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Capelatus prykei gen. et sp.n. (Coleoptera: Dytiscidae: Copelatinae) - a phylogenetically isolated diving beetle from the Western Cape of South Africa

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1 *Capelatus prykei* gen. et sp. n. (Coleoptera: Dytiscidae: Copelatinae) - a
2 phylogenetically isolated diving beetle from the Western Cape of South Africa

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27 **Abstract**

28

29 *Capelatus prykei* **gen. et sp. n.**, a distinctive new lineage of copelatine diving beetle,
30 is described from the greater Cape Town area of the Western Cape Province, South
31 Africa on the basis of both morphological and molecular data. The genus-level
32 phylogeny of Copelatinae is reconstructed using a combination of nuclear and
33 mitochondrial DNA regions, demonstrating that *Capelatus* **gen. n.** has no close
34 relatives within the Afrotropical region, instead forming a clade with the Palaeartic
35 *Liopterus* and largely Australasian *Exocelina*. *Capelatus* **gen. n.** apparently
36 represents a striking example of a phylogenetically isolated Cape lineage, which also
37 appears to be narrowly endemic and endangered by ongoing habitat loss.

38 **Introduction**

39

40 The Western Cape of South Africa hosts one of the world's hottest biodiversity
41 hotspots (Myers *et al.*, 2000), having one of the most diverse and highly endemic
42 floras on earth, supporting around 20% of the vascular plant species known from the
43 whole of sub-Saharan Africa (Manning & Goldblatt, 2012; Valente & Vargas, 2013).
44 Whilst this remarkable floristic richness is not fully matched in terms of animal
45 diversity, the region is a significant centre of endemism for a number of taxa,
46 including reptiles, amphibians, freshwater fish and insect groups (Picker & Samways,
47 1996; Verboom *et al.*, 2009; Sole *et al.*, 2013), many of which are highly endangered
48 (e.g. Samways *et al.*, 2011). Some endemic southern African insect taxa belong to
49 clades with strikingly disjunct or relictual distributions, and apparently lack close
50 relatives elsewhere in the Afrotropical region. This includes groups with Gondwanan
51 affinities such as some montane chironomid midges (Saether & Ekrem, 2003) and
52 canthonine dung beetles (Roets & Oberlander, 2010), alongside Mediterranean Basin
53 – southern African disjunctions (e.g. Bologna *et al.*, 2008; Caldara *et al.*, 2008; Kirk-
54 Spriggs & McGregor, 2009). In addition, the Western Cape supports a number of
55 apparently relictual, phylogenetically isolated taxa which are otherwise absent from
56 the southern Hemisphere including the Aspidytidae, or cliff water beetles (Ribera &
57 Bilton, 2007; Balke *et al.*, 2003, 2005). Whilst the origins and maintenance of Cape
58 endemic diversity are complex and remain poorly understood, it is believed that the
59 combination of relative climatic stability since the Pliocene (Meadows & Sugden,
60 1991; Manning & Goldblatt, 2012) and the geological age of the Cape Fold
61 Mountains, whose basic topography has remained relatively unchanged since the
62 Cenozoic (65 MYA) are two important factors, reducing extinction rates within
63 lineages and at the same time promoting allopatric speciation.

64 With over 660 described species (Nilsson, 2014), Copelatinae is one of the
65 most diverse subfamilies of diving beetles (Dytiscidae), especially in the wet tropical
66 and subtropical forests of the world (e.g., Balke, 2004, 2008; Bilardo & Rocchi,
67 2011). Copelatines show very high levels of local endemism, particularly in running-
68 waters (e.g. Balke, 1998; Wewalka *et al.*, 2010; Shaverdo *et al.*, 2012; Shaverdo *et*
69 *al.*, 2013). Many species of the subfamily have been described recently or remain
70 undescribed; recent field work in tropical regions such as New Guinea producing very
71 high proportions of new species (Toussaint *et al.*, 2014a). Despite this high species

72 richness, known Copelatinae are morphologically rather homogenous beetles, most
73 taxa being oval, weakly convex and between 3–10mm in length. Generic diversity in
74 the subfamily is consequently modest, with only eight genera currently being
75 recognised worldwide (Shaverdo *et al.*, 2008; Miller & Bergsten, 2014; Nilsson,
76 2014), and around 90% of species belonging to the megadiverse *Copelatus* Erichson
77 and *Exocelina* Broun. Here we describe *Capelatus prykei* **gen. et sp. n.**, a highly
78 distinctive new taxon from the Western Cape of South Africa, which has escaped
79 detection until recently, and cannot be placed in any of the existing genera of
80 Copelatinae. Using DNA sequence data from a combination of mitochondrial and
81 nuclear regions we establish the phylogenetic position of this new taxon,
82 demonstrating that it is not closely related to any of the numerous copelatine diving
83 beetles previously described from sub-Saharan Africa and Madagascar, appearing
84 instead to represent a striking example of a phylogenetically isolated Cape endemic
85 lineage.

