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## SHORT COMMUNICATION

**A new *Copelatus* with small eyes from the Eastern Cape Wild Coast, South Africa (Coleoptera: Dytiscidae)**David T. BILTON<sup>1,2)</sup> & Musa C. MLAMBO<sup>3)</sup><sup>1)</sup> School of Biological and Marine Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK; e-mail: d.bilton@plymouth.ac.uk<sup>2)</sup> Department of Zoology, University of Johannesburg, PO Box 524, Auckland Park, Johannesburg 2006, South Africa<sup>3)</sup> Department of Freshwater Invertebrates, Albany Museum, Rhodes University Affiliated Research Institute, Grahamstown 6140, South Africa; e-mail: musa.mlambo@gmail.comAccepted:  
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**Abstract.** A new diving beetle, *Copelatus mkambati* sp. nov., is described from the Mkambati Nature Reserve in the Eastern Cape Province, South Africa. The new species is compared with other Afrotropical taxa with two elytral stria and no submarginal (the *macellus* species group of *Copelatus* Erichson, 1832). A combination of small eyes, rather weak ornamentation, flattened, subparallel habitus, relatively large head and collecting circumstances all suggest that the new species may be semisubterranean in lifestyle.

**Key words.** Aquatic Coleoptera, Dytiscidae, *Copelatus*, new species, South Africa

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**Introduction**

*Copelatus* Erichson, 1832 is the most species-rich genus of diving beetles on earth, particularly diverse in forested tropical and subtropical areas. To date, over 450 species are known (NILSSON & HÁJEK 2021), usually arranged across a number of species groups, based on the number and position of the elytral striae, as first suggested by SHARP (1882; see also ZIMMERMANN 1919, 1934; GUIGNOT 1961; NILSSON et al. 1997). BALKE et al. (2004a) showed that elytral striation does not always reflect phylogeny, demonstrating that these characters are quite labile and homoplastic within the genus. Indeed, the number of striae can differ markedly between closely related species, and even on occasion between individuals of the same species (e.g. OMER-COOPER 1965, MANUEL et al. 2018). Despite this, strial configuration remains a convenient character set on which to order species within this megadiverse genus, particularly in the absence of any obviously better system.

In the Afrotropical Region, *Copelatus* diversity is concentrated in the wet tropical forests of West and Central Africa (NILSSON et al. 1997) and Madagascar (RANARILALATIANA & BERGSTEN 2019, RANARILALATIANA et al. 2019), where most species are associated with small streamside pools in primary forest (e.g. BILARDO & ROCCHI 1995) and many apparently narrowly endemic. The fauna of Southern Africa is, in contrast, rather species poor, with a total of 15

species reported to date from the Republic of South Africa, six of which are apparently endemic (OMER-COOPER 1965, STALS & DE MOOR 2008). The *macellus* species group comprises species which share two discal elytral striae and no submarginal stria. It currently includes four species, one Neotropical (*C. substriatus* Kirsch, 1873 from Peru), one Oriental/Palaearctic (*C. filiformis* Sharp, 1882 from the Himalaya) and two Afrotropical (*C. macellus* Guignot, 1950 from Zaire and *C. basilewskyi* Bilardo & Pederzani, 1979 from Angola) (GUIGNOT 1950, 1961; BILARDO & PEDERZANI 1979; NILSSON et al. 1997; NILSSON & Hájek 2021). Here we describe a new species of the *macellus* group from the Eastern Cape Pondoland Wild Coast of South Africa which, on the basis of its narrow, flattened habitus, small eyes and collecting circumstances, may be semisubterranean in lifestyle.

**Materials and methods**

Beetles were collected using a D-framed pond net with a 1 mm mesh. Specimens were studied using Leica MZ8 and 205C stereomicroscopes, with LED gooseneck lights diffused using a tracing paper collar and tubes derived from opaque white plastic film canisters. Habitus and genital photographs were taken with a Canon EOS 5D mark IV camera fitted to a Leica 205C stereomicroscope, with a 1x objective lens. Specimens were illuminated by gooseneck



