





# Checklist of the pimeliine darkling beetles of the Vhembe Biosphere Reserve, South Africa (Coleoptera: Tenebrionidae: Pimeliinae)

## Authors

Colin S. Schoeman<sup>1</sup>   
Dawn Cory Toussaint<sup>1,2</sup>   
Precious Tshililo<sup>1</sup>   
Stefan H. Foord<sup>1,2,3</sup>   
Michelle Hamer<sup>4,5</sup> 

## Affiliations

<sup>1</sup>Department of Zoology, University of Venda, Private Bag X5050, Thohoyandou 0950, South Africa.

<sup>2</sup>South African Research Chair on Biodiversity Value & Change, University of Venda, Thohoyandou, 0950, South Africa.

<sup>3</sup>Core Team Member of the Centre for Invasion Biology, University of Stellenbosch, Stellenbosch, 7602, South Africa.

<sup>4</sup>Biosystematics Division, South African National Biodiversity Institute, South Africa, Private Bag X101, Silverton, 0184, South Africa.

<sup>5</sup>School of Life Sciences, University of KwaZulu-Natal, Private Bag X101, Scottsville, 3209, South Africa.

## Corresponding Author

Colin Schoeman,  
colin.schoeman@gmail.com

## Dates:

Submitted: 5 April 2019  
Accepted: 19 May 2020  
Published: 30 July 2020

## How to cite this article:

Schoeman, C.S., Toussaint, D.C., Tshililo, P., Foord, S.H. & Hamer, M., 2020, 'Checklist of the pimeliine darkling beetles of the Vhembe Biosphere Reserve, South Africa (Coleoptera: Tenebrionidae: Pimeliinae)', *Bothalia* 50(1), a8. <http://dx.doi.org/10.38201/btha.abc.v50.i1.8>

**Abstract:** A checklist of genera and species of the Pimeliinae (Tenebrionidae: Coleoptera) of the Vhembe Biosphere Reserve is provided. A total of 36 species are recorded. We provide brief biological notes on the tribes recorded from the Vhembe Region.

**Keywords:** Darkling beetles, biological notes, Savanna Biome, Limpopo Province, Soutpansberg

## Introduction

Of the ground-living beetles, Tenebrionidae Latreille 1802 (darkling beetles) rank as the seventh most speciose group of beetles (Kergoat et al. 2014). They are important detritivores and granivores, and constitute a significant food source for reptiles and small mammals, especially in arid and semi-arid environments (Polis et al. 1998).

The darkling beetles of Africa are poorly known, with few taxonomists available to describe new species, revise groups and offer assistance in determination of specimens. Yet these beetles show possibly higher levels of diversity in the southern hemisphere than in the northern hemisphere, and latitudinal gradients in diversity do not quite follow trends observed north of the equator (Platnick 1991). The Cape Floristic Region is abundant in tenebrionid tribes that have few or no representatives in the sub-tropical savannah (Botes, McGeoch & Chown 2007; Endrödy-Younga 1988; Kamiński 2016), inadvertently giving the impression that this family is species poor in the rest of South Africa (Gerlach, Samways & Pryke 2013).

The Tenebrionidae are remarkably diverse in the arid and semi-arid western regions of southern Africa (Koch 1962a) including the Northern Cape, Namibia and southern Angola; some groups, such as *Caenocrypticus*, are restricted to this region (Endrödy-Younga 1996). Nevertheless, arid associated taxa (Koch 1962a) are encountered in the northern bushveld, especially the Limpopo Valley north of the Soutpansberg. At least 40 tribes are known to occur in sub-Saharan Africa (Heyns 1959). Many of the southern African Pimeliinae were reviewed earlier by Koch (1955) as part of his delineation of the sub-family 'Tentyriinae', according to which the abdomen has an intersegmental membrane between the distal segments, a still useful morphological feature in separating members of the subfamily from others. The largest tribe in South Africa is the Sepidiini Eschscholtz, 1829, or *toktokkies*, which can be distinguished from other tribes by the presence of a trochantin on the meso-coxae. Koch (1955) provides a key to the tribes.

This checklist covers only the pimeliine darkling beetle fauna of the Vhembe Biosphere Reserve, which is known to have rich plant (Hahn 1994) and spider (Foord, Dippenaar-Schoeman & Van der Merwe 2002) diversity, but with significant gaps in our knowledge of other hyper-diverse taxa in the region. The classification is that of Bouchard et al. (2005).

