniderma*, can be separated from other species via size, microtuberculation, and male hind tibia structure (see respective diagnoses for separating this species from *E. barbosai* and *E. graniderma*).

Material examined

Holotype, male **TMNH** (Fig. T20): "Warmb. 20.2.04 5308; A. spec. Nov. 5308; Holotype No: 1847 Eurynotus thermarum KOCH; thermarum Koch".

TMNH: "Marble Hall V.1962, TV. RORKE", "Marble Hall V.1962, TV. RORKE (two specimens)".

Distribution

South Africa: Limpopo (Map 17).



Map 17. Distribution of *Eurynotus thermarum* Koch.

C. *Phylacastus* lineage

Genera included (1)

Phylacastus Fairmaire.

ii. Genus *Phylacastus* Fairmaire

Phylacastus Fairmaire, 1897: 116.– Koch 1954a: 275, 1954b: 2, 1956: 27; Iwan 2001: 352; Kamiński 2016: 245; Kamiński *et al*. 2019: 92, 2021: 152; Lumen & Kamiński 2023: 4, 2024a: 4, 2024b: 138; Lumen *et al*. 2025: 2.

Type species: *Phylacastus striolatus* Fairmaire; designated by monotypy.

Diagnosis

Within Eurynotina, *Phylacastus* largely resembles *Capidium* and *Eurynotus*. All three have relatively sharp basal pronotal angles, rather than broadly rounded as is the case in the majority of the rest of Eurynotina. The only other exception is *Oncotus* which has basal angles of the pronotum right-angled, though slightly less angular) and is separable by prosternal process shape (rounded rather than angular in lateral view), much rounder/transverse body shape than *Phylacastus*, tibial morphology (foretibia greatly expanded apically and with a sharp lateral projection), and coloration (species may be bicolored and/or testaceous in color) (Kamiński 2016, Lumen *et al*. 2025). *Phylacastus* can be easily separated from all other subtribal representatives by the form of the prosternal process, which is angular rather than rounded in lateral view, and the pronotum with basal angles sharper rather than rounded, and presence of relatively weak tubercles on the apical declivity of the elytra (versus taxa with stronger tubercles such as *Eurynotus*).

Species included (5)

P. ancoralium Lumen & Kamiński, *P. crypticoides* Koch, *P. makskacymirowi* Lumen & Kamiński, *P. rhodesianus* Koch, *P. striolatus* Fairmaire.

Key to species of *Phylacastus* after Lumen & Kamiński (2023) (See Plate ii for figures):

1. Well-defined tubercles present on apical declivity of elytra (Fig. 1) **2**

— Well-defined tubercles absent on apical declivity of elytra (smooth or at most only with small bumps or undulations) (Figs 2–3) **3**

2. Parameres widely spaced with large dorsal opening exposing median lobe (Fig. 4). Mentum parallel-sided and broad (Fig. 6). Elytral intervals densely punctate. Generally larger (6–8mm) ..... ***Phylacastus rhodesianus***

— Parameres not widely spaced, with small dorsal opening exposing at most only the tip of the median lobe (Fig. 5). Mentum narrowing apically (Fig. 7). Elytral intervals less densely punctate. Generally smaller (4–6mm) ..... ***Phylacastus makskacymirowi***

3. Aedeagus with ancorae (Fig. 8). Ratio of ovipositor coxites I–IV to paraprocts nearly 1:1 (Fig. 10). Elytra smooth, with at most weakly impressed striae on elytral disc, absent stria on apical declivity (Fig. 2) ..... ***Phylacastus ancoralium***

— Aedeagus lacking ancorae (as in Fig. 9). Ratio of ovipositor coxites I–IV to paraprocts distinctly <1:1 (Fig. 11). Elytra with or without bumps and with more clearly impressed elytral striae (as in Fig. 3) **4**

4. Mentum with narrow carina/keel running up median (Fig. 12). Fifth abdominal sulcus narrowly separated from apex (Fig. 13) ..... ***Phylacastus crypticoides***

— Mentum lacking narrow carina/keel running up median. Fifth abdominal sulcus widely separated from apex (Fig. 14) ..... ***Phylacastus striolatus***

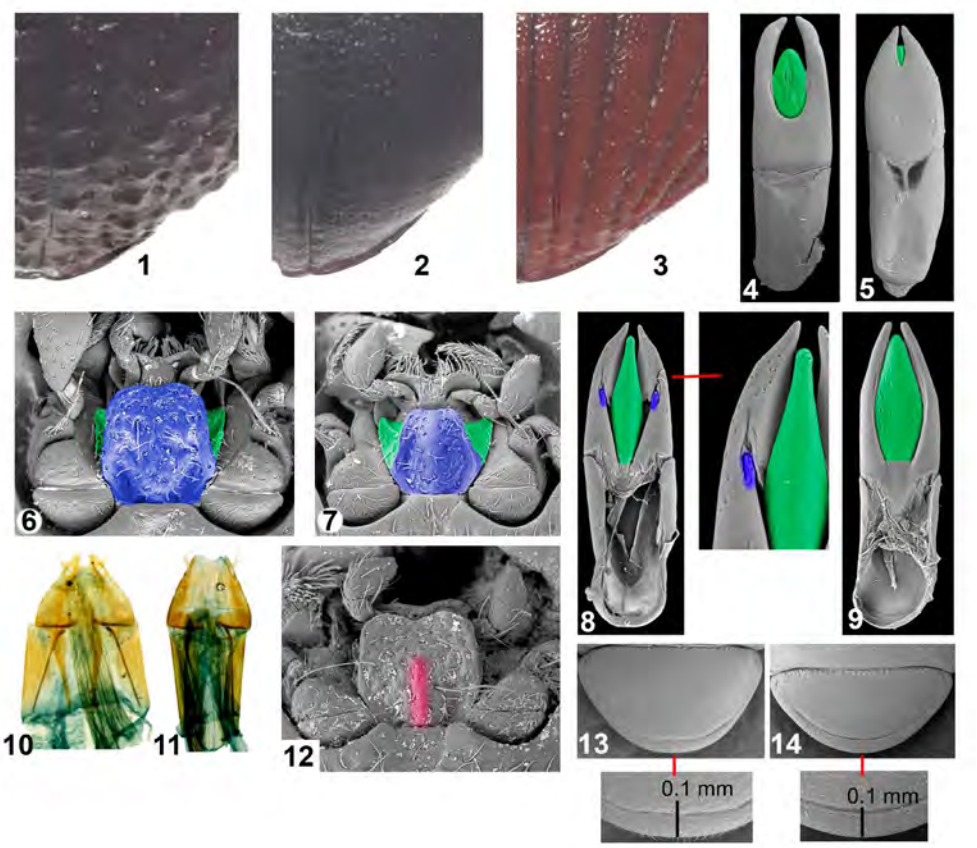


Plate ii. *Phylacastus* species diagnostic features. **Anatomic features**: Elytral declivity (1–3). Aedeagus (Dorsal: 4–5; Ventral: 8–9). Ovipositor (10–11). Mentum (6–7, 12). Abdominal ventrite V (13–14). **Taxa depicted**: *Phylacastus ancoralium* (2, 8, 10). *Phylacastus crypticoides* (9, 11–13). *Phylacastus makskacymirowi* (5). *Phylacastus rhodesianus* (1, 4, 6–7). *Phylacastus striolatus* (3, 14). **Colorcoding**: Figures 6-7; Blue = Mentum, Green = Mentum wings. Figures 4-5 & 8-9; Blue = Ancorae, Green = Penis. Figure 12; Pink = Keel.

1. *Phylacastus ancoralium* Lumen & Kamiński

Phylacastus ancoralium Lumen & Kamiński 2023: 6.– Lumen & Kamiński 2024a: 6; Lumen *et al*. 2025: 10.

Diagnosis

Phylacastus ancoralium is highly modified compared with its congeners. In addition to its wide geographic separation from other species (Lesotho), it can be separated from all other species of *Phylacastus* via the elytra (with extremely weak to absent elytral striae), prosternum (weakly produced between forecoxae, rather than projecting more strongly beyond), aedeagus with ancorae on the ventral surface of the parameres, and ovipositor relatively short compared to other species (ratio of ovipositor coxites I–IV to paraprocts nearly 1:1, rather than more distinctly <1:1). To date, this is the only species within the subtribe Eurynotina with ancorae.

Material examined

Holotype, male **TMNH** (Fig. T21): "S.Afr.;E. Lesotho Hodson's Peak 300m 29.37S - 29.17 E; 11.3.1976;E-Y:1069 fr.und.stones, 3150m leg. Endrödy-Younga." With an additional label on red paper: "Holotype: Phylacastus ancoralium Lumen & Kamiński". **Paratypes MIZ-PAN**: "Same data as Holotype (two specimens)". "S.Afr.Basutoland Makheke Mnts 15 miles ENE Mokhotlong. 8.IV.51 No. 268;Swedish South Africa Expedition 1950-1951; red label.". **TMNH**: "S.Afr., Lesotho Drakensbg,Black Mt. 29.31 S - 29.12 E; 9.3.1976;E-Y:1060 from under stones leg. Endrödy-Younga.", "S.Afr.;E. Lesotho Hodson's Peak 300m 29.37S - 29.17 E; 11.3.1976;E-Y:1067 from under stones leg. Endrödy-Young (five specimens)", "S.Afr., E.Lesotho Sani Pass Valley 29.39 S - 29.12 E; 10.3.1976; E-Y:1066 from under stones leg. Endrödy-Younga (two specimens)".

Distribution

Lesotho: Mokhotlong district (Map 18).



Map 18. Distribution of *Phylacastus ancoralium* Lumen & Kamiński.

2. *Phylacastus crypticoides* Koch

Phylacastus crypticoides Koch, 1954a: 286.– Kamiński 2016: 245; Lumen & Kamiński 2023: 9, 2024a: 7; Lumen *et al*. 2025: 13.

= *Phylacastus pretoriensis* Koch, 1954a: 285.– Kamiński 2016: 245; Lumen & Kamiński 2023: 9 (syn.).

Diagnosis

This species is best separated by ruling out other *Phylacastus*. Unlike *P. ancoralium*, this species has tubercles or more rugose intervals on the apical decline of the elytra, as well as lacking the smaller ancorae or grooves (as in *P. makskacymirowi*) of the aedeagus. Additionally, some representatives of *P. crypticoides* have a prominent keel on the mentum (absent in other species). Further, *P. maksacymirowi* and *P. rhodesianus* have stronger tuberculation of the apical decline of the elytra than other species. *Phylacastus crypticoides* is separable from *P. striolatus via* the size (6–7mm vs 8mm) and placement of the 5th abdominal subapical sulcus (smaller and closer to the apex in *P. crypticoides*).



Map 19. Distribution of *Phylacastus crypticoides* Koch.

Material examined

Phylacastus crypticoides: **Holotype**, sex undetermined **TMNH** (Fig. T22): "Lydenburg Distr. 1896 P.A. Krantz; Phylacastus crypticoides DET.C.KOCH 1953; Holotype No: 1873 Phylacastus crypticoides KOCH; crypticoides Koch; Eurynotus? Sp.."

Phylacastus pretoriensis: **Holotype** sex undetermined **TMNH** (Fig. T24): "Pretoria N., 19.I.1949. G. van Son.; Holotype No 1850; Phylacastus pretoriensis KOCH".

TMNH: "S.Afr.,N.Transvaal Nylsvley Met.Sta. 24.40 S - 28.42 E; 285.1975; E-Y:1160 humus, Berlese, open leg. Endrödy-Younga.", "S.Afr.,N.Transvaal Nylsvley, Smith frm 24.40 S - 24.42E 15.11.1975; E-Y: 952 cattle dung leg. Endrödy-Younga; trench; rep: 5 cage mesh 9mm 7 day aft.sett."*, "S.Afr.,N.Transvaal Nylsvley Met.Sta. 24.40 S - 28.42 E; 29.3.1976; E-Y:1112 sifted litter, open leg. Endrödy-Younga.", "S.Afr.;Limpopo Prov. Lindani Nat Res 1336m 24.02 S - 28.23 E; 8.12.2005; E-Y:3687 single, bushveld leg. Gusmann, Müller.", "S.Afr.,N.Transvaal Nylsvley, Smith frm 24.40 S - 24.42E 8.1.1976; E-Y: 990 sifted litter. Endrödy-Younga"*, "S.Afr.Tvl.Waterbg Lapalala Wilderness 23.49 S - 20.17 E; 16.8.1975; E-Y:829 from under stones leg. Endrödy-Younga (seven specimens)"*.

Lumen & Kamiński (2023) noted that some collecting events (marked *) are likely to be erroneous in their coordinates and should be represented in Northeastern South Africa (circa -24.40, 28.42); however, the coordinates as written on the labels referred to far-off localities in Botswana. As such, while the labels are recorded here (as well as by Lumen & Kamiński 2023), the points are omitted from the species range maps presented here.

Distribution

South Africa: Gauteng, Limpopo, and Mpumalanga (Map 19).

3. *Phylacastus makskacymirowi* Lumen & Kamiński

Phylacastus makskacymirowi Lumen & Kamiński 2023: 12.– Lumen & Kamiński 2024a: 6.

Diagnosis

This is the smallest species of the genus (4–6mm vs 6–8mm). In addition to its size, this species is further defined by the presence of well-defined tubercles on the apical declivity of the elytra–a trait shared only by *P. rhodesianus*, which is larger and can be further differentiated by: punctures on elytral intervals (more numerous and dense in *P. rhodesianus*), the shape of the mentum is broad, not tapered, further concealing the lateral wings in *P. rhodesianus*, tapers apically, exposing lateral wings in *P. makskacymirowi*, aedeagus with a wide space between parameres, exposing large portion of median lobe in *P. rhodesianus*, narrow exposing only the tip of the median lobe in *P. makskacymirowi*.



Map 20. Distribution of *Phylacastus makskacymirowi* Lumen & Kamiński.

Material examined

Holotype, male **TMNH** (Fig. T23): "S.Afr.,E.Transvaal Berlin;Karst plat. 25.31 S - 30.46 E; 20.9.1986; E-Y:2279 groundtraps, 33 days leg. Endrödy-Younga; ground trap with meat bait." With an additional label on red paper: "Holotype: Phylacastus makskacymirowi Lumen & Kamiński". Paratypes **MIZPAN**: Three additional specimens with same data as holotype. **TMNH**: "S.Afr.,E.Transvaal Berlin;Karst plat. 25.31 S - 30.46 E; 23.10.1986; E-Y:2001 groundtraps, 42 days leg. Endrödy-Younga; ground trap with meat bait.", "S.Afr.,E.Trans-

vaal Berlin;Karst plat. 25.31 S - 30.46 E; 4.2.1986 E-Y:2414 under fungous logs leg. Endrödy-Younga.", "S.Afr.;Mpumalanga 10km E Kaapsehoop 25.36 S - 30.43 E; 4-6.1.2014: E-Y:3943 sifting; indigenous forest leg. Ruth Müller.", "S.Afr.;Mpumalanga Sjonajona, Badplaas 24.44 S - 30.40 E; 11.11.2002; E-Y:3565 general collect. 1410m leg. TMSA staff (four specimens)", "S.Afr.,E.Transvaal Berlin;Karst plat. 25.31 S - 30.46 E; 8.12.1986 E-Y:2363 fungous Pinus logs leg. Endrödy-Younga."

Distribution

South Africa: Mpumalanga (Map 20).

4. *Phylacastus rhodesianus* Koch

Phylacastus rhodesianus Koch, 1954a: 287.– Kamiński 2016: 245; Lumen & Kamiński 2023: 15, 2024a: 8.

Diagnosis

In addition to its unique distribution – Zimbabwe, *Phylacastus rhodesianus* is one of two species with clearly defined tubercles of the elytra. The other species (*P. maskacymirowi*) is smaller (4–6 mm vs 6–8mm), has a more strongly narrowed mentum, differently structured aedeagus (smaller apical opening), and less puncate elytrae. *Phylacastus crypticoides* and *P. striolatus* are best identified by ruling out other species first (see *P. crypticoides* diagnosis for more details).

Material examined

Holotype, sex undetermined **TMNH** (Fig. T25): "Marandella Mashld XI.97 GKMarshall; Holotype No: 1877 Phylacastus rhodesianus KOCH; Phylacastus rhodesianus Koch DET.C.KOCH; rhodesianus Koch."

MNHN: "9.VI.1970 Vumba SUD RHODESIE Cl. Besnard leg. 8.VI.1970 Inyanga SUD RHODESIE Cl. Besnard leg (10 specimens)".

Distribution

Zimbabwe: Manicaland and Mashonaland East (Map 21).



Map 21. Distribution of *Phylacastus rhodesianus* Koch.

5. *Phylacastus striolatus* Fairmaire

Phylacastus striolatus Fairmaire, 1897: 117.– Koch 1954a: 287, 1954b: 2; Kamiński 2016: 245; Lumen & Kamiński 2023: 15, 2024a: 6.

Diagnosis

Closest to *P. crypticoides* and *P. rhodesianus*. While separable from *P. rhodesianus* geographically and by the sculpture of the elytra, other species (such as *P. makskacymirowi* and *P. ancoralium*) are best ruled out first for their stronger morphology (e.g., lack of tuberculation and ancorae in *P. ancoralium* and strong tuberculation and small size of *P. makskacymirowi*). For more information, see *P. crypticoides*.

Material examined

Lectotype, sex undetermined, designated by Lumen & Kamiński (2023) **MNHN** (Fig. T26): "Makapan (TR.) E. Simon 1893; Phylacastus striolatus ? Cafrar?". With an additional label on red paper: "Lectotype: Phylacastus striolatus Fairmaire". Paralectotype **MNHN**: single specimen with same data as lectotype.

MIZPAN: "Transvaal Soutpansberg Mphome Magd Knothe S (two specimens)".

Distribution

South Africa: Limpopo (Map 22).



Map 22. Distribution of *Phylacastus striolatus* Fairmaire.

D. *Schyzoschelus* lineage

Genera included (3)

Heteropsectropus Kaszab, *Muelleropsectropus* Lumen & Kamiński, *Schyzoschelus* Koch.

Key to genera of *Schyzoschelus* lineage after Lumen & Kamiński (2024b) (see Plate D for figures):

1. Epipleural base evenly narrowed beyond humeral angle (Fig. 1). Elytron with additional striae terminating before shoulder, resulting in 11 intervals posteriorly (Fig. 1). Ovipositor long (length of coxites 1–4 to paraprocts ratio <1:1) (Fig. 3). Bursa copulatrix with terminal "bulb" (Fig. 5) ..... ***Schyzoschelus***

— Epipleural base abruptly narrowed beyond the humeral angle (Fig. 2). Elytra without prematurely terminating striae–with ten intervals. Ovipositor short (length of coxites 1–4 to paraprocts ratio = 1) (Fig. 4). Bursa copulatrix without terminal "bulb" **2**

2. Prementum without median emargination (Fig. 6). Subapical sulcus on abdominal ventrite V present; ventrite not concave (Fig. 8). Female without furrow running along extreme apical edge of abdominal V, and without median notch. Bursa copulatrix without additional pouches ..... ***Heteropsectropus***

— Prementum with median emargination (Fig. 7). Subapical sulcus on abdominal ventrite V absent; ventrite slightly concave (Fig. 9). Female with furrow running along extreme apical edge of abdominal ventrite V, and with median notch (Fig. 9). Bursa copulatrix with two additional pouches on base (Fig. 10) ..... ***Muelleropsectropus***

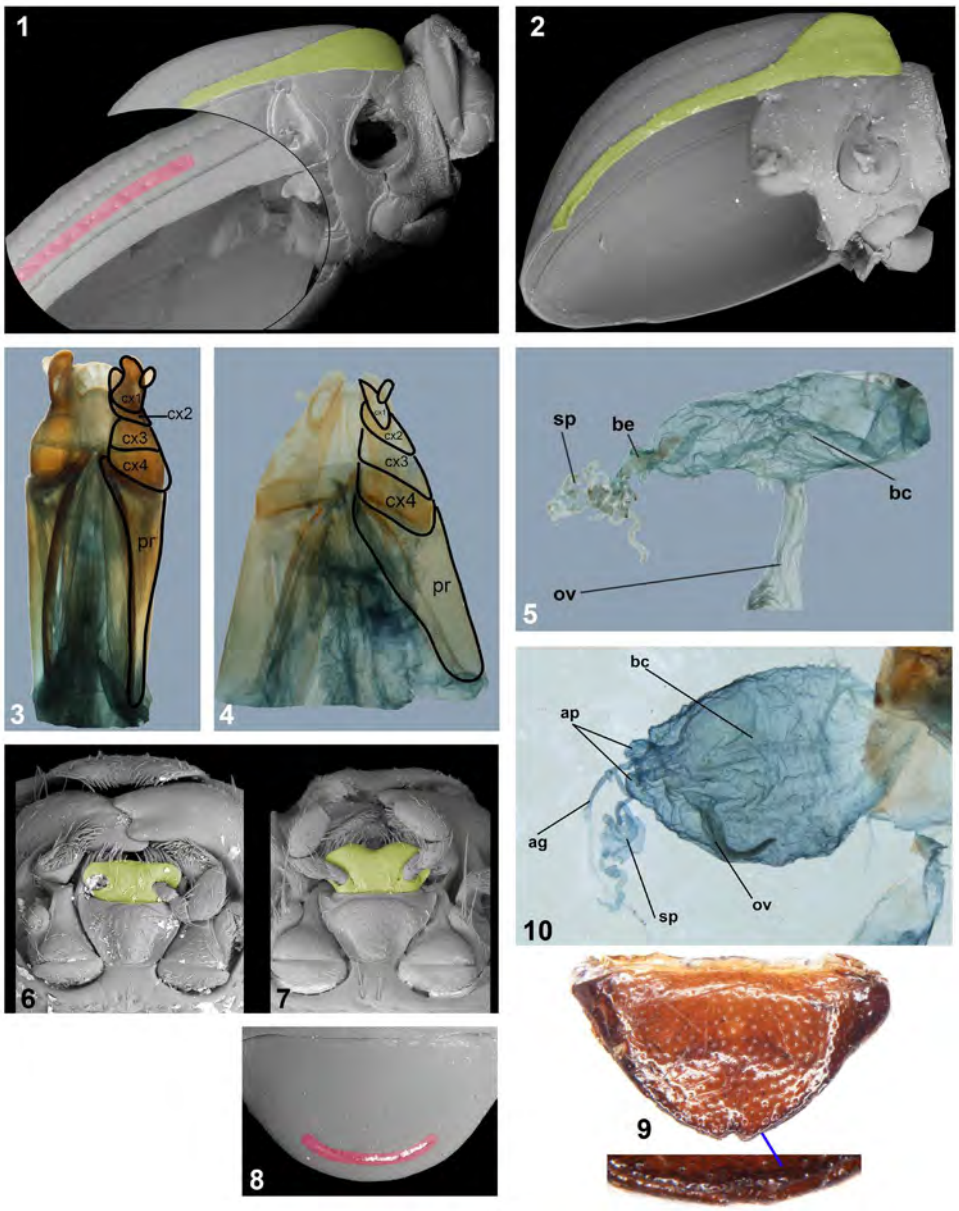


Plate D. *Schyzoschelus* lineage. Genera diagnostic features. **Anatomic features**: Epipleuron (1–2). Ovipositor (3–4). Bursa copulatrix (5, 10). Prementum (6–7). Abdominal ventrite V (8–9). **Taxa depicted**: *Shyzoschelus kaszabi* (1, 3, 5, 7). *Heteropsectropus difficilis* (2, 4, 6, 8). *Muelleropsectropus malaisei* (9–10). **Abbreviations**: ag = accessory gland, ap = additional pouch(es), bc = bursa copulatrix, be = bursa copulatrix "bulb", sp = spermatheca, ov = oviduct.

iii. Genus *Heteropsectropus* Kaszab

Heteropsectropus Kaszab 1941: 34.– Koch 1954b: 71, 1956: 27; Kamiński 2016: 237; Kamiński *et al*. 2019: 92, 2021: 152; Lumen & Kamiński 2024a: 12, 2024b: 127; Lumen *et al*. 2025: 2.

Type species. *Heteropsectropus aenescens* Kaszab; by original designation.

Diagnosis

Heteropsectropus is well-defined within the *Schyzoschelus* lineage of Eurynotina by the straight apical margin of the clypeus, straight/unexpanded foretibiae, rounded basal angles of the pronotum, abdominal ventrite V with a subapical sulcus, and parameres with a longitudinal groove running from the apex down to the base. The genus is further distinguished from other genera within the group by the following suite of characters: epipleura abruptly narrowing at the humeral region (gradually narrowing in *Schyzoschelus*), with a subapical sulcus on abdominal ventrite V in both males and females (present on extreme apex in females of *Schyzoschelus* and *Muelleropsectropus*), with a single large puncture bearing a strong seta above each eye (absent in *Schyzoschelus* except for *S. ladini*), flat or convex abdominal ventrite V (concave in male *Schyzoschelus* and *Muelleropsectropus*), female abdominal ventrite V without apical emargination or notch (present in *Schyzoschelus*, though species described based only on males require future confirmation, and in *Muelleropsectropus*), males with straight, unmodified tibiae—except for a patch of dense setae running down apex of hind tibiae (curved or strongly modified tibiae with setal patches in both *Schyzoschelus* and *Muelleropsectropus*), larger punctures bearing strong setae on abdominal ventrite V restricted largely to outer edge (throughout center in *Schyzoschelus*, and present on other abdominal ventrites in *Muelleropsectropus* and *Schyzoschelus*). *Heteropsectropus* males also have a relatively long penis (>half the length of the parameres) and a more pronounced curvature, or hook, at the end of the penis (also present in *Muelleropsectropus*, but at most weakly pronounced in *Schyzoschelus*–except for *S. aeneomicans*, which has a long penis and pronounced hook).

Species included (3)

H. aenescens Kaszab, *H. difficilis* Koch, *H. longantennatus* Koch.

Key to species of *Heteropsectropus* after Lumen & Kamiński (2024b) (see plate iii for figures):

1. Antennae short (at most just exceeding base of pronotum). Elytra striae not deeply impressed (Fig. 1) **2**

— Antennae long (far exceeding base of pronotum). Elytral striae more deeply impressed (Fig. 2) ..... ***Heteropsectropus longantennatus***

2. Rounder in cross-section. Lateral-most, ventrally reflected elytral intervals narrow (~2–3x epipleural width). Parameres upturned and widened apically, penis with strong apical hook (Fig. 4) ..... ***Heteropsectropus aenescens***

— Flatter in cross-section. Lateral-most, ventrally reflected elytral intervals wide (~3–5x epipleural width) (Fig. 3). Parameres flat and narrowed apically, penis with weak apical hook (Fig. 5) ..... ***Heteropsectropus difficilis***

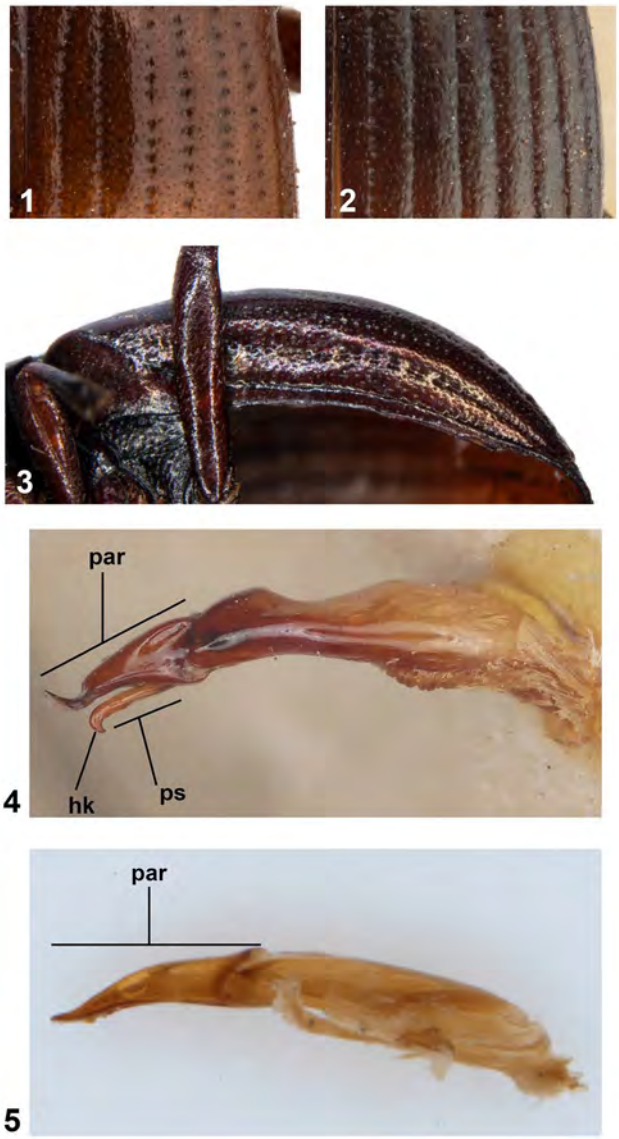


Plate iii. *Heteropsectropus* species diagnostic features. **Anatomic features**: Elytron (Dorsal: 1–2; Lateral: 3). Aedeagus (4–5). **Taxa depicted**: *Heteropsectropus aenescens* (4). *Heteropsectropus difficilis* (1, 3, 5). *Heteropsectropus longantennatus* (2). **Abbreviations**: hk = hook, par = parameres, ps = penis.

1. *Heteropsectropus aenescens* Kaszab

Heteropsectropus aenescens Kaszab, 1941: 34.– Koch 1954b: 73; Kamiński 2016: 237; Lumen & Kamiński 2024b: 130.

Diagnosis

Heteropsectropus aenescens has a distinct coppery shine. Though it is strongly pronounced in *H. aenescens*, other species may display a similar luster and therefore other characters may be useful to diagnose them. *Heteropsectropus aenescens* is separable from *H. longantennatus* by the degree of impression of the elytral striae, which are shallow to unimpressed. *Heteropsectropus aenescens* has more convex elytrae than its congeners, which have an overall flatter elytral disc. The lateral edges of the pronotum can also be used to distinguish *H. aenescens* (with numerous large, well-defined punctures bearing large setae; few such punctures and setae in other species). The lateral-most elytral intervals reflected ventrally are also narrower in *H. aenescens* (~2–3x width of epipleura) compared to *H. longantennatus* and *H. difficilis* (~>3x width of epipleura). Other species are also generally wider (3–4.25mm *H. aenescens*; 3.25mm–4.75mm *H. difficilis*; 3–4.5mm *H. longantennatus*). The humeri of the elytra in the dorsal view are more rounded in *H. aenescens* compared to the other species (which are generally broader or square-shaped). The aedeagus is strongly sclerotized, with apically upturned parameres and a pronounced hook on the apex of the penis (Fig 6B) (less-sclerotized, absent, and weak respectively in *H. difficilis* (Fig. 6D); parameres less strongly upturned and hook on the apex of penis less pronounced in *H. longantennatus*). *Heteropsectropus aenescens* is also restricted to the South East region of South Africa (Eastern Cape and KwaZulu-Natal), whereas *H. longantennatus* and *H. difficilis* are distributed more northward.



Map 23. Distribution of *Heteropsectropus aenescens* Kaszab.

Material examined

The holotype (described by Kaszab in 1941) should be in **NHMB** with label data "Griqualand. Matatiela". While the type specimen of this species was not directly studied, our diagnoses, discussion, and concepts are based upon both Kaszab's (1941) and Koch's (1954b) publications. Koch was able to directly compare his specimens with Kaszab's type; and we in turn were able to examine Koch's specimens.

NHMUK: "Umtata Caffraria C. Greaves, Heteropsectropus aenescens Kaszab C. Koch det. 1956, Brit. Mus. 1951-55, with yellow circle PARATYPE label and white QR-code label with code NHMUK014663109". **TMNH**: "Umtata Caffraria C. Greaves Menederes det. Peringuey (three specimens)", "15m SE Barkley east. C.P. II.67. L.SCHULZE", "SA KZN Kamberg 13 29.37331°S 29.62798°E 1814m Grassland Ground Search 08-Nov-2005 III-UKZN (two specimens, bearing two different codes: MDTP 55645 and MDTP 1100)". **MIZPAN**: "TB#26351 -29.65, 29.44, Heteropsectropus".

Distribution

South Africa: Eastern Cape, KwaZulu-Natal (Map 23).

2. *Heteropsectropus difficilis* Koch

Heteropsectropus difficilis Koch, 1954b: 76.– Kamiński 2016: 237; Kamiński & Lumen 2024b: 131; Lumen *et al*. 2025: 8.

= *Heteropsectropus amaroides* Koch, 1954b: 75.– Kamiński 2016: 237; Kamiński & Lumen 2024a: 3, 2024b: 131 (syn.).

= *Heteropsectropus natalensis* Koch, 1954b: 75.– Kamiński 2016: 238; Kamiński & Lumen 2024b: 131 (syn.).

= *Heteropsectropus transvaalensis* Koch, 1954b: 74.– Kamiński 2016: 238; Kamiński & Lumen 2024b: 131 (syn.).

Diagnosis

Heteropsectropus difficilis is the most widespread species of the genus–with its range extending from the eastern coast of KwaZulu-Natal to Johannesburg. Formerly represented under four species names, *H. difficilis* is relatively variable compared to its congeners. This species is most easily separable *via* elimination of the other two. Otherwise, *H. difficilis* is sharply separable by aedeagal morphology (less sclerotized and without upturned paramere apex and with weak apical hook of the penis; compared with the other species with more sclerotized aedeagi and more pronounced hooks and upturned parameres). Superficially, *H. difficilis* more resembles *H. longantennatus* in body shape (more squared elytral humeri, less metallic than *H. aenescens*, wider reflected elytral intervals). However, *H. difficilis* differs from *H. longantennatus* by the length of the antennae (short—at most only slightly surpassing base of pronotum; rather than long—distinctly surpassing the base of the pronotum).

Material examined

Heteropsectropus difficilis: **Holotype**, female **TMNH** (Fig. T28): "Christiana Transvaal Dr. Brauns. Holotype No: 1782 Heteropsectropus difficilis KOCH difficilis Koch".

Heteropsectropus amaroides: **Paratype**, female **TMNH** (Fig. T27): "'N' Kandhla Forest Zululand R.F. Lawrence Jan 1937. Paratype No: 1781 Heteropsectropus amaroides KOCH". **NHMUK**: "Malvern Natal 7.97 8477? Marshall Coll. 1911–263. Heteropsectropus amaroides C.Koch Det, Koch 1954" (also with yellow circle "Paratype" label and QR code label with code NHMUK014663128.).

Heteropsectropus natalensis: **Holotype**, female **TMNH** (Fig. T31): "Karkloof Natal 2.97 Marshall Coll. 1911–263. Heteropsectropus natalensis C. Koch det., 1954" (Also with red

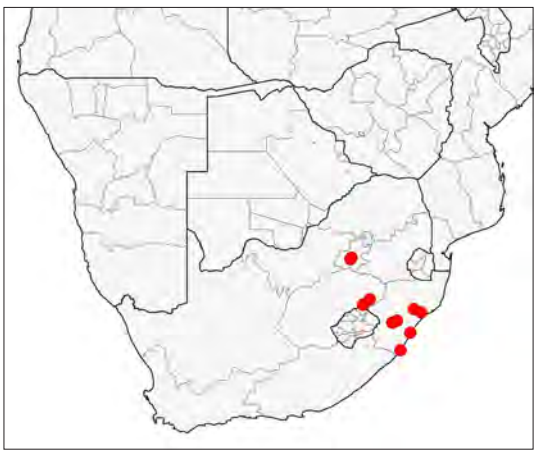
circle "Type" label, Red square "HOLOTYPE natalensis Koch" label, and QR code label with code NHMUK014663129.) **Paratype**, male **TMNH**: same data as holotype with additional labels (Paratype No: 1779 Heteropsectropus natalensis KOCH).

Heteropsectropus transvaalensis: **Holotype**, female **TMNH** (Fig. T32): "Highlands J'burg T Sept 1901 under stones Heteropsectropus transvaalensis Koch C. Koch det., 195 transvaalensis Koch".

SANC: "Johannesberg Mondeor TVL 27-9-1959 C. H. Draper (two specimens; one with year 1960)". "Natal RT Lawrence Feb 1938", "Nr. Balgowan Natal Jan 1953 D.W. Rorke". **TMNH**: "S.Afr.,Ntl-Drakensb Cathedral Peak for. 28.57S - 29.12 E 15.3.1976; E-Y: 1088 from under stones leg. Endrödy-Younga", "Golden Gate Nat. Park I.1968. R.Jones Heteropsectropus sp. FROM INSECTARIUM NO. 807 (four adult specimens, 2 pupae, several larvae)", "Golden Gate Southern O.F.S. 1.3.67. L.SCHULZE.".

Distribution

South Africa: Free State, Gauteng, KwaZulu-Natal (Map 24).



Map 24. Distribution of *Heteropsectropus difficilis* Koch.

3. *Heteropsectropus longantennatus* Koch

Heteropsectropus longantennatus Koch, 1954b: 76.– Lumen & Kamiński 2024b: 134; Lumen *et al*. 2025: 14.

= *Heteropsectropus montisdraconis* Koch, 1954b: 77.– Lumen & Kamiński 2024b: 134 (syn.).

Diagnosis

Heteropsectropus longantennatus is sharply separable from all other species by its geographic location (largely restricted to the Drakensberg mountain range and extending northward along the borders of KwaZulu-Natal and Free State), antennae (long—extending distinctly beyond pronotum base; short—barely exceeding the pronotum base in other species), and elytra (with strongly impressed striae; weakly impressed in other species).

Material examined

Heteropsectropus longantennatus: **Holotype**, male **TMNH** (Fig. T29): "Volksrust 1.1922. A.Rob. & G.V. Dam. Holotype No: 1783 heteropsectropus longantennatus KOCH Heteropsectropus longantennatus Koch C. Koch Det., 195 Longantennatus Koch".

Heteropsectropus montisdraconis: **Holotype**, male **NHMUK** (Fig. T30): S.Africa R.E.Turner. Brit.Mus.1927–25. Natal: Van Beenen Drakensberg Dec.1926 HoloTYPE montis-draconis Koch unique holotype!! Heteropsectropus montis-draconis Koch C. Koch Det., 195" (Also bearing bearing white QR label with code NHMUK 014663130 and red, circled "Type" label).

MIZPAN: "-28.68741, 28.947903, 18/1/18, leg. MJ. Kamiński" (also bearing blue Tenebrionidbase QR label with ID# 26352).

Distribution

South Africa: KwaZulu-Natal, Mpumalanga (Map 25).



Map 25. Distribution of *Heteropsectropus longantennatus* Koch.

iv. Genus *Muelleropsectropus* Lumen & Kamiński

Muelleropsectropus Lumen & Kamiński 2024b: 135.– Lumen *et al*. 2025: 2.

Type species. *Schyzoschelus malaisei* Koch; by original designation.