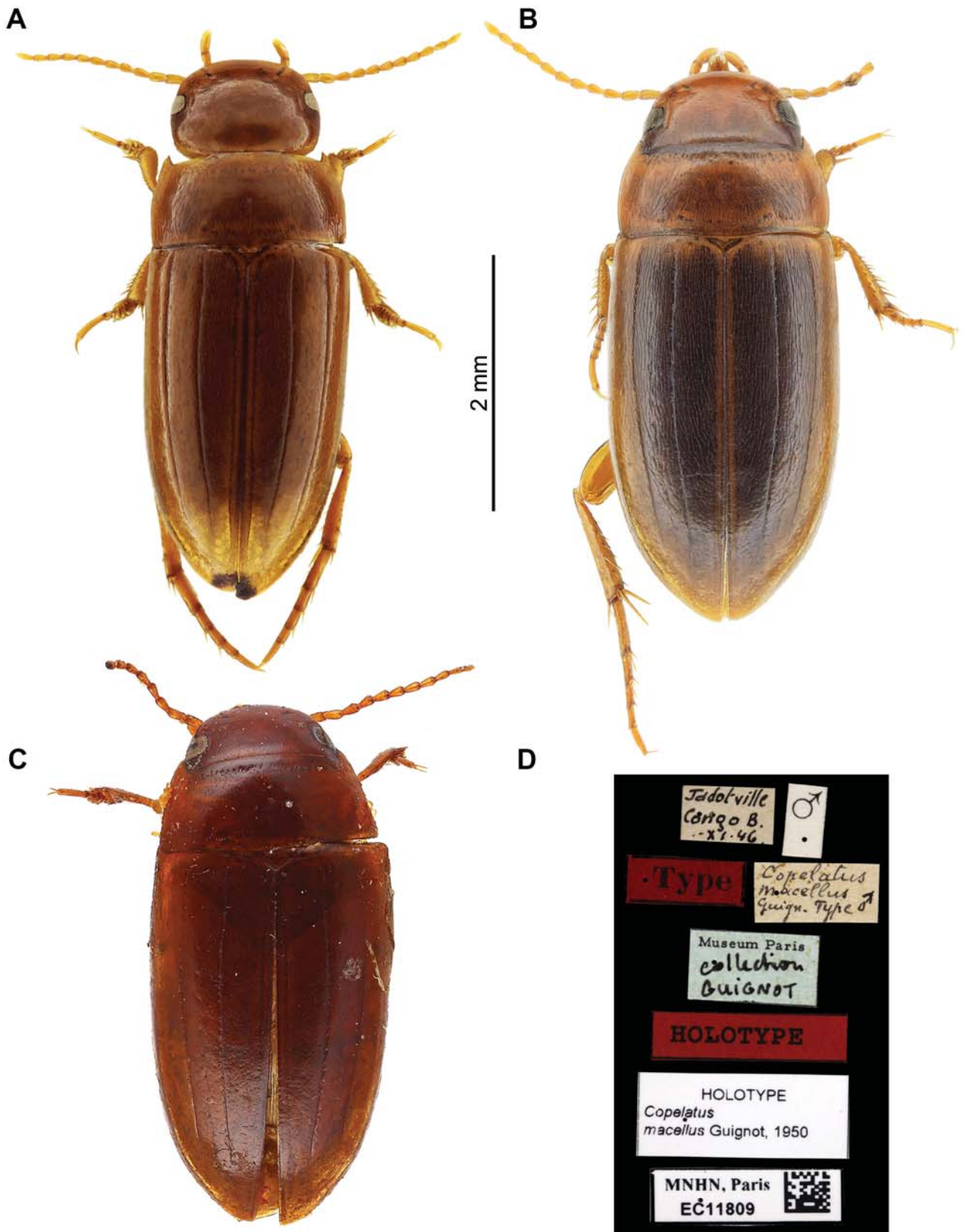


Fig. 1. *Copelatus* species. A–C. *mkambati* sp. nov. holotype habitus; B–C. *mkambati* sp. nov., paratype female habitus; C – *C. macellus* Guignot, 1950, holotype habitus; D – *C. macellus*, holotype labels. Scale bar applies to A–C.