## Methods and Materials

Twenty sites in the VBR Vhembe Biosphere Reserve (VBR), situated in Limpopo Province, South Africa were sampled using pitfall traps (maps were drawn using vector layers from DIVA-GIS) (Figure 1). These sites were located in the following vegetation units (Mucina & Rutherford 2006): Makhado Sweet Bushveld (3 sites), Soutpansberg Summit Sourveld (4 sites), Northern Mistbelt Forest (4 sites), Roodeberg Bushveld (2 sites), Soutpansberg Mountain Bushveld (4 sites), Musina Mopane Bushveld (2 sites), and Limpopo Ridge Bushveld (1 site) (Figure 2). Pitfall traps (7 cm diameter, 12 cm deep) were dug into the ground and a quarter filled with propylene glycol. Left out for seven days, as was done here, it is possible to attain inventory completion for each point. After collection, the contents of each trap were washed using a fine net, and stored in 96% ethanol. Thereafter, the specimens from each trap were sorted into pill vials with acquisition numbers placed in each.

Darkling beetles were then sorted to morphospecies and where possible identified to the tribe level using Koch (1955). Tenebrionidae identifications were then confirmed to genus and species level by Ruth Müller (Ditsong National Museum of Natural History), and Mary Louise Penrith (retired entomologist). Vouchers of each species are housed in the Coleoptera Collection of the Ditsong Museum of Natural History and in the UNIVEN Natural History Collection.

In this paper we present photos, depicting 26 species of Tenebrionidae found in the VBR (Figure 3), and representing 16 genera. The photos were taken with a Canon 450D camera with a F2.8 100 mm lens by Dawn Cory Toussaint, who also edited the images to remove shadows and increase clarity and contrast.

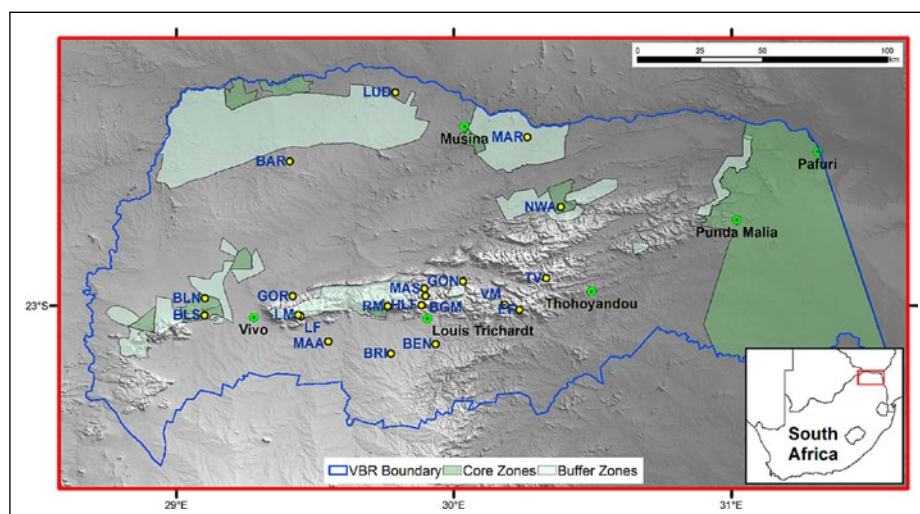
This checklist of the pimeliine darkling beetles of the VBR is the first published record of a major ground-dwelling beetle family for the region. Intraspecific taxa are not distinguished in the checklist presented here. We include suspected species (designated with cf.) and morphospecies (identified to genus and tribe) in the checklist, highlighting future taxonomic research needs.

