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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 Aspitytidae, 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.zerene.com](http://www.zerene.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  $\alpha$ -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 micropunctation 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 km<sup>2</sup>, 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

539 **References**

540

541 Balke, M. (1998) Revision of New Guinea *Copelatus* Erichson, 1832 (Insecta:  
542 Coleoptera: Dytiscidae): The running water species, Part I. *Annales Naturhistorisches*  
543 *Museum Wien*, **100B**, 301–341.

544

545 Balke, M., Ribera, I. & Beutel, R.G. (2003) Aspidytidae: on the discovery of a new  
546 beetle family: morphological analysis, description of a second species, and key to  
547 fossil and extant adepagan families (Coleoptera). In: *Water beetles of China* Volume  
548 3 (ed. by M. A. Jäch & L. Ji) pp. 53–66. Zoologisch-Botanische Gesellschaft in  
549 Österreich and Wiener Coleopterologenverein, Wien.

550

551 Balke, M., Ribera, I. & Vogler, A.P. (2004) MtDNA phylogeny and biogeography of  
552 Copelatinae, a highly diverse group of tropical diving beetles (Dytiscidae). *Molecular*  
553 *Phylogenetics and Evolution*, **32**, 866–880.

554

555 Balke, M., Ribera, I. & Beutel, R.G. (2005) The systematic position of Aspidytidae,  
556 the diversification of Dytiscoidea (Coleoptera, Adepaga) and the phylogenetic signal  
557 of third codon positions. *Journal of Zoological Systematics and Evolutionary*  
558 *Research*, **43**, 223–242.

559

560 Balke, M., Gómez-Zurita, J., Ribera, I., Vilorio, A., Zillikens, A., Steiner, J., Garcia,  
561 M., Hendrich, L. & Vogler, A.P. (2008) Ancient associations of aquatic beetles and  
562 tank bromeliads in the Neotropical forest canopy. *Proceedings of the National*  
563 *Academy of Sciences, USA*, **105**, 6356–6361.

564

565 Balke, M., Ribera, I., Hendrich, L., Miller, M.A., Sagata, K., Posman, A., Vogler, A.P.  
566 & Meier, R. (2009) New Guinea highland origin of a widespread arthropod  
567 supertramp. *Proceedings of the Royal Society of London Series B*, **276**, 2359–2367.

568

569 Billardo, A. & Rocchi, S. (2011) Noteridae, Dytiscidae (Coleoptera) du Gabon (8ème  
570 partie). Monts de Cristal. *Atti della Società italiana di scienze naturali e del Museo*  
571 *civico di storia naturale di Milano*, **152**, 177–231.

572

573 Bilton, D.T. (2013a) *Prosthetops wolfbergensis* sp. nov. – a giant amongst the ‘minute  
574 moss beetles’, with new data on other members of the genus (Coleoptera,  
575 Hydraenidae). *Zootaxa*, **3666**, 345–357.

576

577 Bilton, D.T. (2013b) A revision of South African *Sharphydrus* (Coleoptera,  
578 Dytiscidae, Bidessini), with the description of two new species. *Zootaxa*, **3750**, 26–  
579 36.

580

581 Bilton, D.T. (2014) New species and new records of *Pterosthetops*: eumadiculous  
582 water beetles of the South African Cape (Coleoptera, Hydraenidae). *Zootaxa*, **3811**,  
583 438–462.

584

585 Bilton, D.T. & Gentili, E. (2014) *Laccobius leopardus* sp. nov. from the Western  
586 Cape of South Africa (Coleoptera: Hydrophilidae). *Zootaxa*, **3835**, 397–400.

587

588 Bologna, M.A., Di Giulio, A. & Pitzalis, M. (2008) Examples of disjunct distributions  
589 between Mediterranean and southern or eastern Africa in Meloidae (Coleoptera,  
590 Tenebrionidae). *Biogeographia*, **29**, 81–98.  
591

592 Brancucci, M. (1986) Revision of the genus *Lacconectus* Motschultsky (Coleoptera,  
593 Dytiscidae). *Entomological Basiliensia*, **11** 81–202.  
594

595 Caldara, R., Colonnelli, E. & Osella, G. (2009) Curculionidae Curculioninae:  
596 relationships between Mediterranean and southern African species (Coleoptera).  
597 *Biogeographia*, **29**, 133–156.  
598