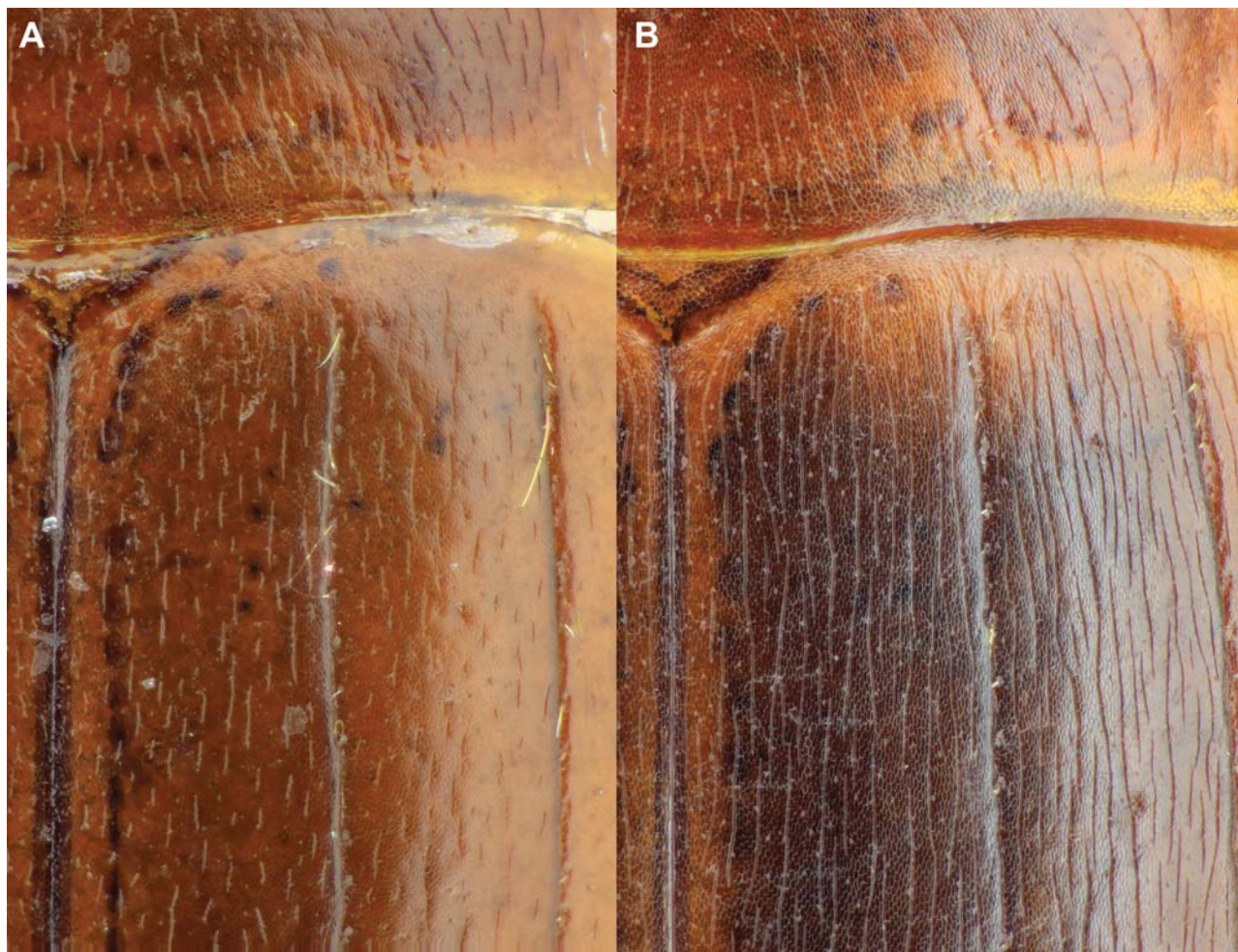


Fig. 2. *Copelatus mkambati* sp. nov. dorsal sculpture. A – holotype male; B – paratype female.

lights, diffused with a film canister tube. Genitalia were mounted on glass slides in Kisser's glycerol gelatine (see RIEDEL 2005). All image stacks were produced by hand, and combined using Zerene Stacker software ([www.zerene-systems.com](http://www.zerene-systems.com)).

Exact label data are cited for specimens. / indicates new line in label text.

#### Abbreviations:

AMGS	Albany Museum, Grahamstown, South Africa;
CDTB	Collection D.T. Bilton, Plymouth, UK;
BL	Body length (front of labrum to elytral apices);
BL-H	Body length – head (front margin of pronotum to elytral apices).
EL	Elytral length (outer angle of shoulder to apex);
EW	Elytral width at widest point.

## Taxonomy

### *Copelatus mkambati* sp. nov.

(Figs 1–4)

**Type material.** HOLOTYPE: m\*, '7/ix/2019 South Africa EC / Mkambati Nature Reserve / Mgwegwe River / 31°17'36.28"S / 29°59'50.83"E, 58 m / Wet 211, D T Bilton leg.' (AMGS). With red Holotype label. PARATYPES: 1 m\* (CDTB), same data as holotype; 1 f\*, '9/ix/2019 South Africa EC / Mkambati Nature Reserve / Diwa River / 31°17'44.49"S / 29°58'52.15"E, 57 m / Wet 215, D T Bilton leg.' (AMGS). With red Paratype labels.

**Description. Male** (holotype). Body shape (Fig. 1A)

elongate, subparallel, relatively flat; head relatively large and broad. Head testaceous; infuscated at anterior margin of clypeus, around clypeal suture, and eyes; very weak infuscation towards posterior temples. Pronotum testaceous with faint infuscation on disc and irregular row of dark spots visible through cuticle inside anterior and posterior margins. Elytra testaceous; each elytron weakly infuscated over most of area inside outer stria, with the exception of narrow, paler region adjacent to suture; Dark line visible through cuticle outside this pale strip, breaking down into spots along base and close to apex. Venter testaceous, prosternum, prosternal process and margins of cuticular plates infuscated; all appendages testaceous.

Head broad, width 0.77 pronotal width (Figs 1A, 4A) shining, microreticulate, meshes isodiametric on frons and vertex, elongate laterally on temples; finely micropunctate, most micropunctures bearing short, peg-like setae, some with long, fine, adpressed setae. Eyes small, occupying approximately one fourth side of head, with 9–11 ommatidia in longest series. Pronotum (Figs 1A, 2A) shining, isodiametrically microreticulate and micropunctate as head; with fine impressed longitudinal strioles, densest and longest laterally and posteriorly, sparsest and shortest on disc. Disc with shallow, weakly impressed longitudinal furrow in central fourth. Puncture row behind anterior

