Systematic
Entomology

Systematic Entomology (2015), **40**, 520–531 DOI: 10.1111/syen.12128

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

Introduction

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

With over 660 described species (Nilsson, 2014), Copelatinae is one of the most diverse subfamilies of diving beetles (Dytiscidae), especially in the wet tropical and subtropical forests of the world (e.g., Balke *et al*., 2004, 2008; Bilardo & Rocchi, 2011). Copelatines show very high levels of local endemism, particularly in running waters (e.g. Balke, 1998; Wewalka *et al*., 2010; Shaverdo *et al*., 2012, 2013). Many species of the subfamily have been described recently or remain undescribed; recent fieldwork in tropical regions such as New Guinea producing very high proportions of new species (Toussaint *et al*., 2014). Despite this high species richness, known Copelatinae are morphologically rather homogenous beetles, most taxa being oval, weakly convex and between 3 and 10 mm in length. Generic diversity in

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the subfamily is consequently modest, with only eight genera currently being recognised worldwide (Shaverdo *et al*., 2008; Miller & Bergsten, 2014; Nilsson, 2014), and around 90% of species belonging to the megadiverse *Copelatus* Erichson and *Exocelina* Broun. Here we describe *Capelatus prykei* **gen. et sp.n.**, a highly distinctive new taxon from the Western Cape of South Africa that has escaped detection until recently, and cannot be placed in any of the existing genera of Copelatinae. Using DNA sequence data from a combination of mitochondrial and nuclear regions we establish the phylogenetic position of this new taxon, demonstrating that it is not closely related to any of the numerous copelatine diving beetles previously described from sub-Saharan Africa and Madagascar, appearing instead to represent a striking example of a phylogenetically isolated Cape endemic lineage.

Materials and methods

Morphology

Specimens were studied with a Leica MZ8 stereomicroscope at ×8–80, lighted with a swan-neck illuminator, diffused using a tracing paper collar close to the specimen (to enable study of microsculpture). The terminology to denote the orientation of the male genitalia follows Miller & Nilsson (2003).

Digital photographs were taken with a Canon EOS 500D camera on a Leica Z6 Apo macroscope, fitted with a 1× or 2× objective lens. Specimens were illuminated using a Leica LED5000 HDI dome illuminator to avoid shadow. Genitalia were mounted on glass slides in Kisser's glycerol gelatine (see Riedel, 2005) and imaged using the same Leica system and a combination of transmitted and incident light. Image stacks were produced by hand, and combined using Zerene Stacker software (www.zerenesystems.com). For scanning electron microscopy, material was air-dried overnight at 60°C before being mounted onto metal stubs using double-sided carbon conducting tape. Specimens were examined and photographed at low vacuum in a JEOL JSM6610LV Scanning Electron Microscope (SEM).

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

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

Molecular analysis

In order to investigate the phylogenetic relationships of the new taxon, novel DNA sequences were generated for representatives of known extant genera of the subfamily Copelatinae [with the exception of *Rugosus* García, a little-known genus of two species from the Venezuelan Amazon, recently transferred to Copelatinae by Miller & Bergsten (2014)], in addition to data retrieved from GenBank (see Table S1). Total genomic DNA was extracted from leg, thoracic and head tissues of specimens kept in 96% ethanol using the DNeasy kit (Qiagen, Hilden, Germany). PCR protocols followed Toussaint *et al*. (2014) to amplify the following gene fragments: mitochondrial cytochrome c oxidase I (*cox1*, 732 bp), cytochrome c oxidase II (*cox2*, 552 bp) and cytochrome b (*cob*, 306 bp), and nuclear histone 3 (*H3*, 315 bp), histone 4 (*H4*, 156 bp), 18S ribosomal DNA (*18S*, 546 bp), Carbomoylphosphate synthase (*CAD*, 849 bp) and α-Spectrin (*Asp*, 792 bp). All gene fragments were chosen because of their proven efficiency in disentangling dytiscid phylogenetics at the generic level (see Ribera *et al*., 2008; Balke *et al*., 2009; Hawlitschek *et al*., 2012; Toussaint *et al*., 2014, 2015). Forward and reverse DNA sequences were assembled and mismatches corrected with Geneious R6 (Biomatters, http://www.geneious.com/), aligned using Muscle (Edgar, 2004) and reading frames checked in Mesquite 2.75 (http://mesquiteproject.org). Overall the concatenated molecular matrix contained 4248 aligned nucleotide positions. All new sequences were deposited in GenBank (see Table S1 for accession nos.).