Diagnosis

Muelleropsectropus is well-defined within the *Schyzoschelus* lineage by the straight apical margin of the clypeus, straight/unexpanded foretibiae, rounded basal angles of the pronotum, abdominal ventrite V with a sulcus, and parameres with a longitudinal groove running from the apex down to the base. The genus is further distinguished from other genera within the *Schyzoschelus* lineage by the following suite of characters: epipleura abruptly narrowing at the humeral region (gradually narrowing in *Schyzoschelus*), sulcus present on extreme apex in females (*Heteropsectropus* with a subapical sulcus on abdominal ventrite V in both males and females), with a single large puncture bearing a strong seta above each eye (absent in *Schyzoschelus*, except for *S. ladini*), flat or concave abdominal ventrite V (flat to convex in Heteropsectropus), female abdominal ventrite V with apical emargination or notch (absent in some *Schyzoschelus* and in *Heteropsectropus*), males with curved or strongly modified tibiae with setal patches (straight, unmodified tibiae—except for a patch of dense setae running down apex of hind tibiae in *Heteropsectropus*), larger punctures bearing strong setae on abdominal ventrites with those on ventrite V restricted largely to outer edge (throughout center in *Schyzoschelus*, and absent on other abdominal ventrites in *Heteropsectropus*). Aedeagus similar to *Heteropsectropus* (long penis with sclerotized hook at apex).

Species included (Monotypic)

M. malaisei (Koch).

1. *Muelleropsectropus malaisei* (Koch)

Schyzoschelus malaisei Koch, 1954b: 78.– Kamiński 2016: 247; Lumen & Kamiński 2024b: 135; Lumen *et al*. 2025: 10.

Diagnosis

See diagnosis of *Muelleropsectropus*.

Material examined

Holotype, female **TMNH** (Fig. T33): "Marieps Mnt. IV: 1932 G. van Son. HOLOTYPE No: 1784 Schyzoschelus malaisei KOCH Malisei Koch".

TMNH: "S.Afr.,E.Transvaal Berlin; Karst plat. 25.31S - 30.46E 4.2.1987; E-Y:2414 under fungous logs leg. Endrody-Younga", "S.Afr;E.Tvl. Uitsoek high alt.grassveld 25.15 S - 30.34 E 12.12.1986; E-Y:2381 grassnetting leg. Endrody-Younga", "Transvaal Mt. Anderson 29.1.1955 I.Rudebeck (two specimens)", "E.Y.Western Coll. B.M. 1924–176 Transvaal".

Distribution

South Africa: Mpumalanga (Map 26).



Map 26. Distribution of *Muelleropsectropus malaisei* (Koch).

v. Genus *Schyzoschelus* Koch

Schyzoschelus Koch, 1954b: 72.– Koch 1956: 27; Iwan 2001: 352; Kamiński 2016: 264; Kamiński *et al*. 2019: 92, 2021: 152; Lumen & Kamiński 2024a: 12, 2024b: 136; Lumen *et al*. 2025: 2.

Type species: *Schyzoschelus kaszabi* Koch; by original designation.

Diagnosis

Schyzoschelus has a straight clypeal apical margin, rounded pronotal margins, unexpanded tibiae, and longitudinal groove of the aedeagus of the other genera within the lineage. Setting the genus apart from *Heteropsectropus* and *Muelleropsectropus* is the particular morphology of the abdominal sterna. In particular, many species (all except *S. aeneomicans*, *S. dumosicola*, and *S. jenkinsae*) bear stridulatory structures on the abdominal ventrites I and II in males. Additionally, *Schyzoschelus* is well-defined within Eurynotina by the strong modifications of the foretibiae (more exaggerated in males): slightly curved with hollowed-out and/or toothed margins, and various additional accouterments such as granulations or ridges. The aedeagus of *Schyzoschelus* is also different from other eurynotines in that it is almost entirely closed ventrally. Additionally, abdominal ventrite V in males of many species are strongly concave, with many strong setae. The general habitus of *Schyzoschelus* is also diagnostic, as many species are more elongate (body length much greater than width, similar only to some *Menederes*) rather than squat or rounded as is the case in the majority of other genera in Eurynotina.

Species included (14)

S. aeneomicans Koch, *S. aetheculus* **sp. nov.**, *S. africanus* (Kaszab), *S. bispinosus* (Kaszab), *S. braunsi* Koch, *S. capensis* (Kaszab), *S. dumosicola* Koch, *S. jenkinsae* Koch, *S. kaszabi* Koch, *S. ladini* Koch, *S. karrooensis* Koch, *S. simplicipes* Koch, *S. sympatrius* Koch, *S. validus* (Fairmaire).

Key to species of male *Schyzoschelus* after Koch (1954b) (see plate v part 1 and 2 for figures):

The classification of the genus is largely based on male features, impeding identification of female specimens. Due to the relative rarity of the genus in collections and scarcity of specimens, the key provided below is largely based upon males. Until more material is available it will remain difficult to delineate some species reliably (e.g., the *capensis* group)–especially without males.

1. Tip of elytra with projecting pair of teeth (Fig. 1) ..... ***Schyzoschelus bispinosus***

— Tip of elytra broadly rounded or almost truncated **2**

2. Anterior edge of first and second abdominal ventrites with transverse rugose areas (Fig. 2). Underside of front tibiae hollowed, usually with a tooth-like extension (Fig. 3). Pronotum always transverse, broader than long **3**

— First and second abdominal ventrites without rugosities, evenly shiny, covered with punctures. Front tibiae relatively simple, not hollowed, and without tooth-like extensions (Fig. 4). Pronotum either narrow, rectangular, and then only little wider than head (Fig. 5), or transverse (Fig. 6) **12**
(*dumosicola* species-group: *Schyzoschelus aeneomicans, S. dumosicola, S. jenkinsae*)

3. Lower edge of the outer surface of the hind femora emarginate, apically forming more or less sharply rectangular projection (Figs 7–8). Body usually smaller (most 7-10.25 mm long, single larger species up to 12mm long) ..... **4 (*capensis* species-group: *Schyzoschelus aetheculus* sp. nov., *S. africanus*, *S. braunsi*, *S. capensis*, *S. karrooensis*, *S. simplicipes*, *S. sympatrius*)**

— Hind femorae simple, the lower edge of the outer surface straight up to the tip (Fig. 9). Body usually larger (8.25-12 mm long) ..... **10 (*kaszabi* species-group: *Schyzoschelus kaszabi*, *S. ladini*, *S. validus*)**

4. Forelegs strongly chamfered and sculptured on inner margins (Fig. 10 & 11). Large (~12mm long) ..... ***Schyzoschelus aetheculus* sp. nov.**

— Forelegs at most weakly chamfered on inner margin. Smaller (7–10.25 mm long) **5**

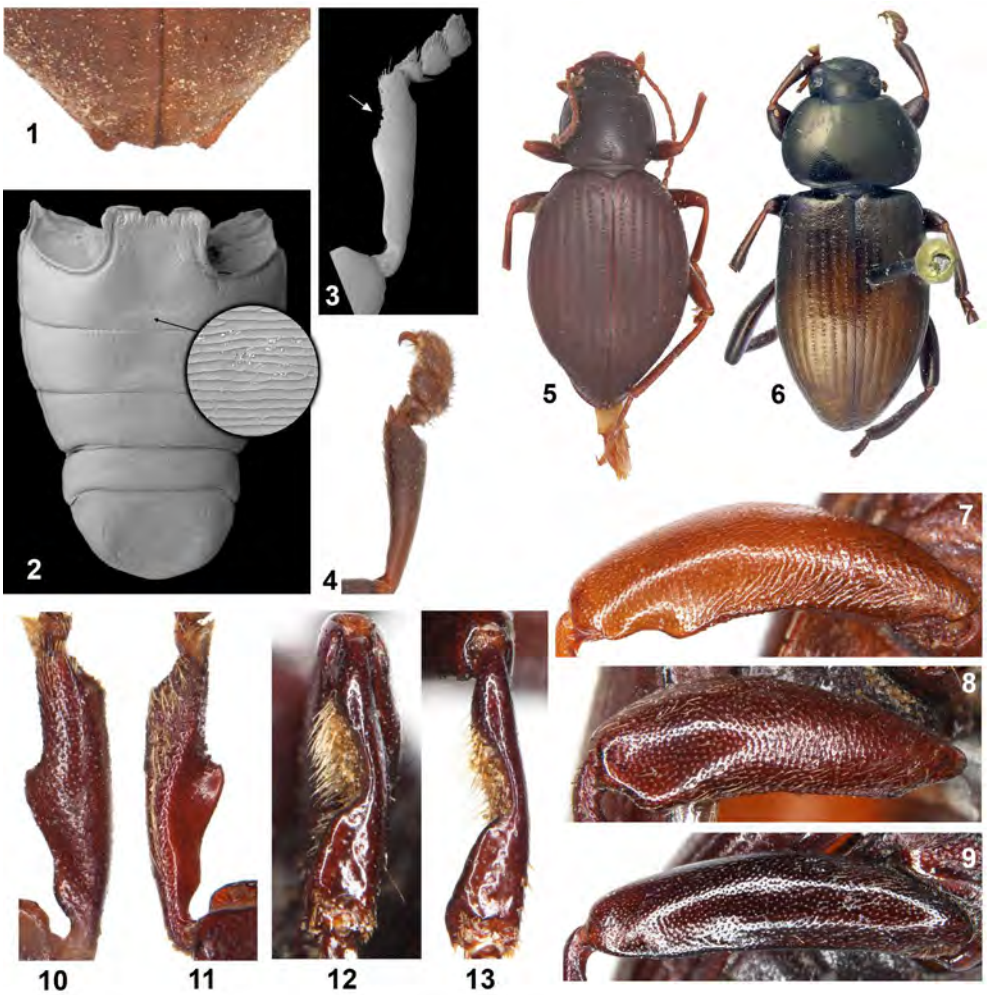


Plate v. part 1. *Schyzoschelus* species diagnostic features: **Anatomic features**: Elytra (1). Abdominal ventrites (2). Foreleg (Tibia: 3–4, 10–11). Midleg (Tibia: 12–13). Hindleg (Femur: 7–9). **Taxa depicted**: *Schyzoschelus aeneomicans* (4, 6). *Schyzoschelus aetheculus* (8, 10–11). *Schyzoschelus africanus* (7). *Schyzoschelus bispinosus* (1). *Schyzoschelus jenkinsae* (5). *Schyzoschelus karrooensis* (12–13). *Schyzoschelus kaszabi* (2–4). *Schyzoschelus ladini* (9).

5. Middle tibia strongly narrowed and emarginated medially, hollowed, and covered with dense setation; underside without post basal extension; lower contours straight (in lateral view) (Figs 12–13) ..... ***Schyzoschelus karrooensis***

— Middle tibia not strongly narrowed and emarginated medially; underside with strong post-basal extension, visible as rounded prominence of the lower contours of the lateral surfaces (in lateral view) **6**

6. Underside of middle tibiae with median tooth-like extension ..... ***Schyzoschelus capensis***

— Underside of middle tibiae without median tooth-like extension, often with rounded, more or less strong postbasal extension anterior to the middle **7**

7. Lower edge of the outer surface of the hind femora with strong, postmedian extension/curve (Fig. 7) ..... ***Schyzoschelus africanus***

— Lower edge of the outer surface of the hind femora without additional curve (Fig. 9) ... **8**

8. Outer lateral surface of the front tibiae not raised covering underside projection. Underside of middle tibiae simple, without extensions ..... ***Schyzoschelus simplicipes***

— Outer lateral surface of the front tibiae strongly raised basally exposing underside projection (Figs 14–15). Underside of middle tibiae with post basal or an apical extension **9**

9. Underside projection of front tibiae sharp (angular) (Fig. 15) ..... ***Schyzoschelus braunsi***

— Underside projection of front tibiae blunt (Fig. 14) ..... ***Schyzoschelus sympatrius***

10. Hind tibiae strongly chamfered basally, strongly widened, often with strongly keeled edge (Fig. 16). Middle tibiae without dense brush-like setae ..... ***Schyzoschelus validus***

— Hind tibiae weakly chamfered, less strongly widened, with weak to absent keel on edge (Fig. 17). Middle tibiae with dense brush-like setae (Fig. 18) **11**

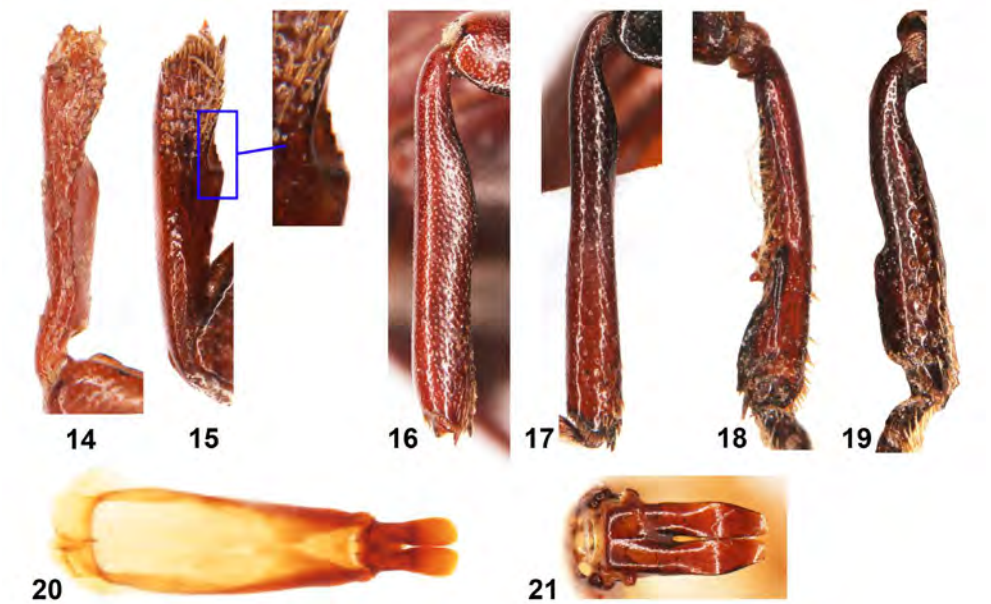


Plate v. part 2. *Schyzoschelus* species diagnostic features: **Anatomic features**: Foreleg (Tibia: 14–15). Midleg (Tibia: 18–19). Hindleg (Tibia: 16–17). Aedeagus (20–21). **Taxa depicted**: *Schyzoschelus braunsi* (15). *Schyzoschelus kaszabi* (17–20). *Schyzoschelus ladini* (21). *Schyzoschelus sympatrius* (14). *Schyzoschelus validus* (16).

11. Middle tibiae strongly constricted medially, strongly widened apically (Fig. 19). Parameres truncate-rounded and slightly divergent apically (Fig. 20) ... ***Schyzoschelus kaszabi***

— Middle tibiae weakly constricted medially, less-strongly widened apically. Parameres more parallel and pointed apically (Fig. 21) ..... ***Schyzoschelus ladini***

12. Body slender, habitually different from all other Eurynotina, and reminiscent of Tentyriini Eschscholtz. Pronotum narrow, only slightly wider than long, rectangular, only little wider than head and about as wide as elytra; dull, very trongly punctured; without coarser, bristle-bearing punctures; basal angles obtuse. Antennae elongate, laid back far exceeding the base of the pronotum. Middle and hind tibiae simple (Fig. 5) ..... ***Schyzoschelus jenkinsae***

— Body broad, habitually consistent with other *Schyzoschelus*. Pronotum broad, transverse, discoid, much (up to two-thirds) wider than head, and not much narrower than elytra; shiny, less sparsely punctured; laterally with coarser, bristle-bearing punctures; basal angles broadly rounded. Antenne moderately long, laid back, barely exceeding pronotal base. Middle tibiae widened internally or emarginated and setose on the distal two-thirds; hind tibiae with densely setose inner surface **13**

13. Dorsal side of body with metallic luster. Middle tibiae gradually widened internally from base to apex. Hind tibiae without distinct post basal widening, shallowly flared internally (see Fig. 6) ..... ***Schyzoschelus aeneomicans***

— Dorsal side of body without metallic luster. Middle tibiae with post-basal expansion, curved between middle apex, and distinctly emarginated. Hind tibiae inside with clear post-basal widening, deeply flared internally (See Figs T39-40) ..... ***Schyzoschelus dumosicola***

1. *Schyzoschelus aeneomicans* Koch

Schyzoschelus aeneomicans Koch, 1954b: 90.– Kamiński 2016: 246; Lumen & Kamiński 2024b: 129; Lumen *et al*. 2025: 2.

Diagnosis

Member of the *dumosicola* species-group. This species is reminiscent of *Heteropsectropus*, e.g., setation (pronotal sides dorsally with large, widely spaced setae and punctures situated on lateral edges), coloration (presence of aeneous and/or cupreous luster), and aedeagus (long penis and pronounced hook vs hook weakly pronounced in other *Schyzoschelus*). Upon closer examination during this revision, other *Schyzoschelus* species possess similar pronotal setation (e.g., *S. dumosicola*). The taxonomic position of *S. aeneomicans* should be tested with molecular data; unfortunately the holotype is the only known specimen. To date, this species fits the definition of *Schyzoschelus* as proposed by Koch (1954b) and Lumen & Kamiński (2024b).

Material examined

Holotype, male **TMNH** (Fig. T34): "Nutwoods Arminel-Alice C.P.-Walker leg. Holotype No: 1818 Schyzoschelusd aeneomicans KOCH Paracharactes aeneomicans Koch C. Koch det.,195 aeneomicans Koch".

Distribution

South Africa: Eastern Cape (Map 27).



Map 27. Distribution of *Schyzoschelus aeneomicans* Koch.

2. *Schyzoschelus aetheculus* sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:B49A101E-EEFF-4EFE-B169-4CC1CD0E3A03

Diagnosis

Member of the *capensis* species-group. This species is unique within the group for its size, which is reminiscent of the *kaszabi*-group (~12mm long). However, in addition to the abdominal striae characteristic of both groups, this species possesses the hind femoral emar-

gination of the apex typical of the capensis group. Additionally, *S. aetheculus* has uniquely strongly chamfered foretibiae. As of this revision and description, this species is represented by only three male specimens with vague locality information (e.g., Cap. Bon Esperance).

Description

Length 12mm, width 5mm. **Head**: finely punctate, punctures widely spaced, separated by ≥1 feature diameter. Mentum with prominent median portion and exposed wings. Submentum pentagonal. Eye slightly impressed by genal canthus, well-developed. **Prothorax**: Pronotum finely punctate, punctures separated by ~1 feature diameter. Apical, lateral, and basal margination of pronotal disc complete. Hypomeron almost impunctate, lightly sculptured/wrinkled. Prosternal process rounded in lateral view. **Pterothorax**: Elytron without tubercles on disc. With wrinkling to weak tubercles on apical decline. Rows puncto-striate, with punctures separated by ≤1 feature diameters. Intervals very finely punctate. Elytral interval X terminates before hind coxae and elytra base, with division giving rise to eleventh interval. Epipleuron narrower than width of elytral interval 10. Elytral intervals not obscured by epipleuron in ventral view. **Abdomen**: Punctate with larger setigerous punctures interspersed. Males with transverse rugosities on apex of abdominal ventrites I & II, and central concavity on ventrite V. **Legs**: Male hind femora with slight apical emargination, hind tibiae slightly chamfered and expanded. Male pro/meso tarsi enlarged, with ventral, tomentose pads. **Male terminalia**: Basal part longer than parameres. Parameres broadening towards apex, truncate and concave/curved in lateral view.

Etymology

From the Greek *aeth* meaning unusual with the latin diminutive suffix *culus*; in reference to the small differences (size and chamfered forelegs) separating this taxon from the rest of the *capensis*-species group.

Material examined

Holotype, male **ZMHB** (Fig. T35): "Dr. Smith S. Afr. 44-6, and red label: S. aetheculus Holotype". **Paratypes**, male **ZMHB**: "c femoralis c.b.sp. tuch?, and yellow label: S. aetheculus Paratype", "c femoralis x Reich c.b.sp, and yellow label: S. aetheculus Paratype".

Distribution

South Africa; further specificity impossible based on label data.

3. *Schyzoschelus africanus* (Kaszab)

Psectropus africanus Kaszab, 1941: 36.

Schyzoschelus africanus (Kaszab, 1941).– Koch 1954b: 82; Kamiński 2016: 246; Lumen & Kamiński 2024b: 136; Lumen *et al*. 2025: 7.

Diagnosis

Member of the *capensis* species-group. This species differs from all other *Schyzoschelus* by the strong postmedian extension of the lower edge of the hind femora, giving the impression of a double-extension of the apical margin.

Material examined

According to Kaszab (1941), three syntypes were deposited in the private collection of Hans Gebien and bear the following labels: "Capland" (single male specimen), and two female spec-

imens labeled "Caffraria" and "Sterkstroom" respectively. For this study we were able to examine the Sterkstroom specimen; however, we are not designating it as a lectotype as the most diagnostic characters are restricted to males.

Syntype, female **NHMUK** (Fig. T36): "Cap Sterkstroom Typus Psectropus africanis m. 1938 Kaszab Type Brit. Mus. 1947-241 Psectropus 2partitus Sol. Psectropus bipartitus Sol TYPUS Psectropus africanus Exam. C. Koch".

TMNH: "Willowmore Capland Dr. Brauns (four specimens) and another specimen with the same data and two additional labels: "S.A.M. Psectropus africanus Kasz. C.Koch det.,1957".

Distribution

South Africa: Eastern Cape (Map 28).



Map 28. Distribution of *Schyzoschelus africanus* (Kaszab).

4. *Schyzoschelus bispinosus* (Kaszab)

Psectropus bispinosus Kaszab, 1941: 38.

Schyzoschelus bispinosus (Kaszab, 1941).– Koch 1954b: 77; Kamiński 2016: 246; Lumen & Kamiński 2024b: 136.

Diagnosis

Easily diagnosable from other *Schyzoschelus* due to its elytra with strong apical projecting teeth. As this species is known only from female specimens, its affiliation towards any of the recognised species groups of *Schyzoschelus* cannot currently be determined.

Material examined

Holotype, female **TMNH** (Fig. T37): "CAPE col. Dunbrody. J. A. O'niel 1901 bispinosus (Kaszab)".

Distribution

South Africa: Eastern Cape (Map 29).



Map 29. Distribution of *Schyzoschelus bispinosus* (Kaszab).

5. *Schyzoschelus braunsi* Koch

Schyzoschelus braunsi Koch, 1954b: 83.– Kamiński 2016: 246; Lumen & Kamiński 2024b: 136.

Diagnosis

Member of the *capensis* species-group. All representatives of this group possess an emargination at the apex of the hind tibiae of males. While describing this species Koch (1954b) mentioned its close affiliation with *S. africanus*. Both species coexist in the surroundings of Willowmore (South Africa). Contrary to *S. africanus*, *S. braunsi* lacks the postmedian extension of the lower edge of the hind femora. The species concepts within the *capensis*-group are based on a limited number of specimens in a small geographical area, which does not preclude the possibility that some morphological definitions represent interspecific diversity. The following species of *capensis* species-group are especially taxonomically challenging and all are known from the surroundings of Willowmore: *Schyzoschelus africanus*, *S. braunsi*, *S. simplicipes*, *S. sympatrius*. New material and/or molecular studies will be necessary to more thoroughly test the concepts of the members of this group.



Map 30. Distribution of *Schyzoschelus braunsi* Koch.

Material examined

Holotype, male **TMNH** (Fig. T38): "Willowmore Capland Dr. Brauns. Holotype No: 1786 Schyzoschelus braunsi KOCH Braunsi Koch".

TMNH: "Triangle 83, 2:20", two specimens.

Distribution

South Africa: Eastern Cape (Map 30).

6. *Schyzoschelus capensis* (Kaszab)

Psectropus capensis Kaszab, 1941: 37.

Schyoschelus capensis (Kaszab, 1941).– Koch, 1954b: 80; Kamiński 2016: 246; Lumen & Kamiński 2024b: 136.

Diagnosis

Member of the *capensis* species-group (see *S. braunsi*); distinguished by the prominent tooth on the midtibiae.

Material examined

The type specimen was not studied. Though the original description states the type is deposited at **NHMB** (Kaszab 1941), an investigation of their type material did not uncover any record of the type specimen. An additional search of **HNHM** was undertaken as some of Kaszab's material is also deposited there (see Merkl *et al*. 2015); however, we were still unable to locate the type specimen.

Despite not locating the holotype, we elected not to designate a neotype, as we were only able to examine a single specimen, which was damaged and difficult to identify with certainty. Further, two specimens identified by Koch (1954b) examined here (locality "Triangle") actually belonged to *S. braunsi*; therefore, it is likely additional specimens from this area identified by Koch may not be *S. capensis*. According to the original description, the holotype should bear the following label: "Capland. Touns R.".

MNHN: "MUSEUM PARIS Afriquer austr. (L. Peringuey) Coll. L. FAIREMAIRE 1906".

Distribution

South Africa; further specificity impossible based on label data.

7. *Schyzoschelus dumosicola* Koch

Schyzoschelus dumosicola Koch, 1954b: 91.– Kamiński 2016: 247; Lumen & Kamiński 2024b: 137.

= *Schyzoschelus dumosicola* var. *diversipenis* Koch, 1954b: 91.– Kamiński 2016: 246; Lumen & Kamiński 2024b: 137 (syn.).

Diagnosis

Member of the *dumosicola* species-group. While the general morphology of the species within the *dumosicola* group is overall consistent with *Schyzoschelus* (e.g., the *capensis* and *kaszabi* groups), they lack the striate abdominal ventrites in males. Species in the *dumosicola*

group are separable from each other based on their individual irregular morphology (see *S. aeneomicans* and *S. jenkinsae*).

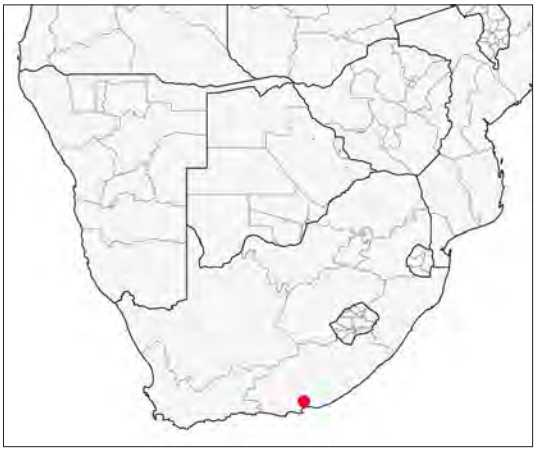
Material examined

Schyzoschelus dumosicola dumosicola: **Holotype**, male **TMNH** (Fig. T40): "Algoa Bay Capland Dr. Brauns 30.8.96, Dumosicola Koch, HOLOTYPE No: 1819 Schyzoschelus dumosicola KOCH.". **Paratype**, **NHRS**: same data as holotype.

Schyzoschelus dumosicola diversipenis: **Holotype**, male **TMNH** (Fig. T39): "Algoa Bay Capland. Dr. Brauns. V.diversipenis HT Koch.". **Paratype**, **TMNH**: "Addo Bush, Juli 1919, leg. J. Drury".

Distribution

South Africa: Eastern Cape (Map 31).



Map 31. Distribution of *Schyzoschelus dumosicola* Koch.

8. *Schyzoschelus jenkinsae* Koch

Schyzoschelus jenkinsae Koch, 1954b: 88.– Kamiński 2016: 247; Lumen & Kamiński 2024b: 136.

Diagnosis

Member of the *dumosicola* species-group. Easily diagnosable by its body shape, which is habitually different from all other Eurynotini, and reminiscent of Tentyriini Eschscholtz, 1831. In particular, the pronotum is especially narrow and elongated.

Material examined

Holotype, male **TMNH** (Fig. T41): "Zwartberg C.P. nr. Avondrust Vii.1950.E.A.Pienaar Jenkinsae Koch HOLOTYPE No: 1815 Schyzoschelus jenkinsae KOCH". **Paratypes**, male and female **NHMB**: "96/67 Paratype Schyzoschelus jenkinsae KOCH", "Matjesfontein, leg. R. Lightfoot".

Distribution

South Africa: Western Cape (Map 32).



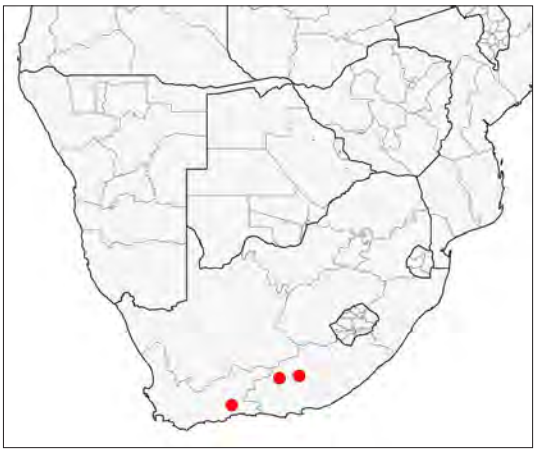
Map 32. Distribution of *Schyzoschelus jenkinsae* Koch.

9. *Schyzoschelus karrooensis* Koch

Schyzoschelus karrooensis Koch, 1954b: 79.– Kamiński 2016: 247; Lumen & Kamiński 2024b: 136.

Diagnosis

Member of the *capensis* species-group (see *S. braunsi*). When diagnosing this species Koch (1954b) compared it to *S. kaszabi* (member of the *kaszabi* species group) as it shares a similar structure of male midtibiae (underside with a tooth-like extension). However, unlike *S. kaszabi*, the midtibial tooth of *S. karrooensis* is located near the tip of the tibia. Separable from *S. capensis* and *S. africanus* by the middle tibiae: strongly narrowed and emarginated medially, hollowed, and covered with dense setation; underside without post basal extension and with lower contours straight in lateral view (conversely *S. africanus* and *S. capensis* without strongly narrowed middle tibiae and with strong postbasal extensions visible as rounded prominence of lower contours of lateral surface – in lateral view).



Map 33. Distribution of *Schyzoschelus karrooensis* Koch.

Material examined

While the holotype was not examined, it should be preserved in **IMSA** with matching collection data as the examined paratype (Oudtshoorn) (Koch 1954b).

Paratype, female **TMNH** (Fig. T42): "Oudtshoorn 7 06 PARATYPE No: 1785 Schyzoschelus Karooensis KOCH Paratypus Schyzoschelus Karrooensis C. Koch sp.n.".

SANC: "Mt Zebra nl. Park Cape Prov.R.S.A. 13/14.Viii.89 G.Minet Recolt", (four specimens).

Distribution

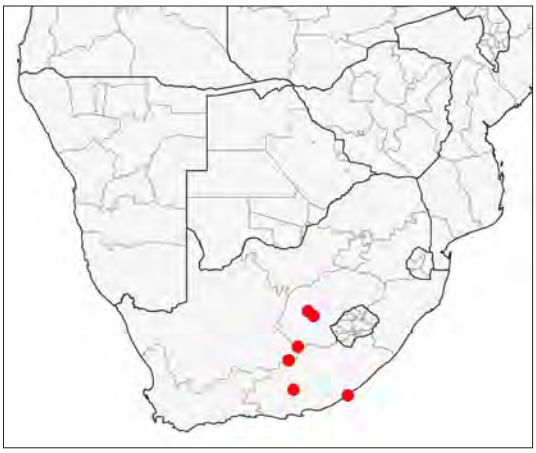
South Africa: Eastern Cape, Western Cape (Map 33).

10. *Schyzoschelus kaszabi* Koch

Schyzoschelus kaszabi Koch, 1954b: 85.– Kamiński 2016: 246; Lumen & Kamiński 2024b: 136; Lumen *et al*. 2025: 8.

Diagnosis

Member of the *kaszabi* species-group. Most resembles *S. ladini* from which it is separable by the constriction of the middle tibiae (strong, rather than weakly constricted in the case of *S. ladini*), and specific shape of the parameres (wide, truncate, and slightly divergent apically).



Map 34. Distribution of *Schyzoschelus kaszabi* Koch.

Material examined

Holotype, male **TMNH** (Fig. T43): "Naauwpoort, C.P. 27-x-1948 Koch & van Son Kaszabi koch HOLOTYPE No: 1795 Schyzoschelus kaszabi KOCH".

TMNH: "Bloemfontein, O.R.C. 2-9-05 G. A. K. Marshall. 1908–213", "S.Afr.,Cape-Karoo Welwood farm 31.58 S - 24.28E 14.9.1983; E–Y:2007 groundtraps, 98 days leg. Penrith groundtrap with meat bait (two specimens)", "S.Afr.,Cape-Karoo Vanwykafontein farm 30.38S - 25.23E 22.9.1983; E–Y:2019 groundtraps,90 days leg. Penrith groundtrap with meat bait", "S.Afr.,Cape-Karoo Woodcliff farm 31.57S - 24.38E 13.9.1983; E–Y:2004 singled day leg. Penrith". **SANC**: "South Africa CP Middelburg 31.3.S 25.0 E 25/viii/1989 M

de Jager AcLG1151 ex unbaited pitfalls near Pentzia spp NATIONAL COLL. OF INSECTS Pretoria.S.Afr (four specimens, 5 additional specimens with different date: 7/IX/1989)", "S. Africa, O.F.S. Krugersdrift Dam BLOEMFONTEIN SE 2926 Aa NATIONAL COLL. OF INSECTS Pretoria.S.Afr (two specimens)".

Distribution

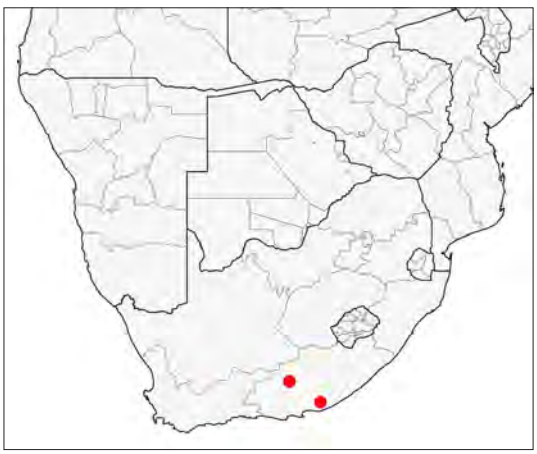
South Africa: Eastern Cape, Northern Cape, Free State (Map 34).

11. *Schyzoschelus ladini* Koch

Schyzoschelus ladini Koch, 1954b: 88.– Kamiński 2016: 247; Lumen & Kamiński 2024b: 137; Lumen *et al*. 2025: 8.

Diagnosis

Member of the *kaszabi* species-group. Most resembles *S. kaszabi* from which it is separable by the constriction of the middle tibiae (weakly constricted versus strongly in the case of *S. kaszabi*), and specific shape of the parameres (narrow, somewhat pointed, and parallel).



Map 35. Distribution of *Schyzoschelus ladini* Koch.

Material examined

Holotype, male **TMNH** (Fig. T44): "Resolution Albany Distr VI 1928 A. Walton. Ladini Koch HOLOTYPE No: 1805 Schyzoschelus ladini KOCH". **Paratype**, **TMNH**: same data as holotype.

SANC: "SOUTH AFRICA: ECape Asante Sana Game Reserve ca 41km E Graaf-Reinett 32°15.934'S 24°58.801E 1400m T1S1d 23.x.2010 J.M. Midgley NATIONAL COLL. OF INSECTS Pretoria.S.Afr Midgley donation 2021", "SOUTH AFRICA: ECape Asante Sana Game Reserve ca 43.5km E Graaf-Reinett 32°17.092'S 24°00.521E 1024m T2S1c 23.x.2010 J.M. Midgley NATIONAL COLL. OF INSECTS Pretoria.S.Afr Midgley donation 2021", "SOUTH AFRICA: ECape Asante Sana Game Reserve ca 38km E Graaf-Reinett 32°15.689'S 24°57.099E 1419m T3S1c 23.x.2010 J.M. Midgley NATIONAL COLL. OF INSECTS Pretoria.S.Afr Midgley donation 2021", "SOUTH AFRICA: ECape Asante Sana Game Reserve ca 41km E Graaf-Reinett 32°15.894'S 24°58.962E 2004m T1S4a 15.iv.2010 J.M. Midgley NATIONAL COLL.

OF INSECTS Pretoria.S.Afr Midgley donation 2021", "SOUTH AFRICA: ECape Asante Sana Game Reserve ca 43km E Graaf-Reinett 32°15.128'S 24°00.418E 2011m T2S5d 25.xi.2009 J.M. Midgley NATIONAL COLL. OF INSECTS Pretoria.S.Afr Midgley donation 2021".

Distribution

South Africa: Eastern Cape (Map 35).

12. *Schyzoschelus simplicipes* Koch

Schyzoischelus simplicipes Koch, 1954b: 84.– Kamiński 2016: 247; Lumen & Kamiński 2024b: 138.

= *Schyzoschelus simplicipes willowmorensis* Koch, 1954b: 85.– Kamiński 2016: 248; Lumen & Kamiński 2024b: 138 (syn.).

Diagnosis

Member of the *capensis* species-group (see *S. braunsi*). Enigmatic species closely affiliated with *Schyzoschelus africanus*, *S. braunsi*, and *S. sympatrius*. All of these species are known to coexist in the surroundings of Willowmore (South Africa). The only available diagnostic features concern the shape of male legs (see the key).

Material examined

While the holotype of *Schyzoschelus simplicipes simplicipes* was not examined, it should be preserved in **IMSA** with matching collection data as the examined paratype.

Schyzoschelus simplicipes simplicipes: **Paratypes**, sex undetermined **TMNH** (Fig. T45): "George dist. C.P., C. Thorne Aug. 193? Paratypus SCHYZOSCHELUS simplicipes C. Koch sp.n. (two specimens)".

Schyzoschelus simplicipes willowmorensis: **Holotype**, male **TMNH** (Fig. T46): "Willowmore, C.P. 1-XI-1948 Koch & van Son Paracharactes simplicipes ssp. willowmorensis C. Koch det., 195 KOCH ssp. willowmorensis HT Koch." **Paratype**, **TMNH**: same data as holotype.

Distribution

South Africa: Eastern Cape (Map 36).



Map 36. Distribution of *Schyzoschelus simplicipes* Koch.

13. *Schyzoschelus sympatrius* Koch

Schyzoschelus sympatrius Koch, 1954b: 84.– Kamiński 2016: 247; Lumen & Kamiński 2024b: 137.

Diagnosis

Member of the *capensis* species-group (see *S. braunsi*). Closely affiliated with *Schyzoschelus africanus*, *S. braunsi*, and *S. simplicipes*; all are known to coexist in the surroundings of Willowmore (South Africa). The only available diagnostic features concern the shape of male legs (relatively simple middle tibiae versus other species in the group with post basal or apical extensions).

Material examined

Holotype, male **TMNH** (Fig. T47): "Willowmore cape of g. Hope Dr. Brauns. HOLOTYPE No:1789 Schyzoschelus sympatrius KOCH synpatrius Koch".

MNHN: "MUSEUM PARIS Afr australe (L. Peringuey) Coll. L. FAIRMAIRE 1906".

Distribution

South Africa: Eastern Cape (Map 37).



Map 37. Distribution of *Schyzoschelus sympatrius* Koch.

14. *Schyzoschelus validus* (Fairmaire)

Psectropus validus Fairmaire, 1894: 661.– Gebien 1938: 391; Kaszab 1941: 35.

Schyzoschelus validus (Fairmaire, 1894).– Koch 1954b: 87; Kamiński 2016: 248; Lumen & Kamiński 2024b: 137.

Diagnosis

Member of the *kaszabi* species-group, within which it is diagnosable by the shape of its hind legs (strongly widened and chamfered, the only similar species is *S. africanus*, which belongs to the *capensis* group), and lack of setae on the middle tibiae (separating it from other members of the *kaszabi* group (*S. ladini* and *S. kaszabi*).