## Results and Biological Notes

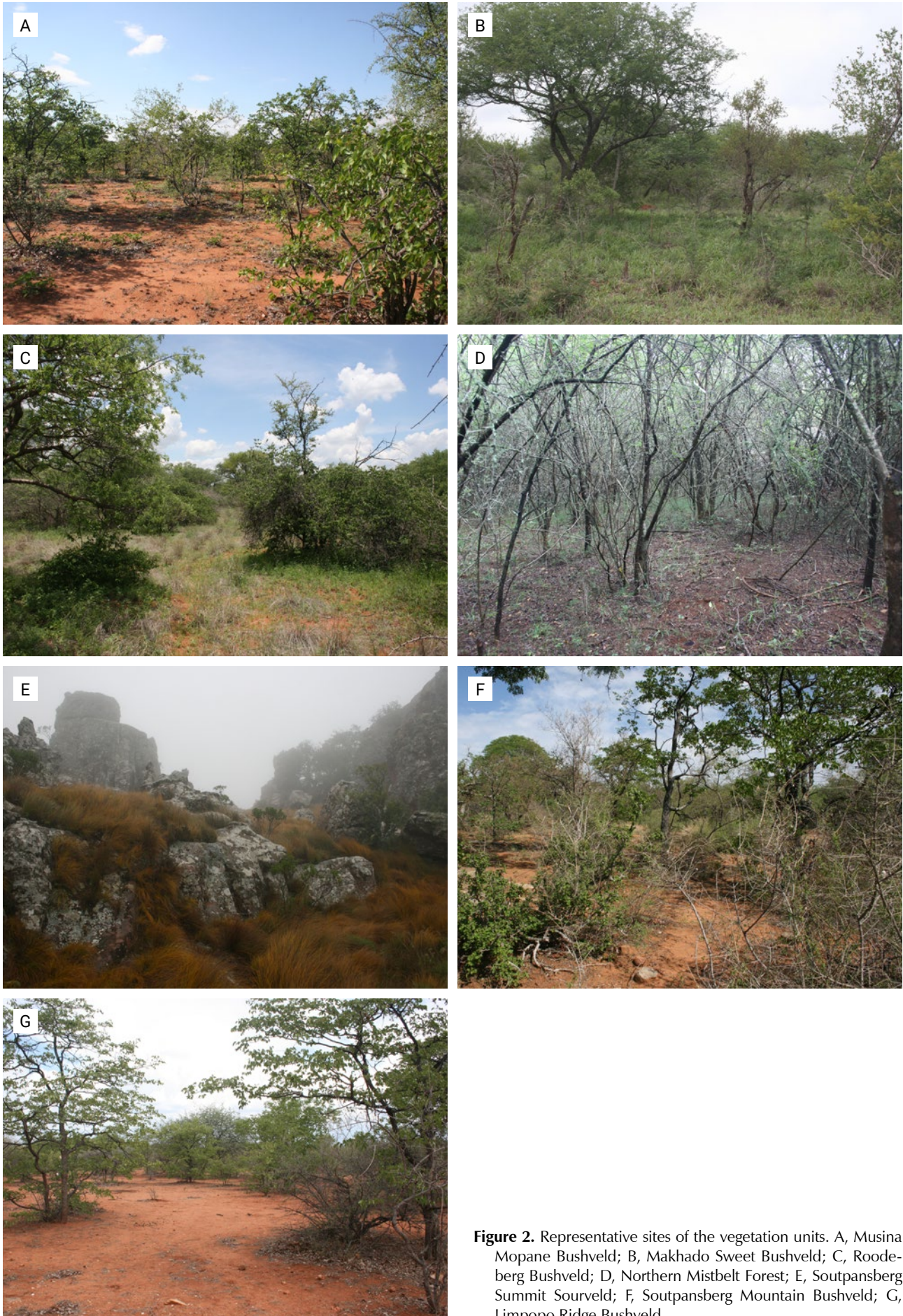
A total of 36 Pimeliine darkling beetles were sampled distributed in seven tribes. Provided is a quick overview of each tribe occurring in the VBR.

The Adesmiini are pear-shaped beetles with slender, spindly mid- and hind-legs, often longer than the anterior legs, and distinctive elytral sculpturation. They are sun-loving, flightless, fast running beetles that occupy the savannah, grassland and desert biome. Their centre of diversity is Namibia and Botswana. Adesmiini were treated by Koch (1951), and Penrith (1979a, 1986) who provides keys to the genera and species. Three species were sampled in the VBR.

Most sub-Saharan genera of Asidini are endemic to southern Africa and Madagascar (Koch 1962b). The head is partly hidden from above, the pronotum has prominent lobes located antero-laterally, while the elytra are strongly convex with ridges and tubercles present, sometimes with a pair of sharply elevated costae.



**Figure 1.** Map of the Vhembe Biosphere Reserve showing distribution of existing core and buffer zones and transition areas; current core areas in dark green and buffer zones in lighter green, and outline of the reserve in blue. The remainder of the area outlines in blue is transition area.