Phylogeny reconstruction

We used Bayesian Inference (BI), Maximum-Likelihood (ML) and Parsimony (MP) to reconstruct phylogenetic relationships. The BI analyses were conducted on a concatenated dataset using MrBayes 3.2.1 (Ronquist *et al*., 2012). The partitions and corresponding optimal models of substitution were searched using PartitionFinder 1.1.1 (Lanfear *et al*., 2012) using the *greedy* algorithm, either the *MrBayes* or *RAxML* sets of models and with the Akaike Information Criterion corrected (AICc) to compare the model fits. PartitionFinder analyses were carried out using 22 pre-defined data blocks, one for each codon position of the seven protein coding genes and one for *18S*. The analyses consisted of two simultaneous and independent runs of four Metropolis-coupled Markov chain Monte Carlo (MCMC, one cold and three incrementally heated) chains run for 50 million generations with a tree sampling every 1000 generations to calculate posterior probabilities (PP). In order to investigate the convergence of the runs, we investigated the standard deviation of the split frequencies and Effective Sample Size (ESS) of all parameters, and plotted the log-likelihood of the samples against the number of generations in Tracer 1.5 (http://BEAST.bio.ed.ac.uk/Tracer). A value of ESS >200 was acknowledged as a good indicator of convergence. All of the trees that predated the time needed to reach a log-likelihood plateau were discarded as burn-in, and the remaining samples were used to generate a 50% majority rule consensus tree. The ML analyses were conducted with RAxML (Stamatakis, 2006) with the concatenated dataset partitioned under the optimal scheme recovered by PartitionFinder. We performed 1000 Bootstrap replicates (BS) to investigate the level of support at each node. The MP analyses were carried out with TNT 1.1 (Goloboff *et al*., 2008) with the *Sectorial Searches*, *Tree Ratchet*, *Tree Fusing* and *Tree Drifting* algorithms (Goloboff, 1999) and

100 random addition sequences. In order to assess the level of support at each node, we performed 1000 replicates using the *Symmetric Resampling* (SR) with a probability fixed to 10. A calculated PP above 0.95 or a BS/SR above 70 was considered to indicate strong support for a given clade (Erixon *et al*., 2003; Felsenstein, 2004).

Results

Molecular biology and phylogenetics

Results of the different phylogenetic methods conducted on the concatenated molecular dataset summarized in Fig. 1, whilst gene regions successfully amplified and sequenced from sampled Copelatinae are detailed in Table S1, with partitions and substitution models recovered by PartitionFinder presented in Table S2. All genera of Copelatinae were monophyletic with optimal support in BI, ML and MP. *Lacconectus* Motschulsky was sister to the rest of the subfamily with strong support in all analyses. *Copelatus* (including taxa from the Afrotropics, Australasia and the Neotropics) was sister to all genera except *Lacconectus*, with strong support, in every analysis except BI, where it was moderately supported. The other genera fell into two separate well supported clades (*Agaporomorphus* Zimmermann + *Madaglymbus* Shaverdo & Balke and *Capelatus* **gen.n.** + *Liopterus* Dejean + *Exocelina*) in both BI and ML analyses (see Fig. 1 and Figure S1). In MP, most relationships between genera were congruent with the results of the probabilistic methods, albeit with low SR scores (Figure S1). In this analysis, however, *Aglymbus* Sharp was recovered as sister to *Agaporomorphus* + *Madaglymbus* with low support (Figure S1). A clade comprising *Capelatus* **gen.n.**, *Exocelina* and *Liopterus* was recovered in all analyses; highly supported in BI and ML, less so in MP (Fig. 1; Figure S1). Despite globally moderate supports, the relationships within this clade were consistent across all three phylogenetic methods; *Capelatus* **gen.n.** and *Liopterus* forming a separate clade, itself sister to *Exocelina*. The relatively low support values for *Capelatus* + *Liopterus* in BI and MP analyses are likely to have resulted from missing genetic coverage in *Capelatus* and *Liopterus*, for which some gene fragments would not amplify (see Table S1). Data from other loci would be useful in the future to robustly assess the placement of these two genera relative to *Exocelina*. Our phylogenetic analyses all unambiguously place *Copelatus cheesmanae* J. Balfour-Browne, 1939 well within *Exocelina* (Fig. 1; Figure S1). Consequently we introduce the following **new combination**: *Exocelina cheesmanae* (J. Balfour-Browne, 1939). Our unpublished data suggest that *E. cheesmanae* is closely related to the New Caledonian *E. aubei* (Montrouzier, 1860).

