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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 pigmentation, 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. basilenskyi 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. Habitats 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.
lights, diffused with a film canister tube. Genitalia were mounted on glass slides in Kissér’s glycerol gelatine (see RIEDEL 2005). All image stacks were produced by hand, and combined using Zerene Stacker software (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 striae, 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
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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 strioles 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; strioles 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 micoreticulate and micropunctate. Micoreticulation meshes mostly small and isodiametric; transverse on metaventrite, elongate on me-

Fig. 3. *Copelatus* species male genitalia. A – *C. macellus* Guignot, 1950, median lobe; B – *C. basilowskii* 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.
tacoxae. Lateral wings of metaventrite narrow. Metacoxae with sparse, elongate, longitudinal strioles. Metacoxal lines well impressed, becoming finer towards metaventrite 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: m* BL 4.0 mm; BL-H 3.5 mm; EL 2.8 mm; EW 1.65 mm. f* 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. Micropunctation as male. Strioles denser, deeper and longer than in male, also present on frons and vertex of head, where they are

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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).
orientated transversally centrally and longitudinally posteriorly and laterally. Protiabae 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, micropunctation 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. 2B). Additionally, *C. mkambati* sp. nov. has relatively smaller 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 (Hamet & 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 highly 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 mauoshomi* 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 groundwater systems rather than a genuine absence.

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