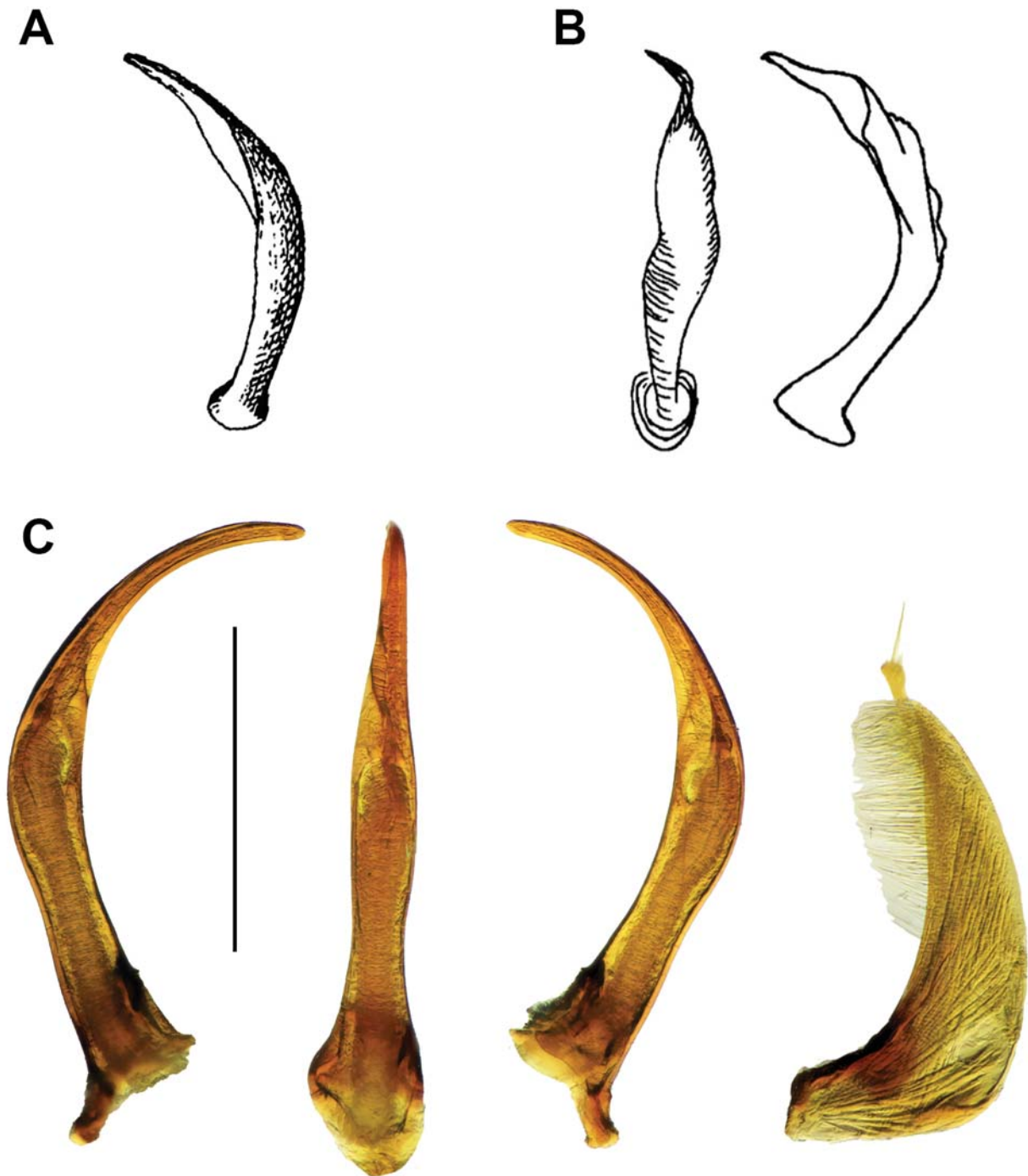


Fig. 3. *Copelatus* species male genitalia. A – *C. macellus* Guignot, 1950, median lobe; B – *C. basilewskyi* Bilardo & Pederzani, 1979, median lobe; C – *C. mkambati* sp. nov., median lobe and paramere. Scale bar in C = 0.5 mm. Note that lines on the paramere represent musculature, not surface ridges. A & B after GUIGNOT (1961) and BILARDO & PEDERZANI (1979), respectively.

pronotal margin irregular, shallow and weakly evident, most punctures with fine, adpressed amber-coloured setae; similar punctures and setae close to lateral and posterior margins. Each elytron with two well-impressed discal striae, extending from base to ca. 0.1 from apex. Each stria with sparse, medium punctures, bearing long, amber-coloured setae. No submarginal stria; irregular row of longitudinal striae and punctures, the latter bearing long, fine, adpressed setae, present on anterior 0.6 of outermost elytral edge, where submarginal striae are typically located

in *Copelatus*. Elytral disc between striae (Fig. 2A) shining, sculptured as pronotum; striae much sparser outside of second stria, and almost absent in posterior fourth, where reticulation is somewhat obsolete and more transverse than on disc. Legs with basal three pro- and mesotarsomeres dilated, each foot bearing four transverse rows of suction setae. Protibiae broadly expanded distally.