Taxonomy

Capelatus gen.n. Turner & Bilton

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

Generic diagnosis. Male protarsomere 4 with strongly protruding anterodistal process furnished with four stout, spine-like setae (Fig. 3B–D). Female protarsomere 4 simple, but with four stout setae at anterodistal angle (Fig. 3A). Male pro- and mesotarsomeres 1–3 with large stalked adhesive discs, arranged in four rows (Fig. 3D). Female metatibia and metatarsus with only dorsal row of natatorial setae. Median lobe of aedeagus with well-developed internal sac sclerites (Fig. 2B). Paramere with distal stylus (Fig. 2B). Paramere setae sparse, restricted to paramere margin and apex of distal stylus. Bursa copulatrix present; strongly sclerotized, with thick walls. Elytra without striae, and with distinct longitudinal strioles in the only known species (Fig. 4 – note these are also present in some species of other copelatine genera). Metacoxal lines present but weak, restricted to an indistinct ridge on outer margins of process in the only known species, not reaching posterior borders of metaventrite. *Capelatus* **gen.n.** can be distinguished from all other genera of Copelatinae by the above combination of characters. The modified structure of the male protarsomere 4 is a unique apomorphy of this genus in the world fauna. It differs from *Liopterus*, its apparent sister genus (see above), in the modification of this tarsal segment, which lacks the spinose anterodistal process in *Liopterus*, as well as in the absence of setae on the inner faces of the parameres (long, dense hair-like setae present in *Liopterus*) and the weak metacoxal lines in the only known species (strong and reaching posterior borders of the metaventrite in both known *Liopterus*).

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

Male. Protibia simple, with approximately triangular outline. Pro- and mesotarsomeres 1–3 distinctly dilated, ventrally