**Figure 2.** Representative sites of the vegetation units. A, Musina Mopane Bushveld; B, Makhado Sweet Bushveld; C, Roodeberg Bushveld; D, Northern Mistbelt Forest; E, Soutpansberg Summit Sourveld; F, Soutpansberg Mountain Bushveld; G, Limpopo Ridge Bushveld.



**Figure 3.** A, *Renatiella reticulata*; B, *Amachla schmidtii*; C, *Amachla sulcicollis*; D, *Amachla echinoderma*; E, *Amachla* sp. A; F, *Machlomorpha* cf. *evanida*; G, *Machlomorpha* cf. *mossambica*; H, *Himatismus* sp. A; I, *Eurychora barbata*; J, *Eurychora* sp. A; K, *Pogonobasis ovatus*; L, *Serrichora fahraei*; M, *Amiantus* cf. *gibbosus*; A–M, scale = 1 cm



**Figure 3 (continued).** N, *Amiantus pusillus*; O, *Dichtha cubica*; P, *Moluris discoidea*; Q, *Psammodes rowleianus*; R, *Ocnodes (Ocnodes) scrobicolle*; S, *Psammodes cf. janitor*; T, *Psammodes cf. ventricosus*; U, *Psammophanes sp. A*; V, *Somaticus (Trichotrichus) angulatus*; W, *Somaticus (Trichotrichus) varicollis*; X, *Somaticus (Somaticus) aeneus*; Y, *Ossiporis terrena fragilis*; Z, *Zophosis (Oculosis) sp. A*; N–Z, scale = 1 cm.

Koch (1962b) revised the sub-Saharan genera, of which there are seven: *Amachla*, *Machla*, *Asidomorpha*, *Machlomorpha*, *Machleida*, *Afrasida* and *Cryptasida*. They are found predominantly in montane habitat and afro-montane forest in undergrowth and may be hard to collect (Koch 1955). A total of six species are recorded.

The Adelostomini, referred to by Koch (1955) and Scholtz and Holm (1985) as Eurychorini Solier, 1837, are specialised tenebrionids with approximately 20 endemic South African genera (Koch 1955). The vertex of the head is slightly concave in dorsal view, with a narrow neck, the pronotum has broad lateral flanges. The elytra are also very broad. Several genera have stridulatory organs on the inner surface of the middle femora (Schawaller 2007). They often bear soil particles and other debris held by long hairs on the dorsal surface, which may be indicative of myrmecophily (Schawaller 2007). Koch (1952) provides keys to the different genera. Brown (1958) summarises information on the distribution of the genera in South Africa. Genera recorded from the VBR are *Eurychora*, *Pogonobasis* and *Serrichora*. Other genera that may occur in the Vhembe region (not sampled for this study) include *Geophanus*, *Prunasipila* and *Phytolostoma*.

The Sepidiini, referred to by Koch (1955) and Scholtz and Holm (1985) as Molurini Solier, 1834 are flightless beetles, usually strongly convex and globular; the elytra are extremely variable in shape, and loosely attached to the pronotum. The presence of a membrane between the distal sternal segments, of a trochantin on the mesocoxae, and a very broad scutellum above the elytra serve to differentiate the Sepidiini, or *toktokkies*, from other Tenebrionidae. Sepidiini generally show a smooth, punctate or costate type of elytral sculpturation in which raised longitudinal costal elements dominate the sculpture patterns – these may be smooth, denticulate or irregular (Koch 1955). Their common name derives from the habit of rapidly tapping the ground with the abdomen to attract a mate. About 1000 species and many genera occur over the African continent. The Sepidiini are a mostly sub-Saharan group, but with representatives in the Sahara and the Middle-East. Koch (1955) provides a key to subtribes. Kamiński et al. (2019) has produced a catalogue of the world fauna of this tribe. This was by far the most diverse tribe with 16 species sampled.

Zophosini or coffee-bean beetles are often seen running very rapidly over bare ground (Picker, Griffiths & Weaving 2004). When caught they are usually covered with a fine yellow dust, which rubs off when handled. The tribe is monogeneric, but there are many sub-genera and species and they are often the most abundant beetles in pitfalls (Penrith 1977). The elytra may display small pits, raised costae, or be completely smooth. Their centre of diversity is the arid western part of southern Africa, including Angola (Koch 1958). Penrith (1977, 1979b–1983) revised the tribe.