86

87

88 **Materials & methods**

89

90 *Morphology*

91

92 Specimens were studied with a Leica MZ8 stereomicroscope at x8 – 80, lighted with a
93 swan-neck illuminator, diffused using a tracing paper collar close to the specimen (to
94 enable study of microsculpture). The terminology to denote the orientation of the
95 male genitalia follows Miller & Nilsson (2003).

96 Digital photographs were taken with a Canon EOS 500D camera on a Leica
97 Z6 Apo macroscope, fitted with a 1x or 2x objective lens. Specimens were
98 illuminated using a Leica LED5000 HDI dome illuminator to avoid shadow.

99 Genitalia were mounted on glass slides in Kisser's glycerol gelatine (see Riedel,
100 2005) and imaged using the same Leica system and a combination of transmitted and
101 incident light. Image stacks were produced by hand, and combined using Zerene
102 Stacker software (www.zerenesystems.com). For scanning electron microscopy
103 material was air-dried overnight at 60°C, before being mounted onto metal stubs
104 using double-sided carbon conducting tape. Specimens were examined and

105 photographed at low vacuum in a JEOL JSM6610LV Scanning Electron Microscope
106 (SEM).

107 Female reproductive tract structures were studied as follows: Abdomens were
108 removed from ethanol preserved material, and rehydrated for 10 min in distilled
109 water. Terga were opened with dissecting scissors, and the whole abdomen
110 macerated for 20 min in 10% aqueous potassium hydroxide at 60°C. The
111 reproductive tract and associated sclerites were then removed from the abdomen, and
112 stained for 5 min in 1% aqueous chlorazol black, before observation of structures in
113 distilled water.

114 Exact label data for specimens are cited in quotation marks. A double slash (//)
115 indicates separate labels.

116

117 *Molecular analysis*

118

119 In order to investigate the phylogenetic relationships of the new taxon, novel
120 DNA sequences were generated for representatives of known extant genera of the
121 subfamily Copelatinae (with the exception of *Rugosus* García, a little-known genus of
122 two species from the Venezuelan Amazon, recently transferred to Copelatinae by
123 Miller & Bergsten (2014)), in addition to data retrieved from GenBank (see Table
124 S1). Total genomic DNA was extracted from legs, thoracic and head tissues of
125 specimens kept in 96% ethanol using the DNeasy kit (Qiagen, Hilden, Germany).
126 PCR protocols followed Toussaint *et al.* (2014a) to amplify the following gene
127 fragments: mitochondrial cytochrome c oxidase I (*cox1*, 732bp), cytochrome c
128 oxidase II (*cox2*, 552bp) and cytochrome b (*cob*, 306bp) and nuclear histone 3 (*H3*,
129 315bp), histone 4 (*H4*, 156bp), 18S ribosomal DNA (*18S*, 546bp),
130 Carbomoylphosphate synthase (*CAD*, 849bp) and α -Spectrin (*Asp*, 792bp). All gene
131 fragments were chosen because of their proven efficiency in disentangling dytiscid
132 phylogenetics at the generic level (see Ribera *et al.*, 2008; Balke *et al.*, 2009;
133 Hawlitschek *et al.*, 2012; Toussaint *et al.*, 2014a,b). Forward and reverse DNA
134 sequences were assembled and mismatches corrected with Geneious R6 (Biomatters,
135 <http://www.geneious.com/>), aligned using Muscle (Edgar 2004) and reading frames
136 checked in Mesquite 2.75 (<http://mesquiteproject.org>). Overall the concatenated
137 molecular matrix contained 4,248 aligned nucleotide positions. All new sequences
138 were deposited in GenBank (see Table S1 for accession nos.).

139

140

141 *Phylogeny reconstruction*

142

143 We used Bayesian Inference (BI), Maximum Likelihood (ML) and Parsimony
144 (MP) to reconstruct phylogenetic relationships. The BI analyses were conducted on a
145 concatenated dataset using MrBayes 3.2.1 (Ronquist *et al.*, 2012). The partitions and
146 corresponding optimal models of substitution were searched using PartitionFinder
147 1.1.1 (Lanfear *et al.*, 2012) using the *greedy* algorithm, either the *MrBayes* or *RAxML*
148 sets of models and with the Akaike Information Criterion corrected (AICc) to
149 compare the model fits. PartitionFinder analyses were carried out using 22 pre-
150 defined data blocks, one for each codon position of the 7 protein coding genes and
151 one for 18S. The analyses consisted of two simultaneous and independent runs of four
152 Metropolis-coupled Markov chain Monte Carlo (MCMC, one cold and three
153 incrementally heated) chains run for 50 million generations with a tree sampling
154 every 1,000 generations to calculate posterior probabilities (PP). In order to
155 investigate the convergence of the runs we investigated the standard deviation of the
156 split frequencies and Effective Sample Size (ESS) of all parameters, and plotted the
157 log-likelihood of the samples against the number of generations in Tracer 1.5
158 (<http://BEAST.bio.ed.ac.uk/Tracer>). A value of ESS > 200 was acknowledged as a
159 good indicator of convergence. All the trees that predated the time needed to reach a
160 log-likelihood plateau were discarded as burn-in, and remaining samples were used to
161 generate a 50% majority rule consensus tree. The ML analyses were conducted with
162 RAxML (Stamatakis, 2006) with the concatenated dataset partitioned under the
163 optimal scheme recovered by PartitionFinder. We performed 1,000 Bootstrap
164 replicates (BS) to investigate the level of support at each node. The MP analyses were
165 carried out with TNT 1.1 (Goloboff *et al.*, 2008) with the *Sectorial Searches*, *Tree*
166 *Ratchet*, *Tree Fusing* and *Tree Drifting* algorithms (Goloboff, 1999) and 100 random
167 addition sequences. In order to assess the level of support at each node, we performed
168 1,000 replicates using the *Symmetric Resampling* (SR) with a probability fixed to 10.
169 A calculated PP above 0.95 or a BS/SR above 70 was considered to indicate strong
170 support for a given clade (Erixon *et al.*, 2003; Felsenstein, 2004).