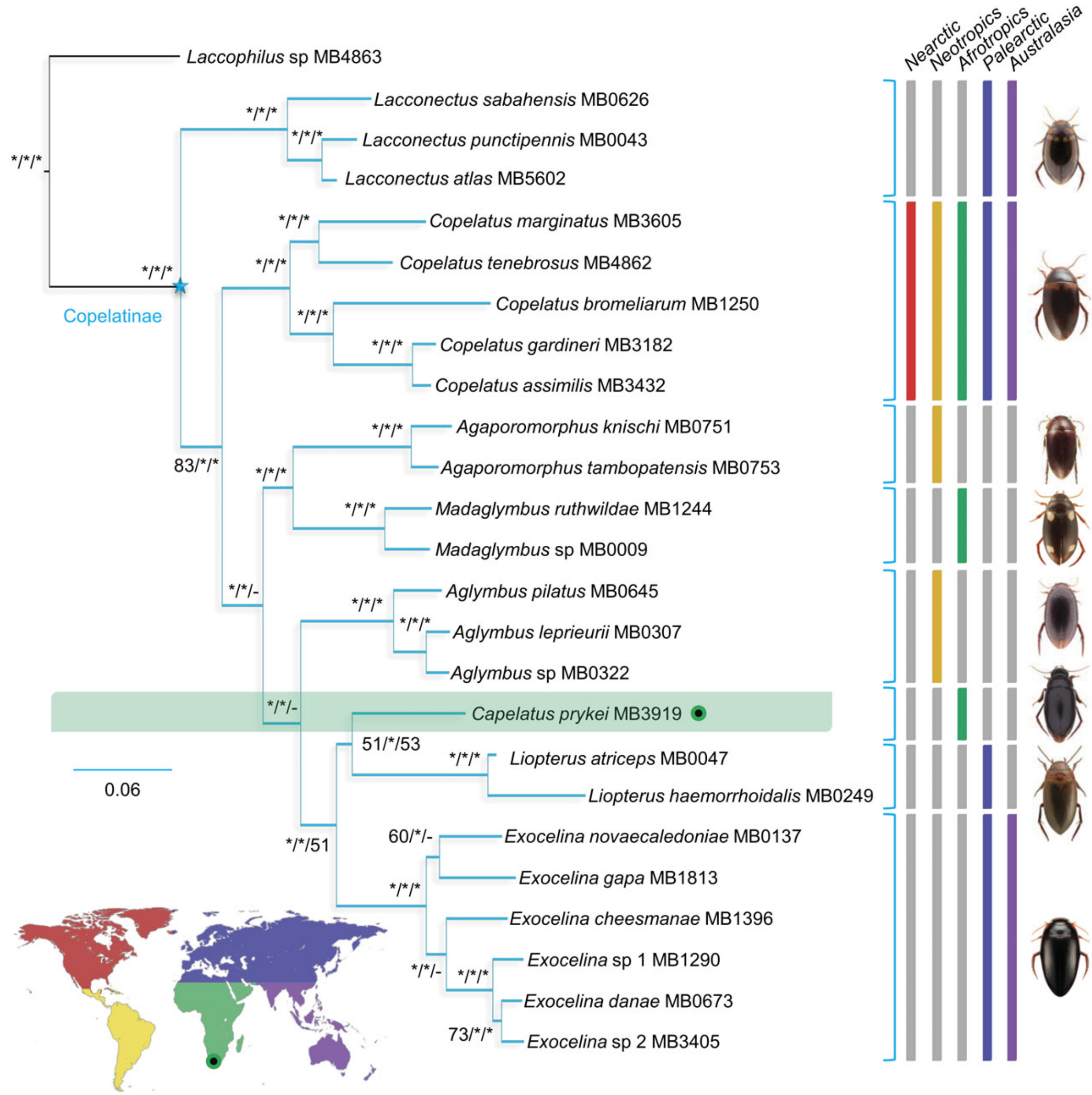

Fig. 1. Bayesian phylogenetic relationships amongst Copelatinae diving beetles. Nodal support values for analyses are presented at each node of the consensus tree from the MrBayes analysis (BI/ML/MP, respectively). Asterisks indicate a PP ≥ 0.95 or a BS/SR ≥ 70 in BI, ML and MP analyses. Hyphens indicate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

with four rows of stalked adhesive setae. Protarsomere 4 with protruding anterodistal process bearing four stout, blade-like setae which are ventrally curved to apices (Fig. 3B, D). Protarsomere 5 simple, long and narrow, ventrally with short, sparse setae. Protarsal claws simple, evenly curved, anterior slightly longer than posterior. Metatibia and metatarsus with dorsal and ventral rows of natatorial setae. Median lobe (Fig. 2B) with protruding endophallic sclerites. Paramere (Fig. 2B) with distal stylus. Setae restricted to paramere margin and apex of distal stylus.

Female. Dorsal surface with microreticulation slightly stronger than in males. Strioles of pronotal margins and elytral disc denser than in males. Metatibia and metatarsus with

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

only dorsal rows of natatorial setae. Bursa copulatrix present, strongly sclerotized. Gonocoxa and gonocoxosternum as in other genera of Copelatinae (see Miller, 2001).

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

Capelatus prykei sp.n. Turner & Bilton

Type material. Holotype (male) 'Stn. No. 347// S.Africa, Cape Flats, Ca. 3–5 mls. S.E. of Philippi 5.viii.1954// J.