599 Edgar, R.C. (2004) MUSCLE: Multiple sequence alignment with high accuracy and  
600 high throughput. *Nucleic Acids Research*, **32**, 1792–1797.  
601

602 Erixon, P., Svennblad, B., Britton, T., & Oxelman, B. (2003). Reliability of Bayesian  
603 posterior probabilities and bootstrap frequencies in phylogenetics. *Systematic  
604 biology*, *52*(5), 665–673.  
605

606 Felsenstein, J. (2004) *Inferring Phylogenies*. Sinauer Associates, Sunderland,  
607 Massachusetts.  
608

609 Galley, C. & Linder, H.P. (2006) Geographical affinities of the Cape flora. *Journal of  
610 Biogeography*, **33**, 236–250.  
611

612 García, M. (2001) Nuevos Colymbetinae (Coleoptera; Dytiscidae) del sur de  
613 Venezuela. *Boletín del Centro de Investigaciones Biológicas*, **35**, 339–347.  
614

615 Gehrke, B. & Linder, H.P. (2009) The scramble for Africa: pan-temperate elements  
616 on the African high mountains. *Proceedings of the Royal Society of London Series B*,  
617 **276**, 2657–2665.  
618

619 Goloboff, P.A. (1999) Analyzing large data sets in reasonable times: solutions for  
620 composite optima. *Cladistics*, **15**, 415–428.  
621

622 Goloboff, P.A., Farris, J. S., & Nixon, K. C. (2008) TNT, a free program for  
623 phylogenetic analysis. *Cladistics*, **24**, 774–786.  
624

625 Harrison, J.A., Minter, L. & Channing, A. (2004) *Microbatrachella capensis*. In:  
626 IUCN 2004. *2004 IUCN Red List of Threatened Species*. www.redlist.org.  
627

628 Hawlitschek, O., Hendrich, L., Espeland, M., Toussaint, E.F.A., Genner, M.J. &  
629 Balke, M. 2012. Pleistocene climate change promoted rapid diversification of aquatic  
630 invertebrates in Southeast Australia. *BMC Evolutionary Biology*, **12**, 142.  
631

632 IUCN (2012) *IUCN Red List Categories and Criteria: Version 3.1*. Second edition.  
633 Gland, Switzerland and Cambridge, UK: IUCN. iv + 32pp.  
634

635 Kirk-Spriggs, A.H. & McGregor, G. (2009) Disjunctions in the Diptera (Insecta)  
636 fauna of the Mediterranean Province and southern Africa and a discussion of

637 biogeographical considerations. *Transactions of the Royal Society of South Africa*, **64**,  
638 32–52.  
639  
640 Manning, J.C. & Goldblatt, P. (2012) The Greater Cape Floristic Region I: the Core  
641 Cape Flora. *Strelitzia*, **29**, 1–853. South African national Biodiversity Institute,  
642 Pretoria.  
643  
644 Meadows, M.E. & Sugden, J.M. (1991) A vegetation history of the last 14,000 years  
645 on the Cederberg, southwestern Cape Province. *South African Journal of Science*, **87**,  
646 33–43.  
647  
648 Miller, K.B. (2001) On the phylogeny of the family Dytiscidae Linnaeus (Insecta:  
649 Coleoptera) with an emphasis on the morphology of the female reproductive tract.  
650 *Insect Systematics and Evolution*, **32**, 45–92.