171

172 **Abbreviations**

173

174	BMNH	Natural History Museum, London
175	CDTB	Collection D.T. Bilton, Plymouth, UK
176	CTP	Collection C. R. Turner, Plymouth, UK
177	ISAM	Iziko South African Museum, Cape Town, South Africa
178	SANC	South African National Collection of Insects, Pretoria, South Africa
179	ZSM	Zoologische Staatssammlung, München, Germany
180	EL	Elytral length
181	MW	Maximum width
182	TL	Total length

183

184

185 **Results**

186

187 *Molecular biology and phylogenetics*

188

189 Results of the different phylogenetic methods conducted on the concatenated
190 molecular dataset summarized in Fig. 1, whilst gene regions successfully amplified
191 and sequenced from sampled Copelatinae are detailed in Table S1, with partitions and
192 substitution models recovered by PartitionFinder presented in Table S2. All genera of
193 Copelatinae were monophyletic with optimal support in BI, ML and MP. *Lacconectus*
194 Motschulsky was sister to the rest of the subfamily with strong support in all
195 analyses. *Copelatus* (including taxa from the Afrotropics, Australasia and the
196 Neotropics) was sister to all genera except *Lacconectus*, with strong support, in every
197 analysis except BI, where it was moderately supported. The other genera fell into two
198 separate well supported clades (*Agaporomorphus* Zimmermann + *Madaglymbus*
199 Shaverdo & Balke and *Capelatus* **gen. n.** + *Liopterus* Dejean + *Exocelina*) in both BI
200 and ML analyses (see Figs. 1 and S1). In MP, most relationships between genera were
201 congruent with the results of the probabilistic methods, albeit with low SR scores
202 (Fig. S1). In this analysis *Aglymbus* Sharp was, however, recovered as sister to
203 *Agaporomorphus* + *Madaglymbus* with low support (Fig. S1). A clade comprising
204 *Capelatus* **gen. n.**, *Exocelina* and *Liopterus* was recovered in all analyses; highly
205 supported in BI and ML, less so in MP (Figs. 1 & S1). Despite globally moderate
206 supports, the relationships within this clade were consistent across all three

207 phylogenetic methods; *Capelatus* **gen. n.** and *Liopterus* forming a separate clade,
208 itself sister to *Exocelina*. The relatively low support values for *Capelatus* + *Liopterus*
209 in BI and MP analyses are likely to have resulted from missing genetic coverage in
210 *Capelatus* and *Liopterus*, for which some gene fragments would not amplify (see
211 Table S1). Data from other loci would be useful in the future to robustly assess the
212 placement of these two genera relative to *Exocelina*. Our phylogenetic analyses all
213 unambiguously place *Copelatus cheesmanae* J. Balfour-Browne, 1939 well within
214 *Exocelina* (see Figs. 1 & S1). Consequently we introduce the following **new**
215 **combination**: *Exocelina cheesmanae* (J. Balfour-Browne, 1939). Our unpublished
216 data suggest that *E. cheesmanae* is closely related to the New Caledonian *E.*
217 *aubei* (Montrouzier, 1860).

218
219

220 **Taxonomy**

221

222 ***Capelatus* gen. n. Turner & Bilton**

223

224 *Type species. Capelatus prykei* **sp. n.**

225

226 *Generic diagnosis.* Male protarsomere 4 with strongly protruding anterodistal
227 process furnished with four stout, spine-like setae (Fig. 3B - D). Female protarsomere
228 4 simple, but with four stout setae at anterodistal angle (Fig. 3A). Male pro- and
229 mesotarsomeres 1-3 with large stalked adhesive discs, arranged in 4 rows (Fig. 3D).
230 Female metatibia and metatarsus with only dorsal row of natatorial setae. Median
231 lobe of aedeagus with well-developed internal sac sclerites (Fig. 2B). Paramere with
232 distal stylus (Fig. 2B). Paramere setae sparse, restricted to paramere margin and apex
233 of distal stylus. Bursa copulatrix present; strongly sclerotized, with thick walls.
234 Elytra without striae, and with distinct longitudinal striae in the only known species
235 (Fig. 4 – note these are also present in some species of other copelatine genera).
236 Metacoxal lines present but weak, restricted to an indistinct ridge on outer margins of
237 process in the only known species, not reaching posterior borders of metaventricle.
238 *Capelatus* **gen. n.** can be distinguished from all other genera of Copelatinae by the
239 above combination of characters. The modified structure of the male protarsomere 4
240 is a unique apomorphy of this genus in the world fauna. It differs from *Liopterus*, its