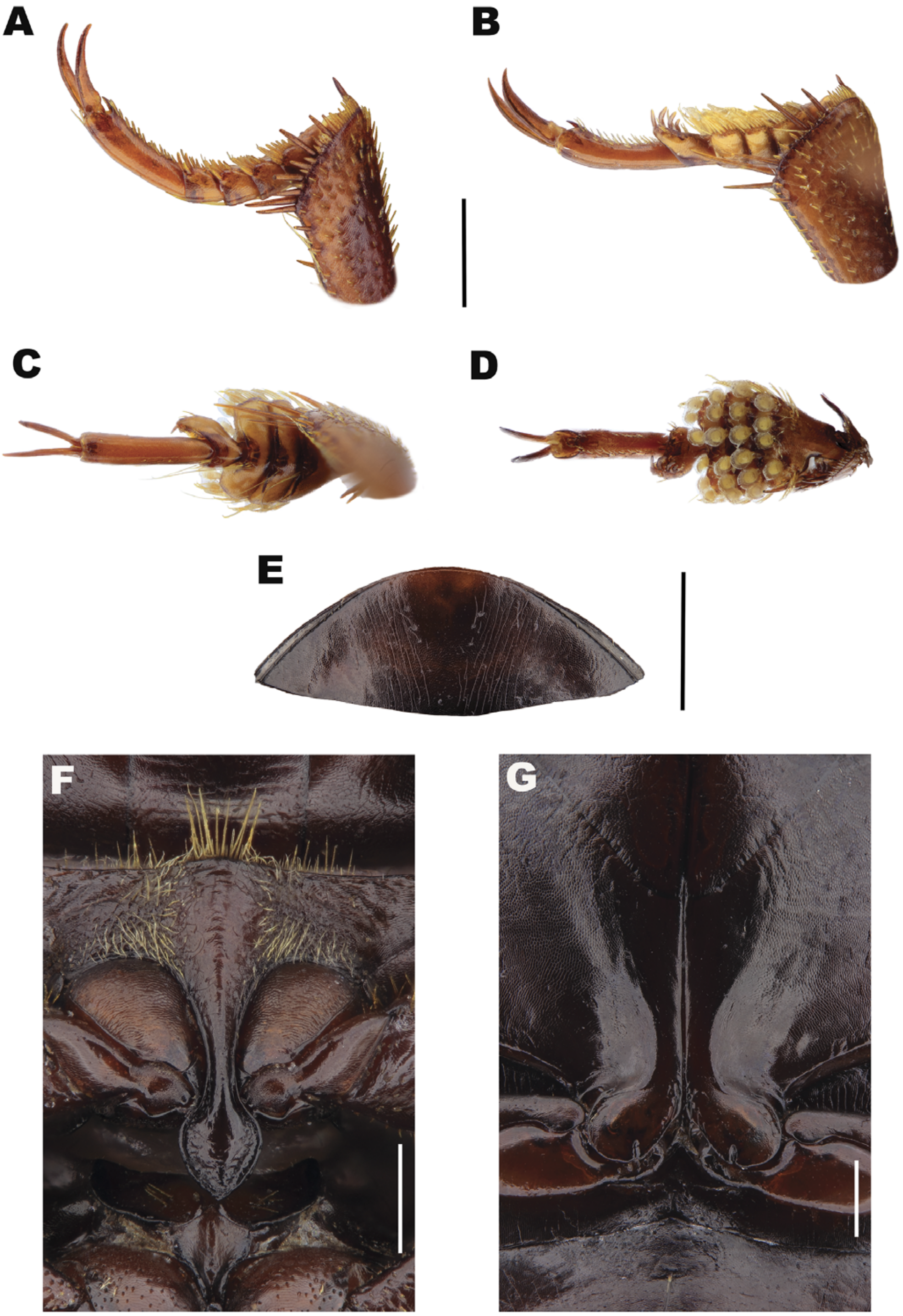

Fig. 3. *Capelatus prykei* **gen. et sp.n.** paratypes. (A) Female protarsus, lateral view; (B) male protarsus, lateral view; (C) male protarsus, dorsal view; (D) male protarsus, ventral view; (E) male abdominal ventrite 6; (F) prosternal process; (G) metacoxal process. Scale bars = 0.5 mm.