651 Miller, K.B. (2014) *Agaporomorphus sharynae*, a new species of diving beetle  
652 (Coleoptera: Dytiscidae: Copelatinae) from Venezuela. *Zootaxa*, **3790**, 177–184.  
653  
654 Miller, K.B., & Bergsten, J. 2014. The phylogeny and classification of diving beetles  
655 (Coleoptera: Dytiscidae). In: *Ecology, Systematics, and Natural History of*  
656 *Predaceous Diving Beetles (Coleoptera: Dytiscidae)* (ed. D.A. Yee) pp. 49–172.  
657 Springer, New York.  
658  
659 Miller, K.B. & Nilsson, A.N. (2003) Homology and terminology: Communicating  
660 information about rotated structures in water beetles. *Latissimus*, **17**, 1–4.  
661  
662 Mucina, L. & Rutherford, M.C. (2006). (eds.). The vegetation of South Africa,  
663 Lesotho and Swaziland. *Strelitzia*, **19**, 1–807.  
664  
665 Myers, N, Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B & Kent, J. (2000)  
666 Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.  
667  
668 Nilsson, A.N. (2014) *A World Catalogue of the Family Dytiscidae, or the Diving*  
669 *Beetles (Coleoptera, Adephaga)*. Version 1.I.2014. Distributed by the author  
670 from the URL <http://www2.emg.umu.se/projects/biginst/andersn/>.  
671  
672 Omer-Cooper, J. (1966) Coleoptera: Dytiscidae. Chapter 2 in: Hanström, B., Brinck,  
673 P. & Rudebeck, G. (eds.) *South African Animal Life*, **6**, 59–214.  
674  
675 Lanfear, R., Calcott, B., Ho, S. Y., & Guindon, S. (2012). PartitionFinder: combined  
676 selection of partitioning schemes and substitution models for phylogenetic  
677 analyses. *Molecular Biology and Evolution*, **29**, 1695–1701.  
678  
679 Perkins, P.D. (2005) A revision of the African hygropetric genus *Coelometopon*  
680 Janssens, and description of *Oomtelecopon* new genus (Coleoptera: Hydraenidae).  
681 *Zootaxa*, **949**, 1–103.  
682  
683 Perkins, P.D. (2008). New species and new collection records of Prosthetopine water  
684 beetles from southern Africa (Coleoptera: Hydraenidae). *Zootaxa*, **1864**, 1–124.  
685

686 Perkins, P.D. & Balfour-Browne, J. (1994). A contribution to the taxonomy of aquatic  
687 and humicolous beetles of the family Hydraenidae in southern Africa. *Fieldiana*  
688 *Zoology (N.S.)*, **77**, 1–159.

689  
690 Picker, M.D. & Samways, M.J. 1996. Faunal diversity and endemism of the Cape  
691 Peninsula - a first assessment. *Biodiversity and Conservation*, **5**, 591–606.

692  
693 Ribera, I. (2008) Habitat constraints and the generation of diversity in freshwater  
694 macroinvertebrates. In: *Aquatic Insects: Challenges to Populations*. (ed. by J.  
695 Lancaster & R.A. Briers) pp. 289–311. CAB International, UK.

696  
697 Ribera, I., Beutel, R.G., Balke, M. & Vogler, A.P. (2002) Discovery of Aspidytidae, a  
698 new family of aquatic Coleoptera. *Proceedings of the Royal Society of London Series*  
699 *B*, **269**, 2351–2356.

700  
701 Ribera, I. & Balke, M. (2007) Recognition of a species-poor, geographically restricted  
702 but morphologically diverse Cape lineage of diving beetles (Coleoptera: Dytiscidae:  
703 Hyphydrini). *Journal of Biogeography*, **34**, 1220–1232.

704  
705 Ribera, I. & Bilton, D.T. (2007) Aspidytidae. In: *Guides to the Freshwater*  
706 *Invertebrates of Southern Africa, Volume 10: Coleoptera*. (ed. by R. Staals & I.J. de  
707 Moor, I.J) pp. 85–88. Water Research Commission, Pretoria, South Africa.

708  
709 Ribera, I., Vogler, A. P., & Balke, M. (2008) Phylogeny and diversification of diving  
710 beetles (Coleoptera: Dytiscidae). *Cladistics*, **24**, 563–590.

711  
712 Riedel, A. (2005) Digital imaging of beetles (Coleoptera), and other three-  
713 dimensional insects. In: *Digital Imaging of Biological Type Specimens. A Manual of*  
714 *Best Practice*. (ed. by C. Häuser, A. Steiner, J. Holstein & M.J. Scoble) pp. 222–250.  
715 Results from a study of the European Network for Biodiversity Information, Stuttgart,  
716 Germany.

717  
718 Roets, F. & Oberlander, K.C. (2010) *Silvaphilus*: a new relict forest-endemic  
719 Canthonini dung beetle genus from the Western Cape Province of South Africa  
720 (Coleoptera: Scarabaeidae: Scarabaeinae). *African Entomology*, **18**, 369–373.

721  
722 Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S.,  
723 Larget, B., Liu, L., Suchard, M.A., Huelsenbeck, J.P. (2012) MrBayes 3.2: Efficient  
724 Bayesian Phylogenetic Inference and Model Choice Across a Large Model  
725 Space. *Systematic Biology*, **61**, 539–542.