241 apparent sister genus (see above) in the modification of this tarsal segment, which
242 lacks the spinose anteriodistal process in *Liopterus*, as well as in the absence of setae
243 on the inner faces of the parameres (long, dense hair-like setae present in *Liopterus*)
244 and the weak metacoxal lines in the only known species (strong and reaching
245 posterior borders of the metaventrite in both known *Liopterus*).

246

247 *Generic description.* Body elongate, with lateral outline more or less
248 continuous in dorsal view (Fig. 3A). Large in comparison to most Copelatinae; TL =
249 8.4 – 10.0 mm. Dorsal and ventral surfaces with distinct microreticulation (Fig. 4A –
250 B), this being more strongly impressed on the dorsum. Head, pronotum and elytron
251 with fine sparse micropunctuation and longitudinal striae. Head, pronotum and elytra
252 with distinct fields or rows of setiferous punctures, bearing long, white, hair-like
253 setae. Clypeus with medially interrupted marginal bead. Antenna simple; slightly
254 flattened dorsoventrally. Pronotum with distinct lateral bead. Scutellum transversely
255 triangular; 3x wider than long. Ventral surface with fine, sparse punctuation;
256 longitudinal striae also present on metacoxal plates. Prosternum (Fig. 3F) tectiform,
257 with distinct, low, rounded ridge in centre. Prosternal ridge continuous with raised
258 central portion of blade of process. Blade of prosternal process broadly ovate; bluntly
259 pointed, with longitudinal convexity and thick marginal bead, particularly behind
260 procoxae. Blade with scattered setiferous punctures, especially immediately inside of
261 bead line. Metacoxal lines weak (see Fig. 3G), restricted to an indistinct ridge on
262 outer margin of process; not reaching posterior border of metaventrite. Posterior
263 margin of metacoxal process with distinct incision. Last ventrite apically rounded
264 (Fig. 3E). Metatibia with irregular medial longitudinal row of spiniferous punctures
265 on anterior surface. Pro- and mesotibiae with irregular spiniferous punctures over
266 entire anterior surface. Metatarsus with anterior claw slightly longer and straighter
267 than posterior.

268

269 *Male.* Protibia simple, with approximately triangular outline. Pro- and
270 mesotarsomeres 1–3 distinctly dilated, ventrally with four rows of stalked adhesive
271 setae. Protarsomere 4 with protruding anteriodistal process bearing four stout, blade-
272 like setae which are ventrally curved to apices (Fig. 3B – D). Protarsomere 5 simple,
273 long and narrow, ventrally with short, sparse setae. Protarsal claws simple, evenly
274 curved, anterior slightly longer than posterior. Metatibia and metatarsus with dorsal

275 and ventral rows of natatorial setae. Median lobe (Fig. 2B) with protruding
276 endophallic sclerites. Paramere (Fig. 2B) with distal stylus. Setae restricted to
277 paramere margin and apex of distal stylus.

278

279 *Female.* Dorsal surface with microreticulation slightly stronger than in males.
280 Strioles of pronotal margins and elytral disc denser than in males. Metatibia and
281 metatarsus with only dorsal rows of natatorial setae. Bursa copulatrix present,
282 strongly sclerotized. Gonocoxa and gonocoxosternum as in other genera of
283 Copelatinae (see Miller, 2001).

284

285 *Etymology.* The generic epithet *Capelatus* is a combination of *Copelatus*, the
286 type genus of Copelatinae, and the Cape, the region of South Africa in which this new
287 taxon has been discovered.

288

289 ***Capelatus prykei* sp. n. Turner & Bilton**

290

291 *Type material. Holotype* (male) “Stn. No. 347// S.Africa, Cape Flats, Ca.3-5
292 mls. S.E. of Philippi 5.viii.1954// J. Balfour-Browne Brit. Mus. 1954-797// grassy
293 flood pools, Algae, Aponogeton and Hydrodictyon”. With our red Holotype label
294 “Holotype *Capelatus prykei* Turner & Bilton” (BMNH). Paratypes (19): 5♂ 6♀ same
295 data as holotype (4♂ 5♀ BMNH, 1♂ 1♀ CTP); 1♂ 1♀ “South Africa, Western Cape
296 Province, ref: col605, leg. James Pryke, wetland, Nordhoek, Cape Peninsula, 15 Jul
297 2006, 34 06.500S 18 22.390E, presented to C. R.Turner coll. 2007” (ISAM); 1♂ 1♀
298 “South Africa, Western Cape Province, ref: col131, leg. James Pryke, wetland,
299 Nordhoek, Cape Peninsula, 31 July 2007, 34.10858S 18.37306E, presented to
300 C.R.Turner coll. 2007” (CTP); 1♀ “South Africa, Western Cape Province, ref:
301 col131, leg. James Pryke, wetland, Nordhoek, Cape Peninsula, 31 July 2007,
302 34.10858S 18.37306E, presented to C.R.Turner coll. 2007// DNA, M.Balke, 3919
303 [green label]” (ZSM); 1♀ “James Pryke, Noordhoek, 31-07-2007, col 131// Wetland,
304 S34.10858, E18.37306” (SANC); 1♂ 1♀ “23/ix/2010 South Africa WC, Table
305 Mountain National Park, Noordhoek Wetlands – seasonal pans with iron ochre mud
306 and deep litter, below *Juncus* and restios, D. T. Bilton leg.”. (CBP) All with our red
307 paratype labels “Paratype *Capelatus prykei* Turner & Bilton”.