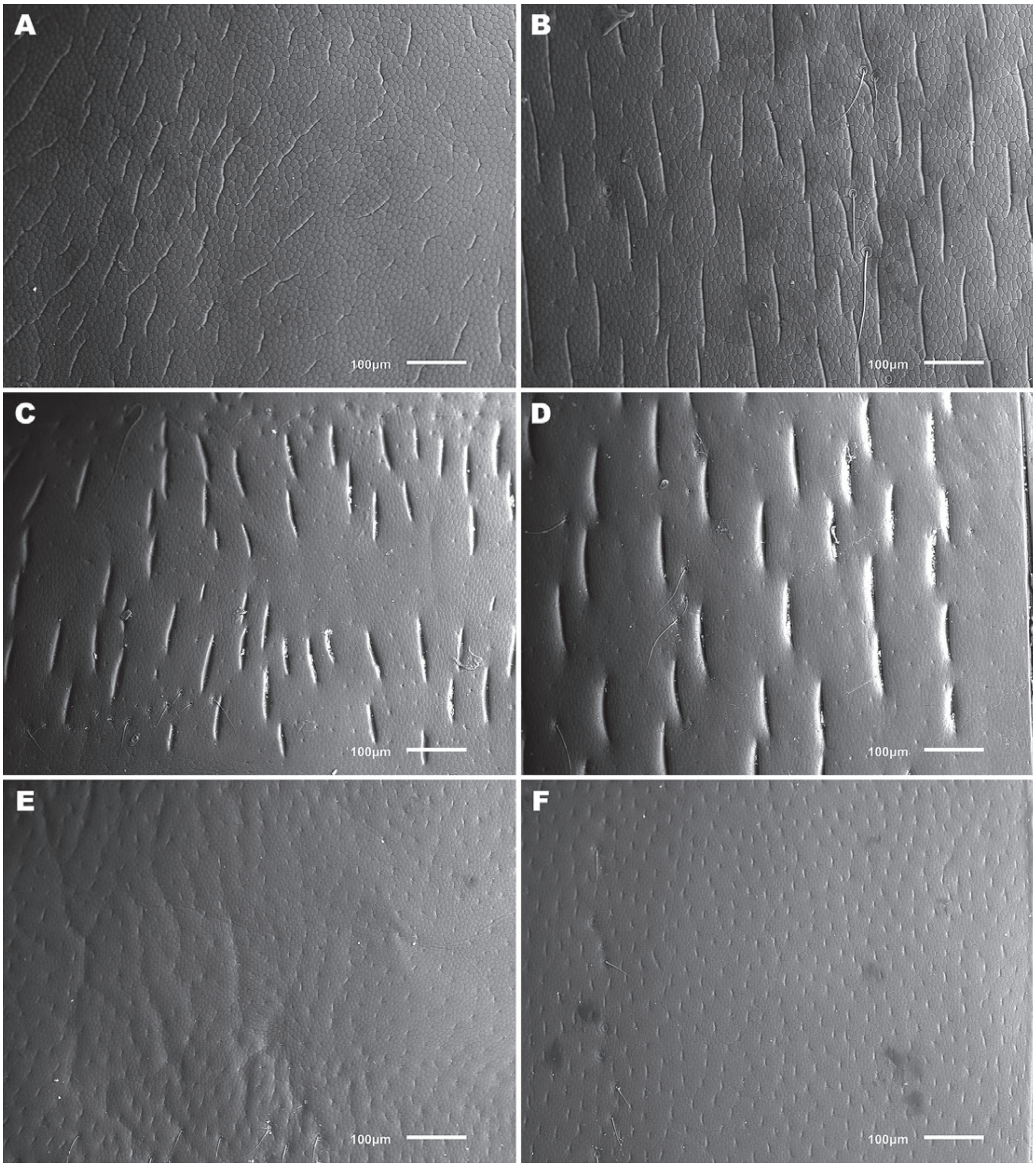

Fig. 4. Examples of dorsal sculpture with strioles in male Copelatinae. (A, B) *Capelatus prykei* **gen. et sp.n.**; (C, D) *Exocelina* sp. (Australia, S Queensland, Manorina NP, 10/x/2006, L. Hendrich leg.); (E, F) *Liopterus haemorrhoidalis* (Fabricius). (A, C, E) show pronotal and (B, D, F) elytral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