726  
727 Saether, O.A. & Ekrem, T. (2003). Biogeography of afrotropical Chironomidae  
728 (Diptera), with special reference to Gondwanaland. *Cimbebasia*, **19**, 123–139.

729  
730 Samways, M.J., Pryke, J.S. & Simiaka, J.P. (2011) Threats to dragonflies on land  
731 islands can be as great as those on oceanic islands. *Biological Conservation*, **144**,  
732 1145–1151.

733

734 Sanmartín, I., Anderson, C.L., Alarcon, M., Ronquist, F. & Aldasoro, J.J. (2010)  
735 Bayesian island biogeography in a continental setting: the Rand Flora case. *Biology*  
736 *Letters*, **6**, 703–707.  
737

738 Shaverdo, H., Hendrich, L. & Balke, M. (2012) Introduction of the *Exocelina ekari-*  
739 *group* with descriptions of 22 new species from New Guinea (Coleoptera, Dytiscidae,  
740 Copelatinae). *Zookeys*, **250**, 1–76.  
741

742 Shaverdo, H., Hendrich, L. & Balke, M. (2013) *Exocelina baliem* sp. n., the only  
743 pond species of New Guinean *Exocelina* Broun, 1886 (Coleoptera, Dytiscidae,  
744 Copelatinae). *Zookeys*, **304**, 83–99.  
745

746 Shaverdo, H., Monaghan, M.T., Lees, D., Ranaivosolo, R. & Balke, M. (2008) A  
747 new genus of Malagasy endemic diving beetles and description of a highly unusual  
748 species based on morphology and DNA sequence data (Dytiscidae: Copelatinae). -  
749 *Systematics and Biodiversity*, **6**, 43–51.  
750

751 Sole, C.L., Scholtz, C.H. Ball, J.B. & Mansell, M.W. (2013) Phylogeny and  
752 biogeography of southern African spoon-winged lacewings (Neuroptera:  
753 Nemopteridae: Nemopterinae). *Molecular Phylogenetics and Evolution*, **66**, 360–368.  
754

755 Stamatakis, A. (2006). RAxML-VI-HPC: maximum likelihood-based phylogenetic  
756 analyses with thousands of taxa and mixed models. *Bioinformatics*, **22**, 2688–2690.  
757

758 Toussaint, E.F.A., Hall, R., Monaghan, M., Sagata, K., Ibalim, S., Shaverdo, H.V.,  
759 Vogler, A.P., Pons, J. & Balke, M. 2014a. The towering orogeny of New Guinea as a  
760 trigger for arthropod megadiversity. *Nature Communications*, **5**, 5001.  
761

762 Toussaint, E.F.A., Condamine, F.L., Hawlitschek, O., Watts, C.H., Porch, N.,  
763 Hendrich, L., & Balke, M. (2014b) Unveiling the diversification dynamics of  
764 Australasian predaceous diving beetles in the Cenozoic. *Systematic Biology*, syu067,  
765 doi:10.1093/sysbio/syu067.  
766

767 Vaillant, F. (1956) Recherches sur la faune madicole de France, de Corse et d’Afrique  
768 du Nord. *Memoires du Muséum National d’Histoire Naturelle Series A Zoologie*, **11**,  
769 1–252.  
770

771 Valente, L.M. & Vargas, P. (2013) Contrasting evolutionary hypotheses between two  
772 mediterranean-climate floristic hotspots : the Cape of southern Africa and the  
773 Mediterranean Basin. *Journal of Biogeography*, **40**, 2032–2046.  
774

775 Vane-Wright, R.I., Humphries, C.J. & Williams, P.H. (1991). What to protect -  
776 systematics and the agony of choice. *Biological Conservation*, **55**, 235–254.  
777

778 Verboom, G.A., Dreyer, L.L. & Savolainen, V. (2009) Understanding the origins and  
779 evolution of the world’s biodiversity hotspots: The biota of the African ‘Cape  
780 Floristic Region’ as a case study. *Molecular Phylogenetics and Evolution*, **51**, 1–4.  
781

782 Wewalka, G., Balke, M. & Hendrich, L. (2010) Dytiscidae: Copelatinae (Coleoptera).  
783 In: *Monographs on Coleoptera, Volume 3, Water beetles of New Caledonia (part 1)*

784 (ed. by M.A. Jäch & M. Balke) pp. 45–128. Naturhistorisches Museum, Wein,  
785 Austria.  
786  
787  
788  
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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.

815

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).