308

309 *Diagnosis.* Males of this species are readily distinguished from all other
310 known Copelatinae by the unique modifications to protarsomere 4 (Fig. 3B - D), and
311 the structure of the genitalia (Fig. 2B). Within the Afrotropical fauna the species is
312 also recognized by a combination of its relatively large size (8.4 – 10 mm), the
313 strongly microreticulate dorsum with marked longitudinal striae, and the absence of
314 elytral striae (Fig. 4A – B).

315

316 *Description.* In addition to the characters mentioned in the generic diagnosis
317 and description, the new species possesses the following features.

318 Size: Holotype: TL = 9.7 mm; EL = 7.6 mm; MW = 4.8 mm. Paratypes:
319 Males: TL = 8.4 – 9.8 mm; EL = 6.4 – 7.3 mm; MW = 4.15 – 4.8 mm. Females: TL =
320 9.4 – 10.0 mm; EL = 7.3 – 7.6 mm; MW = 4.6 – 5.1 mm.

321 Colour: Dorsum (Fig. 2A) black to very dark pitchy-brown; paler dark
322 reddish-brown on vertex and towards lateral margins of pronotum. Legs dark reddish
323 brown; tibiae darker than tarsi. Clypeus, antenna and palpi paler reddish brown.
324 Venter reddish brown; paler than dorsum. Darker on blade of prosternal process and
325 around discum in centre of metaventricle.

326 Head: Broad, transverse, with large eye, which bulges slightly and occupies
327 *ca.* 1/3 of lateral margin of head. Clypeus somewhat thickened around marginal bead.
328 Labrum distinct, with marked circular apicomedial emargination furnished with dense
329 golden setae. Upper surface of labrum with distinct isodiametric microreticulation.
330 Entire dorsal surface of head capsule with impressed isodiametric microreticulation,
331 giving a slightly dull appearance. Sparse, fine micropunctures on frons and vertex;
332 short longitudinal striae present laterally on vertex and temples. Frontoclypeal
333 suture weakly visible laterally. Frons with lateral row of setiferous punctures situated
334 on either side just behind line of frontoclypeal suture, each bearing a long white
335 decumbent seta. Circular row of similar punctures inside lateral and anterior margins
336 of each eye.

337 Pronotum: Strongly transverse, rectangular, broadest close to base. Sides
338 rounded, narrowed in front to acutely rounded anterior angles which are marked by a
339 small cluster of short, stout, spine-like golden setae. Posterior angles obtusely
340 rounded. Anterior margin evenly curved, posterior margin straight. Disc with
341 shallow median longitudinal furrow, most visible posteriorly. Shallow, irregular
342 lateral longitudinal impressions also visible in some specimens. Entire surface

343 relatively dull, with well-impressed isodiametric microreticulation. Disc with sparse
344 fine micropunctures. Longitudinal striae (Fig. 4A) present laterally and along
345 posterior margin; shorter anteriorly. Pronotal striae predominantly orientated
346 antero-posteriorly; some orientated more laterally towards the posterior margin. Front
347 margin bordered by an irregular row of median setiferous punctures, each bearing a
348 long, white, hair-like seta. A similar row of setiferous punctures present along lateral
349 margin, curving inwards in posterior 1/3, and ending close to the outer margin of the
350 scutellum.

351 Elytron: Elongate, broadest behind middle. Rounded to shoulders, almost
352 parallel-sided or slightly divergent over anterior 2/3, then rounded to posterior angles.
353 Elytra distinctly asymmetrical at apex; one side with apical angle protruding more
354 than the other (Fig. 2A). Entire elytral surface rather dull, with strong isodiametric
355 microreticulation, sparse fine micropunctuation and strong longitudinal striae, which
356 are denser than on the pronotum, and orientated antero-posteriorly (see Fig. 4B).
357 Each elytron with three irregular rows of medium setiferous punctures on disc, each
358 bearing a long, white, hair-like decumbent seta. Setal rows beginning just behind
359 elytral shoulder, and visible until approx. apical 1/3. Similar setiferous puncture rows
360 present close to lateral margin, particularly in apical 2/3.