Venter weakly shining; finely microreticulate and micropunctate. Microreticulation meshes mostly small and isodiametric; transverse on metaventrite, elongate on me-



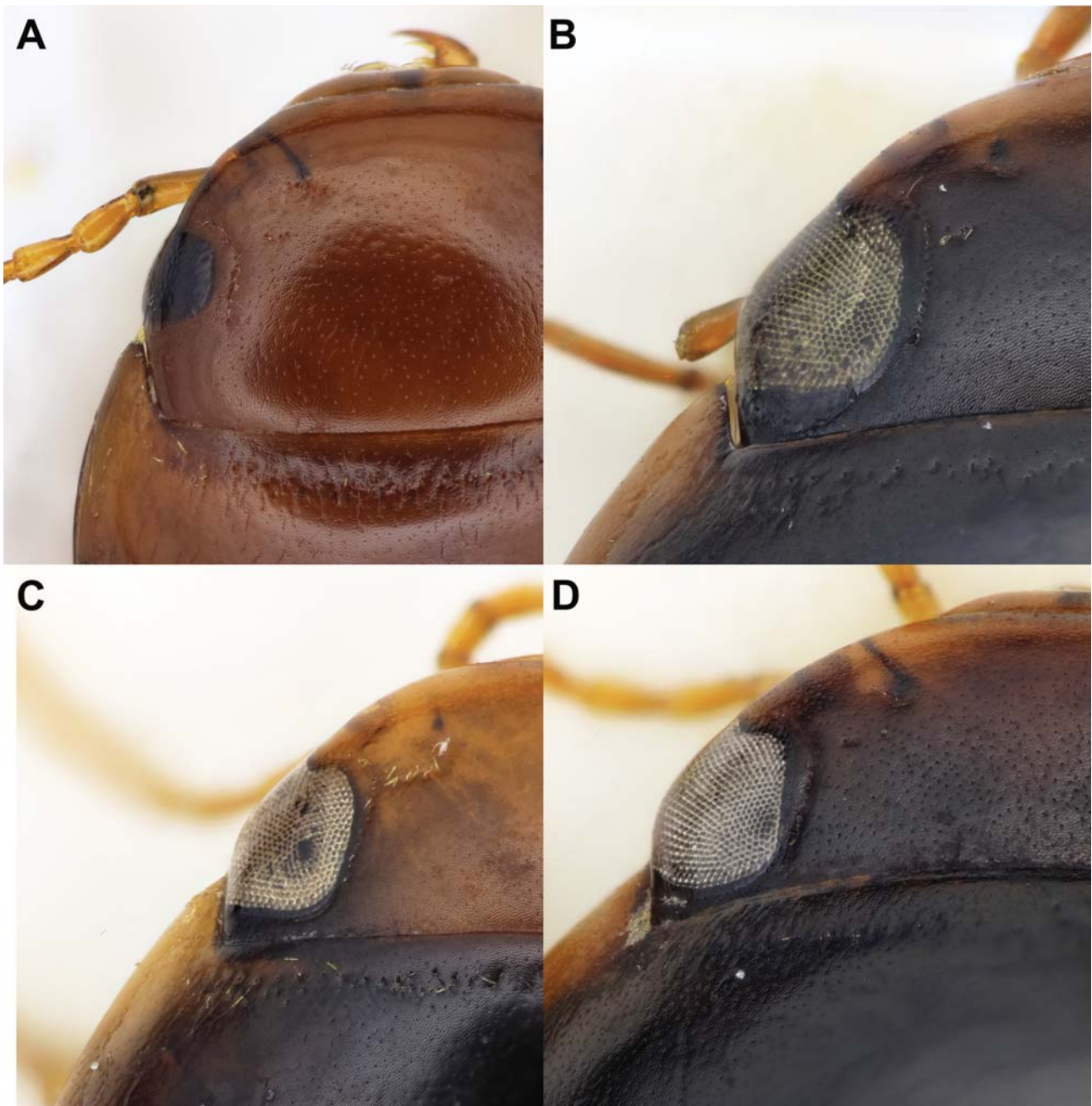


Fig. 4. Southern African *Copelatus* species compound eyes, all to same scale. A – *C. mkambati* sp. nov., paratype male; B – *C. capensis* Sharp, 1882 (Groote River, South Africa); C – *C. erichsoni* Guérin-Méneville, 1847 (St Lucia, South Africa); D – *C. pulchellus* (Klug, 1834) (St Lucia, South Africa).

tacoxae. Lateral wings of metaventricle narrow. Metacoxae with sparse, elongate, longitudinal striae. Metacoxal lines well impressed, becoming finer towards metaventricle and absent in basal fifth of metacoxae. Abdominal ventrites I–III with narrow, elongate, fine longitudinal ridges laterally, particularly marked on ventrite II. Abdominal ventrite IV with irregular transverse row of punctures halfway down length, each bearing a long, fine, adpressed seta. Abdominal ventrite VI with cluster of small punctures laterally, halfway down length, each bearing similar setae.

**Male genitalia.** Median lobe of aedeagus (Fig. 3C) relatively simple, evenly curved in lateral view, with small oval opening medially on right side (see right hand lateral view

in Fig. 3C). Rather straight in ventral view; apex flattened and bluntly pointed. Paramere as in Fig 3C.

**Measurements.** Holotype: BL 3.9 mm; BL-H 3.45 mm; EL 2.7 mm; EW 1.50 mm. Paratypes: ♂ BL 4.0 mm; BL-H 3.5 mm; EL 2.8 mm; EW 1.65 mm. ♀ BL 4.3 mm; BL-H 3.65 mm; EL 3.0 mm; EW 1.75 mm.