The tribe Cryptochilini is very poorly represented in the VBR, as their centre of diversity is the arid southwest of Africa, occurring especially in the Northern Cape, Namibia and Angola. Penrith & Endrödy-Younga (1994) revised the tribe.

## Discussion

Subsets of the Tenebrionidae community of the VBR show strong regional associations, influenced not just by environmental variables, but by biogeography, such as the psammophyllous Sepidiini associated with the mega-Kalahari deep-sands (Koch 1962a), and Platynotina radiations associated with the Bushveld Igneous complex (Endrödy-Younga 1988, Kamiński & Iwan 2013). Otherwise summer-rainfall faunas dominate the taxonomic composition, even at tribal level, with distributions extending into the tropics: a trend observed in other families as well (Davis, Frolov & Scholtz 2008).

There is a need to generate data on species turnover affected by broad scale environmental variables (Hawkins et al. 2003), beetle biogeography and zoogeographic provinces in the light of new data (Holm et al. 1984; Wharton & Robert, 1982). Furthermore, very little has been done on studying the ecosystem services provided by Tenebrionidae and Carabidae, especially in arid ecosystems where these taxa are particularly prominent.

The major purpose of this study is to highlight the necessity of continuing to sample and compare faunal assemblages between major biogeographic regions or biomes, focusing on poorly sampled regions. The South African National Survey of Arachnida (Dippenaar-Schoeman et al. 2015) provides a tried and tested protocol that can be emulated to catalogue and promote the beetle diversity of South Africa, generating biodiversity data that can provide valuable information to the scientific community.

## Checklist

### TENEBRIONIDAE Latreille, 1802

#### PIMELIINAE Latreille, 1802

#### Adesmiini Lacordaire, 1859

**Cephaladesmia arachnoides** Gerstaecker (?) LUD

**Renatiella reticulata** (Gerstaecker, 1854) Fig. 3A, MAR, BAR, BLN, GON, LUD, NWA

**Stenocara aenescens** Haag, 1875 LUD

**Table 1.** Index of geographical names and abbreviations used in the checklist

Abbreviation	Site	Vegetation type	Latitude	Longitude
BAR	Barries Farm	Musina Mopane Bushveld	-22.48	29.41
BEN	Ben Lavin Nature Reserve	Makhado Sweet Bushveld	-23.13	29.92
BGM	Bluegumspoort (Farm)	Soutpansberg Summit Sourveld	-22.96	29.89
BLN	Blouberg NR North	Roodeberg Bushveld	-22.98	29.12
BLS	Blouberg NR South	Roodeberg Bushveld	-23.02	29.09
BRI	Bristow Farm	Makhado Sweet Bushveld	-23.17	29.76
EF	Entabeni State Forest	Northern Mistbelt Forest	-23.01	30.24
GON	Gondeni (Communal land)	Soutpansberg Mountain Bushveld	-22.91	30.06
GOR	Goro Game Reserve	Soutpansberg Mountain Bushveld	-22.93	29.42
HLF	Hanglip State Forest	Northern Mistbelt Forest	-22.99	29.88
LF	Lajuma Forest	Northern Mistbelt Forest	-23.03	29.44
LM	Lajuma Mistbelt	Soutpansberg Summit Sourveld	-23.02	29.43
LUD	Ludwig's Lust Farm	Limpopo Ridge Bushveld	-22.25	29.78
MAA	Mara Research Station	Makhado Sweet Bushveld	-23.14	29.55
MAR	Maremani Game Reserve	Limpopo Ridge Bushveld	-22.39	30.23
MAS	Mashovela Lodge	Soutpansberg Mountain Bushveld	-22.93	29.89
NWA	Nwanedi Game Reserve	Soutpansberg Mountain Bushveld	-22.64	30.37
RM	Happy Rest	Soutpansberg Summit Sourveld	-23.01	29.75
TV	Thatevondo State Forest	Northern Mistbelt Forest	-22.91	30.33
VM	Vhuvha (Communal land)	Soutpansberg Summit Sourveld	-22.99	30.18