Material examined

Despite extensive efforts, FAIRMAIRE's original (1894) holotype could not be located. Therefore, under the provisions of Article 75.3 of the ICZN (1999), the designation of a neotype is warranted. A specimen from **MNHN** matching the type locality in FAIRMAIRE's original description ("Cafrerie"), originating from his collection, and falling well-within the morphological concepts presented by both FAIRMAIRE (1894) and KOCH (1954b) is here chosen as the neotype to stabilize this species.

Neotype here designated, male **MNHN** (Fig. T48): "Port Elizbt. / Museum Paris / 1906 / coll. L. Fairmaire."

TMNH: "Resolution Albany Distr. VI 1928 A. Walton", "Port Eliz. 90.49. Psectropus validus Fairm Schyzoschelus Validus (Fairm) C. Koch det., 1954". SANC: "Grahamstown, CP. 26-2-1955 G.A. Gill. AcC. 2992. NATIONAL COLL. OF INSECTS Pretoria.S.Afr". MNHN: "Mars 1875 Baltrasna highl ds GRAHAMSTOWN Afrique du Sud Museum Paris Coll. P. Ardoin 1978".

Distribution

South Africa: Eastern Cape (Map 38).



Map 38. Distribution of *Schyzoschelus validus* (FAIRMAIRE).

E. *Psectrapus* lineage

Genera included (6)

Byrrhoncus Koch, *Capidium* Koch, *Colophonesthes* Koch, *Colophonexsula* Lumen & Kamiński, *Isoncophallus* Koch, *Psectrapus* Solier.

Key to genera of *Psectrapus* lineage (see Plate E for figures):

While most specimens can be identified to genus through this key and/or a combination of features in the subsequent diagnoses; as of this revision only males have reliable characters for species identification for the genera *Colophonesthes*, *Colophonexsula*, *Isoncophallus*, and *Psectrapus*.

1. Abdominal ventrite V relatively broad (Fig. 1); males never with subapical sulcus, females with or without subapical sulcus **2**

— Abdominal ventrite V more-or-less quadrate to elongate, relatively flat, without or with weak convexity; subapical sulcus present in males and females (Fig. 2), or absent in both **3**

2. Males with greatly expanded fore- and midtarsus (Fig. 3). Females with sulcus on abdominal ventrite V. Abdominal ventrite V convex or bulbous (Fig. 1). Aedeagus with relatively narrow paramere window and parameres overall parallel and evenly tapered apically (Fig. 4); sclerotized penis with apical hook (sometimes bifurcated) (Figs 5–6) .... ***Psectrapus***

— Males with weakly expanded fore- and midtarsus. Females without sulcus on abdominal ventrite V. Abdominal ventrite V weakly to not-convex nor bulbous. Male aedeagi with extremely wide paramere window and greatly inwardly curved apical tips that are not tapered apically (Figs 7–8); penis without apical hook ..... ***Byrrhoncus***

3. Foretibiae cylindrical and slender. Pronotum with produced basal angles (Fig. 9). Abdominal ventrite V never with sulcus. Aedeagus with large paramere window (Fig. 10). Bursa copulatrix with two accessory pouches ..... ***Capidium***

— Foretibiae flattened and distally expanded. Pronotum without produced basal angles (however, see *Isoncophallus angulicollis*, Fig. T68). Abdominal ventrite V with subapical sulcus in males and females (Fig. 2), or absent in both. Bursa copulatrix without accessory pouches **4**

4. Abdominal ventrite V in both males and females with subapical sulcus (Fig. 2) .... ***Isoncophallus***

— Abdominal ventrite V without sulcus **5**

5. Aedeagus not tapered, rounded apically, with narrow opening (Fig. 11), with or without apical hook on penis ..... ***Colophonesthes***

— Aedeagus slightly tapered, not rounded apically, with wide opening exposing penis (Fig. 12), never with apical hook ..... ***Colophonexsula***

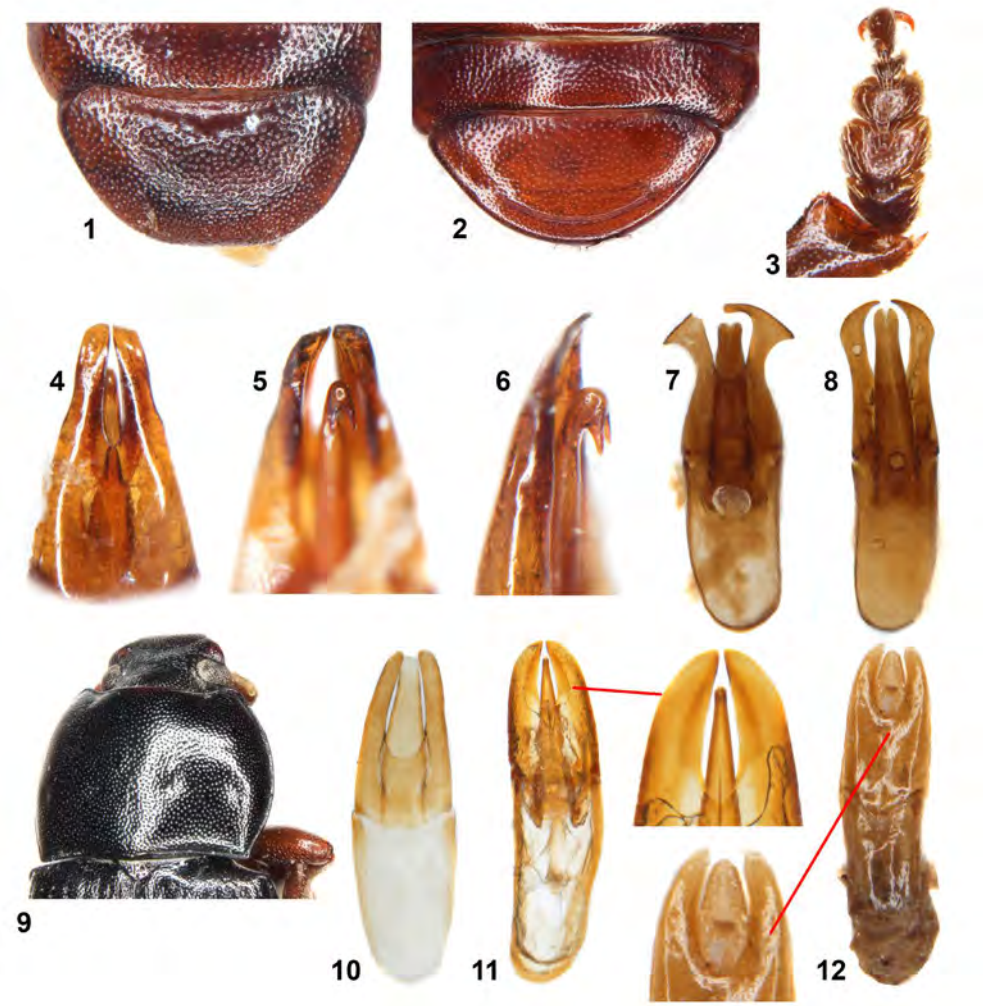


Plate E. *Psectrapus* lineage. Genera diagnostic features. **Anatomic features**: Abdominal ventrite V (1–2). Foretarsus (3). Aedeagus (4–8, 10–12). Pronotum (9). **Taxa depicted**: *Byrrhonchus monticola* (7). *Byrrhonchus parvithorax* (8). *Capidium bipunctatum* (9–10). *Colophonesthes montisatri* (11). *Colophonexsula puerilis* (12). *Isoncophallus campester* (2). *Psectrapus bipartitus* (4–6). *Psectrapus latimentulum* (1). *Psetrapus simplicimentulum* (3).

vi. Genus *Byrrhoncus* Koch

Byrrhoncus Koch, 1954b: 49.– Koch 1956: 27; Kamiński 2016: 233; Kamiński *et al*. 2019: 92, 2021: 152; Bouchard *et al*. 2021: 128; Lumen *et al*. 2025: 2.

Type species. *Byrrhoncus monticola* Koch; by original designation.

Diagnosis

Byrrhoncus has been a difficult genus to identify or clearly define–largely because the concept of the genus is based on very few (12) specimens, and the original description(s) and figure(s) of species are most helpful use only male characteristics. The most similar genera are *Isoncophallus*, *Psectrapus*, *Colophonesthes*, and *Colophonexsula*, which all have a similar habitus and relatively simple legs that may be slightly curved or 'scoop-shaped'. *Byrrhoncus* can be separated from *Isoncophallus* and *Psectrapus* based on the lack of sulcus on abdominal ventrite V (present in both males and females of *Isoncophallus* and females of *Psectrapus*). Additionally, while most species of *Psectrapus* have greatly expanded foretarsi (see *Psectrapus* diagnoses & descriptions), *Byrrhoncus* also has expanded foretarsi; however, *Isoncophallus* lacks them. Finally, in males, the aedeagus of *Byrrhoncus* is distinct within Eurynotina, with its long, thin parameres, which diverge medially before converging apically, giving a pincer- or scythe-like appearance, and leaving a characteristically large window exposing the penis.

Species included (2)

B. monticola Koch, *B. parvithorax* Koch.

Key to species of *Byrrhoncus* (see Plate vi for figures):

1. Glossy or shiny dorsum (Fig. 1). Pronotum large, more than twice as wide as the head, punctures crowded, with space between them almost smaller than their diameter. Aedeagus with paramere apices scythe-like (Fig. 2) ..... ***Byrrhoncus monticola***

— Entire dorsum silky matte (or elytra slightly more shiny than the anterior), with a greasy shimmer (Fig. 3). Pronotum narrow, only half wider than the head with fine, but less crowded punctation, space between punctures significantly larger than their diameter. Aedeagus with paramere apices pincer-like (Fig. 4) ..... ***Byrrhoncus parvithorax***



Plate vi. *Byrrhonchus* species diagnostic features. **Anatomic features**: Pronotum (1,3). Aedeagus (2, 4). **Taxa depicted**: *Byrrhonchus monticola* (1–2). *Byrrhonchus parvithorax* (3–4).

1. *Byrrhoncus monticola* Koch

Byrrhoncus monticola Koch, 1954b: 53.– Banaszkiewicz 2006: 63; Kamiński 2016: 233.

Diagnosis

The simplest way to separate *B. monticola* from *B. parvithorax* is the shape of the thorax and the texture/luster of the dorsal habitus. In *B. monticola* the dorsum is shinier, with crowded punctation. Additionally, the pronotum is large (~2x the size of the head) and is nearly the size of the base of the elytra. Finally, in males of *B. monticola*, the parameres of the aedeagus have a distinctive, scythe-like shape.

Material examined

Holotype male **TMNH** (Fig. T49): "Zwartberg, oberhalb Avondrust, Juli 1950, leg. E. A. Pienaar". **Paratypes**, male and 4 females **IMSA**, **TMNH** (Fig. T50): same data as holotype, two specimens. TMNH, IMSA: "Matjesfontein, 1902, leg. R. Lightfoot". SU: "Montagu, Juli".

CASC: "Cape Prov. Cape Point elev. 0 m. IV-26-58 CASENT 8590254 QR Label".

Distribution

South Africa: Western Cape (Map 39).



Map 39. Distribution of *Byrrhoncus monticola* Koch.

2. *Byrrhoncus parvithorax* Koch

Byrrhoncus parvithorax Koch, 1954b: 54.– Kamiński 2016: 233.

Diagnosis

Byrrhoncus parvithorax is distinguished by the lack of luster of its dorsum, and the shape of the pronotum (narrower than the elytra, and less than twice the width of the head). The punctation of the pronotum is also less dense. Finally, in males of *B. parvithorax*, the parameres of the aedeagus converge apically in a more simple, pincer-like shape, which is down-turned in lateral-view.

Material examined

Holotype female **TMNH** (Fig. T51): "Van Rhynsdorp, Juli–August 1927, leg. G. van Son". **Paratypes** male and female **IMSA**: "Garies, Juni 1930, leg. Mus. Personal", two specimens.

CASC: "SOUTH AFRICA: Cape Province, Floriskraal Dam, 18 road km SE Laigns-burg 730m, 25 October 1985 J.T. Doyen, C.E.Griswold, T.M. Griswold collectors CASENT 8590269 QR Label".

Distribution

South Africa: Northern Cape, Western Cape (Map 40).



Map 40. Distribution of *Byrrhoncus parvithorax* Koch.

vii. Genus *Capidium* Koch

Capidium Koch, 1954b: 44.– Koch 1956: 27; Iwan 2001: 352; Kamiński 2016: 233; Kamiński *et al*. 2019: 92, 2021: 13; Bouchard *et al*. 2021: 133; Lumen & Kamiński 2023: 4; 2024a: 12; Lumen *et al*. 2025: 2.

Type species. *Oncotus tardus* Solier; by original designation.

Diagnosis

Capidium is unique (aside from the *Eurynotus* and *Phylacastus* lineages) within Eurynotina for the shape of its pronotum (with produced basal angles). Within the *Psectrapus* lineage, *Capidium* has particularly strong tuberculation of the elytra (in most species), and the most angular basal pronotal angles (with one close exception, see *Isoncophallus angulicollis*). *Capidium* lacks a sulcus on the fifth abdominal ventrite (present in *Isoncophallus* males & females, and in females of *Psectrapus*) as well as a well-defined sulcus circumscribing the lateral edges of the pronotum (present in all other genera). The aedeagus has a wide paramere opening (relatively narrow in most other *Psectrapus*-lineage genera except *Byrrhoncus*). The bursa copulatrix has two accessory pouches, separating them from other related genera.

Species included (4)

C. bipunctatum (Thunberg), *C. hessei* Koch **stat. res.**, *C. tuberculatum* Koch, *C. vicarium* Koch.

Key to species of *Capidium* (see Plate vii for figures):

1. Elytra tuberculate (Figs 1–3) **2**

— Elytra without tubercles ..... ***Capidium bipunctatum***

2. Elytra with weak tubercles restricted to apical decline (Fig. 2) ... ***Capidium vicarium***

— Elytra with intermittent large, prominent tuberculation (Figs 1 & 3) **3**

3. Hypomeron strongly punctate (Fig. 4). Elytral humerus with weak knob (Fig. 3) .... ***Capidium tuberculatum***

— Hypomeron not strongly punctate (Fig. 5). Elytral humerus with prominent knob (Fig. 1) ..... ***Capidium hessei***

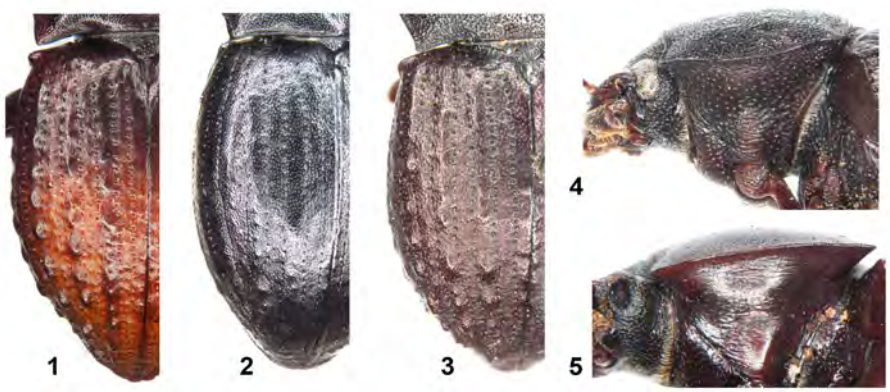


Plate vii. *Capidium* species diagnostic features: **Anatomic feature**: Elytron (1–3). Hypomeron (4–5). **Taxa depicted**: *Capidium hessei* (1, 5). *Capidium tuberculatum* (3–4). *Capidium vicarium* (2).

1. *Capidium bipunctatum* (THUNBERG)

Blaps bipunctata THUNBERG, 1821: 165.– FERRER 2009: 117.

Capidium bipunctatum (Thunberg, 1821).– FERRER 2009: 117; KAMIŃSKI 2016: 233; LUMEN *et al*. 2025: 10.

= *Blaps striatula* THUNBERG, 1821: 166 **syn. nov.**

= *Oncotus tardus* SOLIER, 1848: 219.– GEMMINGER & HAROLD 1870: 1911; GEBIEN 1910: 271, 1938: 393; FERRER 2009: 117 (syn.).

Capidium tardum (SOLIER, 1848).– KOCH 1954b: 46; IWAN 2001: 372; FERRER 2009: 117.

= *Onchotus tardus* var. *pedellus* SOLIER, 1848: 219.– GEBIEN 1910: 271, 1938: 393; FERRER 2009: 117 (syn.).

Diagnosis

Within *Capidium*, *C. bipunctatum* is unique in its lack of tubercles on the elytra. Other species have either prominent tuberculation of the elytra (e.g., *C. tuberculatum* or *C. hessei*), or some presence of at least weak tuberculation on the apical decline (as in *C. vicarium*). *Capidium bipunctatum* is the most sexually dimorphic species within the genus, and as such has generated some confusion especially when it comes to male and female specimens (e.g., *Blaps striatula* THUNBERG **syn. nov.** treated as separate from *Blaps bipunctata* THUNBERG). Access to larger material collections and type specimens showed that the differences between *B. striatula* and *B. bipunctata* can be associated with variation (tuberculation reduced/absent) and/or sexually dimorphic (widened versus narrow-bodied). To further fix the taxonomic status of *C. bipunctatum* and its junior synonyms as well as resolve/prevent confusion, lectotypes are designated here for *Oncotus tardus* and *Onchotus tardus* var. *pedellus* from SOLIER type material uncovered in **MNHN**.

Material examined

Blaps bipunctata: **Holotype**, sex undetermined **UUZM** (Fig. T52): "Uppsala Univ. Z-.Mus. Thunbergsaml. Type 6335 Blaps bipunctata Cap. TYP 2punctata cap. 14 Capidium bipunctata (Thunb) comb. Det. nov. det. J. Ferrer".

Blaps striatula: **Holotype**, sex undetermined **UUZM** (Fig. T56): "Uppsala Univ. - Mus. Thunbergsam - Type 6349 Blaps striatula Cap. TYP striatula cap. 28".

Oncotus tardus: **Lectotype**, sex undetermined, here designated **MNHN** (Fig. T57): "Du Cap de Bonne Espérance, Red TYPE label".

Onchotus tardus var. *pedellus*: **Lectotype**, sex undetermined, here designated **MNHN** (Fig. T55): "Cap. b. Sp. Coll R. Oberthür ex coll. Deyrolle, Oncotus pedellus Gory C.B. Esp., Red SYNTYPE label".

MNHN: "Cap. b. Sp. Coll R. Oberthür ex coll. Deyrolle, (four specimens)". "Museum Paris Afr. Australe (E.Peringuey) Coll. L. Fairmaire 1906, (two specimens)". "Museum Paris Cap De Bonne Esperance Verreaux 1835, (four specimens)". "Museum Paris Colonie Du Cap J. Verreaux 1866", "Museum Paris Env De Cape Town A. Raffray 1899, (10 specimens)". "De Vylder Cap. B. Esp. (three specimens)", "S. Africa R.E. Turner 1920-342 Lion's Head. Cape Town Aug. 1920, (32 specimens)". "CAPE TOWN XII.1953 B.W. Zenziger", "South Africa E.Y. Western Coll. B.M.1924-176", "Cape Town Distr. Aug, 1968 C.G.C. Dickson", "Richmond Natal XII 54, (nine specimens)". **TMNH**: "Cape Town 20.8.1967", "Cape Town 27.9.1967", "Darling 10.6.50 illegible second label", "South Africa Stellenbosch 194", "Tafelberg Capstat Dr. Brauns 1915 (nine specimens with variations of Cap. Bon. Esp. labels)".

Distribution

South Africa: Western Cape (Map 41). Although extralimital records in KwaZulu-Natal based on specimen data are included here, whether they represent real established populations is questionable.



Map 41. Distribution of *Capidium bipunctatum* (Thunberg).

2. *Capidium hessei* Koch stat. res.

Capidium hessei Koch, 1954b: 46.– Ferrer 2009: 117; Kamiński 2016: 233; Lumen *et al*. 2025: 10.

Diagnosis

Capidium hessei is most similar to *C. tuberculatum*, as both species possess prominent tubercules on the elytra; however, they can be differentiated by the sculpture of the hypomeron (large or strong punctation in *C. tuberculatum*), the presence of a large knob on the elytral humeri (small to absent in all other species), and a slight metallic luster (less common in other species of *Capidium*).

Upon examination and comparison of Koch's types, additional material loaned from **TMNH**, and Thunberg's types for *Blaps striatula* and *B. bipunctata*, it is clear that Koch's concept for *Capidium hessei* is a distinct and diagnosable species. *Capidium hessei* was erroneously synonymized with *B. striatula* (Ferrer 2009). Though it might be due to the Thunberg type specimen having a somewhat similar body shape, no justification was given for the synonymy, and cross-examination with Koch's (1954b) type material, as well as additional specimens from multiple collections, showed clear differences (e.g., much greater sculpturing of the elytra and more rearwardly projecting basal pronotal angles in *C. hessei*).

Material examined

Holotype, male **TMNH** (Fig. T53): "CAPE G.H., F. Bates 81 19, HOLOTYPE No: 1686 Capidium hessei KOCH Hessei Koch". **Paratype**, **NHMUK** (Fig. T54): "Fry Coll. 1905.100. C.Bon. Spei yellow circle "Paratype" label Paratype hessei Koch NHMUK014663123 barcode label."

MNHN: "Simon's Bay Sept 62", two specimens. "Museum Paris 1906 coll. L. Fairmare", two specimens. **MIZPAN**: "Oct 9 2019 South Afr 34.25S 18.46E".

Distribution

South Africa: Western Cape (Map 42).



Map 42. Distribution of *Capidium hessei* Koch.

3. *Capidium tuberculatum* Koch

Capidium tuberculatum Koch, 1954b: 48.– Kamiński 2016: 233.

Diagnosis

Capidium tuberculatum is closest to *C. hessei* morphologically—from other species *C. tuberculatum* is set apart by the strong tuberculation of the elytra and sculpturing of the hypomeron (see *C. hessei* diagnosis). Additional characteristics separating *C. tuberculatum* from *C. hessei* are overall stronger punctation on elytral intervals and more impressed striae, as well as confluent pronotal punctation.

Material examined

The holotype, though unexamined here, should be located in **IMSA** with label data "Cape Town, leg. Purcell".

Paratype, male **TMNH** (Fig. T58): "De Vylder Cap. b sp. PARATYPE No: 1710 Capidium tuberculatum Koch".

MNHN: "Cap. b. Sp. Coll R. Oberthür ex coll. Deyrolle, (three specimens)". "Oncotus tuberculatum F. Bates 18 19 Tuberculatus C. Koch det. 19 ??mberg", "tuberculatum Cap. b. sp. Museum Paris Coll De Marseul 1890 tuberculatus Deyrolle", "Museum Paris Cape Town Rondebosch (E.Peringuey) Coll. L. Fairmaire 1906, (two specimens)". **TMNH**: "South Africa S.W. Cape Stellenbosch Jonkershoek I.X.1966 H. Geertsema", "South Africa S.W. Cape Stellenbosch 27.vi.1965 H. Geertsema, (two specimens)". "South Africa S.W. Cape Stellenbosch 13.vii.1965 H. Geertsema". "Stellenbosch Cape 8 Dec. 1985 R.W.E. Tucker Ag Dp S Afr Pres. by Com. Inst. Ent. BM 1981-315".

Distribution

South Africa: Western Cape (Map 43).



Map 43. Distribution of *Capidium tuberculatum* Koch.

4. *Capidium vicarium* Koch

Capidium vicarium Koch, 1954b: 47.– Kamiński 2016: 234.

Diagnosis

See diagnosis of *C. bipunctatum*.

Material examined

Holotype, male **TMNH** (Fig. T59): "Stellenbosch, 1. Feb. 1915, leg. H. Brauns".

TMNH: "Stellenbosch Cape 8 Dec. 1985 R.W.E. Tucker Ag Dp S Afr Pres. by Com. Inst. Ent. BM 1981-315 Oncotus sp. Nov. ? B.M. G.E. Bryant Det.", "S. Afr., SW Cape Zuurefontein farm 32.50S - 18.34 E 31.8.1981 E-Y: 1872 groundtraps, 59 days leg. Endrödy-Younga ground trap with faeces bait, (two specimens)". **NMNW**: "Bainskloof (Limietberge) 33°33'S., 19°08'E CAPE, R.S.A. 3 Oct 1974 H21379 Namibian National Insect Collection State Museum P.O. Box 1203 WINDHOEK, Namibia".

Distribution

South Africa: Western Cape (Map 44).



Map 44. Distribution of *Capidium vicarium* Koch.

viii. Genus *Colophonesthes* Koch

Colophonesthes Koch 1954b: 47.– Koch 1956: 27; Kamiński 2016: 234; Bouchard *et al*. 2021: 147; Kamiński *et al*. 2021: 152; Lumen *et al*. 2025: 10.

Type species. *Colophonesthes montisatri* Koch; by original designation.

Diagnosis

Colophonesthes can be differentiated from other genera in the *Psectrapus* lineage by the shape of the aedeagi which are rounded/weakly tapered rather than strongly tapered or with extremely wide separation or other accoutrements (see *Byrrhoncus* and *Psectrapus*). Other genera (e.g., *Isoncophallus* and *Capidium*) are separable by the presence of a sulcus on abdominal ventrite V in males and females and produced basal pronotal angles respectively. The last, closest genus is *Colophonexsula*, which is separable by the shape of the aedeagus (similar to *Byrrhoncus* and *Psectrapus*, albeit less ornately so); in *Colophonexsula* the window between the parameres is relatively wide and the parameres slightly tapered—whereas in *Colophonesthes* the parameres are closer together (smaller opening exposing less of the penis) and with a weaker taper (rounded apically). Finally, overall the pronotum of *Colophonesthes* is rounder and wider than in *Colophonexsula* (where the pronotum is slightly more elongate and slightly narrower than the elytra).

Species included (2)

C. barnardi Koch, *C. montisatri* Koch.

Key to species of *Colophonesthes* – males only (see Plate viii for figures):

1. Penis with hook (Fig. 1). Foretibiae with small strip of setae on apex (Fig. 2). Midtibiae with small patch of setae on the apex (Fig. 2) ..... ***Colophonesthes montisatri***

— Penis without hook. No strips or patches of setae on the fore- or midtibiae .... ***Colophonesthes barnardi***



Plate viii. *Colophonesthes* species diagnostic features: **Anatomic features**: Aedeagus (1). Midtibia (2). **Taxon depicted**: *Colophonesthes montisatri* (1–2).

1. *Colophonesthes barnardi* Koch

Colophonesthes barnardi Koch, 1954b: 50.– Kamiński 2016: 234; Lumen *et al*. 2025: 17.

Diagnosis

Psectrapus barnardi was described by Koch (1954b) based on three specimens (male and two females) and is morphologically close to *P. montisatri*. As of this revision, it can be difficult to differentiate this species from *P. montisatri* (with which it co-occurs); however, the aedeagi figured by Koch (1954b) depict a clear difference in that *P. barnardi* lacks a hook on the penis (present in *P. montisatri*). Additionally, *P. montisatri* has a small strip of setae on the apex of the foretibiae, and a small patch of setae on the apex of the midtibiae—both of which are absent in *P. barnardi*.

Material examined

The holotype, though unexamined here, should be located in **IMSA** with the label data "Zwartberg Pass, Prince Albert Div., 5000 bis 6000 Fuss Höhe, Nov. 1929, leg. K. H. Barnard".

Paratypes, 2 females **TMNH** (Fig. T60): same data as holotype.

Distribution

South Africa: Western Cape (Map 45).



Map 45. Distribution of *Colophonesthes barnardi* Koch.

2. *Colophonesthes montisatri* Koch

Colophonesthes montisatri Koch, 1954b: 52.– Kamiński 2016: 234; Lumen *et al*. 2025: 17.

Diagnosis

See *P. barnardi* diagnosis.

Material examined

Holotype, male **TMNH** (Fig. T61): "Southern slope of Zwartberg Pass 3-XI-1948 C.P., Koch & van Son". **Paratypes**, sex undetermined **TMNH** (Fig. T62): "Zwartberg nr. Avondrust Kaingsbg. Dist. 8II.1950 Pienaar". "7 Weeks Poort Berg Ladismith, Cape 5500–7000 ft, two specimens".

Distribution

South Africa: Western Cape (Map 46).



Map 46. Distribution of *Colophonesthes montisatri* Koch.

ix. Genus *Colophonexsula* Lumen & Kamiński

Colophonexsula Lumen *et al*. 2025: 6.

Type species. *Colophonesthes puerilis* Koch; by original designation.

Diagnosis

This genus was erected to contain the species (*C. puerilis*) of *Colophonesthes sensu* Koch (1954b), which diverged phylogenetically in recent phylogenetic analyses (Lumen *et al*. 2025). Further investigation for this monograph revealed additional taxonomic changes are warranted; namely, the inclusion of *C. enisa* and *C. nitens* from *Colophonesthes*. Specifically, closer examination of internal morphology (aedeagal parameres) and comparisons of pronotum firmly separate both *C. enisa* and *C. nitens* from *Colophonesthes*, while affiliating them more strongly with *Colophonexsula* (see *Colophonesthes* diagnosis for further details).

Colophonexsula is best diagnosed by exclusion of other genera, e.g., wide abdominal ventrite V in *Byrrhoncus* and *Psectrapus*, sulcus on abdominal ventrite V in males and females of *Isonocphallus*, strongly produced hind angles of the pronotum and cylindrical forelegs in *Capidium*, weakly tapered and apically rounded parameres in *Colophonesthes*. The habitus of this genus greatly resembles *Psectrapus* and *Colophonesthes*.

Psectrapus females have a sulcus of the fifth abdominal ventrite (absent in *Colophonexsula* and *Colophonesthes*). From *Colophonesthes* this genus can be differentiated based on the general morphology of the aedeagus (rounded with narrow/small window between almost hiding the penis; with wider opening and more tapered in *Colophonexsula*) and the general shape of the pronotum (somewhat wider, base about equal to width of elytra and overall rounder; *Colophonexsula* with somewhat longer pronotum that is slightly narrower than the elytra. Unfortunately, as with other representatives in the *Psectrapus* lineage, two species (*C. enisa*, *C. nitens*) are only known by small type series originally designated by Koch (1954b). New specimens uncovered in future work may shed light on further diagnostic characters which could necessitate further taxonomic shuffling. A new description for the genus is provided below to include the diversity brought about by the newly incorporated species.

Redescription

Length 5.5–8mm, width 3–4.5mm. Colored tenebrous; dark brown to black. **Head**: Coarsely to finely puncate, punctures closely (≤1 feature diameter) to widely (≥1 feature diameter) spaced. Epistoma shallowly emarginate. Prementum straight, with no emargination. Mentum with small ventrally projecting middle portion; lateral wings exposed. Gula with stridulatory file. Eyes constricted in middle and reniform. Antennae 11 segmented, terminal segments forming weak club. **Prothorax**: scutellum small and transversely triangular. Pronotum slightly wider than long in females, and subequally wider than long in males, both males and females with broadly rounded basal angles. Lateral margin well-defined with border running perimeter. Hypomeron nearly smooth to finely wrinkled; with light to absent punctation. Prosternal process round without posterior projection. **Pterothorax**: Elytra with 10 intervals, disc relatively flat to convex. Elytral striae weakly impressed and punctate. Intervals dull and finely punctate in females, shining and more strongly punctate in males, both males and females with few to no bumps or tubercles present on apical declivity. Elytral intervals visible in ventral view. Epipleura broad basally, narrowing after humeral region. Apterous. **Abdomen**: Punctate. Punctures separated by >1 diameter. Abdominal ventrite V flat to slight-

ly convex, subquadrate to slightly elongate, and without subapical sulcus or additional larger setigerous punctation. **Legs**: femurs laterally compressed, slightly curved and strongly thickened. Tibiae straight, foretibiae with small downward pointing, apical lateral protrusion or 'tooth' or apically widened and slightly triangular; males with large setose patch. Tarsi with golden setae and without strongly expanded pro/meso tarsi in males. **Male terminalia**: Tegmen bipartite and without ancorae; basal portion membranous ventrally; dorsally with small, triangular membranous field at base of apical portion. **Female terminalia**: Ovipositor short; (~1:1 paraprocts to coxae ratio). Bursa copulatrix without additional pouches.

Species included (3)

C. enisa (Koch) **comb. nov.**, *C. nitens* (Koch) **comb. nov.**, *C. puerilis* (Koch).

Key to species of *Colophonexsula* – males only (see Plate ix for figures):

1. Foretibiae with downward pointed projection or spur at the apex (Fig. 1) .... ***Colophonexsula puerilis***

— Foretibiae slightly expanded apically (more triangular) and without or with less pointed projection (Fig. 2) **2**

2. Dorsal habitus dull (Fig. 4). Males with, at most, slightly widened tarsi, male with hind tibia with setal strip (Fig. 3) ..... ***Colophonexsula enisa***

— Dorsal habitus shiny (Fig. 5). Males with broad tarsi and without hind tibial setae ..... ***Colophonexsula nitens***

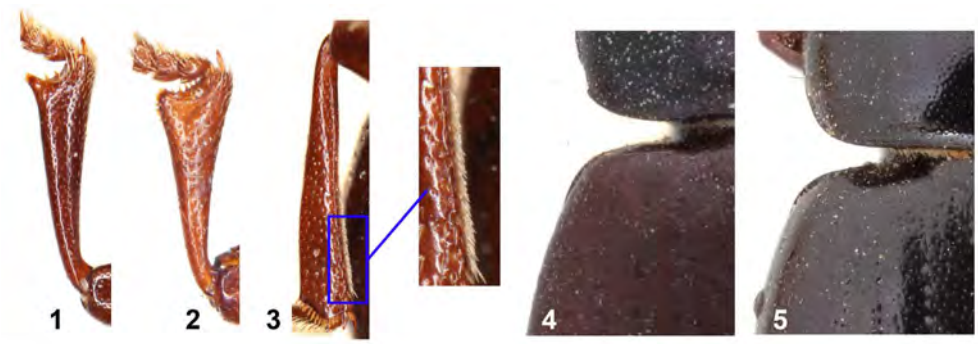


Plate ix. *Colophonexsula* species diagnostic features. **Anatomic features**: Foreleg (1–2). Midleg (3). Elytron and pronotal base (4–5). **Taxa depicted**: *Colophonexsula enisa* (2–4). *Colophonexsula nitens* (5). *Colophonexsula puerilis* (1).

1. *Colophonexsula enisa* (Koch) comb. nov.

Colophonesthes enisa Koch, 1954b: 52.– Kamiński 2016: 234.

Diagnosis

New combination based on reinterpretation of generic boundaries (see genus diagnosis). *Colophonexsula enisa* differs from *C. puerilis* by the absence of a well-defined protuberance of the foretibiae; instead, the foretibiae are widened apically and slightly triangular. *Colophonexsula nitens* differs by its shiny lustre.

Material examined

Holotype, male **TMNH** (Fig. T63): "Cedarbergen Cape 4-5000 ft. K.M. Barnadr Sept. 936 Red HOLOTYPE label". **Paratypes**, 2 males **TMNH** (Fig. T64): same data as holotype.

Distribution

South Africa: Western Cape (Map 47).



Map 47. Distribution of *Colophonexsula enisa* (Koch).

2. *Colophonexsula nitens* (Koch) comb. nov.

Psectrapus nitens Koch, 1954b: 67.– Kamiński 2016: 246 (*Psectropus* sic!); Lumen *et al*. 2025: 20.

Diagnosis

Colophonexsula nitens is unique within the genus for the shiny lustre for which it was originally named by Koch (1954b). The closest species, *C. enisa*, differs in that males have feebly expanded tarsi, while *C. nitens* has more strongly expanded fore- and midtarsi.

Material examined

While the holotype was not examined, it should be deposited at **IMSA** with the label data "Matjesfontein, 1902, leg. R. M. Lightfoot".

Paratype, female **TMNH** (Fig. T65): same data as holotype.

Distribution

South Africa: Western Cape (Map 48).



Map 48. Distribution of *Colophonexsula nitens* (Koch).

3. *Colophonexsula puerilis* (Koch)

Colophonesthes puerilis Koch, 1954b: 51.– Kamiński 2016: 234; Lumen *et al*. 2025: 15.

Diagnosis

Colophonexsula puerilis is the most easily diagnosed species in the genus–with forelegs bearing a small, downward-pointed protuberance on the apex. The other two species (*C. nitens* and *C. enisa*) have more triangular forelegs.

Material examined

Holotype, male **TMNH** (Fig. T66): "Sneeuwgat Valley, Tulbagh Div. Oktober 1934 Red HOLOTYPE label". **Paratype**, female **TMNH** (Fig. T67): Same data as holotype.

TMNH: "Z.A. 99 SedarBerg, 500-1000m Clanwilliam Distr. C.P. Humus under bushes and large stones. IV.1962, N.Leleup N LELEUP leg., (three specimens)". "S.Afr., W.Cape Nieuvoudtville 32.23 S - 19.06 E 21.8.1981; E-Y: 1820 groundtraps, 64 days leg. Endrödy-Younga ground traps with meat bait".

Distribution

South Africa: Western Cape (Map 49).



Map 49. Distribution of *Colophonexsula puerilis* (Koch).

x. Genus *Isoncophallus* Koch

Isoncophallus Koch, 1954b: 55.– Koch 1956: 27; Iwan 2001: 352; Kamiński 2016: 239; Kamiński *et al*. 2019: 92, 2021: 152; Lumen & Kamiński 2024b: 138; Lumen *et al*. 2025: 2.

Type species: *Isoncophallus zabroides* Koch; by original designation.

Diagnosis

Isoncophallus superficially most resembles *Byrrhoncus*, *Colophonexsula*, and *Psectrapus*. However, it differs by the configuration of the sulcus present on abdominal ventrite V. Specifically, it is present in both males and females (absent in males of *Psectrapus*, and absent altogether in *Colophonexsula* and *Byrrhoncus*). *Colophonexsula puerilis* has a unique denticle or protuberance near the apex of the foretibiae which is absent or very differently formed in *Isoncophallus* (i.e., *Isoncophallus dentimanus* has a protuberance, but it is very strongly developed and broader than in *Colophonexsula*). Additionally, *Isoncophallus* is, in general, wider in gestalt than *Colophonexsula* (except in the case of *I. ornatipes*, which can be differentiated by the lack of denticle on the apex of the foretibiae and the abbreviated sulcus on abdominal ventrite V). The parameres of the aedeagus can also be used to differentiate some genera. In particular, *Byrrhoncus* has unique morphology of the parameres (see *Byrrhoncus* section), and *Psectrapus* has parameres that tend to converge apically to close the central window or opening between them. *Isoncophallus* also lacks the strongly expanded tarsus in males present in other genera such as *Psectrapus* and *Byrrhoncus*.

Isoncophallus can be divided into two groups for identification based on foretibial morphology: foretibiae with large apical inset for tarsal attachment (*I. angulicollis*, *I. avontuurensis*, *I. campester*, and *I. zabroides*), or with broader/truncate tibial apex – somewhat resembling some genera in the *Oncotus* lineage (*I. dentimanus*, *I. diffusus*, *I. ovanullum*, *I. crispiformus*, and *I. ornatipes*).

Species included (9)

I. angulicollis Koch, *I. avontuurensis* Koch, *I. campester* Koch, *I. crispiformus* **sp. nov.**, *I. dentimanus* Koch, *I. diffusus* Koch, *I. ovanullum* **sp. nov.**, *I. ornatipes* Koch, *I. zabroides* Koch.