361 Venter: Prementum shining, lacking microreticulation, with broad central
362 convexity and scattered, sparse punctures. Mentum with strongly developed anterior
363 bead, and M-shaped anterior central projection. Mentum shining, entire surface
364 except bead with weak isodiametric to slightly transverse microreticulation.
365 Submentum shining, but with stronger and more transverse microreticulation,
366 particularly transverse towards gula. Irregular transverse fields of long, stout golden
367 bristle present laterally along anterior margin. Gula shining, lacking
368 microreticulation; microsculpture restricted to sparse transverse wrinkles. Gena
369 shining, with evident isodiametric to transverse microreticulation. Pronotal
370 hypomeron shining, with weak isodiametric microreticulation. Centre of front margin
371 of prosternum with stout golden setae, directed anteriorly (Fig. 3F). Central
372 prosternal ridge smooth, lacking microreticulation and sparsely punctate, some
373 punctures bearing long, golden adpressed setae. Prosternum with irregular wrinkles
374 either side of central ridge, and dense, golden hair-like setae. Metathoracic
375 anepisternum, metaventricle, metacoxae and abdominal ventrites shining, with
376 isodiametric microreticulation. Metaventral wings narrow. Metacoxal suture well-

377 impressed, reaching posterior margin of metaventrite. Metacoxal process with deep
378 medium punctures close to junction of lobes, each bearing a short, golden adpressed
379 seta. Ventrites 1-2 with longitudinal scratches in both sexes. Ventrites 3-5 with long,
380 golden setal tuft in centre, inserted $1/3 - 1/2$ of way from anterior margin of ventrite,
381 reaching posterior margin of ventrite.

382 Male: Pro- and mesotarsomeres 1-3 with 23 stalked adhesive setal discs, five
383 in distal row; six in each of three proximal rows. Protarsal claw slightly thickened in
384 comparison to female. Abdominal ventrites with higher density of longitudinal
385 scratches than in females; present on all ventrites. Ventrite 3 raised centrally towards
386 hind margin. Ventrite 5 with small longitudinal apicomedian notch on surface.
387 Ventrites 3-6 with irregular apicolateral depressions; more strongly marked on
388 ventrites 5-6 (ventrite 6 see Fig. 3G). Median lobe of aedeagus (Fig. 2B) TL = 2.25
389 mm, with prominent internal sac sclerites visible ventrally. Left sclerite small, with
390 triangular apex; right sclerite much longer, protruding, with serrated apex. Parameres
391 (Fig. 2B) asymmetrical, with strong, parallel-sided distal stylus, bearing few setae.
392 Scattered setae also present on apical margin of paramere.

393 Variability: In addition to the size variation noted above, some of the Cape
394 Flats paratypes are paler in colouration than the holotype, varying from reddish brown
395 to black, this perhaps reflecting some tenacity.

396

397 *Etymology.* Named after Dr James S. Pryke, Stellenbosch University, whose
398 recent material of this species alerted us to its existence. The specific epithet is a
399 noun in the genitive case.

400

401 *Ecology.* All recent material has been collected from Noordhoek Wetlands
402 (Fig. 5), a Restionaceae-dominated wetland developed over coastal sands, situated
403 within Table Mountain National Park, on the Cape Peninsula. Adult *Capelatus gen.*
404 **n.** were netted from the base of restio and *Juncus* tussocks, mostly in areas of
405 relatively dense vegetation. Specimens found by DTB were in water with reddish,
406 iron oxide-rich sediment, and a mixture of grasses and fine leaved Juncaceae (Fig.
407 5B). Noordhoek Wetlands contains some areas of permanent water, but also
408 fluctuates in level considerably, some parts, including those inhabited by *Capelatus*
409 **gen. n.**, likely to dry out during many summers (J. Pryke, pers. comm.). The
410 Noordhoek site is itself largely situated within modified Cape Flats Dune Strandveld

411 (*sensu* Mucina & Rutherford, 2006), and has benefitted from the recent clearance of
412 invasive alien vegetation. Material from the Cape Flats was, according to label data,
413 taken in grassy flood pools, with algae, *Aponogeton* and *Hydrodictyon*, a description
414 that suggests these were Cape vernal pools (Mucina & Rutherford, 2006). This
415 habitat type harbours a number of specialist endemic plant and animal lineages, and is
416 suspected to be of Pliocene origin (Oberlander *et al.*, 2014). Vernal pools were
417 formerly widespread on the Cape Flats and in adjacent areas of the far southwestern
418 Cape, but have now largely been lost to development, including it would appear those
419 in which *Capelatus* **gen. n.** was collected.