**Female** (Fig. 1B) coloured as male; dorsum matt, reticulation (Fig. 2B) much more strongly impressed than male; meshes larger throughout, isodiametric to elongate on head, slightly elongate on pronotum, elongate on elytral disc, strongly transverse in posterior fourth. Micropunctuation as male. Strioles denser, deeper and longer than in male, also present on frons and vertex of head, where they are

orientated transversally centrally and longitudinally posteriorly and laterally. Protibiae less expanded distally. Venter as male, but with striae on metacoxae very sparse and longitudinal ridges on abdominal sternites weaker and sparser. The single female paratype is somewhat larger and broader than the two known males (see above).

**Differential diagnosis.** A member of the *macellus* species group on the basis of elytral striation, the new species can be distinguished from the two other Afrotropical species with two discal striae as follows. In contrast to *C. mkambati* sp. nov. and *C. macellus*, *C. basilewskyi* lacks longitudinal striae, being microreticulate and micropunctate only dorsally. Compared to *C. macellus* (Fig. 1C), *C. mkambati* sp. nov. is more elongate, paler in colouration, with longer, denser striae dorsally and finer, less strongly impressed, micropunctuation on the elytra, particularly in the posterior third. The three species can also be readily distinguished on the form of their median lobes (see Fig. 2). Additionally, *C. mkambati* sp. nov. has relatively small eyes, with only 8–11 ommatidia in the longest series. In contrast, the holotype of *macellus* (Fig. 1C) has visibly larger eyes, with 18 ommatidia in the longest series. Although we have not been able to study specimens, the description of *C. basilewskyi* makes no mention of the compound eyes, strongly suggesting that these are also normally sized for the genus.

**Etymology.** The new species is named after Mkambati, a beautiful Nature Reserve of natural grassland, forests and wetlands on Natal Group Sandstones in the Pondoland region of the Eastern Cape Province, from which all known specimens have been collected. The specific epithet is a noun in the nominative singular.

**Distribution and ecology.** Known to date only from two close localities in the Mkambati Nature Reserve, Eastern Cape Province, South Africa. Mkambati is on the Pondoland Wild Coast, whose sandstones and forested gorges support a high number of endemic taxa (MUCINA et al. 2006), and is part of the Maputaland-Pondoland-Albany Global Biodiversity Hotspot (MITTERMEIER et al. 2004, PERERA et al. 2011). The invertebrate fauna of the entire Wild Coast region remains poorly studied, even compared with other areas in southern Africa (HAMER & SLOTOW 2017). Recent surveys of aquatic beetles in this region have yielded several new species (e.g. BILTON 2016, 2020; BILTON & MLAMBO, submitted) and often high alpha diversity (PERISSINOTTO et al. 2017, BIRD et al. 2017). All three known specimens were collected from the flooded margins of small streams, in areas where seepage water was entering from nearby small valley wetlands. At the type locality, specimens were taken a day after heavy rainfall, when seepage flow was relatively strong. A return visit four days later, when water levels had receded, produced no further specimens despite an extended search.

## Discussion

Truly subterranean dytiscids are known from a number of parts of the world, being particularly diverse in Australia (e.g. WATTS & HUMPHREYS 2009). Such subterranean species are typically depigmented and blind, or with hi-

ghly reduced eyes, and often have a flattened, carabiform appearance (see MILLER & BERGSTEN 2016 for review). Almost all known underground dytiscids are hydroporines, the others being a handful of copelatines, in both *Exocelina* and *Copelatus* (BALKE et al. 2004b; CAETANO et al. 2013; WATTS et al. 2016; RIBERA & REBOLEIRA 2019; BALKE & RIBERA 2020).

So-called semisubterranean diving beetles are well documented in the Northern Hemisphere, particularly in arid and semi-arid regions of Europe, Western Asia and North Africa. Such species occupy springs, seepages and the hyporheic zones of rivers, including temporary ones, and are morphologically intermediate between surface and subterranean species. Such species are typically somewhat depigmented compared to surface relatives, and may have reduced eyes and a flattened, often subparallel, habitus (see e.g. BILTON & FERY 1996, WEWALKA & BISTRÖM 1998, Hájek & BRANCUCCI 2011, MANUEL 2013).

Compared to all known southern African *Copelatus*, *C. mkambati* sp. nov. has markedly reduced compound eyes; Fig. 4 compares the eyes of the new species with three more typical *Copelatus* from the region. In addition to its reduced compound eyes, the new species is relatively pale, flattened and parallel-sided, with a large head, all characteristics which are strongly developed in many groundwater dytiscids. These morphological features, coupled with the fact that all known specimens were sampled from seepage water at the margins of small streams, leads us to suggest that *C. mkambati* sp. nov. is semisubterranean in habits, and could have been flooded out due to heavy rain. Similar collecting circumstances were documented for morphologically similar, presumably interstitial, Indian *Copelatus maushomi* Sheth, Ghate & Hájek, 2018 (SHETH et al. 2018). *Copelatus mkambati* sp. nov. is similar in many respects also to the Australian *Exocelina australis* (Clark, 1863) and *E. saltusholmesensis* Watts, Hendrich & Balke, 2016, both of which are apparently interstitial (WATTS et al. 2016). Truly subterranean diving beetles are currently unknown in southern Africa, but this probably reflects a lack of investigation of suitable groundwaters rather than a genuine absence.