**Asidini Fleming, 1821****Amachla schmidti** Wilke, 1924 Fig. 3B, BEN, BLS, MAS**Amachla sulcicollis** (Fåhraeus, 1870) Fig. 3C, MAR, BLS, MAA**Amachla echinoderma** Fairmaire, 1899 Fig 3D, VM, LM**Amachla sp. A**, Fig. 3E. BLS**Machlomorpha cf. evanida** Wilke, 1924 Fig. 3F, BEN, LM, VM**Machlomorpha cf. mossambica** Péringuey, Fig. 3G, 1899 EF, VM**Epitragini****Himatismus sp. A**, Fig. 3H, BRI, LM, LUD**Adelostomini Solier, 1834****Eurychora barbarta** Olivier, 1795 Fig. 3I, MAR, BRI**Eurychora sp. A**, Fig. 3J, RM, GON**Pogonobasis ovatus** Fåhraeus, 1870 Fig. 3K, GOR, LM, LF**Serrichora fahraei** (Haag 1872) Fig. 3L, GON, LM, RM**Sepidiini Eschscholtz, 1829****Amiantus cf. gibbosus** Fåhraeus, 1870 Fig. 3M, BLN, BRI**Amiantus pusillus** Péringuey, 1904 Fig. 3N, BLS, BRI**Dichtha cubica** (Guérin-Méneville, 1845) Fig. 3O, BEN, BGM, BRI, GON, GOR, MAS, NWA**Moluris discoidea** (Guérin-Méneville, 1845) Fig. 3P, BAR, BEN, BLN, BLS, BRI, GON, GOR, MAA**Euphrynus carinatus** (Fåhraeus, 1870) BLN**Psammodes rowleianus** (Westwood, 1864) Fig. 3Q, BRI**Ocnodes (Ocnodes) scrobicollis** (Fåhraeus, 1870) Fig. 3R, BGM, BLN, BLS, BRI, GON, GOR, LUD, MAS, NWA**Psammodes cf. janitor** Koch, 1953 Fig. 3S, BRI, MAA**Psammodes cf. ventricosus** Fåhraeus, 1870 Fig. 3T, MAS**Psammodes vialis** (Burcell, 1822) BLN, GON, GOR**Psammophanes sp. A** Fig. 3U, RM, LM**Somaticus cf. (Trichotrichus) metropolis** Koch, 1955 RM**Somaticus (Trichotrichus) angulatus** (Fåhraeus, 1870) Fig. 3V, MAS**Somaticus (Trichotrichus) varicollis** Koch, 1955 Fig. 3W, RM**Somaticus (Somaticus) aeneus** (Solier, 1843) Fig. 3X, TV**Ossiporis terrena fragilis** (Fåhraeus, 1870) Fig. 3Y, BLS**Zophosini Solier, 1834****Zophosis (Zophosis) sp. A** Deyrolle, 1867 BAR, BLS**Zophosis (Hologenosis) sp. A** Fåhraeus, 1870 LUD, MAR, BLS

**Zophosis (Oculosis) sp. A** Solier, 1834 Fig. 3Z, BAR, BLN  
**Zophosis (Oculosis) sp. B** Gerstaecker, 1854 BAR  
**Zophosis (Oculosis) sp. C** Penrith, 1983 BAR, BEN

## Cryptochilini Solier, 1840

**Cychochile pluricostata** Penrith, 1994 LM

## Acknowledgements

We wish to dedicate this paper to Ruth Müller, curator of the Coleoptera collection at the Ditsong Museum of Natural History, in acknowledgement of her expertise

and tireless support, which has made this publication possible.

We are grateful to Isabel Venter (The Soutpansberger) for preparing the photographic plates; Dr Norbert Hahn for the GIS map; the Vhembe Biosphere Reserve Committee, and Prof. Peter John Taylor of the NRF-Chair in Biodiversity and Change (University of Venda – Centre for Invasion Biology) for logistical support; the University of Venda's Research and Publications Committee for their generous funding of this project. Specimens were collected on permit no. CPM-005-00005, provided by Limpopo Department of Economic Development, Environment and Tourism.