420

421 **Discussion**

422

423 As well as being clearly diagnosable on the basis of its adult morphology, *Capelatus*
424 **gen. n.** is phylogenetically isolated within the Afrotropical diving beetles. Our
425 molecular phylogeny unambiguously places *C. prykei* **gen. et sp. n.** in a clade with
426 the Palearctic *Liopterus* and the largely Australasian *Exocelina*. All other
427 Afrotropical copelatines (250+ spp.) belong to the widespread and species-rich
428 *Copelatus*, or *Madaglymbus*, a relatively small genus of 10 species (+ *ca.* 20
429 undescribed – M. Balke, unpublished) restricted to the Malagasy sub-region; neither
430 of these genera being closely related to *Capelatus* **gen. n.** Whilst detailed
431 examination of the divergence times and biogeography of Copelatinae are not the
432 object of this study, our results suggest that the *Exocelina* group of genera (i.e.
433 *Exocelina*, *Liopterus* and *Capelatus* **gen. n.**) forms a well-supported clade within the
434 subfamily, which has colonised most regions of the Old World. Provisional dating
435 (Toussaint, unpublished) suggests that these genera might have diverged around the
436 Eocene-Oligocene boundary, roughly 30–40 Mya, supporting the hypothesis that
437 active dispersal rather than ancient vicariance was the main trigger of their present-
438 day distribution. *Capelatus* **gen. n.**, joins the Cape endemic Hyphydrini (see Ribera
439 & Balke, 2007) as a distinctive member of the region’s diving beetle fauna, whose
440 phylogenetic composition is unique on a global scale.

441 Although the sister-group relationship between *Capelatus* **gen. n.** and
442 *Liopterus* is not unequivocal from our molecular analyses, it is consistently the best
443 supported across all three phylogenetic methods employed. On the basis of these data
444 *Capelatus* **gen. n.** and *Liopterus* form a striking example of a Palearctic – southern

445 African disjunction, a biogeographical pattern seen in a number of other insect groups
446 (e.g. Balke *et al.*, 2003; Bologna *et al.*, 2008; Caldara *et al.*, 2008; Kirk-Spriggs &
447 McGregor, 2009), as well as some elements of the flora (Galley & Linder, 2006). In
448 some cases such distribution patterns are believed to have resulted from relatively
449 recent (Plio-Pleistocene) southward dispersal of Palaearctic taxa through the Eastern
450 Arc mountains of East Africa (Gerhke & Linder, 2009; Kirk-Spriggs & McGregor,
451 2009; Sanmartín *et al.*, 2010), whilst in others, disjunct taxa appear to represent older,
452 relictual lineages which have survived in areas of relative climatic stability (e.g.
453 extant Aspidytidae - Balke *et al.*, 2003, 2005). The degree of molecular divergence
454 observed between *Copelatus* **gen. n.** and *Liopterus* suggests that these taxa belong to
455 this latter category.

456 Understanding of the higher-level phylogeny of Copelatinae has been
457 hampered by the apparent plasticity of characters formerly used to define genera and
458 species groups, such as elytral striation and the presence/absence of striae or
459 metacoxal lines (Balke *et al.*, 2004). Genus-level relationships have previously been
460 investigated by Balke *et al.* (2004) and Shaverdo *et al.* (2008), using a range of
461 mitochondrial DNA markers with somewhat conflicting results. The addition of
462 nuclear DNA sequences in the present study improves our understanding of the
463 interrelationships amongst these beetles, as does inclusion of all but one of the known
464 copelatine genera. The only current genus-level taxon not included in our analyses is
465 *Rugosus*, which was erected for two Neotropical species, largely on the basis of their
466 rugose dorsal sculpture (García, 2001). These taxa appear highly likely to belong to
467 *Aglymbus*, however, which includes other heavily sculptured species in the
468 Neotropics (M. Balke, unpublished), suggesting that their inclusion would not
469 necessarily change the broader conclusions presented here. All included genera were
470 found to be monophyletic and the internal phylogenetic structure of the subfamily was
471 well-resolved, being largely consistent across different phylogenetic methods. Instead
472 of being nested within *Copelatus*, as has been suggested in most previous molecular
473 analyses, the Oriental genus *Lacconectus* (80 spp.) was found to be sister to remaining
474 Copelatinae, a systematic position first suggested by Brancucci (1986) based on both
475 external and male genital morphology. With over 430 described species and many
476 undescribed taxa, the cosmopolitan *Copelatus* is by far the most species-rich genus of
477 Copelatinae and indeed Dytiscidae. Whilst few species of this genus are included in
478 our phylogeny, these do cover much of the global distribution of *Copelatus*, which

479 was recovered as monophyletic with strong support in all analyses, and sister to
480 remaining copelatine groups, excluding *Lacconectus*. The inclusion of
481 *Agaporomorphus*, a small genus of nine Neotropical species (see Miller, 2014), in our
482 analyses placed this rather than *Aglymbus* sister to the Malagasy *Madaglymbus*; these
483 two genera forming a clade which was supported in all analyses. Our work also
484 forces a re-evaluation of the phylogenetic position of *Liopterus*, made up of two
485 closely-related Palaearctic species which have been considered as either sister to
486 *Madaglymbus* (Balke *et al.*, 2004) or sister to all other members of the subfamily
487 based on mtDNA sequence data alone (Shaverdo *et al.*, 2008) and which here instead
488 clearly associated with *Capelatus* **gen. n.** and *Exocelina*. Miller & Bergsten (2014)
489 used a combination of molecules and morphology to investigate phylogenetic
490 interrelationships across the Dytiscidae as a whole. These authors clearly
491 demonstrated the monophyly of Copelatinae, although their analyses included
492 representatives of only four genera (*Agaporomorphus*, *Copelatus*, *Exocelina* and
493 *Lacconectus*), which, together with differences in choice of root position, may explain
494 the somewhat different generic inter-relationships suggested in this study.