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## References

- BALKE M. & RIBERA I. 2020: A subterranean species of *Exocelina* diving beetle from the Malay Peninsula filling a 4,000 km distribution gap between Melanesia and southern China. *Subterranean Biology* 34: 25–37.

- BALKE M., RIBERA I. & VOGLER A. P. 2004a: MtDNA phylogeny and biogeography of Copelatinae, a highly diverse group of tropical diving beetles (Dytiscidae). *Molecular Phylogenetics and Evolution* **32**: 866–880.
- BALKE M., WATTS C. H. S., COOPER S. J., HUMPHREYS W. F. & VOGLER A. P. 2004b: A highly modified stygobiont diving beetle of the genus *Copelatus* (Coleoptera, Dytiscidae): taxonomy and cladistic analysis based on mitochondrial DNA sequences. *Systematic Entomology* **29**: 59–67.
- BILARDO A. & PEDERZANI F. 1979: Descrizione di quattro nuove specie e di tre allotipi di Coleoptera Dytiscidae africani. *Revue de Zoologie Africaine* **93**: 766–774.
- BILARDO A. & ROCCHI S. 1995: Haliplidae e Dytiscidae (Coleoptera) del Gabon con note sistematiche sulle specie di confronto (Parte seconda: Copelatini, Dytiscinae e integrazioni a Hydroporinae). *Atti della Società Italiana di Scienze Naturali di Milano* **134**: 135–167.
- BILTON D. T. 2016: A new species of *Hydrobiomorpha* from iSimangaliso Wetland Park, South Africa (Coleoptera: Hydrophilidae). *Acta Entomologica Musei Nationalis Pragae* **56**: 149–157.
- BILTON D. T. 2021: Differentiation of South African coastal rock pool *Ochthebius* is associated with major ocean currents (Coleoptera: Hydraenidae). *Acta Entomologica Musei Nationalis Pragae* **61**: 253–260.
- BILTON D. T. & FERY H. 1996: Revisional notes on *Rhithrodytes* Bameul 1989, with the description of a new subspecies and the introduction of *Rhithrodytes dorsoplagiatus* (Fairmaire) as a valid species (Coleoptera, Dytiscidae). *Linzer Biologische Beiträge* **28**: 917–931.
- BILTON D. T. & MLAMBO M. C. *subnoveboracensis*: A new species of *Coelometopon* Janssens from the Wild Coast, South Africa (Coleoptera: Hydraenidae). *Suplementos del Boletín de la Asociación Española de Entomología*.
- BIRD M. S., BILTON D. T. & PERISSINOTTO R. 2017: Diversity and distribution of polyphagan water beetles (Coleoptera) in the Lake St Lucia system, South Africa. *ZooKeys* **656**: 51–84.
- CAETANO D. S., BENÁ D. D. C. & VANIN S. A. 2013: *Copelatus cessaima* sp. nov. (Coleoptera: Dytiscidae: Copelatinae): First record of a troglomorphic diving beetle from Brazil. *Zootaxa* **3710**: 226–232.
- GUIGNOT F. 1950: Trente-et-unième note sur les hydrocanthares. *Bulletin de la Société Linnéenne de Lyon* **19**: 25–28.
- GUIGNOT F. 1961: Revision des hydrocanthares d'Afrique (Coleoptera Dytiscoidea [sic!]). 3. *Annales du Musée Royal du Congo Belge, Série 8<sup>vo</sup> (Sciences Zoologiques)* **90**: 659–995.
- HÁJEK J. & BRANCUCCI M. 2011: Order Coleoptera, family Dytiscidae. Pp. 126–143. In: HARTEN A. VAN (ed.): *Arthropod fauna of the UAE IV*. Multiply Marketing Consultancy Services, Abu Dhabi, 832 pp.
- HAMER M. L. & SLOTOW R. 2017: A conservation assessment of the terrestrial invertebrate fauna of Mkambati Nature Reserve in the Pondoland Centre of Endemism. *Koedoe*: **59**: 1–12.
- MANUEL M. 2013: A new semi-subterranean diving beetle of the *Hydroporus normandi*-complex from south-eastern France, with notes on other taxa of the complex (Coleoptera: Dytiscidae). *Zootaxa* **3652**: 453–474.
- MANUEL M., DELER-HERNÁNDEZ A., MEGNA Y. S. & HÁJEK J. 2018: *Copelatus* Erichson from the Dominican Republic, with the description of a new species, comments on elytral striation and faunistic notes on Antillean species (Coleoptera: Dytiscidae: Copelatinae). *Zootaxa* **4399**: 371–385.
- MILLER K. B. & BERGSTEN J. 2016: *Diving beetles of the World. Systematics and biology of the Dytiscidae*. Johns Hopkins University Press, Baltimore, USA, 320 pp.
- MITTERMEIER R. A., ROBLES-GIL P., HOFFMANN M., PILGRIM J., BROOKS T., GOETTSCH C., MITTERMEIER J. L. & DA FONSECA G. A. B. 2004: *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Ecoregions*. CEMEX, Mexico City, Mexico 390 pp.