Key to species of *Isoncophallus* (see Plate x for figures):

1. Foretibiae with off-set tarsal insertion apically (Fig. 1). With or without lateral protuberance or 'tooth' **2**

— Foretibiae truncate without off-set or, at most, very weak off-set tarsal insertion giving a more truncate appearance (Fig. 2) **5**

2. Base of pronotum with slight constriction/indent before basal angles, which are roughly quadrate (Fig. 3) ..... ***Isoncophallus angulicollis***

— Base of pronotum without constriction before basal angles, more-or-less rounded or quadrate (Fig. 4) **3**

3. Males without setal patches on hind tibiae ..... ***Isoncophallus avontuurensis***

— Males with setal patch on hind tibiae (Figs 5–6) **4**

4. Male setal patch relatively small–restricted to middle of hind tibiae (Fig. 5) .... ***Isoncophallus campester***

— Male setal patch long–running along apical 2/3rds of hind tibiae (Fig. 6) .... ***Isoncophallus zabroides***

5. Foretibiae with strong tooth-like process projecting laterally (Fig. 7) .... ***Isoncophallus dentimanus***

— Foretibiae blunt, lacking strong tooth-like process **6**

6. Abdominal ventrite V with abbreviated sulcus (Fig. 8) ..... ***Isoncophallus ornatipes***

— Abdominal ventrite V with complete, unabbreviated sulcus (as in Fig. 9) **7**

7. Abdominal ventrite V with sulcus situated at extreme apex (Fig. 10). Pronotum relatively dull and lightly textured. Elytra with finely textured intervals and striae .... ***Isoncophallus ovanullum* sp. nov.**

— Abdominal ventrite V with subapical sulcus more distant from apex (as in Fig. 9). Pronotum relatively shiny and less textured. Elytra with coarse strial punctation and less-finely punctate intervals **8**

8. Aedeagus with large window, and strongly curved parameres (Fig. 11) .... ***Isoncophallus crispiformus* sp. nov.**

— Aedeagus with narrow, uncurved, tapering parameres ..... ***Isoncophallus diffusus***

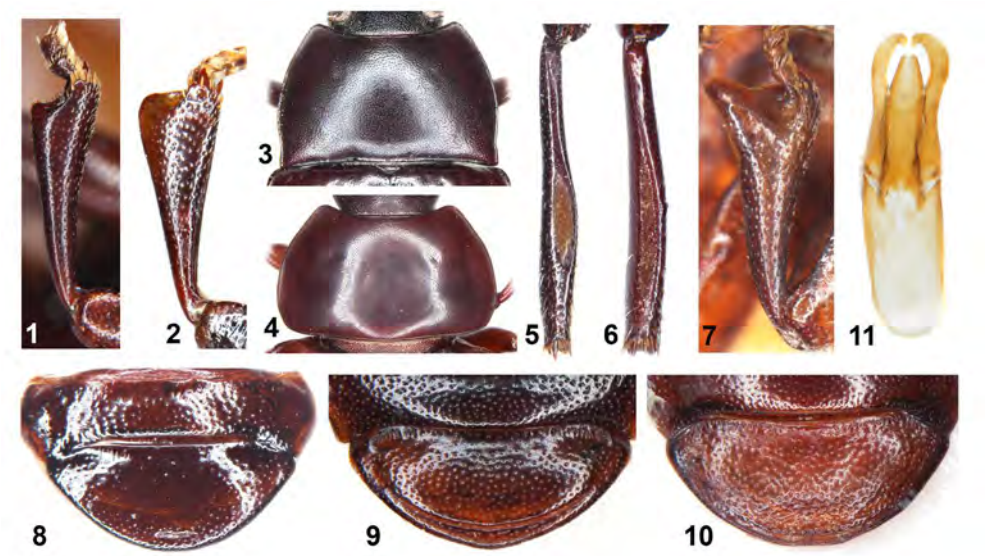


Plate x. *Isoncophallus* species diagnostic features. **Anatomic features**: Foreleg (1–2, 7). Pronotum (3– 4). Hind tibiae (5–6). Abdominal ventrite V (8–10). Aedeagus (11). **Taxa depicted**: *Isoncophallus angulicollis* (3). *Isoncophallus campester* (4, 5). *Isoncophallus crispiformus* (9, 11). *Isoncophallus dentimanus* (7). *Isoncophallus ornatipes* (8). *Isoncophallus ovanullum* (2, 10). *Isoncophallus zabroides* (1, 6).

1. *Isoncophallus angulicollis* Koch

Isoncophallus angulicollis Koch, 1954b: 56.– Iwan 2001: 382; Kamiński 2016: 239.

Diagnosis

This species belongs to the group of *Isoncophallus* with an inset tarsal attachment point of the foretibiae. From all other species it is easily differentiated by the base of the pronotum, which has a unique shape (basal angles nearly 90°, with a small divot or 'pinching' of the margin before the base).

Material examined

Holotype, male **TMNH** (Fig. T68): holotype has no distributional label. **Paratype**, male **TMNH**: paratype has no distributional data.

TMNH: "Stormsriviermond KP. S.Afr. 4.1.71. M.W. Strydom, NATIONAL COLL. OF INSECTS Pretoria S. Afr.". **MNHN**: "20.7.1970 Knysna Cape. Prov. Cl. Besnard Museum Paris Coll. P. Ardoin 1978", "28.VIII.1968 Keurboom River AFRIQUE DU SUD Cl. Besnard Museum Paris Coll. P. Ardoin 1978, two specimens". "RSA W CAPE NATURES VALLEY env., 24.1.2001 LGT. M. SNIZEK".

Distribution

South Africa: Eastern Cape, Western Cape (Map 50).



Map 50. Distribution of *Isoncophallus angulicollis* Koch.

2. *Isoncophallus avontuurensis* Koch

Isoncophallus avontuurensis Koch, 1954b: 58.– Kamiński 2016: 239.

Diagnosis

Of the species with inset tarsal attachments, *I. avontuurensis* is the most difficult to identify. It is easily separated from *I. angulicollis* using the pronotal shape (see *I. angulicollis* diagnosis); however, *I. campester* and *I. zabroides* are only differentiable with male specimens on hand. *Isoncophallus avontuurensis* is the only species without hind tibial setae in the males.

Material examined

Holotype, male **TMNH** (Fig. T69): "Avontuur, 2. Juli 1920, leg. R. E. Turner".

Distribution

South Africa: Western Cape (Map 51).



Map 51. Distribution of *Isoncophallus avontuurensis* Koch.

3. *Isoncophallus campester* Koch

Isoncophallus campester Koch, 1954b: 58.– Kamiński 2016: 239; Lumen *et al*. 2025: 6.

Diagnosis

Similar to *I. avontuurensis*, this is a difficult species to separate from similar congeners (*I. avonturrensis* and *I. zabroides*). As in *I. avontuurensis*, male hind tibiae are the easiest way to diagnose them. *Isoncophallus campester* has a small, thick patch of hind tibial setae situated near the middle. In contrast, *I. zabroides* has a long, thinner patch of setae running the apical 2/3rds of the length of the tibia.



Map 52. Distribution of *Isoncophallus campester* Koch.

Material examined

While the holotype was not examined in this study, it should be located in **IMSA** and bear the label data: "George Distrikt, Aug. 1931, leg. C. W. Thorne".

Paratype, sex undetermined **TMNH** (Fig. T70): "George Capland Dr. Brauns. 6/9/6 PARATYPE No: 1744 Isoncophallus campester KOCH Paratypus ISONCOPHALLUS campester C. Koch sp.n."

MIZPAN: "POI 32 6 Oct Tenebrionidbase Aaron D. Smith 26388". **MNHN**: "14.XII1969 Mossel Bay AFRIQUE DU SUD Cl. Besnard leg. Museum Paris Coll. P. Ardoin 1978 (two specimens)". **SANC**: "SOUTH AFRICA, CP Waboomskraal, Outeniqua Mtns 33.52S 22.22E 7.ii.1985 W. Breytenbach NATIONAL COLL. OF INSECTS Pretoria South Africa".

Distribution

South Africa: Western Cape (Map 52).

4. *Isoncophallus crispiformus* sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:20FF0B29-25D2-4257-BA7C-8C783C381D8E

Diagnosis

This species belongs to the group of *Isoncophallus* without the off-set tarsal insertion of the foretibiae (apex of the foretibiae relatively truncate). From the other species of the group, *I. ornatipes* and *I. dentimanus*, are easily distinguishable based on obvious characteristics (see respective diagnoses). The remaining, most similar species within this group are: *I. ovanullum*, and *I. diffusus*. *Isoncophallus crispiformus* is distinguishable based on the punctation and texture of the pronotum and elytra, which are both far finer and less-shiny than in this species and *I. diffusus*. Finally, the sulcus of abdominal ventrite V is situated on the extreme apex in *I. ovanullum*, which sets it apart from all other representatives of *Isoncophallus*, wherein the sulcus is situated subapically farther from the margin. Finally, *I. crispiformus* is separable from all other species based on the aedeagus, which has parameres that are broadly curved (similar to *Byrrhoncus parvithorax*) and bent downward in lateral view.

Description

Length 8–9mm, width 3.5–4mm. **Head**: finely punctate, punctures somewhat crowded, separated by ≤1 feature diameter. Mentum with prominent median portion and exposed wings. Submentum triangular. Eye slightly impressed by genal canthus, well-developed. **Prothorax**: Pronotum finely punctate, punctures separated by ≥1 feature diameter. Apical, lateral, and basal margination of pronotal disc complete. Hypomeron almost impunctate, lightly sculptured/wrinkled. Prosternal process rounded in lateral view. **Pterothorax**: Elytron without tubercles on disc. With wrinkling to weak tubercles on apical decline. Rows puncto-striate, with punctures separated by ≤1 feature diameters. Intervals finely punctate. Elytral interval X terminates after hind coxae and before elytra base. Epipleuron narrower than width of elytral interval 10. Elytral intervals not obscured by epipleuron in ventral view. **Abdomen**: Finely punctate, with subapical sulcus on abdominal ventrite V. Legs: Male hind- and midtibiae with narrow strip of setae. Male pro/meso tarsi slightly enlarged. **Male terminalia**: Basal part longer than parameres. Parameres widely diverged basally and strongly curved apically and bent downward in lateral view.

Female terminalia: Ovipositor short; paraprocts roughly equal in length to combined length of coxites I–IV. Bursa copulatrix sac-like with thick and coiled spermatheca and with no sclerites or additional pouches.

Material examined

Holotype male **NMNW** (Fig. T71): "Bainskloof (Limietberge) 33°33'S, 19°08'E. CAPE, R.S.A. 3 Oct 1974, H21379, Namibian National Insect Collection State Museum P.O. Box 1203 WINDHOEK, Namibia". **Paratype** female **NMNW**: Same data as holotype.

Etymology

This species is named for the shape of the uniquely (for the genus) curved parameres of the aedeagus.

Distribution

South Africa: Western Cape (Map 53).



Map 53. Distribution of *Isoncophallus crispiformus* **sp. nov.**

5. *Isoncophallus dentimanus* Koch

Isoncophallus dentimanus Koch, 1954b: 59.– Kamiński 2016: 240.

Diagnosis

Isoncophallus dentimanus (along with *I. ornatipes* and *I. angulicollis*) is one of the most straightforward species to diagnose in the genus. The foretibiae lack a strongly inset portion at the apex; however, they have a strong, broad projection or tooth extending laterally from the apex of the foretibiae (resembling *Oncotus*).

Material examined

Holotype female **TMNH** (Fig. T72): "Kogman's Kl., Montague", "R. Lawrence 1922".

MNHN: "Museum Paris Coll De Marseul 1890, blue circle label with faded writing, Cap B Sp".

Distribution

South Africa: Western Cape (Map 54).



Map 54. Distribution of *Isoncophallus dentimanus* Koch.

6. *Isoncophallus diffusus* Koch

Isoncophallus diffusus Koch, 1954b: 60.– Kamiński 2016: 240.

Diagnosis

Most similar to *Isoncophallus ovanullum* and *I. crispiformus*. *Isoncophallus ovanullum* is easily separable by the sulcus on abdominal ventrite V (present on extreme apical margin); however, *I. crispiformus* appears to only be separable by the morphology of the male aedeagus which strongly differs from all other *Isoncophallus* (see *I. crispiformus* diagnosis).

Material examined

While the holotype was not directly examined here, it should be deposited at **IMSA** with the label data "Ceres, 1900, leg. R. Lightfoot".

Paratypes, male **NHMUK** and female **TMNH** (Fig. T73-74): Same data as holotype.



Map 55. Distribution of *Isoncophallus diffusus* Koch.

Distribution

South Africa: Western Cape (Map 55).

7. *Isoncophallus ornatipes* Koch

Isoncophallus ornatipes Koch, 1954b: 58.– Kamiński 2016: 240.

Diagnosis

This species belongs to the truncate foretibia group of *Isoncophallus*. It differs from all other species of *Isoncophallus* by the abbreviated subapical sulcus of abdominal ventrite V, and is generally smaller and slimmer than other species.

Material examined

Holotype, male **TMNH** (Fig. T76): "Cap / Oncotus simplex in litt / Holotype no. 1747 / Isancophallus ornatipes KOCH / Ornatipes / KOCH". **Paratype** (Fig. T75): Same data as holotype instead with allotype label "ALLOTYPE No: 1748 / Isancophallus / ornatipes KOCH".

TMNH: "S.Afr., W.Cape Prov. Calvinia 31.28S - 19.47 E 18.8.1983; E-Y: 1939 groundtraps,78 days leg. Endrödy, Penrith ground trap with banana bait".

Distribution

South Africa: Northern Cape (Map 56).



Map 56. Distribution of *Isoncophallus ornatipes* Koch.

8. *Isoncophallus ovanullum* sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:9BAFB36D-3A92-4092-9E2E-218E3FDB830E

Diagnosis

This species belongs to the group of *Isoncophallus* without the off-set tarsal insertion of the foretibiae (apex of the foretibiae relatively truncate). From the other species of the group, *I. ornatipes* and *I. dentimanus*, are easily distinguishable based on obvious char-

acteristics (see respective diagnoses). The remaining, most similar species within this group are: *I. crispiformus*, and *I. diffusus*. *Isoncophallus ovanullum* is distinguishable based on the punctation and texture of the pronotum and elytra, which are both far finer and less-shiny than in *I. crispiformus* and *I. diffusus*. Finally, the sulcus of abdominal ventrite V is situated on the extreme apex in *I. ovanullum*, which sets it apart from all other representatives of *Isoncophallus*, wherein the sulcus is situated subapically farther from the margin.

Description

Length 8mm, width 3.5–4.5mm. **Head**: finely to coarsely punctate, punctures widely spaced, (separated by ≥1 feature diameter) to closely spaced (≤1 feature diameter). Mentum with prominent median portion and exposed wings. Submentum triangular. Eye impressed by genal canthus, well-developed. **Prothorax**: Pronotum finely punctate, punctures separated by >1 feature diameter. Apical, lateral, and basal margination of pronotal disc complete. Hypomeron almost impunctate, lightly sculptured/wrinkled. Prosternal process rounded in lateral view. **Pterothorax**: Elytron without tubercles on disc. With weak tubercles on apical decline. Rows puncto-striate, with punctures separated by ≤1 feature diameters. Intervals very finely punctate. Elytral interval X terminates after hind coxae and before elytra base. Epipleuron narrower than width of elytral interval 10. Elytral intervals not obscured by epipleuron in ventral view. **Abdomen**: Finely punctate. Abdominal ventrite V with sulcus on extreme apex. **Legs**: Fore- and midtibiae expanded apically. Foretibiae truncate, without offset tarsal insertion. **Female terminalia**: Ovipositor short; paraprocts roughly equal in length to combined length of coxites I–IV. Bursa copulatrix sac-like, spermatheca thick and tube-like. No additional sacs, pouches, or sclerites. Ovoviviparous.

Material examined

Holotype, female **MNHN** (Fig. T77): "Oncotus obtusus cap (D.) Sol, red label (Holotype)". **Paratype**, female **MNHN**: "F. Bates 18.19, folded blue label (Obesus Dej c.b.sp. Rufus Meg?, yellow label (Paratype)".

Etymology

This species is named for the larvae found in the holotype's bursa copulatrix—indicating that this species is likely ovoviviparous.

Distribution

South Africa, further determination impossible based on label data.

9. *Isoncophallus zabroides* Koch

Isoncophallus zabroides Koch, 1954b: 57.– Kamiński 2016: 240; Lumen *et al*. 2025: 7

Diagnosis

The shape of the pronotum and setation of male hind tibiae are the best way to separate this and morphologically similar species. See preceding diagnoses of *Isoncophallus angulicollis*, *I. avontuurensis*, and *I. campester*.

Material examined

Holotype, male **TMNH** (Fig. T78): "Willowmore, 1. Sept. 1900, leg. H. Brauns".

MIZPAN: "Doodsklip 13/11/15 Tenebrionidbase Aaron D. Smith 26341". **SANC**: "Top van Swartberg pas 24-IX-1978 HOLM-SCHULTZ NATIONAL COLL. OF INSECTS Pretoria South Africa Ex UPSA, May 2002, (two specimens)". **TMNH**: "S. Afr. Swartberge Blesberg-E, 2000m 23.25S - 22.41E 7.3.1981; E-Y:1758 singled. night leg. Endrödy-Younga, (two specimens)".

Distribution

South Africa: Eastern Cape, Western Cape (Map 57).



Map 57. Distribution of *Isoncophallus zabroides* Koch.

xi. Genus *Psectrapus* Solier

Psectrapus Solier, 1848: 213.– Lacordaire 1859: 231; Koch 1954b: 63; 1956: 27; Bouchard *et al*. 2005: 510; 2021: 52; Lumen & Kamiński 2024b: 138; Lumen *et al*. 2025: 2.

=*Psectropus* Gemminger & Harold, 1870: 1911 (unjustified emendation).– Gebien 1938: 391; Kaszab 1941: 35, Bouchard *et al*. 2011: 422; Kamiński 2016: 245; Kamiński *et al.* 2021: 152. Type species: *Psectrapus bipartitus* Solier, 1848; by original designation.

Type species: *Psectrapus bipartitus* Solier, by original designation.

Diagnosis

The definition of *Psectrapus* presented here follows Lumen *et al*. (2025). The genus most resembles *Isoncophallus*, *Byrrhoncus*, *Colophonesthes*, and *Colophonexsula* (see respective diagnoses for more details). To reiterate some of what is already mentioned in the preceding diagnoses, *Psectrapus* can be distinguished from *Colophonexsula* by the shape of the pronotum, which is generally rounder and nearly as wide basally as the elytra in *Psectrapus* (more elongate and slightly narrower than elytra in *Colophonexsula*), and with more strongly tapered and closer spaced parameres in males (*Colophonexsula* with wider-spaced parameres with weaker taper). *Psectrapus* also, generally, displays some of the strongest sexual dimorphism in the *Psectrapus* lineage (exception: *Colophonexsula puerilis* where males are markedly more gracile than the females as in *Psectrapus byki*). *Psectrapus* males have strongly exaggerated tarsi, and some species show strong dimorphism in size (e.g., larger females in *P. byki*). While other genera also have larger tarsi in the males, they are either less dilated, or differentiable by the suite of other characteristics presented in the preceding entries. Additionally, only females of *Psectrapus* have a sulcus on abdominal ventrite V (present in males & females of Isoncophallus, absent in *Byrrhoncus*, *Capidium*, *Colophonesthes*, and *Colophonexsula*).

Species included (5)

P. bipartitus Solier, *P. byki* Lumen & Kamiński, *P. distaticum* **sp. nov.**, *P. latimentulum* **sp. nov.**, *P. simplicimentulum* Lumen & Kamiński.

Key to species of *Psectrapus* males (see Plate xi for figures):

Many diagnostic characters are based on male specimens and characteristics—specifically the aedeagus and leg setation; without these, specimens may be difficult or impossible to identify with complete certainty. Additionally, female specimens remain unknown, missing, or otherwise underrepresented for some species, making female identification tenuous. As a result, even some specimens examined during this study remain without confident identifications.

1. Penis bifurcated (with two hooks) (Figs 1–2) **2**

— Penis single, unbifurcated hook **3**

2. Mentum midpart broad, square-shaped and nearly concealing lateral wings (Fig. 3). With large fore- and midtibial setal patches (Figs 5–6). Parameres with smoothly tapered margins (as in Figs 8–10). Pronotum dull (Fig. 11). Elytra dull, with smaller strial punctures and fine interval punctation (Fig. 13). Abdominal ventrite V with well-separated punctation (Fig. 15) ..... ***Psectrapus bipartitus***

— Mentum midpart less broad, rectangular and with well-exposed lateral wings (Fig. 4). With small or narrow strip of setae on fore- and midtibiae. Parameres with lateral sinuation near base before tapering toward the apex (Fig. 7). Pronotum shinier (Fig. 12). Elytra shiny, with larger punctation, interval punctures more well-defined (Fig. 14). Abdominal ventrite V punctation highly crowded–almost convergent/confluent (Fig. 16) .... ***Psectrapus latimentulum* sp. nov.**

3. Pronotal base bisinuate (Fig. 17). Parameres narrowed subapically (resulting in a widened window exposing the penis) (Fig. 8). Two puncture types on abdominal ventrite V (Fig. 19) ... . ***Psectrapus byki***

— Pronotal base not bisinuate. Parameres without subapical narrowing, evenly tapered toward apex (penis window slender/ovular and uniform) (Figs 9–10). Single or two puncture types on abdominal ventrite V **4**

4. Hind tibiae with setal patch (Fig. 18). Abdominal ventrite V with single puncture type .... ***Psectrapus distaticum* sp. nov. (Zimbabwe, Bulawayo)**

— No setal patches on hind tibiae. Abdominal ventrite V with two puncture types (Figs 20–21) ..... ***Psectrapus simplicimentulum* (South Africa, Western Cape)**

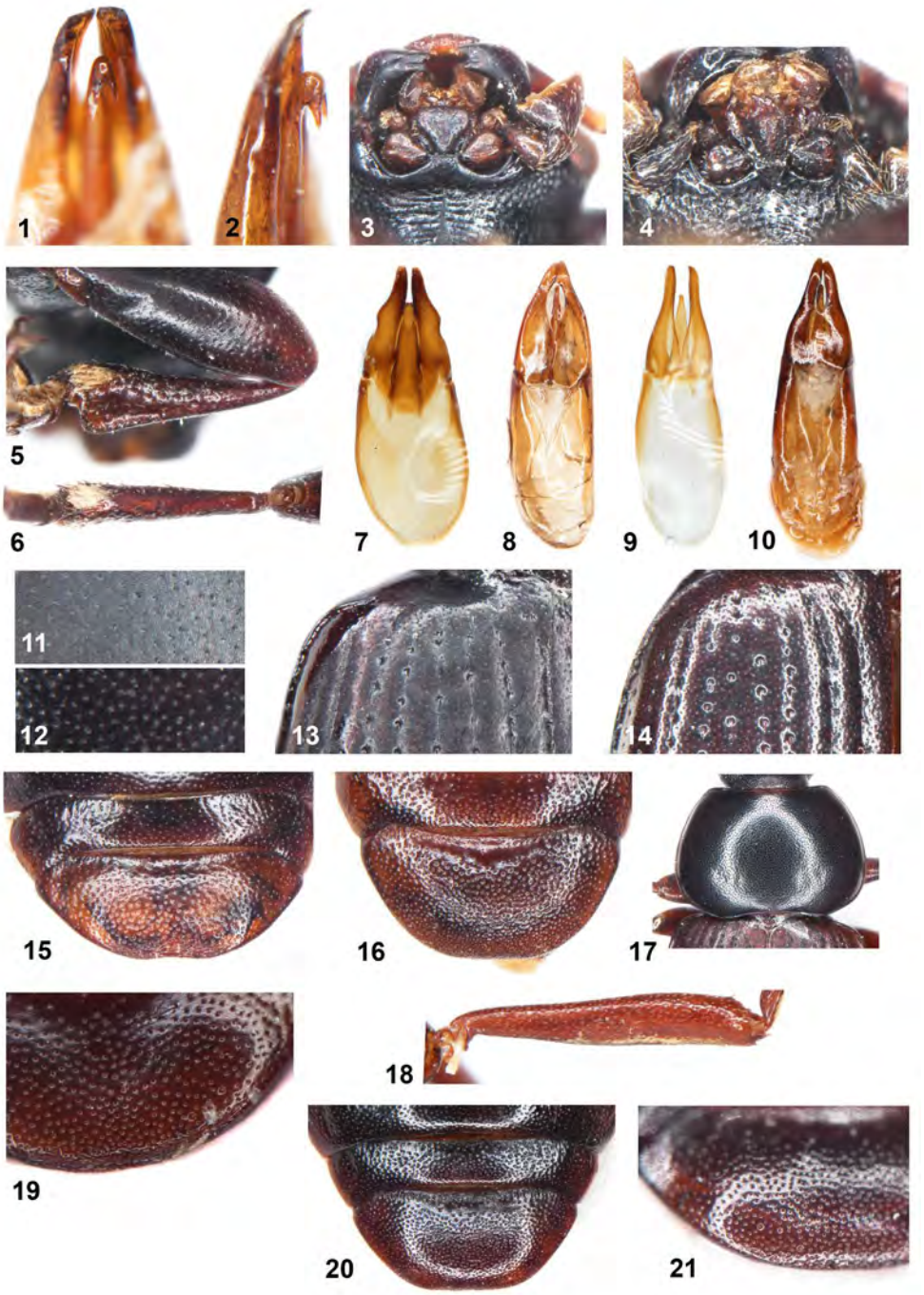


Plate xi. *Psectrapus* species diagnostic features: **Anatomic features**: Aedeagus (1–2, 7–10). Mentum (3–4). Foreleg (5). Midleg (6). Pronotum (Disc punctures: 11-12. Dorsal: 17). Elytron humerus (13–14). Abdominal ventrite V: (15–16, 19–21). Pronotum (17). Hindtibia: 18. Abdominal Ventrite V: 16–17. **Taxa depicted**: *Psectrapus bipartitus* (1, 2, 3, 5, 6, 11, 13, 15). *Psectrapus byki* (8, 17, 19). *Psectrapus distaticum* (9, 10, 18). *Psectrapus latimentulum* (4, 7, 12, 14, 16). *Psectrapus simplicimentulum* (20, 21).

1. *Psectrapus bipartitus* Solier

Psectrapus bipartitus Solier, 1848: 215.– Lacordaire 1859: 231, Bouchard *et al*. 2021: 318; Lumen *et al*. 2025: 10.

Psectropus bipartitus (Solier, 1848).– Gemminger & Harold, 1870: 1911; Gebien 1938: 391; Kaszab 1941: 37; Koch 1954b: 66; Kamiński 2016: 246.

Diagnosis

Psectrapus bipartitus has a uniquely matte or silky habitus. Compared to the rest of the genus, *P. bipartitus* has less-strongly defined punctation of both the elytra and pronotum. Other genera have shinier elytra, pronota, and more well-defined punctation. Additionally, *P. bipartitus* is the only species (aside from *P. latimentulum*) with two hooks on the penis in males. *Psectrapus latimentulum* is further separable based on the shape of the parameres (with subapical lateral protuberances, giving the parameres a spade-like shape versus evenly tapered in *P. bipartitus*).

Material examined

Neotype, male, designated in Lumen *et al*. (2025) **MNHN** (Fig. T79): Blue circle label "Oncotus obtusus Cap. Bon Esp.", White label "Museum Paris Coll. DE MARSEUL 1890" Red label "Psectrapus bipartitus LECTOTYPE".

MNHN: "Caffraria coll. R.Oberthur ex coll. Deyrolle", "Cap. b. sp. coll. R.Oberthur ex coll. Deyrolle Oncotus obtusus Deyr. var. C.B.Esp"

Distribution

South Africa; further specificity impossible based on label data.

2. *Psectrapus byki* Lumen & Kamiński

Psectrapus byki Lumen & Kamiński in Lumen *et al*. 2025: 21.

Diagnosis

Psectrapus byki is unique for the strong medial narrowing of the aedeagal parameres before expanding again toward the apex; giving rise to a uniquely shaped window exposing the penis. Additionally, this species has a more pronounced medial indentation of the pronotal base compared to other species. From *P. bipartitus* the males can be separated by a lessened degree of foretarsal widening: preapical foretarsomere in males of *P. bipartitus* is more than twice as narrow vs. the second tarsomere, in *P. byki* this relation is *ca*. 1.5). The type series is from Gamkaberg.

Material examined

Holotype, male **TMNH** (Fig. T80): "S. Afr: Little Karroo Gamkabg.deBrug 1000m, 33.43 S -21.57 E 15.5.1995: E-Y 3082, groundtraps. 30 days, leg. Tom Berry.". **Paratypes**, female **MIZPAN**: same data as holotype; male **MIZPAN**: "S. Afr: LittleKarroo Gamkaberg 1000m 33.44 S - 21.57 E", "15.5.1994: E-Y: 3074 groundtraps 30 days, leg. Tom Berry"; male **TMNH**: "S. Afr: LittleKarroo Gamka tourist camp, 33.42 S - 21.34 E", "25.10.1993: E-Y: 2903 window trap, leg. Endrödy-Younga"; female **TMNH**: "S. Afr: W Cape Prov. Gamkaberg Nat. Res. 33.42 S - 21.57 E", "1.7.1998: E-Y: 3240 groundtraps, leg. Tom Berry".

Distribution

South Africa: Western Cape (Map 58).



Map 58. Distribution of *Psectrapus byki* Lumen & Kamiński.

3. *Psectrapus distaticum* sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:F2C95DAA-8644-4AA8-BD1D-4BD44EFC59D9

Diagnosis

Psectrapus distaticum is most similar to *P. simplicimentulum*. From the rest of *Psectrapus* it can be differentiated by the structure of the aedeagus (relatively simple; with narrow window between parameres, which are long and tapered, and with a single hook on the penis). Additionally, this species can be differentiated by the tibial setae (missing in *P. simplicimentulum*), and the abdominal punctation (two types in *P. simplicimentulum*, only one in *P. distaticum*). Finally, this species is based on a single male specimen collected in Bulawayo, Zimbabwe, which is far-removed from all other species of *Psectrapus*. Nevertheless, both its morphology and distribution sets it apart from other, similar species (see diagnosis for *P. simplicimentulum*).

Description

Length 6mm, width 3mm. Colored tenebrous; dark brown to black. **Head**: Puncate, punctures crowded (≤1 puncture diameter apart) in distribution. **Prothorax**: dorsally without large, widely spaced setae and punctures situated on lateral edges. **Pterothorax**: Elytral striae strongly impressed and punctate. Intervals with bumps or tubercles present on apical declivity. **Abdomen**: Without larger setigerous punctures intermixed amongst smaller punctures. **Legs**: femurs laterally compressed, slightly curved and thickened. Tibiae straight to slightly curved; males with apical setal strips running apical 2/3rds. **Male terminalia**: Parameres relatively narrowly separate and strongly narrowing apically. Penis strongly sclerotized with pronounced, unbifurcated apical hook.

Material examined

Holotype, male **TMNH** (Fig. T81): "Bulawayo (Rhodesia), G. B. Mal 1913, Red "Holotype" label".

Etymology

Specific epithet refers to the species' type locality (Bulawayo, Zimbabwe)—distant from all other current representatives of the genus restricted to South Africa.

Distribution

Zimbabwe: Bulawayo (Map 59).



Map 59. Distribution of *Psectrapus distaticum* **sp. nov.**

4. *Psectrapus latimentulum* sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:B3FD97B5-AFCB-42A2-8A62-EF441146B858

Diagnosis

Psectrapus latimentulum has unique lateral sinuation or protuberances of the aedeagal parameres, giving them a "spade-like" shape. It is also, aside from *P. bipartitus*, the only species with a bifurcated hook on the apex of the penis. From *P. bipartitus* this species can be differentiated by the luster of the cuticle (shinier or smoother rather than dull/lightly textured in *P. bipartitus*). Type series is from Worcester, South Africa.

Description

Length 6.5–7mm, width 3.0–3.5mm. **Head**: finely punctate, punctures closely spaced, separated by ≤1 feature diameter. Mentum with prominent median portion and exposed wings. **Prothorax**: Pronotum finely punctate, punctures separated by 1-2 feature diameters. **Pterothorax**: Striae punctato-sulcate with coarse punctures separated by 1-2 feature diameters. Intervals finely punctate. **Abdomen**: Finely punctate. Abdominal ventrite V densely punctate, punctures separated by ≤1 feature diameter to confluent. **Legs**: Male hind tibiae very slightly flattened/twisted, appearing bent, covered with setal patch in apical half. Male pro/meso tarsi enlarged, with ventral, tomentose pads. **Male terminalia**: Parameres with lateral protuberances, then strongly narrowed towards apex.

Material examined

Holotype, male **TMNH**: "Cape Province Worcester., 17-31.viii.1928.", "S. Africa, B.E. Turner, Brit. Mus. 1928-421". **Paratypes**, 2 males **TMNH**, **MIZPAN**: same data as holotype.

Etymology

Specific epithet refers to the expansion of the outer perimeter of the parameres in males.

Distribution

South Africa: Western Cape (Map 60).



Map 60. Distribution of *Psectrapus latimentulum* **sp. nov.**

5. *Psectrapus simplicimentulum* Lumen & Kamiński

Psectrapus simplicimentulum Lumen & Kamiński in Lumen *et al*. 2025: 21.

Diagnosis

Superficially most similar to *P. bipartitus* and *P. distaticum* (species with simply tapered parameres and without bisinuate pronotal base); however, can be differentiated from *P. bipartitus* by the penis with a single, unbifurcated hook and denser punctation (penis bifurcated and punctation finer in *P. bipartitus* respectively). *Psectrapus simplicimentulum* lacks secondary sexual characteristics present in other species; namely, the additional setation on the tibiae of males; further, *P. simplicimentulum* possesses two puncture types on abdominal ventrite V (both leg setation and abdominal punctation separate it from *P. distaticum*).



Map 61. Distribution of *Psectrapus simplicimentulum* Lumen & Kamiński.

Material examined

Holotype, male **NHMUK** (Fig. T83): S. Africa. R. E. Turner Brit. Mus. 1921–248., Mossel Bay Cape Province May, 1921, Psectrapubs bipartitus Sol., Psectrapus bipartitus C. Koch det., 1952, Blue label: Tenebrionid Base Aaron D. Smith Catalog # 26334, Red Holotype Label. **Paratype NHMUK**: "Same data as Holotype, additional labels: Psectropus bipartitus Sol. det. ?.G. Blair, Oncotus ? sp. M.J.D.Brendell det. 1975, Yellow "paratype" Label", "S. Afr. Cape Prov. 20 miles SE Swellendam 3.I.51, Swedish South Africa Expedition 1950–1951 Brinck – Rudebeck, yellow "paratype" Label.".

Distribution

South Africa: Western Cape (Map 61).

F. *Oncotus* lineage

***Genera included* (8)**: *Anamenederes*, *Hirtograbies*, *Menederes*, *Ograbies*, *Oncotus*, *Phaleriderma*, *Quadroncotus*, *Stridigula*.

Key to genera of *Oncotus* lineage (see Plate F for figures):

1. Elytra with small setose pit at base (Fig. 1) ..... ***Stridigula***

— Elytra base without setose pit **2**

2. Hypomeron with large, free setae and/or with long setae on the inner margin of forelegs (Figs 2–3) **3**

— Hypomeron without setae or at most with small, appressed setae; never with long setae on inner margin of forelegs **6**

3. Large setae on dorsum of elytra (Fig. 4) (sometimes reduced or absent in *Hirtograbies gariepinus* and *Phaleriderma obscuricollis*). Without well-defined carina on epistoma margin **4**

— Elytra glabrous. Epistoma with well-defined and complete carina on margin (Fig. 5) **5**

4. Epistoma and clypeus differentiable (with clear delineation) (Fig. 6). Anterior border of pronotum incomplete (Fig. 9) ..... ***Phaleriderma***

— Epistoma and clypeus fused (without clear delineation) (Fig. 7). Anterior border of pronotum complete (Fig. 10) ..... ***Hirtograbies***

5. Foretibiae broad, often with slight emargination/narrowing in the middle, giving a "boot" shape, or with strong lateral emargination leaving two projections along lateral edge (Figs 11–12). Elytra delicate or hyaline in most species (Fig. 15). Apical edge of epistoma with complete carina (Fig. 5). Most species with long, free-standing setae on hypomeron (Fig. 2) ..... ***Ograbies***

— Foretibiae expanded apically but without, or with much less-defined, median emargination (Figs 13–14, 18–19). Elytra well-sclerotized. Never with long free-standing setae on hypomeron. Apical edge of epistoma with complete (similar to Fig. 8 as in *Menederes constrictus*) or medially interrupted/obfuscated carina (Fig. 8) **6**

6. Last elytral interval interrupted with large, scattered punctation (Figs 16–17) .... ***Menederes***

— Last elytral interval uninterrupted by punctation **7**

7. Foretibiae with long, skinny, finger-like projection off lateral edge of apex, with additional projection near-to tarsal insertion (Fig. 14) ..... ***Anamenederes***

— Without finger-like apical foretibiae, without additional projection by tarsal insertion ... **8**

8. Outer margin of foretibiae smooth, without irregular bumps or cragginess (Fig. 18). Pronotal disc with fine punctation. Basal angles of pronotum relatively triangular with slight depressions or dimples at the corners (Fig. 20). Antennae longer than head width ..... ***Oncotus***

— Outer margin of foretibiae irregular, bumpy and/or cragged (Fig. 19). Pronotal disc with coarser punctation. Basal angles of pronotum more rounded and without depressions (Fig. 21). Antennae subequal to head width in length ..... ***Quadroncotus***

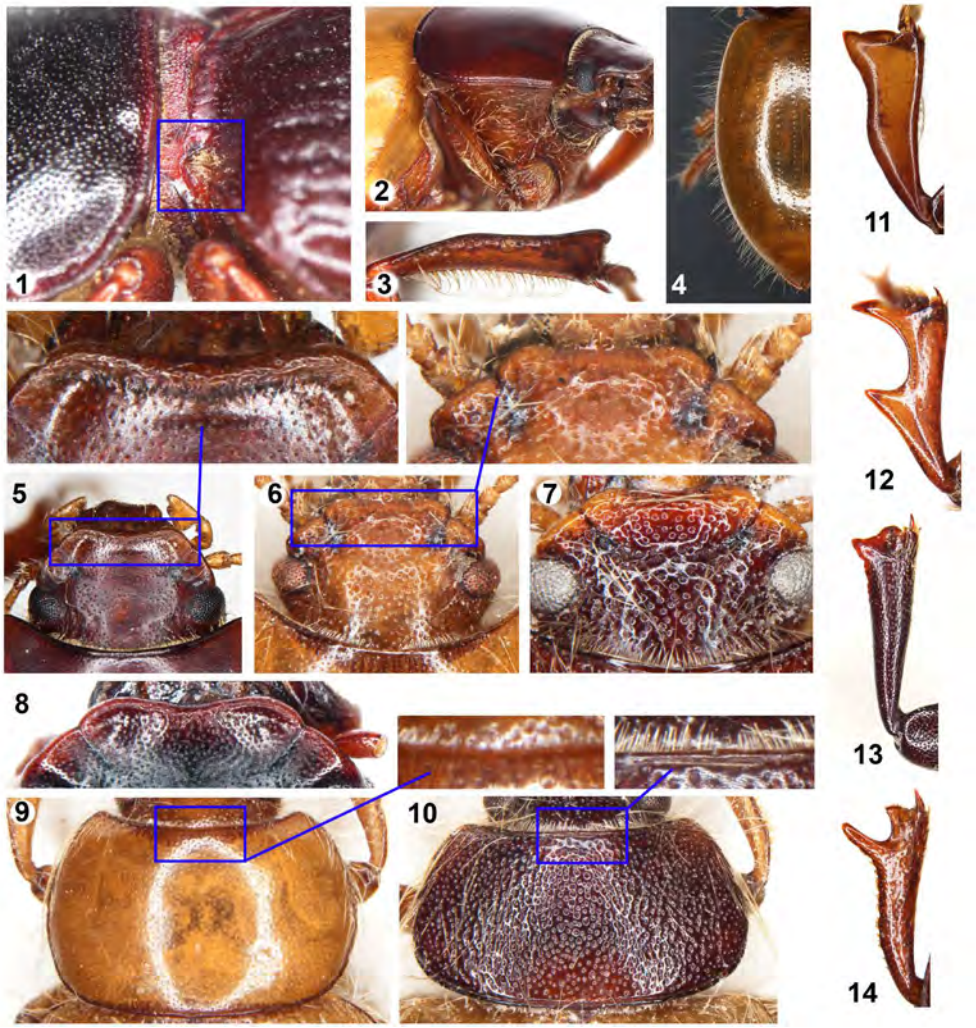


Plate F. part 1. *Oncotus* lineage. Genera diagnostic features. **Anatomic features**: Elyron humeral setose pit (1). Hypomeron (2). Foretibia (Posterior: 3. Anterior: 11–14). Elytron (4). Epistoma (5–8) (Close-up of carina: 5–6, 8). Pronotum (9–10) (with close up of anterior border). **Taxa depicted**: *Anamenederes digitatus* (14). *Hirtograbies canicautis* (7, 10). *Hirtograbies nanus* (4). *Menederes dannheimeri* (13). *Ograbies bidentimanus* (12). *Ograbies testaceus* (2, 3, 5, 11). *Oncotus farctus* (8). *Phaleriderma husserli* (6, 9). *Stridigula planiuscula* (1).