## References

- Botes, A., McGeoch, M.A. & Chown, S.L., 2007, 'Ground-dwelling beetle assemblages in the northern Cape Floristic Region: Patterns, correlates and implications', *Austral Ecology* 32(2): 210–224, <https://doi.org/10.1111/j.1442-9993.2007.01681.x>
- Bouchard, P. Lawrence, J.F., Davies, A.E. & Newton, A.F., 2005, 'Synoptic classification of the world Tenebrionidae (Insecta: Coleoptera) with a review of family-group names', *Annales Zoologici* 55(4): 499–530.
- Brown, H.D., 1958, 'A new species of *Stipsostoma* Koch (Col., Tenebrionidae), with a key to the species and distribution map of the tribe Eurychorini in Southern Africa', *Journal of the Entomological Society of Southern Africa* 21(2): 415–422.
- Davis, A.L.V., Frolov, A.V. & Scholtz, C.H., 2008, *The African dung beetle genera*, Protea Book House, Pretoria.
- Dippenaar-Schoeman, A.S., Haddad, C.R., Foord, S.H., Lyle, R., Lotz, L.N. & Marais, P., 2015, South African national survey of Arachnida (SANSa): review of current knowledge, constraints and future needs for documenting spider diversity (Arachnida: Araneae). *Transactions of the Royal Society of South Africa* 70(3): 245–275, DOI: 10.1080/0035919X.2015.1088486.
- Endrödy-Younga, S., 1988, 'Revision of the Genus *Anomalipus* Latreille, 1846 (Coleoptera: Tenebrionidae: Platynotini)', *Transvaal Museum Monographs* 6: 1–129.
- Endrödy-Younga, S., 1996, 'Revision of the tribe Caenocrypticini: (Coleoptera: Tenebrionidae: Tentyriinae). Taxonomy Tribe Caenocrypticini Genus Caenocrypticus and subgenera' *Transvaal Museum Monographs* 11(1).
- Foord, S.H., Dippenaar-Schoeman, A.S. & Van der Merwe, M., 2002, 'A checklist of the spider fauna of the Western Soutpansberg, South Africa (Arachnida: Araneae)', *Koedoe* 45(2): 35–43, DOI: 10.4102/koedoe.v45i2.25.
- Gerlach, J., Samways, M.J. & Pryke, J., 2013, 'Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups', *Journal of Insect Conservation* 17: 831–850, DOI: 10.1007/s10841-013-9565-9.
- Hahn, N., 1994, *Tree list of the Soutpansberg*, Pretoria: Fan-tique Publishers.
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M. & Porter, E.E., 2003, 'Energy, water, and broad-scale geographic patterns of species richness', *Ecology* 84(12): 3105–3117.
- Heyns, J., 1959, *The secondary sexual characters of some southern African Tenebrionidae*, Unpublished PhD thesis, University of Pretoria.
- Holm, E., Scholtz, C.H., Louw, S. & Penrith, M.L., 1984 'Notes on the coleopterous fauna of the Kalahari', *Koedoe* 27(2): 153–165.
- Kamiński, M.J., 2016, 'Catalogue and distribution of the sub-tribe Eurynotina (Coleoptera: Tenebrionidae: Pedinini)', *Annales Zoologici* 66(2): 227–266, DOI: 10.3161/00034541ANZ2016.66.2.006.
- Kamiński, M.J. & Iwan, D., 2013, 'Taxonomy, distribution and ecological niche models of the Afrotropical platynotoid Platynotina (Tenebrionidae: Pedinini)', *Annales Zoologici* 63(4): 653–733, DOI: 10.3161/000345413X676795.
- Kamiński, M.J., Kanda, K., Lumen, R., Ulmer, J.M., Wirth, C.C., Bouchard, P., Aalbu, R., Mal, N. & Smith, A.D., 2019, 'A catalogue of the tribe Sepidiini Eschscholtz, 1829 (Tenebrionidae, Pimeliinae) of the world', *ZooKeys* 844: 1–121, DOI: 10.3897/zookeys.844.34241. eCollection 2019.
- Kergoat, G.J., Soldati, L., Clamens, A.L., Jourdan, H., Jabour-Zahab, R.O.U.L.A., Genson, G., Bouchard, P. & Condamine, F.L., 2014, 'Higher level molecular phylogeny of darkling beetles (Coleoptera: Tenebrionidae)', *Systematic Entomology* 39(3): 486–499, <https://doi.org/10.1111/syen.12065>.
- Koch, C., 1950, 'The Tenebrionidae of southern Africa. I. First account of the Tenebrionidae collected on the University of California – Transvaal Museum Expedition, 1948', *Annals of the Transvaal Museum* 21: 273–367.
- Koch, C., 1951, 'The Tenebrionidae of southern Africa. VII. Preliminary notes on the South African Adesmiini', *Annals of the Transvaal Museum* 21, 385–417.
- Koch, C., 1952, 'The Tenebrionidae of Southern Africa, 7. Materials for a Monographic study on Eurychorini. Coleoptera', *Bulletin de la Société Royale Fouaud 1er d'Entomologie* 36(1): 1–125.
- Koch, C., 1953, 'The Tenebrionidae of southern Africa. XXI. On some new endemic Opatrinae from the Namib Desert', *Annals of the Transvaal Museum* 22: 231–252.