Balfour-Browne Brit. Mus. 1954-797// grassy flood pools, Algae, Aponogeton and Hydrodictyon'. With our red Holotype label 'Holotype *Capelatus prykei* Turner & Bilton' (BMNH). Paratypes (19): 5♂ 6♀ same data as holotype (4♂ 5♀ BMNH, 1♂ 1♀ CTP); 1♂ 1♀ 'South Africa, Western Cape Province, ref: col605, leg. James Pryke, wetland, Nordhoek, Cape Peninsula, 15 July 2006, 34 06.500S, 18 22.390E, presented to C. R.Turner coll. 2007' (ISAM); 1♂ 1♀ 'South Africa, Western Cape Province, ref: col131, leg. James Pryke, wetland, Nordhoek, Cape Peninsula, 31 July 2007, 34.10858S, 18.37306E, presented to C.R.Turner coll. 2007' (CTP); 1♀ 'South Africa, Western Cape Province, ref: col131, leg. James Pryke, wetland, Nordhoek, Cape Peninsula, 31 July 2007, 34.10858S, 18.37306E, presented to C.R.Turner coll. 2007// DNA, M.Balke, 3919 [green label]' (ZSM); 1♀ 'James Pryke, Noordhoek, 31-07-2007, col 131// Wetland, S34.10858, E18.37306' (SANC); 1♂ 1♀ '23/ix/2010 South Africa WC, Table Mountain National Park, Noordhoek Wetlands – seasonal pans with iron ochre mud and deep litter, below *Juncus* and restios, D. T. Bilton leg.' (CBP) All with our red paratype labels 'Paratype *Capelatus prykei* Turner & Bilton'.

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

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

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

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

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

Pronotum. Strongly transverse, rectangular, broadest close to base. Sides rounded, narrowed in front to acutely rounded anterior angles which are marked by a small cluster of short, stout, spine-like golden setae. Posterior angles obtusely rounded. Anterior margin evenly curved, posterior margin straight. Disc with shallow median longitudinal furrow, most visible posteriorly. Shallow, irregular lateral longitudinal impressions also visible in some specimens. Entire surface relatively dull, with well-impressed isodiametric microreticulation. Disc with sparse fine micropunctures. Longitudinal strioles (Fig. 4A) present laterally and along posterior margin; shorter anteriorly. Pronotal strioles predominantly orientated antero-posteriorly; some orientated more laterally towards the posterior margin. Front margin bordered by an irregular row of medium setiferous punctures, each bearing a long, white, hair-like seta. A similar row of setiferous punctures present along lateral margin, curving inwards in posterior 1/3, and ending close to the outer margin of the scutellum.

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

Venter. Prementum shining, lacking microreticulation, with broad central convexity and scattered, sparse punctures. Mentum with strongly developed anterior bead, and M-shaped anterior central projection. Mentum shining, entire surface except bead with weak isodiametric to slightly transverse microreticulation. Submentum shining, but with stronger and more transverse microreticulation, particularly transverse towards gula. Irregular transverse fields of long, stout golden bristle present laterally along anterior margin. Gula shining, lacking microreticulation; microsculpture restricted to sparse transverse wrinkles. Gena shining, with evident isodiametric to transverse microreticulation. Pronotal hypomeron shining, with weak isodiametric microreticulation. Centre of front margin of prosternum with stout golden setae, directed anteriorly (Fig. 3F). Central prosternal ridge smooth, lacking microreticulation and sparsely punctate, some punctures bearing long, golden adpressed setae. Prosternum with irregular wrinkles either side of central ridge, and dense, golden hair-like setae. Metathoracic anepisternum, metaventrite, metacoxae and abdominal ventrites shining, with isodiametric microreticulation. Metaventral wings narrow. Metacoxal suture well-impressed, reaching posterior margin of metaventrite. Metacoxal process with deep medium punctures close to junction of lobes, each bearing a short, golden adpressed seta. Ventrites 1–2 with longitudinal scratches in both sexes. Ventrites 3–5 with long, golden setal tuft in centre, inserted 1/3–1/2; of the distance from anterior margin of ventrite, reaching posterior margin of ventrite.