Plate F. part 2. *Oncotus* lineage. Genera diagnostic features. **Anatomic features**: Last lateral elytral interval (16–17). Foretibiae (18–19). Pronotum (20–21). **Taxa depicted**: *Menederes dannheimeri* (16, 17). *Ograbies testaceus* (15). *Oncotus cedrimontis* (18). *Oncotus farctus* (20), *Quadroncotus irrepertus* (19, 21).

xii. Genus *Anamenederes* Koch

Anamenederes Koch, 1954b: 68.– Kamiński 2016: 240; Bouchard *et al*. 2021: 100; Lumen *et al*. 2025: 5.

Type species: *Menederes digitatus* Koch; by original designation.

Diagnosis

This monotypic genus is slightly globose, similar to *Oncotus* and *Ograbies*. From *Ograbies* it differs by the shape of the foreleg (broad and boot-shaped in *Ograbies*, less broad and with narrow lateral projection and finger-like projection by tarsus in *Anamenederes*), and setae on the hypomeron (long and free in *Ograbies*, absent or short and appressed in *Anamenederes*. Overall *Oncotus* is more similar to *Anamenederes*; however, they can be separated by the morphology of the pronotum (with basal angles more triangular and with slight depressions or dimples in *Oncotus*; rounded and lacking depressions in *Anamenederes*) and the foreleg (broader lateral projection and without finger-like projection near tarsus in *Oncotus*). Finally, *Anamenederes* is unique within Eurynotina for its morphology of the foretibia, which bears an elongate projection near the tarsus insertion point, and a longer, thinner (compared to *Oncotus*) lateral projection of the tibiae.

Species included (monotypic)

A. digitatus Koch.

1. *Anamenederes digitatus* (Koch)

Menederes (*Anamenederes*) *digitatus* Koch, 1954b: 68.– Kamiński 2016: 240; Bouchard *et al*. 2021: 100.

Anamenederes digitatus (Koch, 1954b).– Lumen *et al*. 2025: 18.

Diagnosis

See diagnosis of the genus *Amanederes*.

Material examined

While the holotype was not examined here, it should be a male specimen at **IMSA** bearing the label data: "Garies, Juni 1930, leg. Mus. Personal".

Paratypes, male and 9 females **IMSA**, **NRS** and **TMNH** (Fig. T84): same data as holotype; female **IMSA**: "Kamieskroon, Sept. 1930, leg. Mus. Personal."

MIZPAN: "Kamieskroon 17May2017 Tenebrionidbase Aaron D. Smith 26347".

Distribution

South Africa: Northern Cape (Map 62).



Map 62. Distribution of *Anamenederes digitatus* (Koch).

xiii. Genus *Hirtograbies* Koch

Hirtograbies Koch, 1954b: 23.– Koch 1956: 27; Kamiński 2016: 238; Bouchard *et al*. 2021: 210; Kamiński *et al*. 2021: 152; Lumen *et al*. 2025: 2.

Type species: *Hirtograbies oograbiensis* Koch; by original designation.

Diagnosis

Globose—similar to many other genera in the *Oncotus* lineage. However, *Hirtograbies* falls into the group of genera that are more hirsute (*Ograbies*, *Phaleriderma*, and *Hirtograbies*), and are separable, *iter alia*, their long, free setae on the hypomeron. *Phaleriderma* and *Hirtograbies* are further differentiable by the strong setation of the pronotal margins. *Ograbies* has uniquely chamfered forelegs that are strongly dilated and emarginated on the outer margin (giving them a "boot" shape) and lacks setation on the elytra. The most similar genus is *Phaleriderma*, which has a similarly hirsuite habitus (setation of the elytra and pronotum) and similarly expanded foretibiae. However, *Phaleriderma* has foretibiae that are widely expanded triangularly without apical projections, and anterior pronotal margin incomplete; while *Hirtograbies* often have slightly less-dilated foretibia with a lateral projection apically (somewhat similar to *Oncotus*), and a complete anterior pronotal margin.

***Species included* (5)**

H. canicautis Koch, *H. gariepinus* Koch, *H. longipilis* (Péringuey), *H. nanus* Koch, *H. oograbiensis* Koch.

Key to species of *Hirtograbies* (see Plate xiii for figures):

1. Basal pronotal margin interrupted medially (Fig. 1). Habitus darkly colored (tenebrous, black to dark brown); unicolored to bicolored; when bicolored, with low contrast between pronotum/head and elytra (both darkly colored). Glabrous elytra (Fig. 6). Largest species (≥7mm) ..... ***Hirtograbies gariepinus***

— Basal pronotal margin uninterrupted medially (Figs 2–5). Habitus mostly lightly colored (tawny/yellow brown to cherry red); when bicolored with high contrast between darker head/pronotum and lighter elytra. Setose elytrae (Figs 7–9). Generally smaller species (most ≤ 8 mm) **2**

2. Pronotum disc widest in middle (Fig. 2) ..... ***Hirtograbies longipilis***

— Pronotum widest basally (Figs 3–5) **3**

3. Pronotum finely and moderately punctured, punctures never confluent. Body colored brown to reddish; head/pronotum slightly darker (Fig. 3) ..... ***Hirtograbies nanus***

— Pronotum coarsely and densely punctured, punctures often (not always) confluent (Figs 4–5). Strongly contrasting dark head/pronotum versus lightly colored yellow to brown elytra **4**

4. Larger (7–9mm). Pronotum strongly transverse (2-3x wider than long), punctures less confluent on disc (Fig. 4) ..... ***Hirtograbies oograbiensis***

— Smaller (5.75–6.5mm). Pronotum less transverse (~2x wider than long), laterally wrinkled, punctures often confluent on disc (Fig. 5) ..... ***Hirtograbies canicautis***

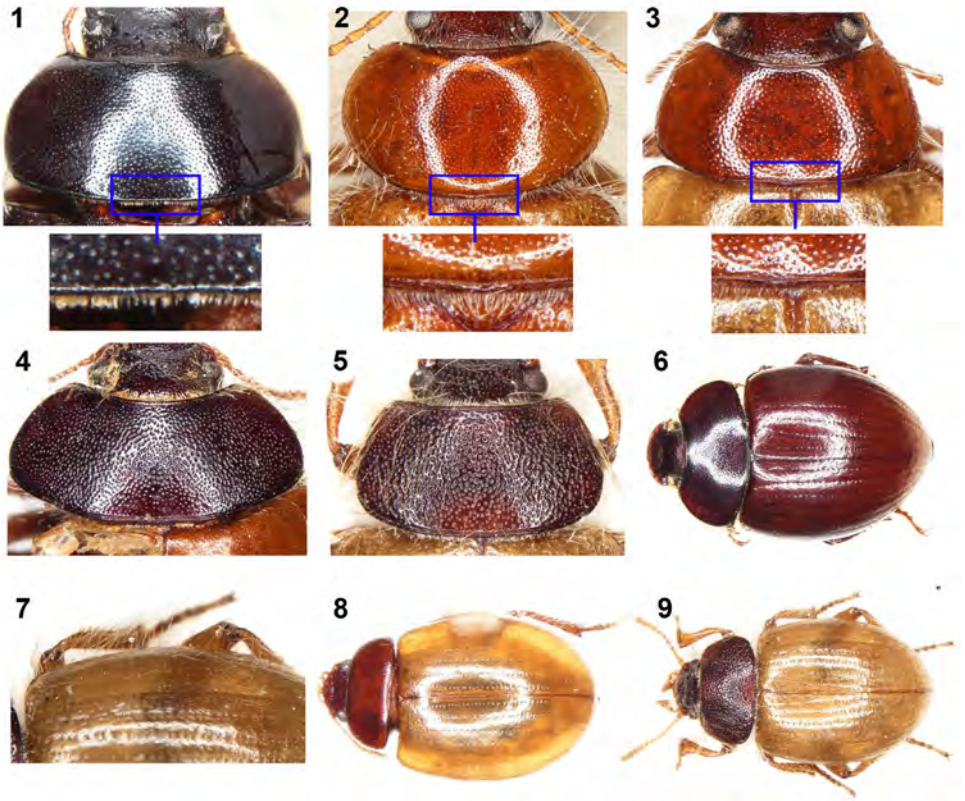


Plate xiii. *Hirtograbies* species diagnostic features. **Anatomical features**: Pronotum (dorsal) (1–5). Elytron (7). **Taxa depicted**: *Hirtograbies canicatus* (5, 7, 9), *Hirtograbies gariepinus* (1, 6), *Hirtograbies nanus* (3, 8), *Hirtograbies longipillis* (2), *Hirtograbies oograbiensis* (4).

1. *Hirtograbies canicautis* Koch

Hirtograbies canicautis Koch, 1954b: 30.– Kamiński 2016: 238, Lumen *et al*. 2025: 7.

Diagnosis

Along with *H. nanus* and *H. longipilis*, one of the smaller species of *Hirtograbies* (5.75–6.5mm). The larger species (*H. gariepinus* and *H. oograbiensis*), in addition to their size (>7 mm), can be differentiated from *H. canicautis* based on glabrous elytra (*H. gariepinus*) and width and transverse-ness of the pronotum–much wider and more transverse in *H. gariepinus* and *H. oograbiensis*. *Hirtograbies canicautus*, along with *H. oograbiensis*, is differentiable from other species by the presence of confluent punctures of the pronotum (laterally wrinkled and with more confluence on the disc in the case of *H. canicautus*); other small species (*H. longipilus* and *H. nanus*) lack confluent punctures of the pronotum. Additionally, *H. canicautis* and *H. oograbiensis* are the only bicolored (dark head/pronotum and tawny/light elytra) species; other species may have slightly darker head/pronota, but are overall more uniformly colored.

Material examined

Holotype, sex undetermined **TMNH** (Fig. T86): "Hondeklip Bay," / "C.P. 15-XI-1948" / "Koch & van Son" / "HOLOTYPE No: 1605" / "Hirtograbies canicautis KOCH" / "canicautis Koch" / "camicantis C.Koch det., 195".

TMNH: "S.Afr., SW Cape Papendorp dunes 31.38 S - 18.12 E 21.8.1981; E-Y: 1826 night, red dunes leg. Endrödy-Younga (five specimens, one with TenebrionidBase Catalog label #26323)", "S.Afr., Northern Cape Noup; 49m 30.07 S - 17.12 E 27.2-3.2010;E-Y 3881 pitfall traps leg. Robin Lyle", "S. Afr.: N Cape Prov. Port Nolloth VII.1978: E. Holm".

Material identified in this study increased the representation of specimens for this species from only the holotype to include seven additional specimens.

Distribution

South Africa: North Cape, Western Cape (Map 63).



Map 63. Distribution of *Hirtograbies canicautis* Koch.

2. *Hirtograbies gariepinus* Koch

Hirtograbies gariepinus Koch, 1954b: 26.– Kamiński 2016: 238, Lumen *et al*. 2025: 6.

Diagnosis

The largest (≥7mm) and most apomorphic species of the genus. While this species lacks setation of the elytra, and has more strongly dilated foretibia compared with other species of the genus, morphological examination always closely allies this species with other *Hirtograbies* (Fig. 2 Introduction). Overall resembling a setose *Oncotus*, this species is clearly affiliated with *Hirtograbies* based on the pronotal setation (strong, free standing on the hypomeron and with strong setae on the pronotal margin).

Material examined

Holotype, sex undetermined **TMNH** (Fig. T87): "Grootderm" / "Na.18.XI." / "1949.Koch" / "HOLOTYPE No: 1573" / "Hirtograbies" / "gariepinus KOCH" / "gariepinus Koch". **Paratype**, **TMNH** (Fig. T88): same data as holotype.

TMNH: "Tc.Alee mts. Richtersvld. II.53.C.Koch (four specimens)", "Anisfontein,Richtersveld, 22.XI.1949 C.Koch (three specimens)", "Brandkross, 2.??.195? Richtersveld. Koch".

Distribution

South Africa: Northern Cape (Map 64).



Map 64. Distribution of *Hirtograbies gariepinus* Koch.

3. *Hirtograbies longipilis* (Péringuey)

Ograbies longipilis Péringuey, 1908: 412.– Gebien 1938: 393.

Hirtograbies longipilis (Péringuey).– Koch 1954b: 28. Kamiński 2016: 239.

=*Hirtograbies brevicornis* Koch, 1954b: 20. **syn. nov.**– Kamiński 2016: 238.

=*Hirtograbies namibensis* Koch, 1954b: 27 **syn. nov.**– Kamiński 2016: 239.

Diagnosis

One of the smallest species (along with *H. canicautis* and *H. nanus* with which it shares some

similarities). *Hirtograbies longipilis* has widely rounded pronotal hind angles and an overall round or 'subquadrate' shape to the pronotum. *Hirtograbies canicautis* and *H. nanus* pronota are both wider at the base (more trapezoidal in shape), and *H. canicautis* has confluent punctures or highly wrinkled sculpturing of the pronotum.

Material examined

Hirtograbies longipilis: **Lectotype**, sex undetermined **NHMB** (Fig. T89): "V.03." / "Prince of" / "Wales-Bay" / "L.Schultze S." / "Coll FREY". Paralectotype, sex undetermined **MNHN** (Fig. T90): "DSW Afrika", "Prince of Wales Bay/L. Schultze S".

Hirtograbies namibensis: **Holotype**, sex undetermined **TMNH** (Fig. T91): "Bogenfels, S." / "Namib,1-XII-" / "48. Koch/Son" / "HOLOTYPE No: 1593" / "Hirtograbies" / "namibensis KOCH" / "namibensis" / "Koch".

Hirtograbies brevicornis: **Holotype**, sex undetermined **TMNH** (Fig. T85): "Grootderm, Rich-" / "tersveld." / "18.XI.1949.Koch" / "HOLOTYPE No: 1594" / "Hirtograbies" / "brevicornis KOCH" / "brevicornis" / "Koch".



Map 65. Distribution of *Hirtograbies longipilis* (Péringuey).

Status

As a result of this investigation, a specimen of *H. longipilis* matching the type locality and description by Péringuey was located from **NHMB**. Comparison with other specimens of *Hirtograbies*—in particular *H. namibensis* and *H. brevicornis* revealed stark similarities. Koch (1954b) described *H. namibiensis* and *H. brevicornis* based on singletons—no specimens have since been uncovered even in the course of this study. The divergences outlined by Koch between these three names (*H. namibensis*, *H. longipilis*, and *H. brevicornis*) include differences in setation which can be attributed to abrasion or specimen damage, and minute differences in measurements of the third antennomere. Further, the geographic distribution of all three entities appears to be coastal, running along the western edge of Sperrgebiet. Other *Hirtograbies* species (e.g., *H. canicautis*) have even larger ranges, supporting the new concept of *H. longipilis* presented here. Combined, we assert that this entity represents a well-delineated lineage within *Hirtograbes* differentiated based on pronotal shape & size.

While Koch (1954b) had a specimen on hand from **TMNH** that he interpreted as a paratype of *H. longipilis*, we found that Peringuey never selected a holotype for the spe-

cies, while the description was based on multiple specimens. We designate the **NHMB** specimen uncovered here as the lectotype for Peringuey's *H. longpilis* to formally fix the status of this species, as well as support our synonomies for *H. namibensis* and *H. brevicornis*.

Distribution

Namibia: ǂKaras (Map 65).

4. *Hirtograbies nanus* Koch

Hirtograbies nanus Koch, 1954b: 28.– Kamiński 2016: 239; Lumen *et al*. 2025: 9.

Diagnosis

See *Hirtograbies longipilis*. The closest species is *H. longipilis*, which can be differentiated by the shape of the pronotum (wider at the base in *H. nanus*) and general coloration (reddish–cherry versus brown).

Material examined

Holotype, sex male **TMNH** (Fig. T92): "Holgat,L.Namaqua-" / "ld., 2.IX.1950" / "C.Koch, G.van Son" / "HOLOTYPE No: 1595" / "Hirtograbies" / "nanus KOCH" / "nanus" / "Koch". **Paratype**, **TMNH**: data matching holotype, paratype label numbered "1598".

CASC: "S. AFRICA: Cape Jakkalsputs 350m 28°42'S, 16°54'E 15/16-IX-85 CL. Bellamy, AV Evans (two specimens, with additional barcode labels: CASENT 8590273 and 8590259)".

Distribution

South Africa: Northern Cape. Namibia: Erongo (Map 66).



Map 66. Distribution of *Hirtograbies nanus* Koch.

5. *Hirtograbies oograbiesensis* Koch

Hirtograbies oograbiensis Koch 1954b: 30.– Kamiński 2016: 239; Banaszkiewicz 2006: 63; Lumen *et al*. 2025: 14.

Diagnosis

Shaped similar to *Oncotus* and *H. gariepinus*, this species is differentiable from *Oncotus* based on *Hirtograbies* setal characteristics (see genus diagnosis) and from *H. gariepinus* by the setation of the elytra and sculpturing of the head/pronotum (with coarse and confluent punctation), and bicolored habitus (dark head/pronotum and light elytra versus darker and less contrasting in *H. gariepinus*). *Hirtograbies canicautis* is also similar in coloration and sculpturing (confluent punctation); however, they differ widely in size (*H. oograbiensis* 7mm–9mm versus *H. canicautis* c.a. 5mm), shape of the pronotum (much wider in *H. oograbiensis*), and in the nature of the sculpturing of their habitus (*H. oograbiensis* pronotum with less confluent punctation on the lateral margins of the dorsum).

Material examined

Holotype, male **TMNH** (Fig. T93): "Oograbies" / "L.Namaqualand" / "HOLOTYPE No: 1606" / "Hirtograbies" / "oograbiesensis" / "KOCH" / "oograbiesen" / "sis Koch". **Paratype**, **NHMB**: "Oograbies, L.Namaquald.,30.VIII.50 C.Koch, G.van Son COLL. FREY".

Distribution

South Africa: Northern Cape (Map 67).



Map 67. Distribution of *Hirtograbies oograbiesensis* Koch.

xiv. Genus *Menederes* Solier stat. nov.

Menederes Solier, 1848: 203.– Koch 1954b: 23; 1956: 27; Kamiński 2016: 238; Bouchard *et al*. 2021: 245; Kamiński *et al*. 2021: 152; Lumen *et al*. 2025: 6.

=*Archinamaqua* Schawaller, 2012: 80.– Kamiński & Schawaller 2019: 291 (syn.). Type species. *Archinamaqua lyleae* Schawaller, 2012; by original designation.

=*Menederopsis* Koch, 1954b: 16 **syn. nov.**– Koch 1956: 26; Kamiński 2016: 241; Bouchard *et al*. 2021: 52.; Kamiński *et al*. 2021: 152; Lumen *et al*. 2025: 2. Type species. *Menederopsis constricta* Koch, 1954b; by monotypy.

=*Menoncotus* Koch, 1954b: 34 **syn. nov.**– Kamiński 2016: 243; Bouchard *et al*. 2021: 246; Lumen *et al*. 2025: 2. Type species. *Oncotus* (*Menoncotus*) *chaetotaxicus* Koch, 1954b; by original designation.

Type species: *Menederes rufilabris* Solier; by original designation.

Status

In his revision of Eurynotina, Koch (1954b) described *Menoncotus* as a subgenus of *Oncotus*. Lumen *et al.* (2025) then revised the concept, noting that the subgenus grouped several atypical forms together and consequently elevated *Menoncotus* to genus rank while transferring two species (*O. capicola* and *O. cedrimontis*) to *Ograbies* and *Oncotus* respectively. The reinterpreted *Menoncotus* was rendered closely related to *Menederes* and *Menederopsis*—the three taxa forming a single clade (see introduction: Fig. 2). Closer investigation of all species here revealed close morphological affiliation(s): scattered punctation on the last elytral interval/stria and apically convergent or pointed parameres. Taking into account these morphological characters with Lumen *et al*.'s (2025) analyses, we propose the following synonymy: *Menederes* (=*Menoncotus* **syn. nov.**, =*Menederopsis* **syn. nov.**).

Diagnosis

Most similar to *Oncotus* and *Quadroncotus*. However, separable by the reduced basal angles of the pronotum (stronger and more angular in *Oncotus* with additional dimples on the hind corners) and scattered punctation of the last elytral interval (absent in both *Oncotus* and *Quadroncotus*). Also, *Quadroncotus* possesses additional sculpturing of the foretibiae (rough or ragged lateral edges, versus smooth and not ragged in *Oncotus* and *Menederes*).

***Species included* (5)**

M. chaetotaxicus (Koch) **comb. nov.**, *M. constrictus* (Koch) **comb. nov.**, *M. dannheimeri* Koch, *M. jokli* (Koch) **comb. nov.**, *M. rufilabris* Solier.

Key to species of *Menederes* (see Plate xiv for figures):

1. Abdominal ventrite V with apical sulcus (sometimes obliterated or otherwise reduced medially) (Figs 1–2) **2**

— Abdominal ventrite V without apical sulcus **3**

2. Foretibiae with weakly projecting apical tooth (Fig. 3). Males with apex of aedeagus upturned (Fig. 5) ..... ***Menederes dannheimeri***

— Foretibiae with more strongly projecting apical tooth (Fig. 4). Males with straight aedeagus (Fig. 6) ..... ***Menederes rufilabris***

3. Antennae long–projecting far beyond pronotal base (Fig. 7). Body elongate (Fig. 8). Epistoma with complete carina along apical edge (Fig. 9) ..... ***Menederes constrictus***

— Antennae short, projecting at most only slightly beyond pronotal base. Body relatively oblong/short. Epistoma without apical carina, or with carina reduced medially **4**

4. Foretibial projection large/produced (Fig. 10). Male hind leg with strip of setae (Fig. 11). Aedeagus narrow with pointed, parallel parameres (Fig. 12) ..... ***Menederes chaetotaxicus***

— Foretibial projection small and sharp (less produced) (Fig. 13). Male hind leg without setae. Aedeagus narrow but with converging, rounded parameres (Fig. 14) .... ***Menederes jokli***

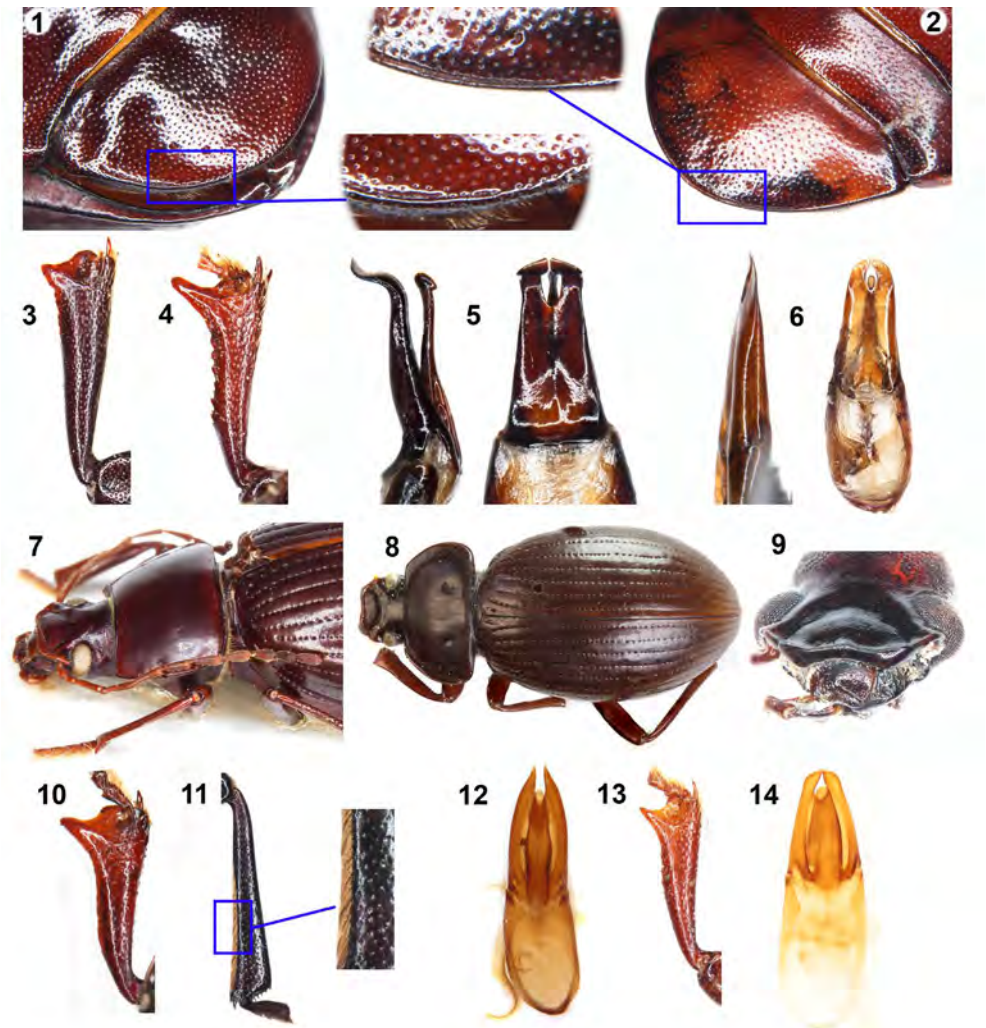


Plate xiv. *Menederes* species diagnostic features. Anatomic features: Abdominal ventrite V (1–2). Foreleg (anterior) (3–4, 10, 13). Aedeagus (5–6, 12, 14). Head and pronotum (lateral) (7). Head (anterior) (9). Hind tibia (11). **Taxa depicted**: *Menederes chaetotaxicus* (10–12), *Menederes constrictus* (7–9), *Menederes dannheimeri* (1, 3, 5), *Menederes jokli* (13–14), *Menederes rufilabris* (2, 4, 6)

1. *Menederes chaetotaxicus* (Koch) comb. nov.

Oncotus (*Menoncotus*) *chaetotaxicus* Koch, 1954b: 38.– Kamiński 2016: 243.

Menoncotus chaetotaxicus Koch, 1954.– Lumen *et al*. 2025: 13.

=*Oncotus* (*Menoncotus*) *sinuatipes* Koch, 1954b: 37 **syn. nov.**– Kamiński 2016: 243; Lumen *et al*. 2025: 13.

Status

On close examination of type material and distribution records, it appears that subtle differences between *O. sinuatipes* and *O. chaetotaxicus* likely represent diversity within a single species. Specifically, *Oncotus chaetotaxicus* is represented by only three specimens from the same collecting event as the holotype of *S. sinuatipes* (Vanrhynsdorp). According to Koch's original diagnoses, the two species differ only in size by a relatively small margin (~2–3mm). Further, examination of internal morphology revealed that the aedeagi of the two entities are identical. As such, we propose here to synonomize the two under *Menederes chaetotaxicus*.

Diagnosis

The most similar species, *M. jokli*, is separable using male characteristics: hind and mid tibial setation (absent in *M. jokli*), and the parallel, pointed shape of the aedeagus (rounded and beveled apically in *M. jokli*).

Material examined

Menoncotus chaetotaxicus: **Holotype**, male **TMNH** (Fig. T94): "v Rhynsdorp / July.Aug. '27 /G. V. Son / Holotype No: 1665 / Oncotus / chaetotaxicus KOCH / chaetotaxicus Koch". **Paratypes TMNH**: "vanRhynsdrop Cape Dr. Brauns. 8 1927 ALLOTYPE No: 1666 Oncotus chaetotaxicus KOCH". **NHMB**: "v Rhynsdorp July.Aug. '27 G. V. Son Holotype No: 1670 Oncotus chaetotaxicus KOCH chaetotaxicus Koch 886 paratype Oncotus chaetotaxicus KOCH PLT021 Coll. FREY".

Menoncotus sinuatipes: **Holotype**, male **TMNH** (Fig. T101): "v Rhynsdorp / July.Aug. '27 / G. V. Son / Holotype No: 1663 / Oncotus / sinuatipes KOCH / HOLOTYPUS / Oncotus / sinuatipes / Dr. C. Koch sp. n.".

Distribution

South Africa: Northern Cape, Western Cape (Map 68).



Map 68. Distribution of *Menederes chaetotaxicus* (Koch).

2. *Menederes constrictus* (Koch) comb. nov.

Menederopsis constricta Koch, 1954b: 16.– Koch 1956: 26; Kamiński 2016: 241; Bouchard *et al*. 2021: 245; Kamiński & Schawaller 2019: 291; Lumen *et al*. 2025: 8.

=*Archinamaqua lyleae* Schawaller, 2012: 80.– Kamiński & Schawaller 2019: 291 (syn.).

Status

Koch (1954b) had trouble assigning to which genus the monotypic *Menederopsis* had the strongest affinity. The distinct morphology of this taxon led to future workers describing a new genus in a different subfamily (*Archinamaqua* Schawaller 2012, Pimeliinae: Tentyriini). Recent analyses (See introduction: Figure 2) recovered *Menederopsis* within a clade including *Menederes* and *Menoncotus*. Closer examination in this context revealed similar morphological traits in the male aedeagus (apically converging/pointed parameres) and elytra (with scattered punctation of the last interval/stria). Taking both the phylogeny and these morphological traits into account, we have chosen to synonomize the genus *Menederopsis* under *Menederes*.

Diagnosis

Although it has a complete epistomal carina as in *Ograbies*, *M. constrictus* is missing the setation and unique foreleg shape of the former. Additionally the species has a diagnostic habitus, which sets it apart from all other *Menederes* (rounded elytral shoulders, elongate body shape, elongate antennae reaching well-past the pronotum). Within *Menederes*, *M. constrictus* most resembles *M. dannheimeri*, which differs in having shorter antennae, incomplete carina of the epistoma, upturned aedeagal parameres (straight in *M. constrictus*), and sclerites in the bursa copulatrix (absent in *M. constrictus*).



Map 69. Distribution of *Menederes constrictus* (Koch).

Material examined

Menederopsis constricta: **Holotype**, male **TMNH** (Fig. T95): "Buffels R. near / Grootmist C.P. / 21-XI-1948 / Koch & van Son / Holotype No: 1481 / Menederopsis / constrictus KOCH".

Archinamaqua lyleae: **Holotype**, male and two **paratypes**, male and female **TMNH** (Fig. T99): "S. Afr.; Northern Cape Noup; 44m 30.06 S - 17.13 E 27.2-3.3.2010;E-Y:3878 pitfall traps, back dune leg. Robin Lyle".

TMNH: "S. Afr., Namaq.Coast Gemsbok VlakteFarm 30.30S - 17.29E 31.8.1977 E-Y: 1362 singled leg. Endrödy-Younga".

Distribution

South Africa: Northern Cape (Map 69).

3. *Menederes dannheimeri* Koch

Menederes (*Menederes*) *dannheimeri* Koch 1954b: 70.– Koch 1956: 26; Kamiński 2016: 241.

Menederes dannheimeri Koch, 1954.– Lumen *et al*. 2025: 9.

Diagnosis

Menederes dannheimeri is most similar to *M. rufilabris*. Both share an apical suclus of the abdominal ventrite V (often reduced or obliterated medially in *M. dannheimeri*) and are more elongate than both *M. chaetotaxicus* and *M. jokli*. The other elongate species, *M. constrictus*, is differentiable based on the length of the antennae (extremely long, protruding well past the pronotal base in *M. constrictus*), and abdominal ventrite V sulcus which is absent in *M. constrictus*. *Menederes dannheimeri* is overall slimmer in build compared to *M. rufilabris* (especially evident in male specimens). Additionally, *M. dannhiemeri* is often darker (black or nearly-so), whereas *M. rufilabris*, as its name appears to denote, is lighter brown to reddish. The foretibiae are also useful to differentiate species (curved/emarginated with weak apical tooth in *M. dannheimeri* and *M. constrictus*, short and sharp tooth in *M. jokli*, straight with more-strongly projecting apical tooth in *M. rufilabris* and *M. chaetotaxicus*). Further, male terminalia clearly separate some species (*M. dannhiemeri* with strongly modified and upwardly-curved parameres, versus most other species with relatively straight parameres). While female specimens of *M. dannheimeri* and *M. rufilabris* aren't possible to differentiate using genitalia, the bursa copulatrix spines in *M. chaetotaxicus* are shorter than in *M. dannheimeri* and *M. rufilabris*, and *M. constrictus* lacks sclerites altogether. Unfortunately, the morphology of the bursa copulatrix of *M. jokli* remains unknown.

Material examined

Holotype, male **TMNH** (Fig. T96): "Brakf,Richters- / veld 18.XI.1933. / G.van Son. / Holotype No: 1775 / Menederes dannheimeri KOCH / Dannheimeri / Koch".

MIZPAN: "Tenebrionidbase Aaron D. Smith 26288", "Kamieskroon 2017/V/ADS South Afr. TenebBase 26354 (2 additional specimens with same data)". **TMNH**: "S. Afr. Richtersv. Doringpoort 28.34S-16.56E 7.9.1976;E-Y:1230 from under stones leg. Endrödy-Younga", "S. Africa (16) Hester Malan N.R. 10mis. E. Springbok 7-8.I.1972 Southern African Ex B.M. 1972-I", "S.Afr.,Namaquald. Springbok Mesklip 29.49S-17.52E 20.8.1976; E-Y:1186 from under stones leg.Endrödy-Younga (two specimens)", "Kleinzee N Namaqualand Museum Staff 1935", "Lekkersing N Namaqualand museum staff 1935", "S. Afr., Richtersveld paradieskloof 28.19 S - 17.00 E 9.9.2001; E-Y: 3416 under stones leg. TMSA staff M. dannheimeri det. Schawaller 2005". **MNHN**: "Sulpius nov. spec. 1955 P. Ardoin Det.". **HNHM**: "??.SW. Afrika Kl.Namaland Kamaggas Nov. Gen. Nov. sp. aff Psectropus det. dr. Kaszab".

Distribution

South Africa: Northern Cape. Namibia: ǁKaras Region (Map 70).



Map 70. Distribution of *Menederes dannheimeri* Koch.

4. *Menederes jokli* (Koch) comb. nov.

Oncotus (*Menoncotus*) *jokli* Koch, 1954b: 39.– Kamiński 2016: 243.

Menoncotus jokli (Koch, 1954).– Lumen *et al*. 2025: 17.

Diagnosis

Most similar to *M. chaetotaxicus* (see *M. chaetotaxicus* diagnosis). Other species of *Menederes* are overall more elongate, or have more specialized morphology (e.g., aedeagus of *M. dannheimeri*, antennae of *M. constrictus*–see other diagnoses for more information).

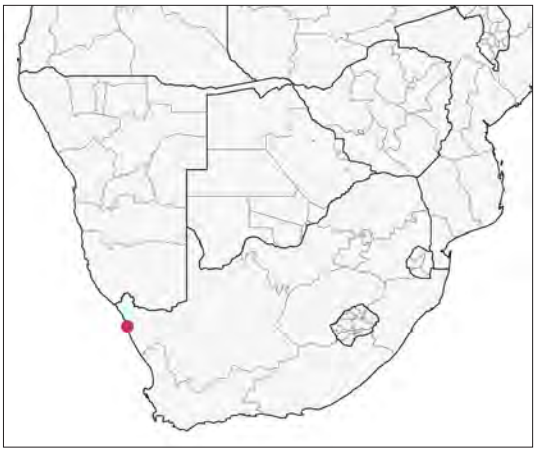
Material examined

While the holotype was not examined here, it should be a male specimen at **IMSA** bearing the label data: "Kleinzee / Marz 1935 leg. Mus. Personal".

Paratypes, male **TMNH** and **NHMB** (Fig. T97-98): Data same as holotype (two specimens).

Distribution

South Africa: Northern Cape (Map 71).



Map 71. Distribution of *Menederes jokli* (Koch).

5. *Menederes rufilabris* Solier

Menederes rufilabris Solier, 1848: 203.

Menederes (*Menederes*) *rufilabris* Solier, 1848.– Koch 1954b: 69; Banaszkiewicz 2006: 63; Kamiński 2016: 241; Lumen *et al*. 2025: 10.

Diagnosis

See diagnosis of *Menederes dannheimeri*. Though previously associated only with *M. dannheimeri*, *M. rufilabris* is also similar to the new inclusion to the genus *M. chaetotaxicus*. *Menederes rufilabris* has a sulcus running along the apex of abdominal ventrite V (also present in *M. dannheimeri*, where it is often reduced medially). Additionally, *M. rufilabris* is differentiable from *M. chaetotaxicus* based on sexual characteristics: strip of setae on the hind femora–absent in *M. rufilabris*; aedeagus parameres with parallel pointed apices–rounded and converging in *M. rufilabris*; bursa copulatrix with two short, toothy sclerites—long and narrow with teeth in *M. rufilabris*.



Map 72. Distribution of *Menederes rufilabris* Solier.

Material examined

Solier (1848) based the species concept on a single male specimen. It follows that Solier's holotype by should be present in **MNHN**; however, despite a thorough search, we were unable to locate it as of this study. Previous reviewers were also unable to locate the specimens. Koch (1954b) asserted that his concept and specimens of *M. rufilabris* matched Solier's (1848) based on the published description, while the range of the species was described as most "southern" among other *Menederes*. Under the provisions of Article 75.3 of the ICZN (1999), the designation of a neotype is warranted. To stabilize the taxonomy of the genus and species respectively, we have chosen to designate a neotype following Koch's assertions and Solier's description and species range.

Neotype, male, here designated, **TMNH** (Fig. T100): "S. Afr., W.Cape Prov. Wiedouw farm 31.43 S - 18.43 E 18.8.1943 singled, night leg. Endrödy, Penrith".