495 *Capelatus prykei* **gen. et sp. n.** was first detected when we received James
496 Pryke's material from Noordhoek Wetlands, where the species is still extant.
497 Subsequent searches in the dytiscid accessions of the BMNH revealed historical
498 material from the Cape Flats, collected in a locality which appears to have been
499 subsequently lost to urban development in the greater Cape Town area. Within an
500 Afrotropical context, the South African dytiscid fauna is relatively well known, the
501 Cape region having been extensively investigated in the past by Joyce Omer-Cooper
502 and others (reviewed by Omer-Cooper, 1966). Whilst a large number of water beetles
503 have been described from the Western Cape in the last 25 years (e.g. Perkins &
504 Balfour-Browne, 1994; Perkins, 2005, 2008; Ribera *et al.*, 2002; Bilton, 2013a-b,
505 2014; Bilton & Gentili, 2014), most of these taxa are non-dytiscids and small, cryptic,
506 and/or occupy macicolous habitats (Vaillant, 1956), largely neglected by earlier
507 workers. The fact that such a large, distinctive diving beetle as *C. prykei* **gen. et sp.**
508 **n.** has apparently remained undetected for so long strongly suggests that the species
509 has a very narrow geographical and ecological range, unusual in lentic freshwater
510 species (see Ribera, 2008). A similar apparent restriction to the extreme southwest of
511 the Cape is seen in a number of stillwater taxa, however, including the dytiscid
512 *Herophydrus capensis* Régimbart, and the Critically Endangered micro frog

513 *Microbatrachella capensis* (Boulenger) (Harrison *et al.*, 2004). Such a pattern may be
514 driven by the combination of strong climatic/ecological gradients, particularly in
515 rainfall, coupled with the relative climatic stability of the region, factors likely to both
516 promote the evolution of narrow-range endemics, and favour their persistence. On
517 the basis of available data, it is suggested that *Capelatus prykei* **gen. et sp. n.** be
518 afforded a provisional IUCN conservation status of Critically Endangered (CR), due
519 to an apparent area of occupancy estimated to be less than 10 km², and the observed
520 decline in extent of occurrence, extent and/or quality of habitat, and number of
521 locations or subpopulations due to urban development in the Cape Town area (B2ab
522 (i, iii, iv)) (IUCN, 2012). If the phylogenetic uniqueness of *Capelatus prykei* **gen. et.**
523 **sp. n.** is also taken into consideration (*sensu* Vane-Wright *et al.*, 1991), it is clear that
524 a better understanding of the range and requirements of this newly discovered taxon
525 represents a priority for conservation, in both a regional and global context.

526

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537

538

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790 **Figure Legends**

791

792 Fig. 1. Bayesian phylogenetic relationships amongst Copelatinae diving beetles.
793 Nodal support values for analyses are presented at each node of the consensus tree
794 from the MrBayes analysis (BI/ML/MP respectively). Asterisks indicate a $PP \geq 0.95$
795 or a $BS/SR \geq 70$ in BI, ML and MP analyses. Hyphens indicate that the corresponding
796 node was not recovered, or with a support of $< 50\%$. Distribution of genera by major
797 biogeographic region is shown with colored vertical bars on the right of the figure,
798 colours corresponding to the world map at the bottom left. The collecting localities of
799 *Capelatus prykei* **gen. et sp. n.** are indicated by the black dot on the map. The habitus
800 of a representative of each genus is displayed to the right of the figure, not to scale.

801

802 Fig. 2. *Capelatus prykei* **gen. et sp.n.** paratype. A) Male habitus; B) male genitalia
803 (aedeagus in lateral and ventral views; parameres). Scale bars A = 1 mm; B = 0.5
804 mm.

805

806 Fig. 3. *Capelatus prykei* **gen. et sp.n.** paratypes. A) Female protarsus, lateral view;
807 B) male protarsus, lateral view; C) male protarsus, dorsal view; D) male protarsus,
808 ventral view; E) male abdominal ventrite 6; F) prosternal process; G) metacoxal
809 process. Scale bars = 0.5 mm.

810

811 Fig. 4. Examples of dorsal sculpture with striae in male Copelatinae. A – B)
812 *Capelatus prykei* **gen. et sp.n.**; C – D) *Exocelina* sp. (Australia, S Queensland,
813 Manorina NP, 10/x/2006, L. Hendrich leg.); E – F) *Liopterus haemorrhoidalis*
814 (Fabricius). A, C & E show pronotal and B, D & F elytral sculpture respectively.

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816 Fig. 5. *Capelatus prykei* **gen. et sp.n.**, habitat. A) Overview of Noordhoek locality
817 (photo J S Pryke); B) detail of microhabitat at the base of tussocks (photo D T Bilton).