- MUCINAL., SCOTT-SHAW C. R., RUTHERFORD M. C., KEMP K. G. T., POWRIE L. W. & HOARE D. B. 2006: Indian Ocean coastal belt. Pp. 568–583. In: MUCINAL. & RUTHERFORD M. C. (eds): *The vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute, Pretoria, viii + 807 pp.
- NILSSON A. N., BILARDO A. & ROCCHI S. 1997: A check list of *Copelatus* Erichson 1832 species (Coleoptera Dytiscidae) from Afro-tropical and Madagascan regions with a review of published penis drawings. *Tropical Zoology* **10**: 11–48.
- NILSSON A. N. & HÁJEK J. 2021: *A World Catalogue of the Family Dytiscidae, or the Diving Beetles (Coleoptera, Adephaga)*. Version 1.1.2021. Distributed as a PDF file via Internet. Available from: [http://www.waterbeetles.eu/documents/W\\_CAT\\_Dytiscidae\\_2021.pdf](http://www.waterbeetles.eu/documents/W_CAT_Dytiscidae_2021.pdf) (accessed December 16, 2021)
- OMER-COOPER J. 1965: Coleoptera: Dytiscidae. A review of the Dytiscidae of Southern Africa, being the results of the Lund University Expedition 1950–1951, with which are incorporated all other records known to the author. Pp. 59–214. In: HANSTRÖM B., BRINCK P. & RUDEBECK G. (eds): *South African Animal Life 11*. Statens naturvetenskapliga forskningsråd, Stockholm, 503 pp.
- PERERA S. J., RATNAYAKE-PERERA D. & PROCHES S. 2011: Vertebrate distributions indicate a greater Maputaland-Pondoland-Albany region of endemism. *South African Journal of Science* **107**: 1–15.
- PERISSINOTTO R., BIRD M. S. & BILTON D. T. 2016: Predaceous water beetles (Coleoptera, Hydradephaga) of the Lake St Lucia system, South Africa: biodiversity, community ecology and conservation implications. *ZooKeys* **595**: 85–135.
- RANARILALATIANA T. & BERGSTEN J. 2019. Discovery of a specialist Copelatinae fauna on Madagascar: highly ephemeral tropical forest floor depressions as an overlooked habitat for diving beetles (Coleoptera, Dytiscidae). *ZooKeys* **871**: 89–118.
- RANARILALATIANA T., RAVAOMANARIVO L. H. R. & BERGSTEN J. 2019: Taxonomic revision of the genus *Copelatus* of Madagascar (Coleoptera, Dytiscidae, Copelatinae): the non-erichsonii group species. *ZooKeys* **869**: 19–90.
- RIBERA I. & REBOLEIRAA. S. P. S. 2019: The first stygobiont species of Coleoptera from Portugal, with a molecular phylogeny of the *Siettitia* group of genera (Dytiscidae, Hydroporinae, Hydroporini, Siettitina). *ZooKeys* **813**: 21–38.
- RIEDEL A. 2005: Digital imaging of beetles (Coleoptera), and other three-dimensional insects. Pp. 222–250. In: HÄUSER C., STEINER A., HOLSTEIN J. & SCOBLE M. J. (eds): *Digital imaging of biological type specimens. A manual of best practice*. Results from a study of the European Network for Biodiversity Information, Stuttgart, 309 pp.
- SHARP D. 1882: On aquatic carnivorous Coleoptera or Dytiscidae. *Scientific Transactions of the Royal Dublin Society* **2**: 179–1003 [+ pls 7–18].
- SHETH S. D., GHATE H. V. & HÁJEK J. 2018: *Copelatus* Erichson, 1832 from Maharashtra, India, with description of three new species and notes on other taxa of the genus (Coleoptera: Dytiscidae: Copelatinae). *Zootaxa* **4459**: 235–260.
- STALS R. & DE MOOR I. J. (eds) 2008: *Guides to the freshwater invertebrates of Southern Africa. Volume 10: Coleoptera*. Water Research Commission, Gezina, Pretoria, South Africa, 263 pp.
- WATTS C. H. S., HENDRICH L. & BALKE M. 2016: A new interstitial species of diving beetle from tropical northern Australia provides a scenario for the transition of epigeal to stygobitic life (Coleoptera, Dytiscidae, Copelatinae). *Subterranean Biology* **19**: 23–29.
- WATTS C. H. S. & HUMPHREYS W. F. 2009: Fourteen new Dytiscidae (Coleoptera) of the genera *Limbodessus* Guignot, *Paroster* Sharp, and *Exocelina* Broun from underground waters in Australia. *Transactions of the Royal Society of South Australia* **133**: 62–107.
- WEWALKA G. & BISTRÖM O. 1998: *Glareadessus* gen. n. with description of two new species from the Persian Gulf region. *Koelopterologische Rundschau* **68**: 53–57.
- ZIMMERMANN A. 1919: Die Schwimmkäfer des Deutschen Entomologischen Museums in Berlin-Dahlem. *Archiv für Naturgeschichte, Abteilung A* **83**: 68–249.
- ZIMMERMANN A. 1934. Monographie der paläarktischen Dytisciden. III. Colymbetinae (I. Teil). *Koelopterologische Rundschau* **20**: 138–214.