TMNH: "S.Afr.W Cape Prov. Vredendal, 20 km W 31.40 S - 18.31 E 19.8.1983;E-Y:1948 groundtraps, 76 days leg. Endrödy, Penrith groundtrap with banana bait (two specimens)", "S.Afr;SW Cape Prov. Clanwilliam,river 32.09 S - 18.53 E 29.8.1989;E-Y:2674 flowering meadow Endrödy & Klimaszewski (two specimens)", "S.Afr.W Cape Prov. Vredendal,20 km W 31.40 S - 18.31 E 19.8.1983;E-Y:1948 groundtraps, 76 days leg. Endrödy, Penrith groundtrap with banana bait Tenebrionidbase 26312", "S. Afr., SW cape Vanrhynspas 31.23 S - 19.02 24.10.1981; E-Y;1891 In roadside gutter leg. Endrödy-Younga", "S. Afr., SW cape Vanrhynspas 31.23 S - 19.02 E 4.11.1983; E-Y;2048 In roadside gutter leg. Endrödy-Younga TenebrionidBase 26339", "Knersvlakte, Na. 14 Nov 1949 C.koch & Malkin", "Calvinia Dist ?? Aston Sep.91 rufliabris C. Koch det., 19", "Vredendal 23-30 July '27 G. v. Son Menederes rufilabris Sol. det AJH.". **SANC**: "SOUTH AFRICA: WCAPE Puts (farm), nr Klawer 31.47,4S 18.41,5E 640m 02.viii.1996 Oberprieler/Stals/Stiller Collected in 1 year old plantation of rooibos tea Aspalathus linearis (FABACEAE)".

Distribution

South Africa: Western Cape (Map 72).

xv. Genus *Ograbies* Péringuey

Ograbies Péringuey, 1899: 293.– Péringuey 1908: 412; Gebien 1938: 393; Koch 1954b: 17, 1956: 26; Kamiński 2016: 241; Bouchard *et al*. 2021: 273; Kamiński *et al*. 2021: 152; Lumen *et al*. 2025: 2.

Type species: *Ograbies singularis* Péringuey; designated by monotypy.

Diagnosis

Ograbies are recognizable by their less-sclerotized cuticle, bi-colored habitus (in many species), distinctive foretibial shape: flat and broad, with slight curvature/emargination on outside edge, giving unique silhouette, and presence of longer, free setae on the hypomeron; short and/or appressed in all genera except *Phaleriderma* and *Hirtograbies*, from which it differs by the lack of setation on the elytral surface. Though recovered close phylogenetically in recent analyses (See introduction: Figure 2), *Oncotus* is morphologically distinguishable by their more dorso-venterally flattened shape, more angular basal angles of the pronotum (with depressions/dimples), apical foretibia projections, and more strongly sclerotized cuticle.

***Species included* (8)**

O. angulatus Koch, *O. bidentimanus* Koch, *O. calumnus* Lumen & Kamiński, *O. campi* Koch, *O. capensis* (Solier), *O. frigidus* Koch, *O. subdentatus* Koch, *O. testaceus* (Solier).

Key to species of *Ograbies* (see Plate xv for figures):

1. Forelegs with strong emargination, giving rise to a medial spine on the outer edge (Fig. 1) ..... ***Ograbies bidentimanus***

— Forelegs with slight to strong emargination, never with well-defined medial spine on outer edge (Figs 2–4) **2**

2. Basal border of pronotum complete (Figs 5–7) **3**

— Basal border of pronotum interrupted or reduced in the middle (Figs 8–9) **7**

3. Bicolored (dark head + prontum and light elytra) and overall larger (8.5mm–12.5mm). Elytra with reduced striae (Fig. 10) ..... ***Ograbies testaceus***

— Bicolored or not. Generally smaller (7.5mm–10mm). Elytral striae not reduced (Fig. 11) ... **4**

4. Hind tibiae with coarse punctation and spines on outer surface (Fig. 12). Head punctation fine; texture of head and pronotum velvety/matte (Fig. 13) ..... ***Ograbies calumnus***

— Hind tibiae without coarse sculpturing on outer surface (Fig. 15). Head punctation coarse (Fig. 14). Texture of head and pronotum relatively shiny (Figs 7 & 14) **5**

5. Hypomeron setae reduced or absent. Long femoral setal patches in males. Aedeagus with long parameres and basal piece (Fig. 16) ..... ***Ograbies capensis***

— Hypomeron setae not reduced nor absent (Fig. 17). Aedeagus with less elongate basal piece (Figs 18–19). Femoral setal patches present or absent **6**

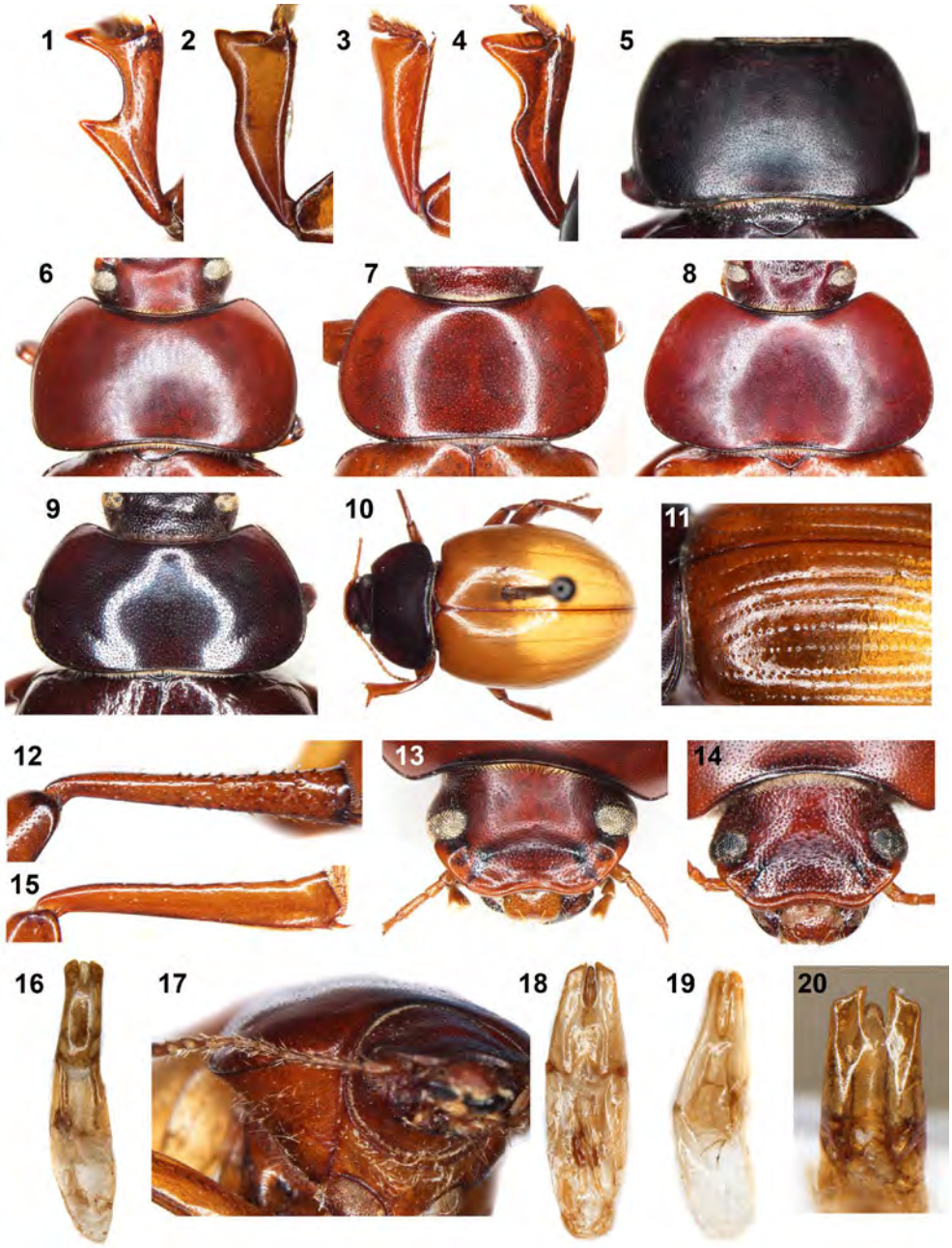


Plate xv. Part 1. *Ograbies* species diagnostic characters. **Anatomic features**: Foreleg (anterior) (1–4). Pronotum (5–9). Elytron (11). Hind tibia (12, 15). Head (13–14). Aedeagus (16, 18–20). Hypomeron (17). **Taxa depicted**: *Ograbies angulatus* (11, 17–18, 20). *Ograbies bidentimanus* (1). *Ograbies capensis* (5, 16). *Ograbies calumnus* (6, 12–13). *Ograbies campi* (7, 14–15, 19). *Ograbies frigidus* (3, 8). *Ograbies subdentatus* (4, 9). *Ograbies testaceus* (2, 10).

6. (males) Aedeagus with short, angular parameres (Fig. 20). Middle and hindfemoral setal patches present (Fig. 21) ..... ***Ograbies angulatus***

— (males) Aedeagus with long parameres and without angular apices (Fig. 19). Middle and hindfemoral setal patches absent (Fig. 22) ..... ***Ograbies campi***

7. Larger (7mm–11mm). Forelegs broad, slightly triangular (Fig. 3). Elytral striae unimpressed (Fig. 23). Pronotum transverse, largely narrowing apically and slightly lunate in shape. Dorsal habitus dull/matte (Fig. 8) ..... ***Ograbies frigidus***

— Smaller (7.5mm–9.75mm). Forelegs emarginate, less triangular (Fig. 4). Elytral striae impressed (Fig. 24). Pronotum less transverse, not lunate. Dorsal habitus shinier (Fig. 9) .... ***Ograbies subdentatus***



Plate xv. Part 2. *Ograbies* species diagnostic characters. **Anatomic features**: Elytron (23–24). Hindfemur (21–22). **Taxa depicted**: *Ograbies angulatus* (21). *Ograbies campi* (22). *Ograbies frigidus* (23). *Ograbies subdentatus* (24).

1. *Ograbies angulatus* Koch

Ograbies angulatus Koch, 1954b: 22.– Kamiński 2016: 241; Lumen *et al*. 2025: 19.

Diagnosis

Most similar to other species with a complete basal pronotal border (*O. testaceus*, *O. capensis*, *O. calumnus*, *O. campi*). Male terminalia separate *O. angulatus* from all other species (short, apically angular parameres; all other species more elongate and/or without angular apex).

Material examined

Holotype, male **TMNH** (Fig. T102): "Saldanha / Bay / 13.XII.57 / K.M. / Dickson / HOLOTYPE / Ograbies / angulatus / Dr. C. Koch sp.n. / HOLOTYPE NO: 1513 / Ograbies angulatus KOCH".

SANC: "SOUTH AFRICA: WCAPE Swartriet Private Nature Reserve, 2km N of Jabos Bay 32°56'50"S, 17°53'13:E 27.xii.2004 PE Reavell HABITAT: Strandveld NATIONAL COLL. OF INSECTS (SANC) Pretoria, South Africa (three specimens)". **MIZPAN**: "ZA October 2019 POI51 Paternoster TenebBase 26350". "cap. b. sp. ex coll. Deyrolle, (three specimens)". "Museum Paris Colonie Du Cap J. Verreaux 1866", "Saldanha Bay, W.OP. 18.XI.1949, Malkin".

Distribution

South Africa: Western Cape (Map 73).



Map 73. Distribution of *Ograbies angulatus* Koch.

2. *Ograbies bidentimanus* Koch

Ograbies bidentimanus Koch, 1954b: 18.– Kamiński 2016: 241.

Diagnosis

Ograbies bidentimanus is sharply separable from all other species of *Ograbies* by the formation of the foretibiae. The distinguishing shape for the genus is especially exaggerated, giving rise to a secondary hook or spur at the midpoint of the foretibiae. All other species have only a slight protuberance or truncate projection that is never so pronounced.

Material examined

Holotype, sex undetermined **TMNH** (Fig. T103): "Strandfontein,Na. / Olifants R. Mouth / 13.XI.1949, C.Koch / HOLOTYPE No: 1482 / Ograbies / bidentimanus KOCH / HOLOTYPUS / Ograbies bidentimanus / Dr. C. Koch sp.n.". **Paratype**, **NHMB**: same data as Holotype.

SANC: "SOUTH AFRICA: WCAPE Uitsig (Farm), near Clanwilliam 380m 31.58,3S 19.07,2E ix.1996-iv.1997 (pit traps) RG Oberprieler & R Stals".

Distribution

South Africa: Western Cape (Map 74).



Map 74. Distribution of *Ograbies bidentimanus* Koch.

3. *Ograbies calumnus* Lumen & Kamiński

Ograbies calumnus Lumen & Kamiński, 2025: 13 in Lumen *et al*. 2025.

Diagnosis

This species is most similar to *O. capensis*, *O. campi*, and *O. angulatus*. *Ograbies calumnus* is separable by the sculpturing of the head capsule (dense and fine) with velvety/matte finish, and hind tibiae with coarse punctation on the outer surface. Other species are separable by size (*O. testaceus* and *O. frigidus* are larger species), coloration (most species are bicolored), and structure of the basal border of the pronotum (complete in this species; incomplete in *O. frigidus* and *O. subdentatus*), and bursa copulatrix sclerites (absent in this species, present in others).

Material examined

Holotype, female **MIZPAN**: "Blue Tenebrionidbase label, Catalog # 26385, POI 45 (-34.244125, 18.410154), 9 Oct, Red label Holotype Ograbies calumnus." **Paratype** (Fig. T104), female **SANC**: "L'Agulas 19.XII.1995, S. Africa Cape Prov. G Minet, Yellow label Paratype Ograbies calumnus."

Distribution

South Africa: Western Cape (Map 75).



Map 75. Distribution of *Ograbies calumnus* LUMEN & KAMIŃSKI.

4. *Ograbies campi* KOCH

Ograbies campi KOCH, 1954b: 21.– KAMIŃSKI 2016: 241; LUMEN *et al*. 2025: 6.

Diagnosis

Most similar to *O. angulatus* and *O. capensis*, from which it can be differentiated by male characteristics: aedeagus less elongate than *O. capensis*, non-angular paramere apices (versus angular in *O. angulatus*), and missing hind tibial setation present in both *O. capensis* and *O. angulatus*.



Map 76. Distribution of *Ograbies campi* KOCH**.**

Material examined

Holotype, male **TMNH** (Fig. T105): "Wallekraal, C.P. / 17-XI-1948 / Koch & van Son / HOLOTYPE No: 1488 / Ograbies / campi KOCH / Campi / Koch / Holotypus / Ograbies / campi / Dr. C. Koch sp.n.".

TMNH: "S.Afr.: Namaqualand Stryd River 188 29.34 S - 17.17 E 27.VII.1996 leg. J. duG.Harris TenebBase 26298", "Wallekraal L. Namaquald", "S.W.Afr. Namib Oranjemund 20.XII.1980; J.Irish".

Distribution

South Africa: Northern Cape. Namibia: ǁKaras Region (Map 76).

5. *Ograbies capensis* (Solier)

Oncotus capensis Solier, 1848: 220.– Gemminger and Harold 1870: 1911; Péringuey 1908: 412. Gebien 1938: 393.

Ograbies capensis (Solier).– Koch 1954b: 22. Kamiński 2016: 242; Lumen *et al*. 2025 syn: 10.

=*Oncotus capicola* Koch 1954b: 36.– Kamiński 2016: 243; Lumen *et al*. 2025 syn: 15.

Diagnosis

Overall *O. capensis* is darker (rarely slightly bicolored), and on the smaller side for the genus (<10mm). Further, *O. capensis* has a characteristic reduction of the hypomeron setation otherwise ubiquitous for the genus (still faintly present, but easily abraded or missing in older specimens). Additionally, the aedeagus for this species is diagnostic (elongate with extremely shallow apical opening of the parameres). Close species (*O. angulatus* and *O. campi*) are separable based on the shape of the male parameres and presence/absence of setae on the hind tibiae (see their respective diagnoses).



Map 77. Distribution of *Ograbies capensis* (Solier).

Material examined

While the holotype for *Oncotus capicola* was not examined here, Koch (1954b) states it should be in **NRS** with the label data "De Vylder, Cap. b. Sp.".

Oncotus capensis: **Neotype**, sex undetermined, designated in Lumen *et al*. (2025) **MNHN** (Fig. T106): "Oncotus / capensis / Sol. C.B.Esp. / Coll. R. Oberthur / ex coll Deyrolle / Cap. b. Sp.".

Oncotus capicola: **Paratypes**, sex undetermined **TMNH** (Fig. T107): "De Vylder" / "Cap. b. Sp." / "PARATYPE No: 1658" / "Oncotus" / "capicola KOCH". NHMB: "891 Paratype Oncotus capicola KOCH Kinb. Cap. B. Sp PARATYPE No: 1660 Oncotus capicola KOCH".

SANC: "Agulhas KP. S.Afr. 16.1.VI M.W. Strydom. NATIONAL COLL. OF INSECTS Pretoria, South Africa Ex UPSA, May 2002 (two specimens)". **MNHN**: "Museum Paris 1906 coll. L. Fairmare", "coll. R. Oberthur ex. coll Deyrolle cap. b. sp. Oncotus capensis Sol. C.B. Esp.". **MIZPAN**: "MEL179 Oncotus sp. 11-1-2017 POI59".

Distribution

South Africa: Western Cape (Map 77).

6. *Ograbies frigidus* Koch

Ograbies frigidus Koch, 1954b: 23.– Kamiński 2016: 242; Lumen *et al*. 2025: 19.

Diagnosis

One of the largest species (7–11mm) (only matched by *O. testaceus* where some specimens can reach 12mm). *Ograbies frigidus* is differentiable from *O. testaceus* by the weak to absent bicoloration (strongly pronounced in *O. testaceus*) and the basal border of the pronotum (interrupted medially; complete in *O. testaceus*). The most similar species, *O. subdentatus*, is generally smaller (7.5-9.75mm), has less triangular forelegs with a stronger emargination on the outer edge of the foretibiae, more impressed elytral striae, and is shiny (*O. frigidus* has a duller cuticular structure).



Map 78. Distribution of *Ograbies frigidus* Koch.

Material examined

Holotype, sex undetermined **TMNH** (Fig. T108): "Buffels R. near / Grootmist C.P. / 21-XI-1948 / Koch & van Son / frigidus / Koch / HOLOTYPUS / Ograbies / frigidus / Dr. C. Koch sp.n. / HOLOTYPE No: 1442 / Ograbies / frigidus KOCH". **Paratype** two specimens, **TMNH**: "same data as Holotype", "Hondesklip Bay. C.P. 15-XI-1948 Koch & van Son 863 Paratype Ograbies frigidus KOCH Paratype no.1558 Ograbies frigidus KOCH Coll. FREY".

TMNH: "3 m. E of Port Nolloth C.P. 22-XI-1948 Koch & Van Son (two specimens)".

Distribution

South Africa: Northern Cape (Map 78).

7. *Ograbies subdentatus* Koch

Ograbies subdentatus Koch, 1954b: 22.– Kamiński 2016: 242; Lumen *et al*. 2025: 19.

Diagnosis

Similar-sized species (i.e., *O. angulatus*, *O. capensis*, and *O. campi*) are separable by the basal bordering of the pronotum (interrupted or missing in *O. subdentatus*). Additionally, *O. capensis* and *O. angulatus* possess unique aedeagal morphology (see respective diagnoses). The only other species with an interrupted basal border of the pronotum is *O. frigidus*, which is separable by the dull lustre of the dorsal habitus (shinier in *O. subdentatus*) and size (overall *O. frigidus* is larger–see diagnosis).

Material examined

Holotype, male **TMNH** (Fig. T110): "12m. Before / Klaver, 12-XI-48 / C.P. Koch/v.Son / HOLOTYPE No: 1515 / Ograbies / subdentatus KOCH / HOLOTYPUS / Ograbies / subdentatus / Dr. C. Koch sp.n. / subdentatus / Koch.". **Paratypes NHMB**: Same data as holotype. **NHMUK**: "Graafwater, C.P. 10-XI-1948 Koch & van Son".

TMNH: "S.Afr., SW Cape Gansbaai 34.35 S - 19.21 E 23.2.1981;E-Y 1745 veget. sand night leg. Endrödy-Younga". MNHN: "c.b.sp Museum Paris Coll De Marseul 1890 (two specimens)", "Museum Paris Colonie Du Cap J. Verreaux 1866", "Cap Town Raffray". **SANC**: "SOUTH AFRICA: WCape Seekoevlei Farm, nr Clanwilliam 360m 32°09.3'S 18°45.1'E 1996-1997 R Stals & RG Oberprieler Collected with unbaited pitfall traps in 5 year old plantation of rooibos tea Aspalathus linearis (FABACEAE) NATIONAL COLL OF INSECTS Pretoria, South Africa (three specimens)". "L'Agulhas 19.XII.1995 S Africa Cape Prov. G. Minet (two specimens)".

Distribution

South Africa: Western Cape (Map 79).



Map 79. Distribution of *Ograbies subdentatus* Koch.

8. *Ograbies testaceus* (Solier)

Oncotus testaceus Solier, 1848: 221.– Gemminger & Harold 1870: 1911; Péringuey 1908: 412. Gebien 1938: 393.

Ograbies testaceus (Solier, 1848).– Koch 1954b: 19; Banaszkiewicz 2006: 63; Lumen *et al*. 2025: 8.

= *Ograbies singularis* Péringuey, 1899: 293.– Gebien 1938: 393; Koch 1954b: 19 (syn); Kamiński 2016: 242.

Diagnosis

Ograbies testaceus is the most easily identified species of the genus (aside from *O. bidentimanus*). It is overall the largest species, with specimens reaching up to 12mm, and is always strongly bicolored (dark head/pronotum with lighter yellowish elytra). The similarly large *O. frigidus* is more unicolored and has an incomplete basal margin of the pronotum. Other bicolored species (e.g., *O. campi*, *O. angulatus*) have more well-defined elytral straie (nearly absent in *O. testaceus*) or, in the case of species such as *O. angulatus* and *O. capensis*, have diagnostic aedeagal features (see respective diagnoses).



Map 80. Distribution of *Ograbies testaceus* (Solier).

Material examined

Both *Oncotus testaceus* and *Ograbies singularis* were described from single specimens by Solier (1834) and Peringuey (1899) respectively. Koch (1954b) synonomized the two species under *O. testaceus* with Peringuey's type specimen on-hand—highlighting their high similarity (e.g., coloration: bi-colored, dark head and pronotum with testaceus or straw-colored elytra). Though our investigations recovered the holotype of *O. singularis* in **TMNH**, the presumed holotype for Solier's *O. testaceus* in **MNHN** was not located. To stabilize the concepts of both the genus *Ograbies* and the species, we hereby designate a neotype for *Oncotus testaceus*. Taking into account Koch's (1954b) revision, as well as Solier's (1848) and Peringuey's (1899) descriptions, we have decided to select the holotype of *Ograbies singularis* as a neotype for *Oncotus testaceus* to objectively confirm the synonymy.

Oncotus testaceus: **Neotype**, here designated: *Ograbies singularis* **Holotype** (see below).

Ograbies singularis: **Holotype**, sex undetermined **TMNH** (Fig. T109): "Port Nolloth".

TMNH: "10km N. Dwarskersbos Cape Prov. SE 32,18, Bb 20-XII-1977 E. HOLM", "Elands bay, C.P. 8-XI-1948 Koch & van Son", "Hondeklip Bay C.P. 15-XI-1948 Koch & van Son TenebBase 26263 (plus 1 additional specimen)", "Port Nolloth (five specimens)", "S.Afr.: Cape Prov. Dwarskersbos 10km N 20.XII.1977; E.Holm (three specimens)", "S. Afr.: Richtersveld Gemsbok Vlakte Farm 30.30S - 17.29 E 28.10.1977; E-Y: 1399 singled on dune leg. Endrödy-Younga (three specimens)".

Distribution

South Africa: Northern Cape, Western Cape (Map 80).

xvi. Genus *Oncotus* Blanchard

Oncotus Blanchard, 1845: 13, 24.– Solier, 1848: 216; Lacordaire 1859: 231; Gemminger & Harold 1870: 1911; Gebien 1938: 393; Koch 1954b: 33; 1956: 27; Iwan 2002: 6, 2004: 739; Kamiński 2016: 242; Bouchard *et al*. 2021: 275; Kamiński *et al*. 2021: 152; Lumen *et al*. 2025: 2.

Type species: *Oncotus farctus* Solier; by subsequent designation (Gebien 1938: 72).

Diagnosis

Oncotus is defined by their relative oblong/short and slightly dorsoventrally flattened shape, epistomal canthus interrupted in the middle (restricted to lateral corners/edges), relatively square/angular basal angles of the pronotum with slight depressions or dimples near the corners (separating the genus from *Menoncotus* and *Quadroncotus*), pronotal lateral edge "eave-like" (overhanging the hypomeron), and foretibiae with lateral margins smooth (versus *Quadroncotus* with jagged lateral margin) and with a laterally projecting apex. Additionally, though *O. andeae* has relatively truncate and apically rounded parameres, *O. farctus* and *O. cedrimontis* both have similar aedeagal morphology (parameres slightly sinuate preapically), which are unique within Eurynotina. *Ograbies* is sharply separable by the form of the forelegs and, along with *Menederes*, are overall more elongate and fusiform in the contour of their elytra. *Hirtograbies* and *Phaleriderma* are separable by setal characteristics and/or size respectively, as *Phaleriderma* are among the smallest taxa in the subtribe (see respective diagnoses).

***Species included* (3)**

O. andreae Koch, *O. cedrimontis* Koch, *O. farctus* Solier.

Key to species of *Oncotus* (see Plate xvi for figures):

1. Last elytral interval wide (~2x the width of the previous interval) (Fig. 1). Parameres constricted subapically, somewhat widely separate, and rounded at apex, not pincer-like, without apical hook on penis (Fig. 2) ..... ***Oncotus cedrimontis***

— Last elytral interval narrow (previous interval subequal) (Fig. 3). Parameres constricted subapically or not, widely or narrowly separate with or without strongly incurved pincer-like apices, and with or without apical hook on penis **2**

2. Parameres truncate apically, with narrow opening between (Fig. 6) ..... ***Oncotus andreae***

— Parameres widely separate with strongly incurved apices, pincer-like, with apical hook on penis (Figs 4–5) ..... ***Oncotus farctus***

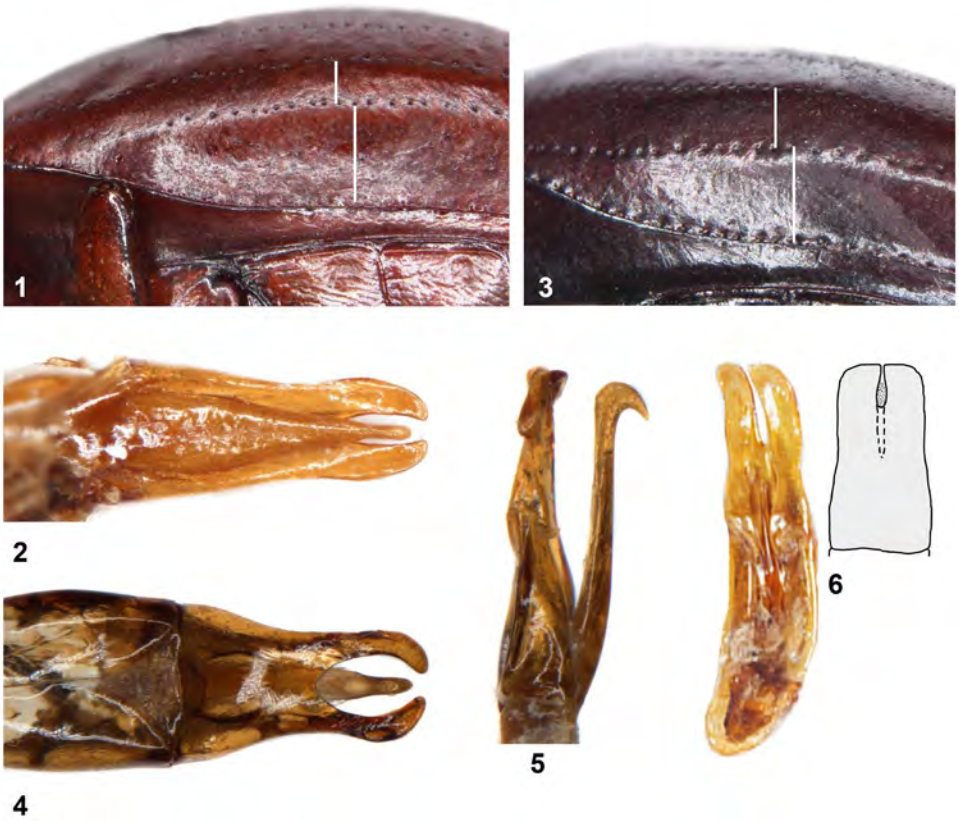


Plate xvi. *Oncotus* species diagnostic features. **Anatomic features**: Elytron last two intervals (lateral) (1, 3). Aedeagus (ventral: 2, dorsal: 4, 6, illustration based on Koch 1954b, lateral: 5). **Taxa depicted**: *Oncotus andreae* (6). *Oncotus cedrimontis* (1, 2). *Oncotus farctus* (4, 5).

1. *Oncotus andreae* Koch

Oncotus (*Oncotus*) *andreae* Koch, 1954b: 42.– Kamiński 2016: 244; Lumen *et al*. 2025: 14.

Diagnosis

Most similar to *O. farctus* from which it is nearly indistinguishable externally. Generally, *O. andreae* is narrower in shape and has less produced basal angles of the elytra (due to an upturned epipleuron). In *O. farctus* and *O. cedrimontis* the base of the elytra is more strongly produced (more triangular, nearly square). Furthermore, the aedeagi of *O. andreae* is particularly distinctive within the genus.

Material examined

Holotype, male **TMNH** (Fig. T111): "J.Jva West., / South Africa / Morreesburg / 14 Julie 1947 / HOLOTYPE No: 1681 / Oncotus / andreae Koch / Andreae / Koch". **Paratype**, female **NHMB**: "A. Ackermann 17.7.47 Morreesburg 884 Paratype Oncotus andreae Koch".

Distribution

South Africa: Western Cape (Map 81).



Map 81. Distribution of *Oncotus andreae* Koch.

2. *Oncotus cedrimontis* Koch

Oncotus (*Menoncotus*) *cedrimontis* Koch, 1954b: 35.– Kamiński 2016: 243; Lumen & Kamiński 2023: 6; Lumen *et al*. 2025: 10.

Diagnosis

Overall very similar to *O. andreae* and *O. farctus*; however, it can be easily differentiated by the shape of the aedeagal parameres (see *O. andreae*) and by the width of the 9th elytral interval—in *O. farctus* and *O. andreae* the 9th interval is relatively narrow (interval 8 subequal to interval 9); whereas in *O. cedrimontis* the 9th interval is wide (nearly twice width of interval 8).

Material examined

Holotype, male **TMNH** (Fig. T112): "Cedarbergen / K. Cameron / 1921 / cedrimontis / HT AT Koch".

TMNH: "Z.A. 99 Seder Berg, 500-1100m Clanwilliam distr.C.P. Humus under bushes and large stones. IV.1962.N. Leleup N.LELEUP leg. (13 specimens)". **SANC**: "South Africa: WCAPE Remhoogte (farm) near Cistrusdal 490m 32.24.5S 19.01E 03.viii.1996 found under stones NATIONAL COLL. OF INSECTS Pretoria, S.Afr.", "South Africa: WCape Papkuilsvlei (farm) near Aurora 32.39.3S 18.38.3E Oberprieler/Stals/Stiller Collected in 3 year old plantation of rooibos tea Aspalathus linearis (FABACEAE) NATIONAL COLL. OF INSECTS Pretoria, S.Afr.", "South Africa W.Koop Doornbaai 18/07/93 C.Loubscher".

Distribution

South Africa: Western Cape (Map 82).



Map 82. Distribution of *Oncotus cedrimontis* Koch.

3. *Oncotus farctus* Solier

Oncotus farctus Solier, 1848: 218.– Gemminger & Harold 1870: 1911; Gebien 1939: 393; Iwan 2002: 12; Lumen *et al*. 2025: 8.

Oncotus (*Oncotus*) *farctus* Solier, 1848.– Koch 1954b: 41; Kamiński 2016: 244.

Diagnosis

See *O. andreae*, which externally is nearly identical. The aedeagus is the best trait to use for separating the two species. *Oncotus cedrimontis*, while also separable using genitalia (*O. farctus* with more strongly bent paramere apices and with a hook on the apex of the penis; *O. cedrimontis* without a hook and with parameres much less dramatically bent/forcep-shaped), is also separable by the width of the last elytral interval (see *O. cedrimontis* diagnosis).

Material examined

Neotype, male, (designated in Lumen *et al*. 2025) **MNHN** (Fig. T113): "MUSEUM PARIS ENV. DE CAPETOWN A. RAFFRAY 1899".

SANC: "Jonhkeshoch Stellenbosch 8.7.1965 H.Geerbema NATIONAL COLL. OF INSECTS Pretoria, S.Afr.". **TMNH**: "Somerset West C.P. TYPUS (stricken) Oncotus farctus ssp. Oblongus (stricken) 1917 C. Koch".

Distribution

South Africa: Western Cape (Map 83).



Map 83. Distribution of *Oncotus farctus* SOLIER.

xvii. Genus *Phaleriderma* Koch

Phaleriderma Koch 1954b: 25.– Koch 1956: 26; Kamiński 2016: 244; Bouchard *et al*. 2021: 295; Kamiński *et al*. 2021: 152; Lumen *et al*. 2025: 2.

Type species: *Oncotus obscuricollis* Solier; by original designation.

Diagnosis

Phaleriderma is, overall, the smallest genus in Eurynotina by body size (5–8mm). While other genera such as *Hirtograbies* or *Phylacastus* have some overlap in size, the genera contain outlying species that are larger and smaller respectively, and are separable based upon other morphology. *Phaleriderma* is most similar to other setose species of Eurynotina (e.g., *Ograbies* and *Hirtograbies*). *Ograbies* are differentiated by glabrous elytra and characteristic forelegs (see *Ograbies diagnosis*) as well as by size (most individuals and species >7mm). The closest taxon to *Phaleriderma* morphologically and phylogenetically is *Hirtograbies*, and the two genera are sister groupings based on recent phylogenetic analyses (See introduction: Figure 2). Despite their close affiliation and similarities, *Phaleriderma* and *Hirtograbies* are differentiable by several characters. Specifically, *Hirtograbies* are differentiable based on the structure of the epistoma (*Phaleriderma* with a clear delineation or divide from the frons; whereas all other Eurynotina have a more fused clypeus+frons). Additionally, *Phaleriderma* has characteristically expanded foretibiae (broadly triangular without apical spurs or projections). *Hirtograbies* have expanded foretibiae that may sometimes resemble *Phaleriderma*; however, in most cases, the foretibiae of *Hirtograbies* are narrower basally before expanding closer to the apex, while *Phaleriderma* are broadly expanded beginning closer to the base of the tibiae.

***Species included* (3)**

P. husserli Koch, *P. iwani* **sp. nov.**, *P. obscuricollis* (Solier).

Key to species of *Phaleriderma* (see Plate xvii for figures):

1. Dorsum of the head strongly sculptured, with large, coarser punctation laterally. Frons/clypeal juncture with a weak to absent indentation (Fig. 1). Conspicuously hirsute. Antennae short (c.a. 1.5x width of the head) (Fig. 2). Distributed on the southeastern coast of Western Cape ..... ***Phaleriderma husserli***

— Dorsum of the head more weakly sculptured, with finer, uniform punctation throughout. Frons/clypeal juncture with strong to weak indentation (Figs 3–4 & 6–7). Less-conspicuously hirsute. Antennae long (~2x width of the head) (Figs 5 & 8). Distributed on the western coast of Western cape **2**

2. Pronotum elongate (~.3 to .5x length of elytra) (Fig. 5). Frons/clypeal indentation relatively weak (Figs 3–4). Overall uniformly colored ..... ***Phaleriderma obscuricollis***

— Pronotum shorter (~.25 to .3x length of elytra) (Fig. 8). Frons/clypeal indentation strong (Figs 6–7). Often bi-colored (dark head/pronotum and lighter elytra) ..... ***Phaleriderma iwani***



Plate xvii. *Phaleriderma* species diagnostic features. **Anatomic features**: Head and pronotum (dorsal) (2, 5, 8). Head (dorsal: 1, 3, 6. latero-dorsal: 3, 6). **Taxa depicted**: *Phaleriderma husserli* (1, 2). *Phaleriderma obscuricollis* (3–5). *Phaleriderma iwani* (6–8).

1. *Phalerideriderma husserli* Koch

Phalerideriderma husserli Koch, 1954b: 32.– Kamiński 2016: 244. Lumen *et al*. 2025: 8.

Diagnosis

The most southern and eastern distributed species. In addition to possessing shorter antennae, *P. husserli* has unique punctation within the group (irregular and with multiple sizes on the lateral margins of the head), and is overall more globose or rotund and setose in comparison.

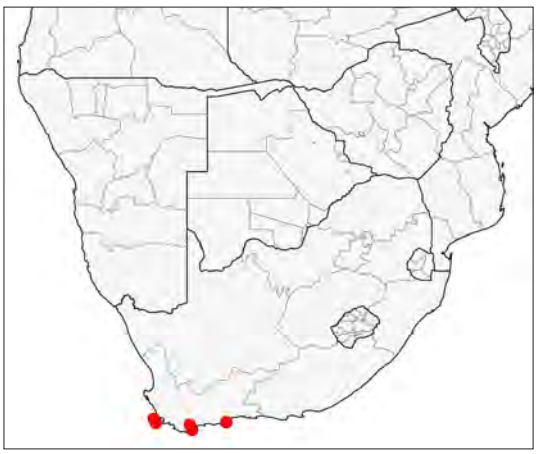
Material examined

Holotype, sex undetermined **TMNH** (Fig. T115): "Muizenberg C.T. / 22.X.1949, Koch / Malkin & Andreae / Husserli / Koch / HOLOTYPE No: 1637 / Phalerideriderma / husserli KOCH".

TMNH: "S.Afr., S.W. Cape Arniston, dunes 34.39 S - 20.13 E 26.10.1983; E-Y: 2023 coastal dunes, night leg. Endrödy-Younga (seven specimens)". **SANC**: "SOUTH AFRICA CP Vleesbaai 34.17S 21.55E 09.ix.1984 W. Breytenbach WB492 NATIONAL COLL. OF INSECTS Pretoria, S.Afr. (two specimens plus 1 additional with TenebrionIDBase Aaron D. Smith #26314 label)".

Distribution

South Africa: Western Cape (Map 84).



Map 84. Distribution of *Phalerideriderma husserli* Koch.

2. *Phalerideriderma iwani* sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:95EBB05B-4129-4DF9-9019-92D1D3B33504

Diagnosis

Phalerideriderma iwani is differentiable from the other two species of *Phalerideriderma* by its (usually) strong bicolored habitus, impressed cypeal/frons indentation. The closest species *P. obscuricollis* has a more elongate pronotum (~0.5x the length of the elytra) whereas *P. iwani* has a shorter pronotum (~0.3x the length of the elytra). Additionally, the elytral striae of *P. iwani* are at most only very weakly impressed (usually unimpressed); while *P. obscuricollis* and *P. husserli* have more prominent elytral striae.