- Koch, C., 1954, 'The Tenebrionidae of southern Africa. XXV. New, forgotten or Palaearctic genera and species of Opatrinae', *Annals of the Transvaal Museum* 22: 419–476.
- Koch, C., 1955, 'Monograph of the Tenebrionidae of southern Africa, Tentyriinae, Molurini I', *Memoirs of the Transvaal Museum* 1: 1–292.
- Koch, C., 1958, 'Tenebrionidae of Angola', *Publicações Culturais da Companhia de Diamantes de Angola* 39: 1–231.
- Koch, C., 1962a, 'The Tenebrionidae of southern Africa. XXXI. Comprehensive notes on the tenebrionid fauna of the Namib Desert', *Annals of the Transvaal Museum* 24: 61–106.
- Koch, C., 1962b, 'Analysis of the Madagascan components of the subfamily Tentyriinae (Tenebrionidae, Coleoptera) with revisions of the generic systematics of the Asidini from Africa south of the Sahara and the African, Asiatic and Palaearctic Epitragina of Tentyriini', *Mémoires de l'institut de la scientifique de Madagascar* 13: 1–146.
- Penrith, M.-L., 1986, 'Relationships in the tribe Adesmiini (Coleoptera: Tenebrionidae) and a revision of the genus *Stenodesia* Reitter', *Annals of the Transvaal Museum* 34(13): 275–302.
- Penrith, M.-L. & Endrödy-Younga, S., 1994, 'Revision of the subtribe Cryptochilina (Coleoptera: Tenebrionidae: Cryptochilini)' *Transvaal Museum Monograph* 9: 1–144.
- Penrith, M.-L., 1977, 'The Zophosini (Coleoptera: Tenebrionidae) of western southern Africa', *Cimbebasia Memoir* 3: 1–291.
- Penrith, M.-L., 1979a, 'Revision of the western southern African Adesmiini (Col. Tenebrionidae)', *Cimbebasia A* 1: 3–94.
- Penrith, M.-L., 1979b–1983, 'Revision of the Zophosini', Part 1–7: *Cimbebasia A*, (1979b) 1, 1–21; (1981) 2, 17–109; (1981) 3, 111–124; (1981) 4, 126–164; (1982) 5, 165–226; (1982) 6, 227–289; (1983) 7, 292–367; (1983) 8, 370–384; (1983) 9, 385–416; (1986) 10, 417–502.
- Picker, M., Griffiths, C. & Weaving, A., 2004, *Field Guide to Insects of Southern Africa*, Struik Publishers, Cape Town.
- Platnick, N.I., 1991, 'Patterns of biodiversity: tropical vs temperate', *Journal of Natural History* 25(5): 1083–1088, <https://doi.org/10.1080/00222939100770701>.
- Polis, G.A., Barnes, J.D., Seely, M.K., Henschel, J.R. & Enders, M.M., 1998, 'Predation as a major cost of reproduction in Namib Desert tenebrionid beetles', *Ecology* 79(7): 2560–2566, [https://doi.org/10.1890/0012-9658\(1998\)079\[2560:PAAMCO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[2560:PAAMCO]2.0.CO;2).
- Mucina, L. & Rutherford, M.C. (eds.), 2006, The vegetation of South Africa, Lesotho and Swaziland, *Strelitzia* 19, South African National Biodiversity Institute, Pretoria.
- Schawaller, W., 2007, 'A new myrmecophilous species of *Cimiciopsis* Koch from Namaqualand in South Africa with a stridulatory organ, and a checklist of the genera of Adelostomini (Coleoptera: Tenebrionidae)', *Annals of the Transvaal Museum* 44: 203–208.
- Scholtz, C.H. & Holm, E., 1985, *Insects of southern Africa*, Pretoria Book House, Pretoria.
- Wharton, M. & Robert, A., 1982, 'Species composition of and biological notes on Tenebrionidae of the lower Kuiseb River and adjacent gravel plain', *Madoqua* 13(1): 5–25.