Map 85. Distribution of *Phaleriderma iwani* **sp. nov.**

Description

Length 5.5–6mm; Width 2.5–3mm. Sometimes bicolored; head and pronotum usually darker, reddish-brown and elytra lighter, tawny. **Head**: Puncate, punctures relatively uniform in size, large and crowded (≤1 puncture diameter apart) in distribution. Frons-clypeus interface strongly indented. **Prothorax**: Disc finely punctured (≥ 1feature diameter apart). **Pterothorax**: Elytra punctio-striate, striae unimpressed. Intervals finely punctate. **Abdomen**: Punctate and setose. Without additional larger punctation on abdominal ventrite V. **Legs**: Anterio-laterally flattened. Mid- and hindtibiae slightly curved, with long setae and peg-like spines. Femora slightly expanded. foretibiae widely triangular, expanding apically. Males without expanded foretarsus, hind tibiae with setose strip running along apical 1/3rd. **Male terminalia**: Parameres tapered, with relatively wide opening exposing penis apex. **Female terminalia**: Ovipositor short; length of paraprocts relatively equal to combined length of coxites 1–4. Bursa copulatrix with one pair of broad sclerites.

Material examined

Holotype, sex undetermined **SANC** (Fig. T116): "SOUTH AFRICA: WCape Uitsig Farm, nr Clanwilliam 380m 31°58.3'S 19°07.2'E 1996-1997 R Stals & RG Oberprieler Collected with unbaited pitfall traps in 4 year old plantation of rooibos tea Aspalathus linearis (FABACEAE) NATIONAL COLL. OF INSECTS Pretoria, South Africa. **Paratypes MIZPAN**: "Same label data as holotype, (two specimens)". **SANC**: "Same label data as holotype, (seven specimens)". "SOUTH AFRICA: WCape Uitsig (farm) near Clanwilliam 31.56,8S 19.05,5E 280m 04.viii.1996 Oberprieler/Stals/Stiller Collected from field of newly established seedlings of rooibos tea Aspalathus linearis (FABACEAE) NATIONAL COLL. OF INSECTS Pretoria, South Africa. (two specimens)". **TMNH**: "S.Afr. SW Cape Elandsbay forestry 32.18 S - 18.21 E 28.8.1981; E-Y 1853 groundtraps, 60 days leg. Endrödy-Younga groundtrap with meat bait", "Graafwater, C.P. 10-XI-1948 Koch & van Son TenebrionIDBase Aaron D. Smith # 26326".

Etymology

This species is named in honor of Professor Dariusz Iwan (Poland, Warszawa)–a prominent worker in tenebrionid systematics in recognition of his significant works on the tribe Platynotini which makes revisions like these possible.

Distribution

South Africa: Western Cape (Map 85).

3. *Phaleriderma obscuricollis* (Solier)

Oncotus obscuricollis Solier, 1848: 221.– Gemminger & Harold 1870: 1911; Gebien 1938: 393.

Phaleriderma obscuricollis (Solier, 1848).– Koch 1954b: 32; Kamiński 2016: 245.

=*Phaleriderma dicksonae* Koch, 1954b: 31 **syn. nov.**– Kamiński 2016: 244; Lumen *et al*. 2025: 8.

Diagnosis

Most similar to *Phaleriderma iwani*; however, *P. obscuricollis* appears to be more coastal in distribution. Can be differentiated by the clypeal/frons indentation, which is much more strongly pronounced in *P. iwani*, and the coloration, which is most often dark and uniform (versus bicolored with lighter elytra in *P. iwani*). This species often has somewhat less pronounced setae (which may easily be abraded)—with some specimens appearing to lack dorsal setation entirely.

In Koch's (1954b) original treatment and designation for the genus, he outlined specimens he likened to Solier's original (1848) description. As he did not have type material at his disposal, he was unable to draw direct comparisons. Upon our investigation of **MNHN**'s holdings, we found a specimen matching Solier's description (based upon a singleton from "Du Cap de Bonne Espérance."). Koch's *Phaleriderma dicksonae* appears to be a junior synonym of *Phaleriderma obscuricollis*. Interestingly, the specimens Koch identified and relegated to *P. obscuricollis* represent a hitherto undescribed species (see *P. iwani*).



Map 86. Distribution of *Phaleriderma obscuricollis* (Solier).

Material examined

Phaleriderma obscuricollis: **Holotype**, sex undetermined **MNHN** (Fig. T117): "obscuricollis. sol 193 Cap b.sp SYNTYPE MUSEUM PARIS COLL. SOLIER 9641-34 MUSEUM PARIS

COLL DE MARSEUL 1890 blue circle label "Oncotus obscuricollis Cape -illegible-".

While the holotype for *Phaleriderma discksonae* was not examined here, the specimen should be housed in **IMSA** bearing the label data: "Blaauwberg / Strand 1897 / Leg. L. Péringuey".

Phaleriderma dicksonae: **Paratype**, sex undetermined **TMNH** (Fig. T114): "Blaurberg L-1?-97 Paratype No: 1633 Phaleriderma dicksonae KOCH Paratypus Phaleriderma dicksonae C. Koch sp.n.".

TMNH: "S.Afr. S.W. Cape Cape Columbine 32.49 S - 17.51 E 22.8.1983; E-Y: 1965 groundtraps, 73 days leg. Endrödy, Penrith groundtrap with faeces bait (four specimens, one with additional TB# label: 26330)", "S.Afr. S.W. Duiker Island 32.43 S - 17.56 E 22.8.1983; E-Y: 1963 grassnetting, coast leg. Endrödy, Penrith (two specimens)."

Distribution

South Africa: Western Cape (Map 86).

xviii. Genus *Quadroncotus* Koch

Oncotus (*Quadroncotus*) Koch, 1954b: 40.– Kamiński 2016: 244; Bouchard *et al*. 2021: 329. Lumen *et al*. 2025: 6

Type species: *Oncotus irrepertus* Koch; by original designation.

Diagnosis

Morphologically the genus superficially resembles *Anamenederes*, *Menoncotus*, or *Oncotus*, but has characteristics similar to *Menederes* (scattered punctation of the last elytral interval) and *Ograbies* (less-strongly sclerotized with reduced elytral punctation). The lateral projection of the foretibia is less pronounced and the outer margin has many irregular spines, protuberances and/or crags present. The basal pronotal angles are also more rounded than *Oncotus* (*Quadroncotus* also lacks the slight depressions on the basal pronotal angles), and *Anamenederes* has an elongate apical projection on the tibia apex as well as an elongate projection near the tarsus insertion point (less-elongate and absent in *Quadroncotus* respectively).

***Species included* (Monotypic)**

Q. irrepertus (Koch).

1. *Quadroncotus irrepertus* (Koch)

Oncotus (*Quadroncotus*) *irrepertus* Koch, 1954b: 40.– Kamiński 2016: 244; Bouchard *et al*. 2021: 329.

Quadroncotus irrepertus (Koch, 1954b).– Lumen *et al*. 2025: 2.

Diagnosis

See diagnosis of *Quadroncotus*.

Material examined

Holotype, female **TMNH** (Fig. T118): "Steinkopf, Namaqua / land, 13-XII-1948 / Koch & Van Son / HOLOTYPE No: 1677 / Oncotus / irrepertus KOCH / irrepertus / Koch". **Paratype**, female **NHMB**: "Steinkopf Na. 15.XII.1949 C. Koch 895 Oncotus irrepertus KOCH Coll. FREY", "Springbok C.P. 17-XI-1948 Koch & van Son 894 Oncotus irrepertus KOCH Coll. FREY".

Distribution

South Africa: Northern Cape (Map 87).



Map 87. Distribution of *Quadroncotus irrepertus* (Koch).

xix. Genus *Stridigula* Koch

Stridigula Koch, 1954b: 60.– Koch 1956: 27; Kamiński 2016: 248; Bouchard *et al*. 2021: 353; Lumen *et al*. 2025: 2.

=*Cilioncotus* Koch, 1954b: 41.– Kamiński 2016: 242; Bouchard *et al*. 2021: 143; Kamiński *et al*. 2021: 152; Lumen *et al*. 2025: 17 (syn.). Type species: *Oncotus namaquanus* Koch, 1954b; by original designation.

Type species: *Stridigula arguta* Koch; by original designation.

Diagnosis

Stridigula is the only genus in Eurynotina with medial pockets of setae on the base of the elytra (though somewhat reduced in *S. namaquana*). Some characteristics separating most species from other genera have exceptions in others that are useful for species delineation. For example, like other genera in the *Oncotus* lineage (e.g., *Ograbies*, *Oncotus*), most *Stridigula* possess sclerites in the bursa copulatrix (except *S. planiuscula*), setting them apart from superficially similar genera from the *Psectrapus* lineage; and females have a sulcus near the apex of abdominal ventrite V (except in *S. namaquana*). Male *Stridigula* lack expanded foretarsi, and have somewhat truncate aedeagi with a relatively small, shallow separation apically and penis without hook(s).

***Species included* (3)**

S. arguta Koch, *S. namaquana* (Koch), *S. planiuscula* (Fairmaire).

Key to species of *Stridigula* (see Plate xix for figures):

1. Strongly dorso-ventrally flattened. Elytral striae impressed with larger and more pronounced punctures (Fig. 1). Bursa copulatrix without sclerites ..... ***Stridigula planiuscula***

— Body convex. Elytral striae weakly to not impressed with smaller punctation (Fig. 2). Bursa copulatrix with sclerites (Figs 5–6) **2**

2. Setose pit at base of elytra large and pronounced. Abdominal ventrite V with single, uniform puncture type (Fig. 3). Bursa copulatrix with small strip-shaped sclerites (Fig. 5). Females with subapical sulcus on abdominal ventrite V (sometimes reduced or interrupted) (Fig. 3) ..... ***Stridigula arguta***

— Setose pit at base of elytra reduced. Abdominal ventrite V with two puncture types (small and large) (Fig. 4). Bursa copulatrix with broad leaf-like sclerites (Fig. 6). Female without subapical sulcus on abdominal ventrite V (Fig. 4) ..... ***Stridigula namaquana***

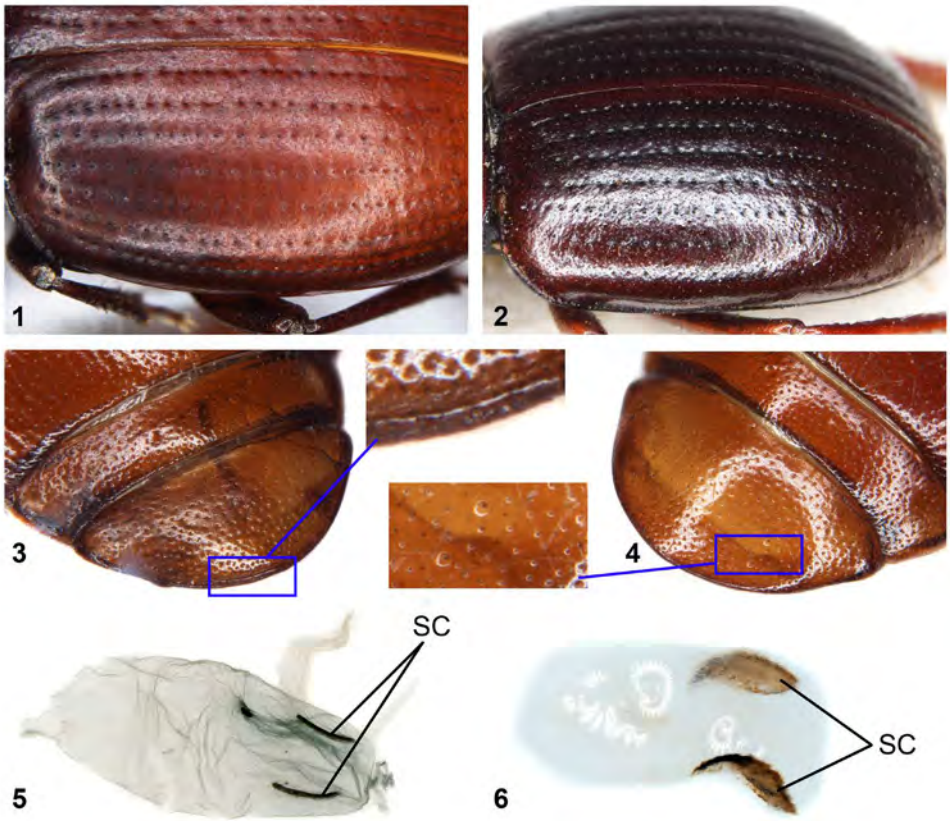


Plate xix. *Stridigula* species diagnostic features. **Anatomic features**: Elytron (1–2). Abdominal ventrites IV and V (3–4). Bursa copulatrix (5–6). **Taxa depicted**: *Stridigula arguta* (2, 3, 5). *Stridigula namaquana* (4, 6). *Stridigula planiuscula* (1). **Abbreviation**: SC = sclerite.

1. *Stridigula arguta* Koch

Stridigula arguta Koch, 1954b: 61.– Kamiński 2016: 248; Lumen *et al*. 2025: 13.

=*Oncotus* (*Cilioncotus*) *humerisetosus* Koch, 1954b: 43.– Kamiński 2016: 243; Lumen *et al*. 2025: 17 (syn.).

Diagnosis

Sharply separable from *S. planiuscula* based on the shape of the body (*S. planiuscula* somewhat elongate and dorsoventrally flattened; *Stridigula arguta* is strongly convex and more globose). The most similar species is *S. namaquana*, which can be separated based on genitalic characteristics (aedeagus angularly convergent apically in *S. arguta*, rounded in *S. namaquana*; bursa copulatrix with narrow strip-shaped sclerites in *S. arguta*, broad and leaf-shaped in *S. namaquana*) and the presence of well-developed setose pits on the elytral base (reduced in *S. namaquana*).

Material examined

Stridigula arguta: **Holotype**, sex undetermined **TMNH** (Fig. T119): "Brandkross, 2. / VI.1953. Rich- / tersveld. Koch / HOLOTYPE No: 1754 / Stridigula / arguta KOCH / arguta / Ko.". **Paratype**, TMNH: Same data as holotype.

Oncotus (*Cilioncotus*) *humerisetosus*: **Holotype**, male **TMNH** (Fig. T120): "Holgat, L.Namaqua- / ld., 2.IX.1950 / C.Koch, G.van Son / HOLOTYPE No: 1684 / Oncotus humerisetosus / KOCH / humerisetosus / Koch".

SANC: "R.S.Africa: Northern Cape Prov.: Koeroegabvlakte (Richtersveld NP) 62km NO Alexander Bay, Succulent-Karoo BIOTA 18.087.2002.07.05.399 28°14'01.9"S/17°01'58.0"E 20 pitfall traps 7.-11.x.2002 leg. M. Uhlig & K Ebert Tenebrionidae gen. Spec. 54 det. M. Uhlig 2003 (two specimens)". **TMNH**: "S. Afr.; Richtersveld De Hoop 28.11 S - 17.11 E 8.9.2001;E-Y:3415 under stones; on ground leg. SATM staff (five specimens)", "Namibia; Namuskluft Zebrafontein 27.45 S - 16.53 E 2-6.IV.2002 leg E. Holm, M.Gebhardt", "S.Afr.;Richtersveld Hellskloof 4km N 28.17 S - 16.59 E 26.9.1991;E-Y:2798 from under stones leg. Endrödy-Younga", "S. Afr.; Richtersveld Kubeos-Ekst. 14kmW 28.33 S - 16.57 E 29.9.1991:E-Y:2812 from under stones leg. Endrödy-Younga", "Richtersveld SWA June ?? HW ??".

Distribution

South Africa: Northern Cape. Namibia: ǁKaras Region (Map 88).



Map 88. Distribution of *Stridigula arguta* Koch.

2. *Stridigula namaquana* (Koch)

Oncotus (*Cilioncotus*) *namaquanus* Koch, 1954b: 43.– Kamiński 2016: 243; Lumen *et al*. 2025: 6.

Stridigula namaquana (Koch, 1954b).– Lumen *et al*. 2025: 6.

Diagnosis

Most similar to *S. arguta* (globose and convex), this species is most easily separated based on a setal pit at the base of the elytra (small/reduced; *Stridigula arguta* has a much more pronounced pit). Further, the shape of the bursa copulatrix sclerites of females and parameres of males can be used to separate the species (see diagnoses of *S. arguta* and *S. planiuscula*).

Material examined

Holotype, male **TMNH** (Fig. T121): "Lilyfontein / Namaqualand / namaquanus / HT KOCH". **Paratype NHMB**: "Kamieskroon / Namaqualand / Museum Staff / Sept 1930 / Coll. FREY / 897 / Paratype / Oncotus / namaquanus / KOCH".

TMNH: "S.Afr.;Richtersveld Ekstienfonteinvall 28.47 S - 17.12 E 28.9.1991;E-Y:2804 from under stones leg. Endrödy-Younga (two specimens)", "S.Afr.Namaqualand Ezelfontein 115m 20.24S - 18.05E 5.9.1977;E-Y:1387 groundtraps, 55 days leg. Endrödy-Younga groundtrap with feces bait", "S.Afr.;Richtersveld Ekstienfont.highval 28.47 S - 17.09 E 28.9.1991;E-Y:2807 from under stones leg. Endrödy-Younga".

Distribution

South Africa: Northern Cape (Map 89).



Map 89. Distribution of *Stridigula namaquana* (Koch).

3. *Stridigula planiuscula* (Fairmaire)

Oncotus planiuscula Fairmaire, 1888: 194.– Gebien 1938: 393; Kamiński 2016: 248.

Stridigula planiuscula (Fairmaire, 1888).– Koch 1954b: 63; Lumen *et al*. 2025: 22.

Diagnosis

Stridigula planiuscula is the most outwardly unique species in the genus by the overall shape of the body (elongate and dorsoventrally flattened). Internally, the species lacks sclerites in

the bursa copulatrix and has an aedeagus with more evenly tapered parameres (the other two species have more truncate parameres; *S. arguta* with sharply angular paramere tips, and *S. namaquana* with a more rounded apex).

Material examined

As Fairmaire never designated a number of individuals nor selected a holotype, to stabilize the taxonomic concept of this species we here nominate a specimen from the syntype series from **MNHN** as a lectotype (see below).

Lectotype, sex undetermined, here designated **MNHN** (Fig. T122): "Nama / sch-illegible- / Oncotus planiuscula / -illegible- / Namaqua".

TMNH: "Witputs gt. Namaq V.53.Koch (three specimens)", "Rek Vlakte, Gt Namaqualand V.1953.C.Koch", "Aus.Gt.Namaquald. 17.IX.1950 C.Koch, G.van Son Tenebrionidbase 26311". **NHMB**: "Witputs gt. Namaq V.53.Koc 925 Stridigula planiuscula FAIRM.".

Distribution

South Africa: Namibia: ǂKaras Region (Map 90).



Map 90. Distribution of *Stridigula planiuscula* (Fairmaire).

IV. Type Photographs
Eurynotus lineage

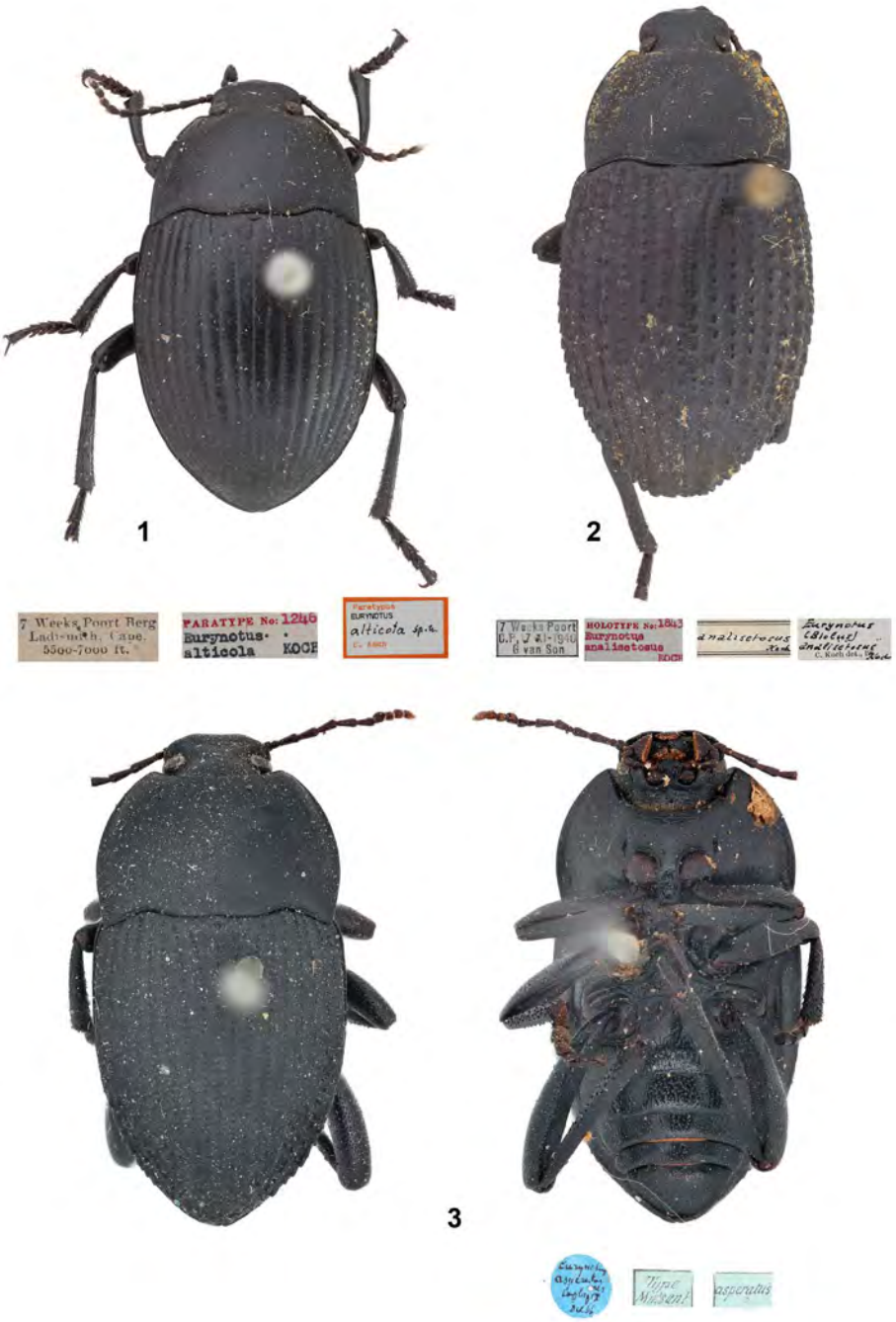


Fig. T1-T3. Type specimens of Eurynotina. Lectotype of *Eurynotus alticola* (1). Holotype of *Eurynotus analisetosus* (2). Lectotype of *Eurynotus asperatus* (3).

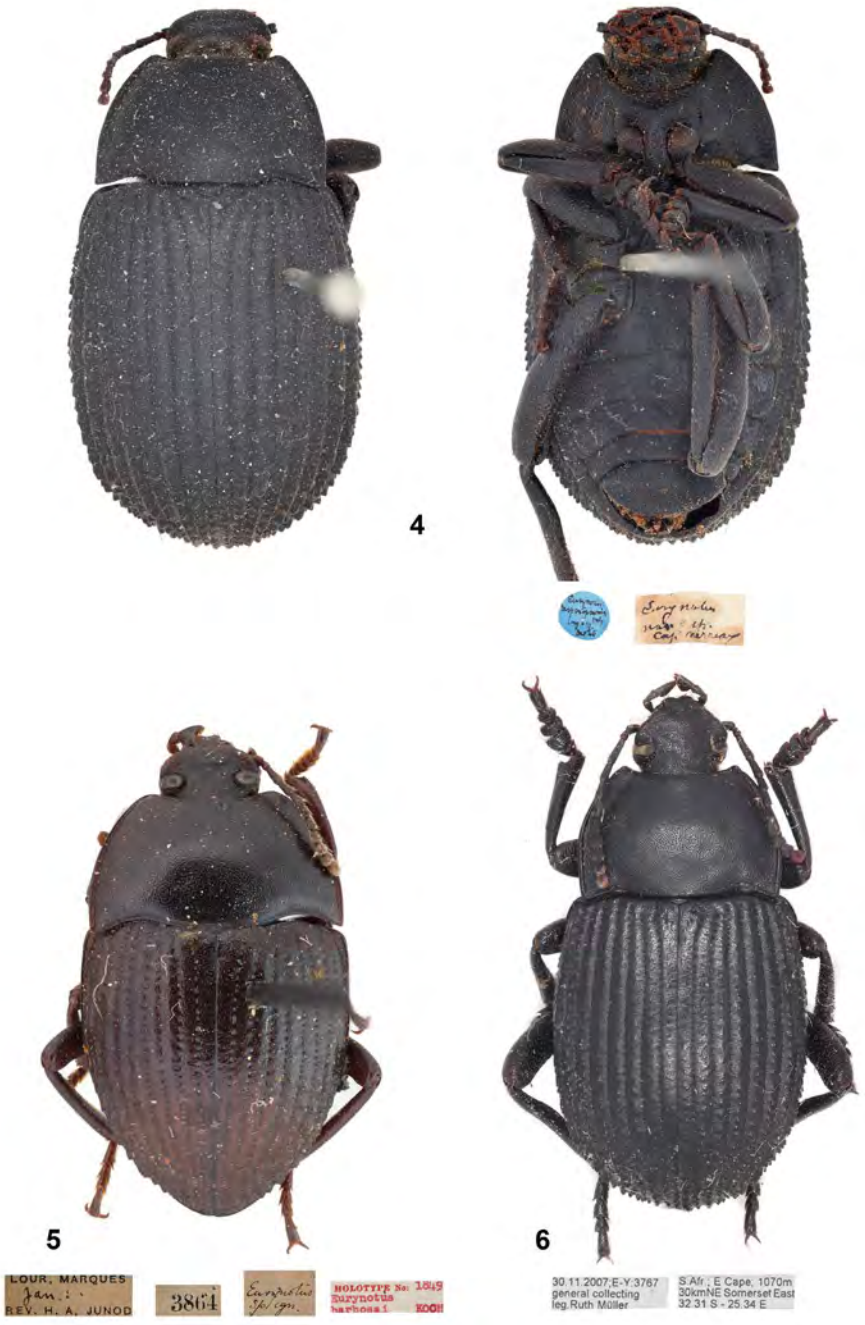


Fig. T4-T6. Type specimens of Eurynotina. Lectotype of *Eurynotus asperipennis* (4). Holotype of *Eurynotus barbosai* (5). Holotype of *Eurynotus brunoi* (6).



Fig. T7-T10. Type specimens of Eurynotina. Lectotype of *Eurynotus capensis* (7). Lectotype of *Eurynotus constrictus* (8). Lectotype of *Eurynotus denticosta* (9). Holotype of *Eurynotus graafi* (10).



Fig. T11-T14. Type specimens of Eurynotina. Holotype of *Eurynotus graniderma* (11). Lectotype of *Eurynotus granulatus* (12). Syntype of *Eurynotus muricatus* synonym of *Eurynotus capensis* (13) – image courtesy Dmitry Telnov, **Natural History Museum London, UK**. Lectotype of *Eurynotus norrisi* synonym of *Eurynotus granulatus* (14).

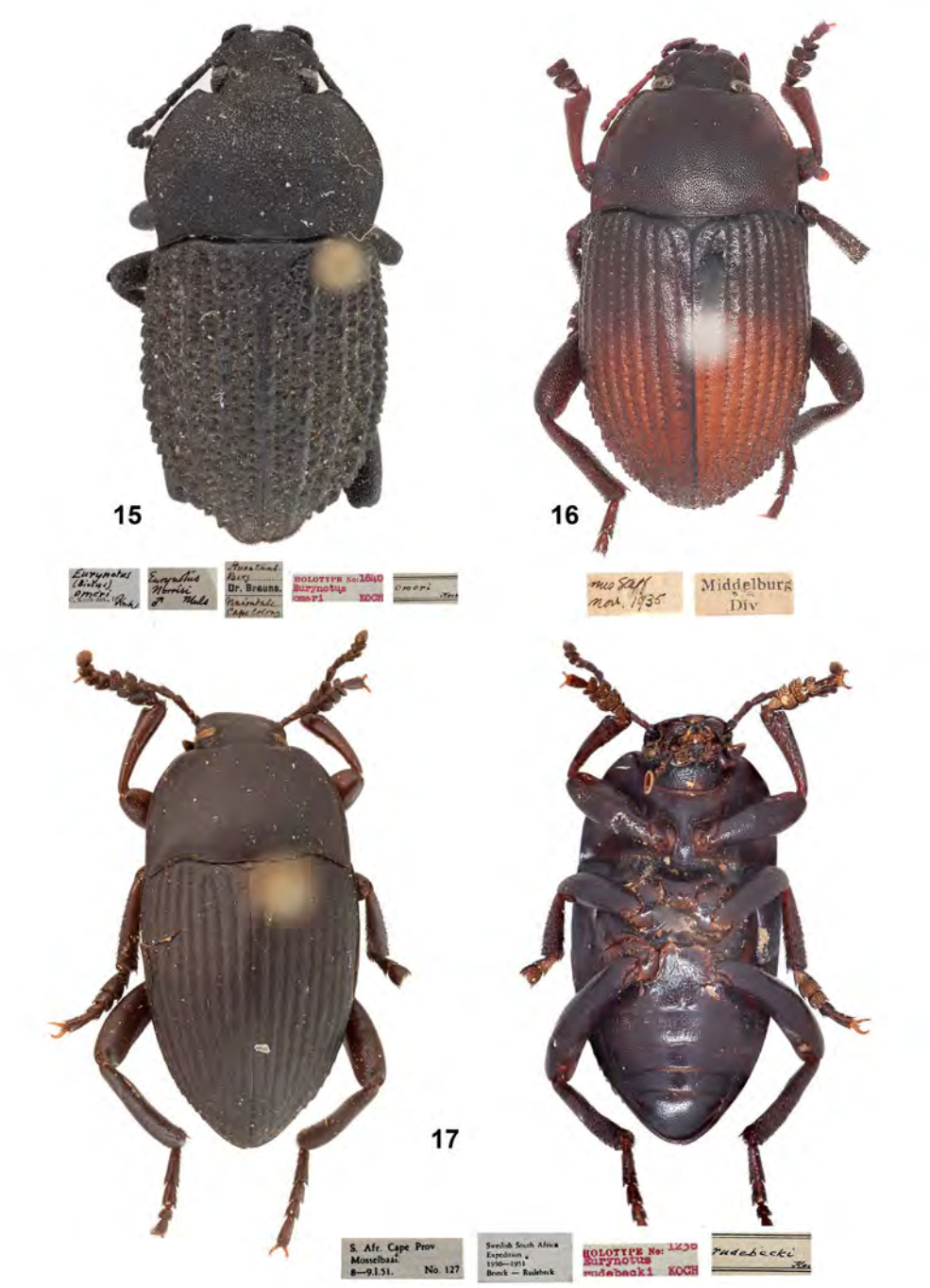


Fig. T15-T17. Type specimens of Eurynotina. Holotype of *Eurynotus omeri* (15). Holotype of *Eurynotus privisolum* (16). Lectotype of *Eurynotus rudebecki* synonym of *Eurynotus asperatus* (17).



Fig. T18-T20. Type specimens of Eurynotina. Holotype of *Eurynotus sauroides* (18). Lectotype of *Eurynotus sulcimargo* (19). Holotype of *Eurynotus thermarum* (20).

***Phylacastus* lineage**

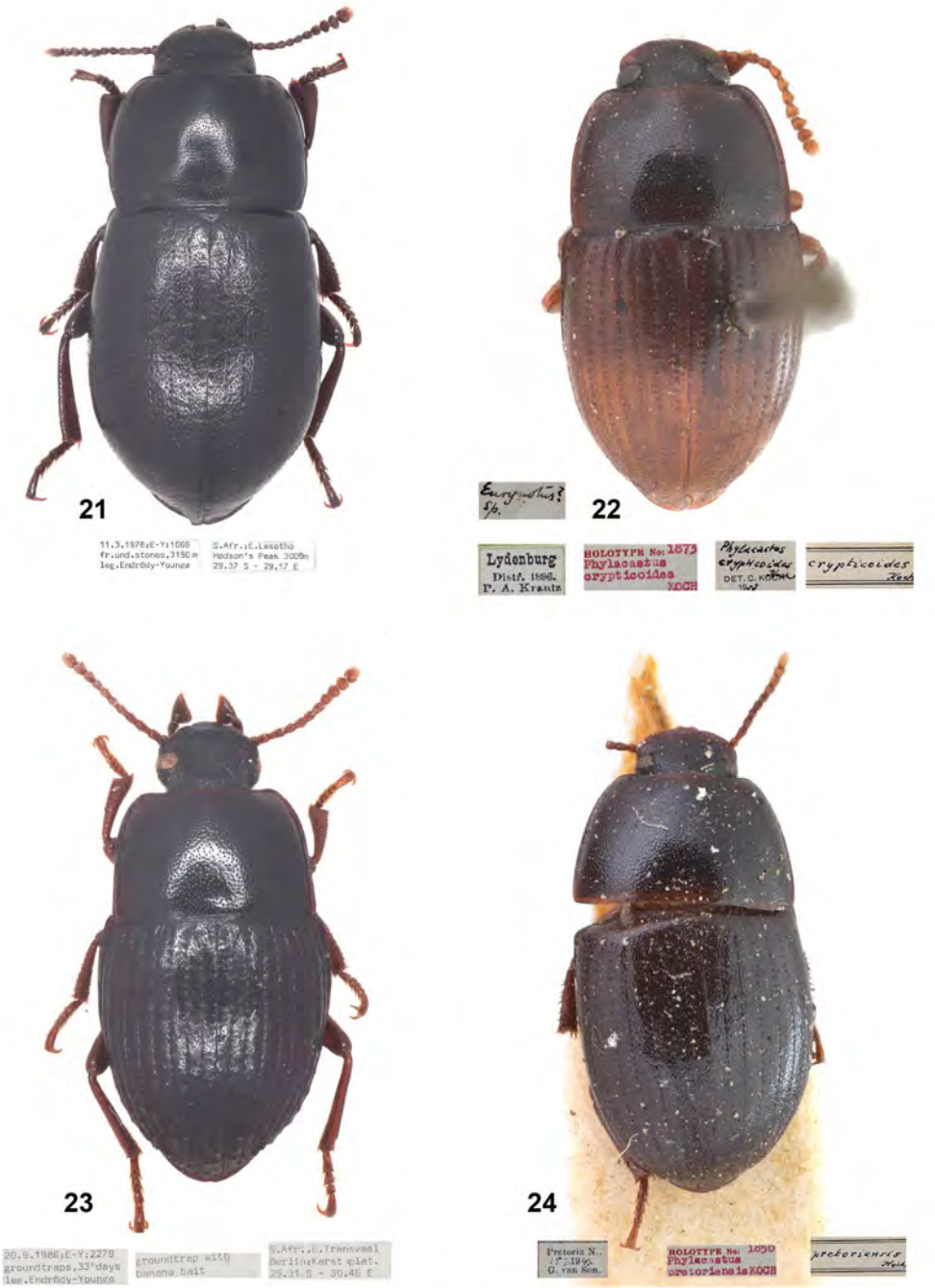


Fig. T21-T24. Type specimens of Eurynotina. Holotype of *Phylacastus ancoralium* (21). Holotype of *Phylacastus crypticoides* (22). Holotype of *Phylacastus makskacymirowi* (23). Holotype of *Phylacastus pretoriensis* synonym of *Phylacastus crypticoides* (24).



Fig. T25-T26. Type specimens of Eurynotina. Holotype of *Phylacastus rhodesianus* (25). Lectotype of *Phylacastus striolatus* (26).

Schyzoschelus lineage



Fig. T27-T29. Type specimens of Eurynotina. Paratype of *Heteropsectropus amaroides* synonym of *Heteropsectropus difficilis* (27). Holotype of *Heteropsectropus difficilis* (28). Holotype of *Heteropsectropus longantennatus* (29).



Fig. T30-T33. Type specimens of Eurynotina. Holotype of *Heteropsectropus montisdraconis* synonym of *Heteropsectropus longantennatus* (30). Paratype of *Heteropsectropus natalensis* synonym of *Heteropsectropus difficilis* (31). Holotype of *Heteropsectropus transvaalensis* synonym of *Heteropsectropus difficilis* (32). Holotype of *Muelleropsectropus malaisei* (33).

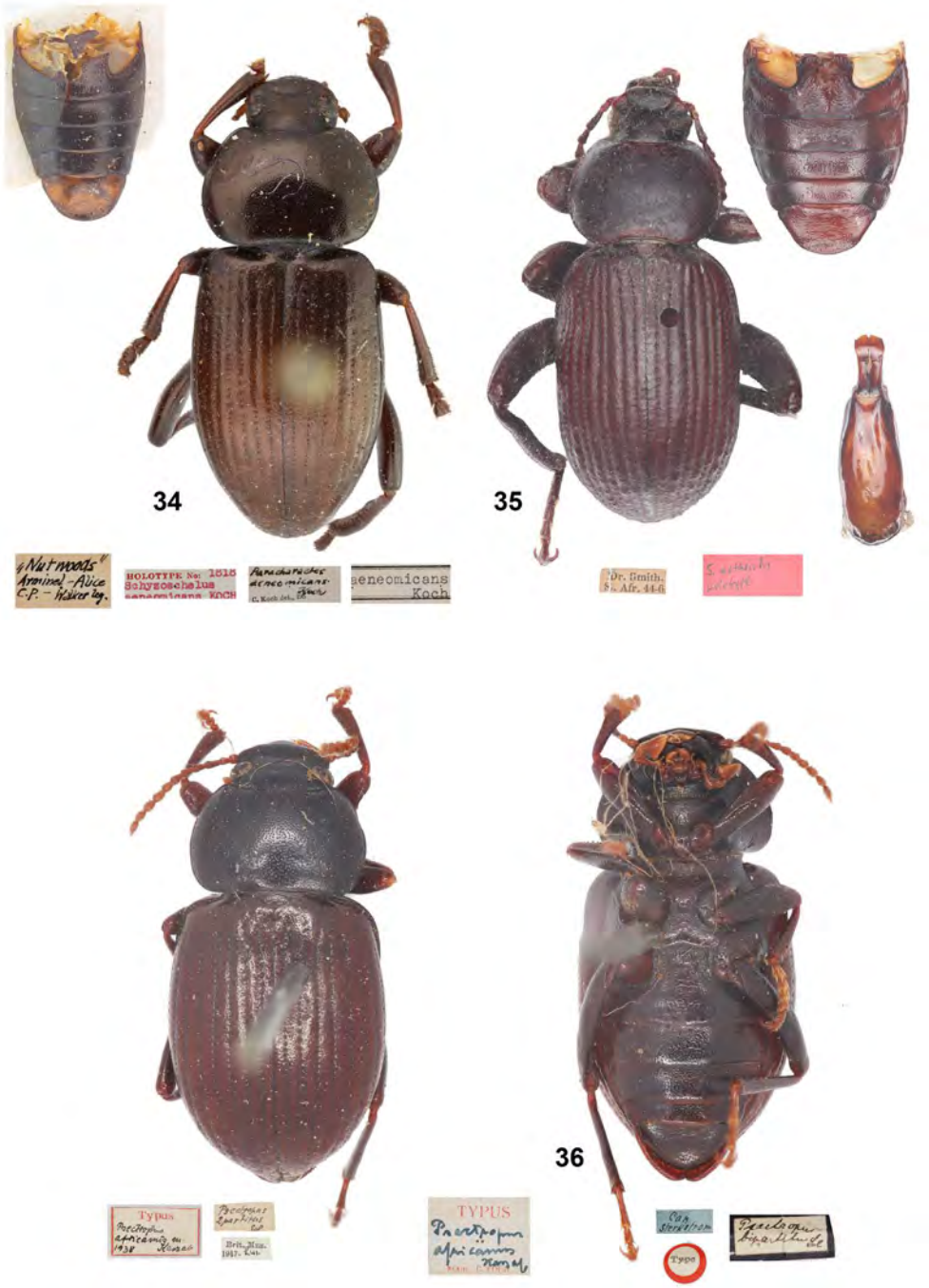


Fig. T34-T36. Type specimens of Eurynotina. Holotype of *Schyzoschelus aeneciomicans* (34). Holotype of *Schyzoschelus aetheculus* (35). Syntype of *Schyzoschelus africanus* (36).

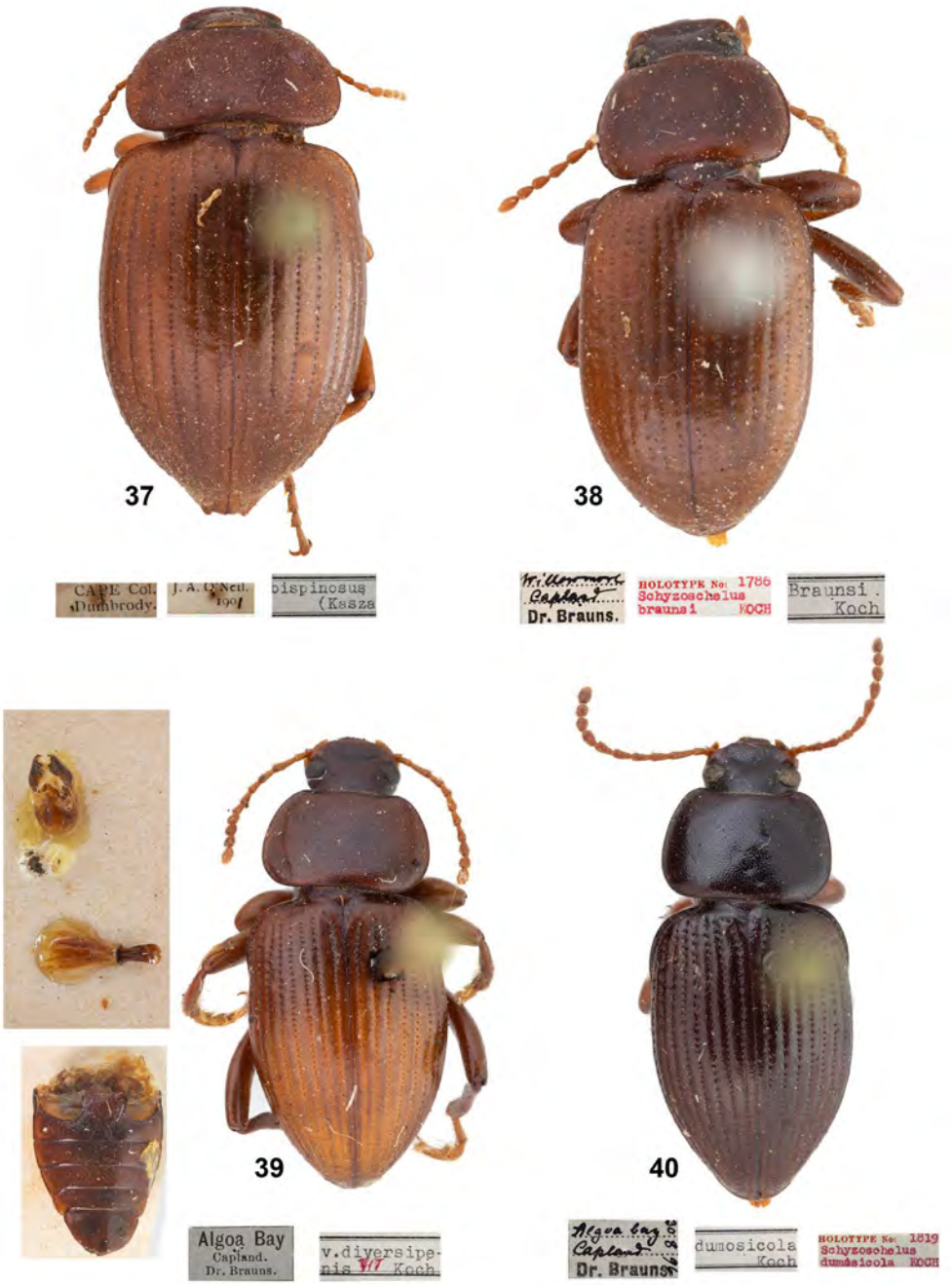


Fig. T37-T40. Type specimens of Eurynotina. Holotype of *Schyzoschelus bispinosus* (37). Holotype of *Schyzoschelus braunsi* (38). Holotype of *Schyzoschelus dumosicola* var. *diversipenis* synonym of *Schyzoschelus dumosicola* (39). Holotype of *Schyzoschelus dumosicola* (40).



Fig. T41-44. Type specimens of Eurynotina. Holotype of *Schyzoschelus jenkinsae* (41). Paratype of *Schyzoschelus karrooensis* (42). Holotype of *Schyzoschelus kaszabi* (43). Holotype of *Schyzoschelus ladini* (44).

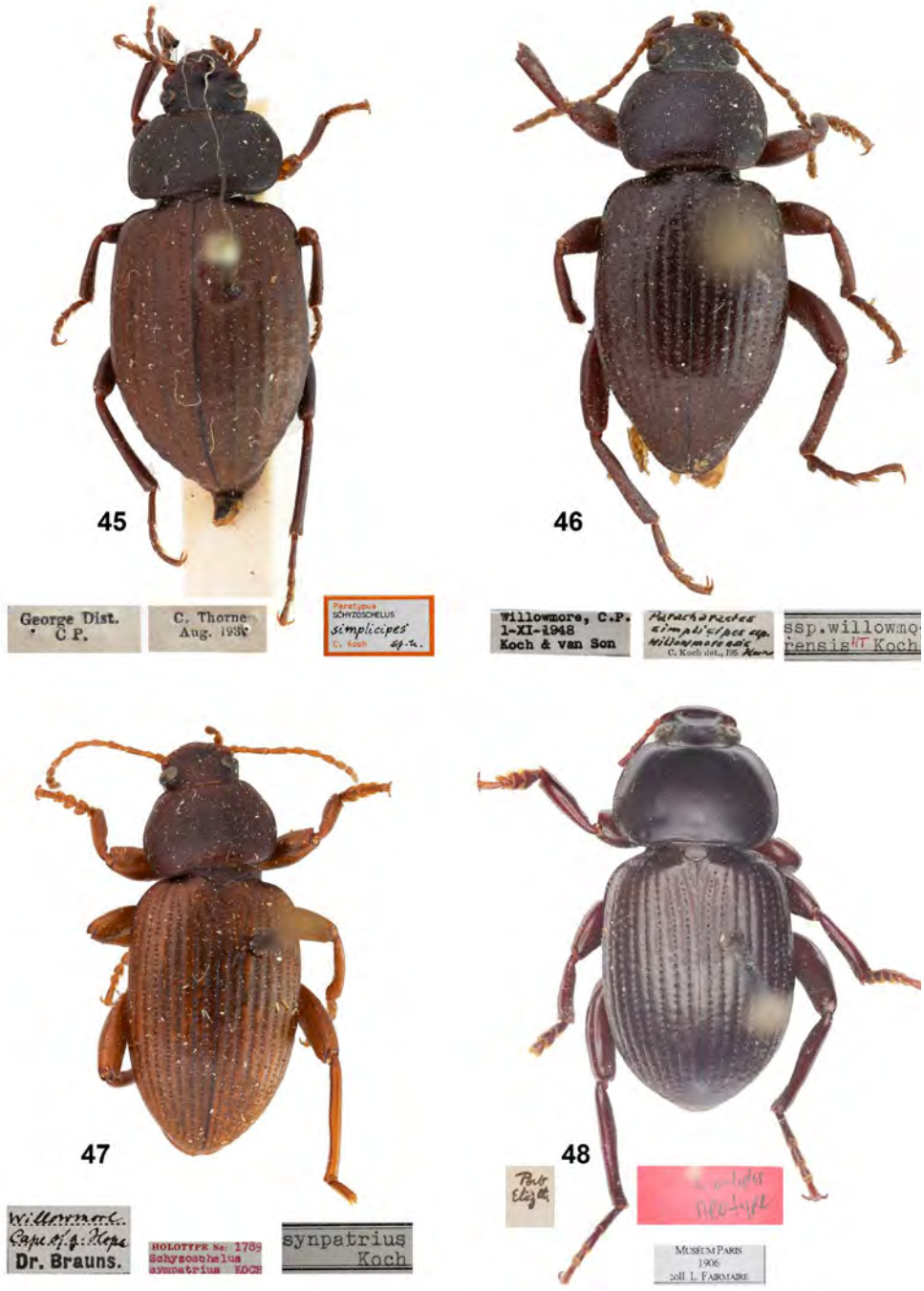


Fig. T45-T48. Type specimens of Eurynotina. Paratype of *Schyzoschelus simplicipes* (45). Holotype of *Schyzoschelus simplicipes willowmorensis* synonym of *Schyzoschelus simplicipes* (46). Holotype of *Schyzoschelus sympatrius* (47). Neotype of *Schyzoschelus validus* (48).

***Psectrapus* lineage**



Fig. T49-T51. Type specimens of Eurynotina. Holotype of *Byrrhoncus monticola* (49). Paratype of *Byrrhoncus monticola* (50). Holotype of *Byrrhoncus parvithorax* (51).



Fig. T52-T55. Type specimens of Eurynotina. Holotype of *Capidium bipunctatum* (52). Holotype of *Capidium hessei* (53). Paratype of *Capidium hessei* (54). Holotype of *Onchotus tardus* var. *pedellus* synonym of *Capidium bipunctatum* (55).



Fig. T56-T59. Type specimens of Eurynotina. Holotype of *Blaps striatula* synonym of *Capidium bipunctatum* (56). Holotype of *Oncotus tardus* synonym of *Capidium bipunctatum* (57). Paratype of *Capidium tuberculatum* (58). Holotype of *Capidium vicarium* (59).



Fig. T60-T61. Type specimens of Eurynotina. Paratypes of *Colophonesthes barnardi* (60). Holotype of *Colophonesthes montisatri* (61).



Fig. T62-T64. Type specimens of Eurynotina. Paratype of *Colophonesthes montisatri* (62). Holotype of *Colophonexsula enisa* (63). Paratype of *Colophonexsula enisa* (64).



Fig. T65-T68. Type specimens of Eurynotina. Paratype of *Colophonexsula nitens* (65). Holotype of *Colophonexsula puerilis* (66). Paratype of *Colophonesthes puerilis* (67). Holotype of *Isoncophallus angulicollis* (68).

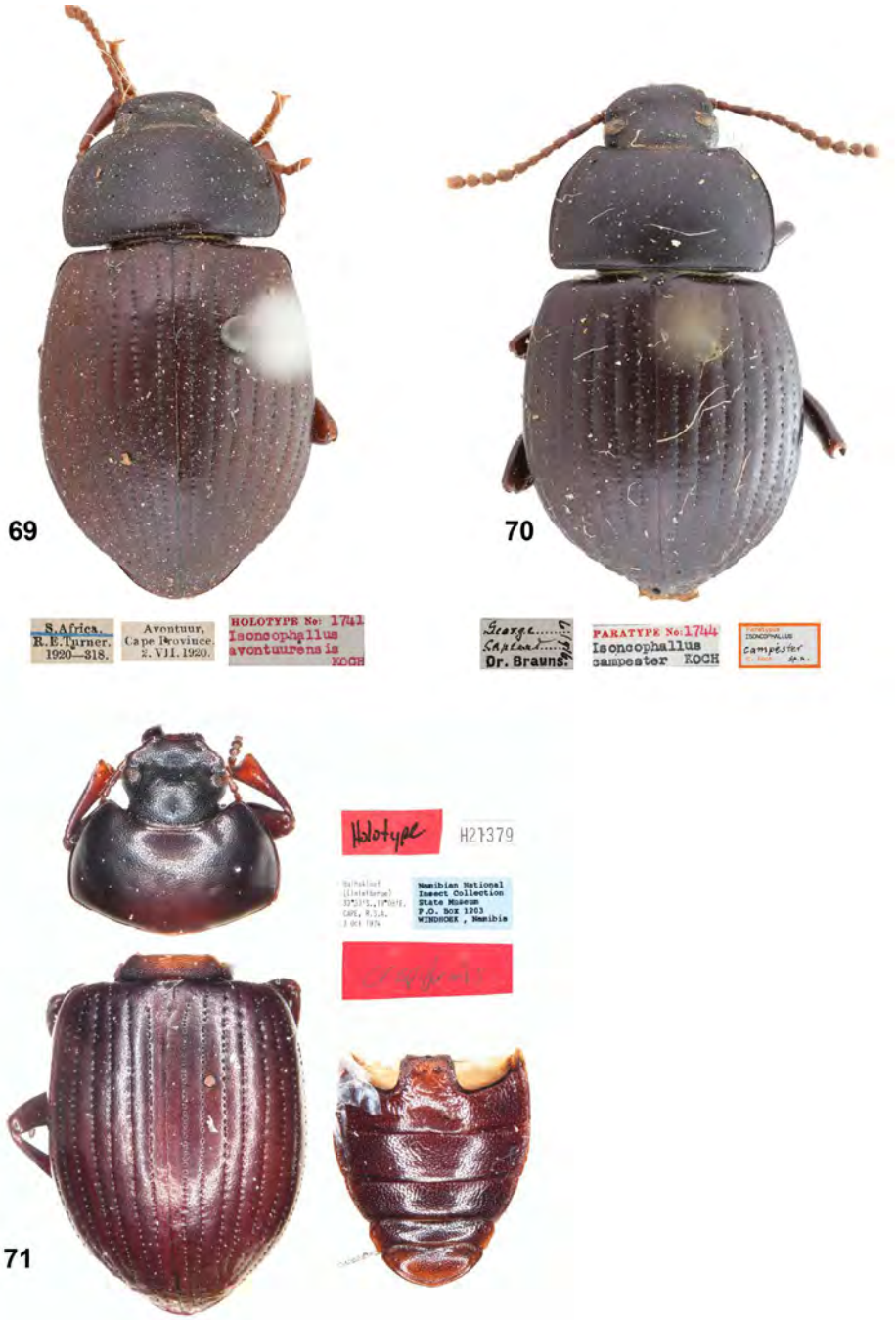


Fig. T69-T71. Type specimens of Eurynotina. Holotype of *Isoncophallus avontuurensis* (69). Paratype of *Isoncophallus campester* (70). Holotype of *Isoncophallus crispiformus* (71).



Fig. T72-T74. Type specimens of Eurynotina. Holotype of *Isoncophallus dentimanus* (72). Paratype of *Isoncophallus diffusus* (73). Paratype of *Isoncophallus diffusus* (74).

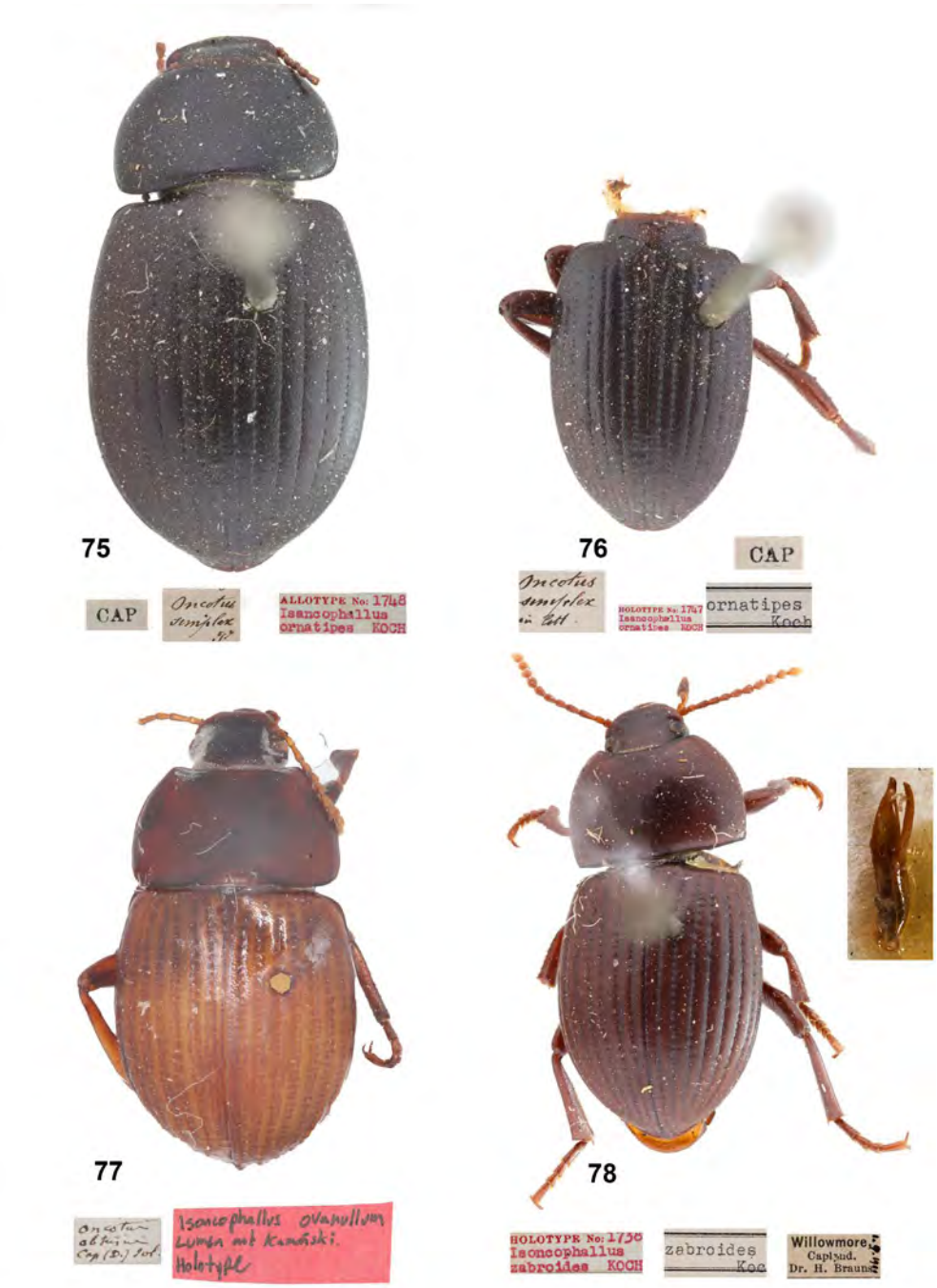


Fig. T75-T78. Type specimens of Eurynotina. Paratype of *Isoncophallus ornatipes* (75). Holotype of *Isoncophallus ornatipes* (76). Holotype of *Isoncophallus ovanullum* (77). Holotype of *Isoncophallus zabroides* (78).



Fig. T79-T82. Type specimens of Eurynotina. Neotype of *Psectrapus bipartitus* (79). Holotype of *Psectrapus byki* (80). Holotype of *Psectrapus distaticum* (81). Paratype of *Psectrapus latimentulum* (82).



Fig. T83. Type specimens of Eurynotina. Holotype of *Psectrapus simplicimentulum* (83).

Oncotus lineage



Fig. T84-T87. Type specimens of Eurynotina. Paratype of *Anamenederes digitatus* (84). Holotype of *Hirtograbies brevicornis* synonym of *Hirtograbies longipilis* (85). Holotype of *Hirtograbies canicautis* (86). Holotype of *Hirtograbies gariepinus* (87).



Fig. T88-T91. Type specimens of Eurynotina. Paratype of *Hirtograbies gariepinus* (88). Lecotype of *Hirtograbies longipilis* (89). Paralectotype of *Hirtograbies longipilis* (90). Holotype of *Hirtograbies namibensis* synonym of *Hirtograbies longipilis* (91).



Fig. T92-T95. Type specimens of Eurynotina. Holotype of *Hirtograbies nanus* (92). Holotype of *Hirtograbies oograbiensis* (93). Holotype of *Menederes chaetotaxicus* (94). Holotype of *Menederes constrictus* (95).



Fig. T96-T98. Type specimens of Eurynotina. Holotype of *Menederes dannheimeri* (96). Paratype of *Menederes jokli* (97). Paratype of *Menederes jokli* (98).



Fig. T99-T102. Type specimens of Eurynotina. Paratype of *Archinamaqua lyleae* synonym of *Menederes constrictus* (99). Neotype of *Menederes rufilabris* (100). Holotype of *Oncotus* (*Menoncotus*) *sinuatipes* synonym of *Menederes chaetotaxicus* (101). Holotype of *Ograbies angulatus* (102).

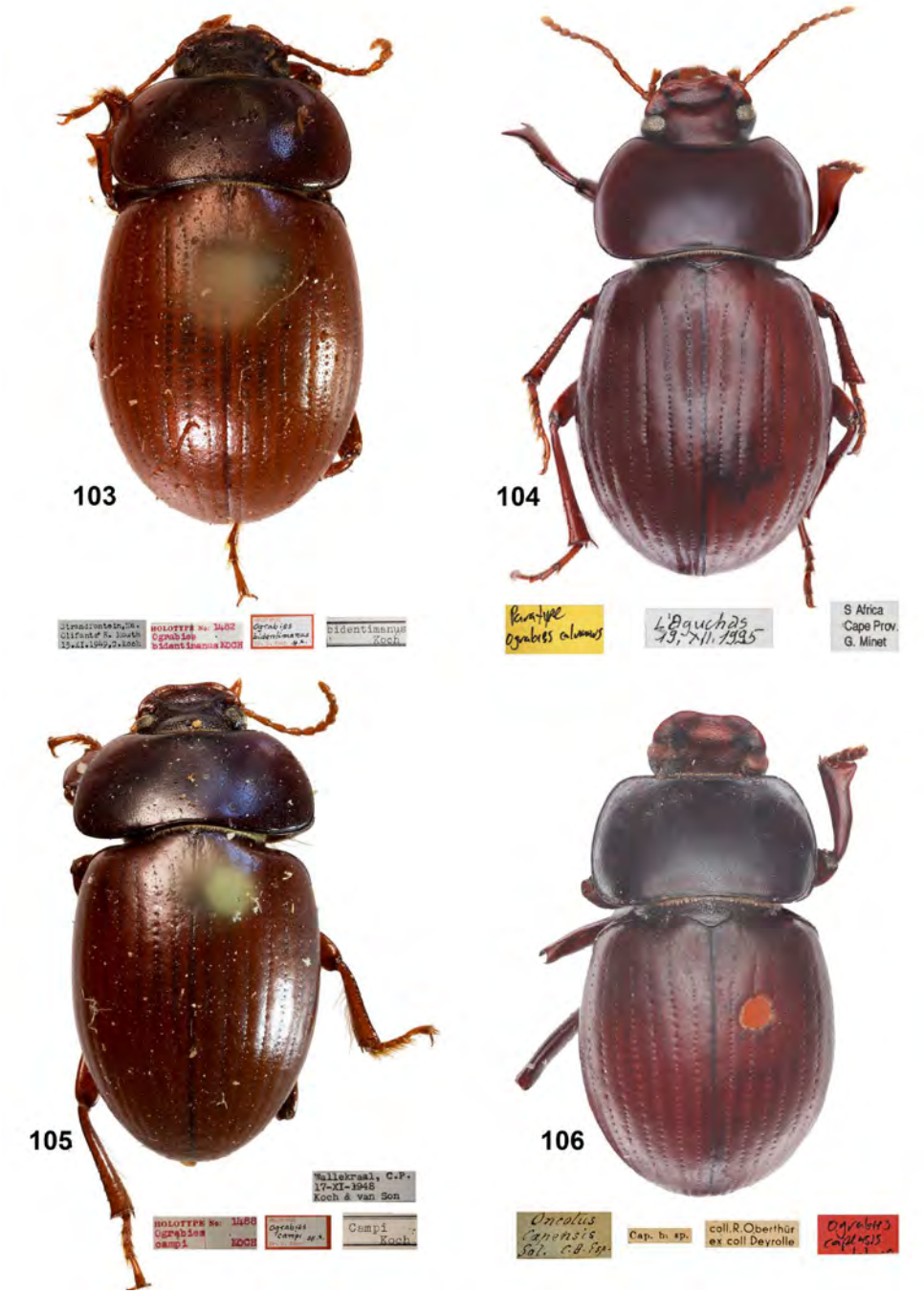


Fig. T103-T106. Type specimens of Eurynotina. Holotype of *Ograbies bidentimanus* (103). Paratype of *Ograbies calumnus* (104). Holotype of *Ograbies campi* (105). Neotype of *Ograbies capensis* (106).

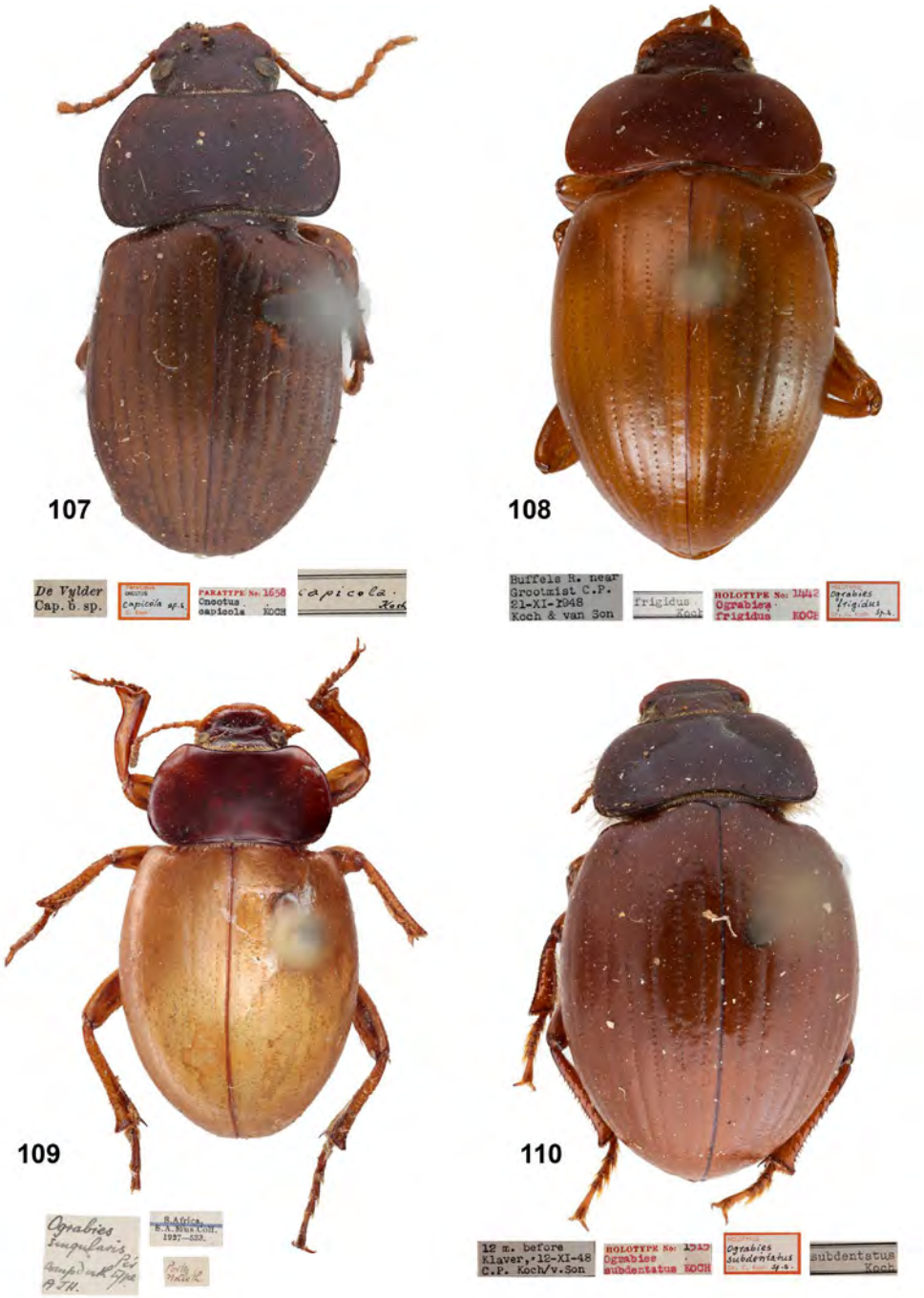


Fig. T107-T110. Type specimens of Eurynotina. Paratype of *Ograbies capicola* synonym of *Ograbies capensis* (107). Holotype of *Ograbies frigidus* (108). Holotype of *Ograbies singularis* and neotype of *Ograbies testaceus* (109). Holotype of *Ograbies subdentatus* (110).

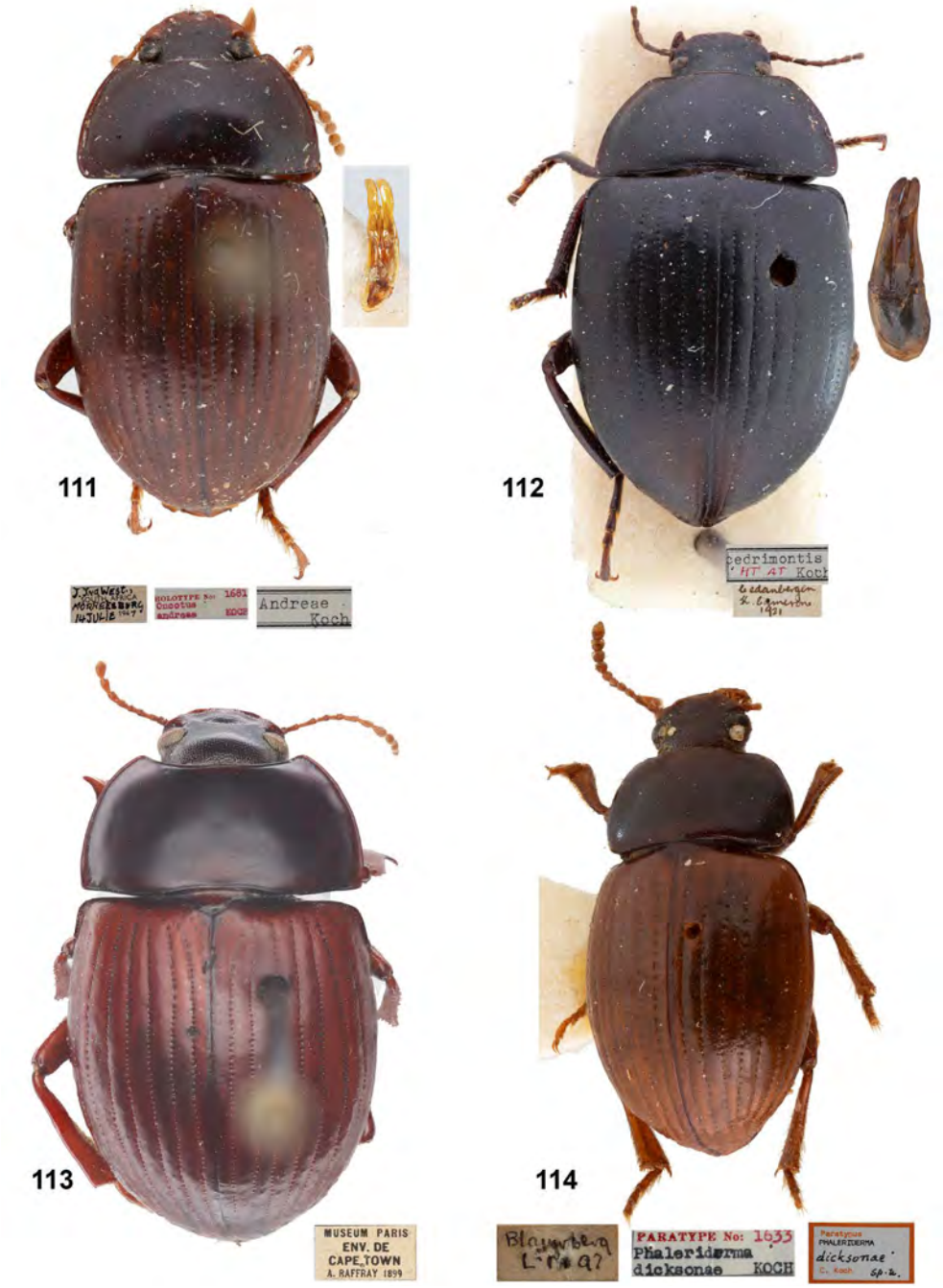


Fig. T111-T114. Type specimens of Eurynotina. Holotype of *Oncotus andreae* (111). Holotype of *Oncotus cedrimontis* (112). Neotype of *Oncotus farctus* (113). Paratype of *Phaleriderma dicksonae* synonym of *Phaleriderma obscuricollis* (114).

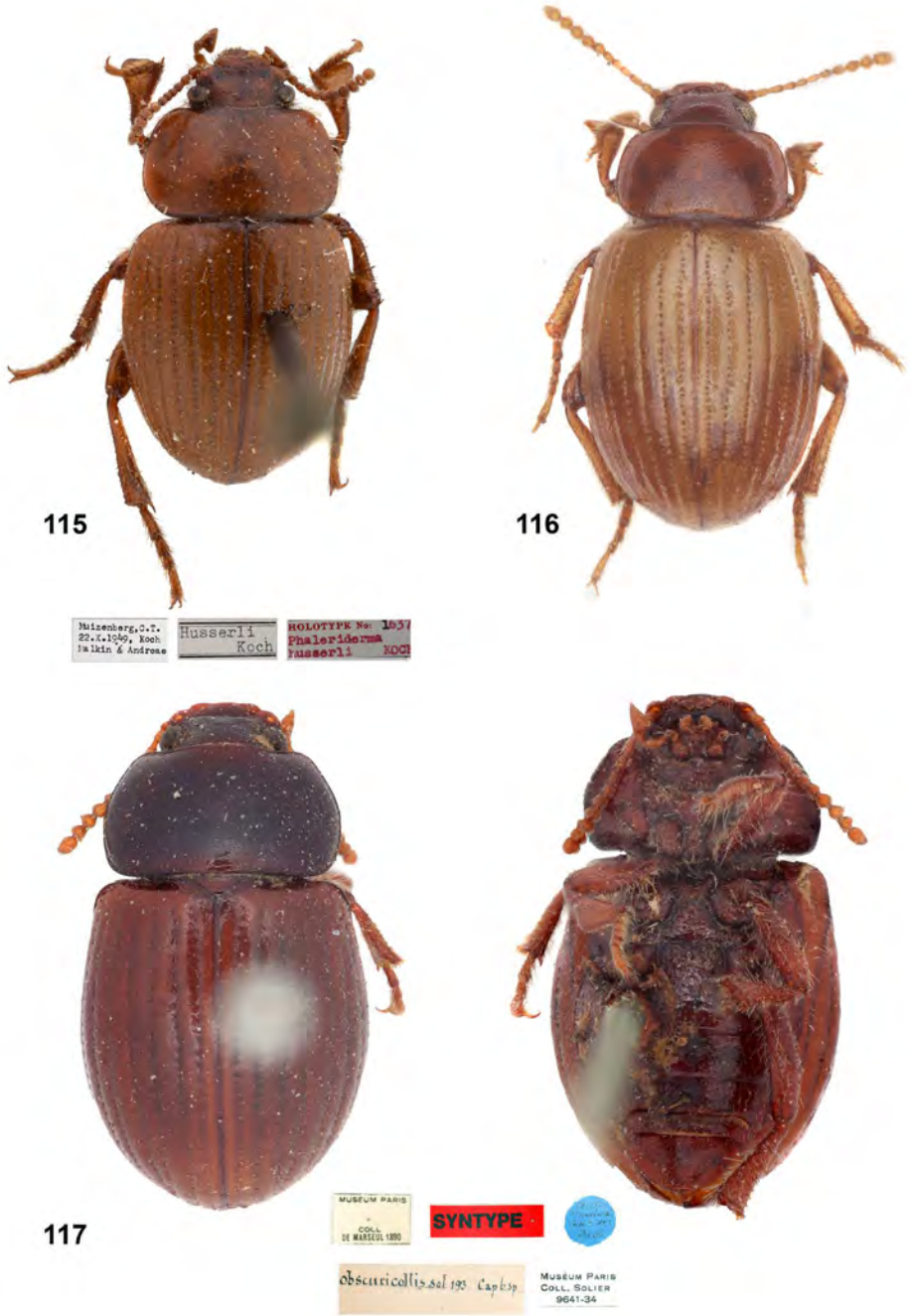


Fig. T115-T117. Type specimens of Eurynotina. Holotype of *Phaleriderma husserli* (115). Holotype of *Phaleriderma iwani* (116). Holotype of *Phaleriderma obscuricollis* (117).



Fig. T118-T121. Type specimens of Eurynotina. Holotype of *Quadroncotus irrepertus* (118). Holotype of *Stridigula arguta* (119). Holotype of *Oncotus* (*Cilioncotus*) *humerisetosus* synonym of *Stridigula arguta* (120). Holotype of *Stridigula namaquanus* (121).



Fig. T122. Type specimens of Eurynotina. Lectotype of *Stridigula planiuscula* (122).

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Storrs, Connecticut, United States of America/17 October 2025

Dr. Adam M. Rork

Institute for Systems Genomics, University of Connecticut, Storrs, Connecticut, USA

DECLARATION

I hereby declare that in the work: **Lumen R, Rork AM, Smith AD, Kamiński MJ. 2025. Complementary genomic and morphological data elucidate the phylogeny of obscure darkling. Systematic Entomology. https://doi.org/10.1111/syen.70012**, my substantive contribution to the preparation, implementation, and development of the research, as well as presenting the work in the form of a publication, is as described in the paper:

Writing (Review of manuscript before submission); software (bioinformatics, troubleshooting, syntax, software functionality).

Adam Rork

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DECLARATION OF THE CO-AUTHOR OF THE PUBLICATION

Lafayette, Indiana, United States of America/17 October 2025

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Department of Entomology, Purdue University, West Lafayette, Indiana, USA

DECLARATION

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Writing (review of manuscript before submission for peer review); data acquisition & sampling (providing specimens and work space for molecular processing); funding acquisition.

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Niniejszym oświadczam, że w pracy: **Lumen R., Kamiński MJ. 2025. Revision of subtribe Eurynotina (Coleoptera: Tenebrionidae: Blaptinae). Natural History Monographs of the Upper Silesian Museum 5: 1–xx. (In press)**, mój merytoryczny wkład w przygotowanie, wdrożenie i rozwój badań, a także w prezentację pracy w formie publikacji, obejmuje:

pisanie (rewizja tekstu przed złożeniem do redakcji); pozyskanie finansowania, administracja projektu; częściowe pozyskanie materiału badawczego; konceptualizacja; przygotowanie i implementacja metodologii (projektowanie badań); wizualizacja.

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(podpis)