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

Variability. In addition to the size variation noted above, some of the Cape Flats paratypes are paler in colouration than the

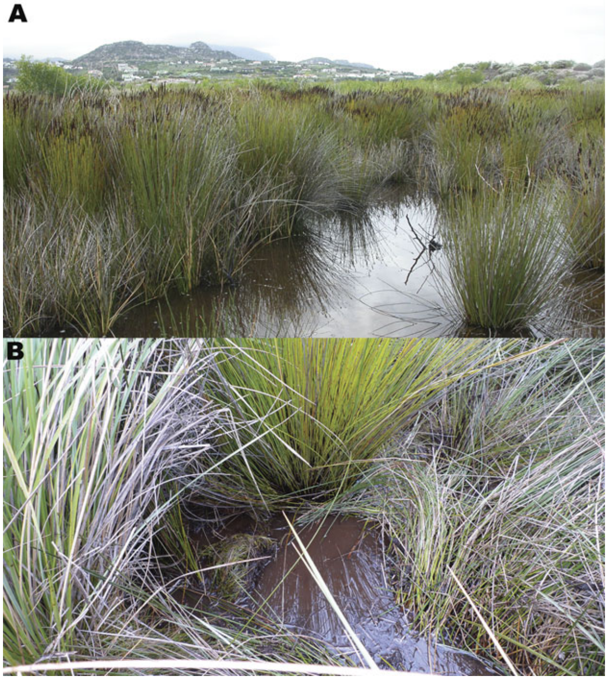

Fig. 5. *Capelatus prykei* **gen. et sp.n.**, habitat. (A) Overview of Noordhoek locality (photo J S Pryke); (B) detail of microhabitat at the base of tussocks (Photo: D T Bilton).

holotype, varying from reddish brown to black, this perhaps reflecting some tenerality.

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

Ecology. All recent material has been collected from Noordhoek Wetlands (Fig. 5), a Restionaceae-dominated wetland developed over coastal sands, situated within Table Mountain National Park, on the Cape Peninsula. Adult *Capelatus* **gen.n.** were netted from the base of restio and *Juncus* tussocks, mostly in areas of relatively dense vegetation. Specimens found by DTB were in water with reddish, iron oxide-rich sediment, and a mixture of grasses and fine leaved Juncaceae (Fig. 5B). Noordhoek Wetlands contains some areas of permanent water, but also fluctuates in level considerably, some parts, including those inhabited by *Capelatus* **gen.n.**, likely to dry out during many summers (J. Pryke, personal communication). The Noordhoek site is itself largely situated within modified Cape Flats Dune Strandveld (*sensu* Mucina & Rutherford, 2006), and has benefitted from the recent clearance of invasive alien vegetation. Material from the Cape Flats was, according to label data, taken in grassy flood pools, with algae, *Aponogeton* and *Hydrodictyon*, a description that suggests these were Cape vernal pools (Mucina & Rutherford, 2006). This habitat type harbours a number of specialist endemic plant and animal lineages, and is suspected to be of Pliocene origin (Oberlander *et al*., 2014). Vernal pools were formerly widespread on the Cape Flats and in adjacent areas of the far southwestern Cape, but have now largely been lost to development, including – it would appear – those in which *Capelatus* **gen.n.** was collected.

Discussion

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

Although the sister-group relationship between *Capelatus* **gen.n.** and *Liopterus* is not unequivocal from our molecular analyses, it is consistently the best supported across all three phylogenetic methods employed. On the basis of these data *Capelatus* **gen.n.** and *Liopterus* form a striking example of a Palaearctic – southern African disjunction, a biogeographical pattern seen in a number of other insect groups (e.g. Balke *et al*., 2003; Bologna *et al*., 2008; Caldara *et al*., 2008; Kirk-Spriggs & McGregor, 2009), as well as some elements of the flora (Galley & Linder, 2006). In some cases such distribution patterns are believed to have resulted from relatively recent (Plio-Pleistocene) southward dispersal of Palaearctic taxa through the Eastern Arc mountains of East Africa (Gehrke & Linder, 2009; Kirk-Spriggs & McGregor, 2009; Sanmartín *et al*., 2010), whilst in others, disjunct taxa appear to represent older, relictual lineages which have survived in areas of relative climatic stability (e.g. extant Aspidytidae; Balke *et al*., 2003, 2005). The degree of molecular divergence observed between *Capelatus* **gen.n.** and *Liopterus* suggests that these taxa belong to this latter category.

Understanding of the higher-level phylogeny of Copelatinae has been hampered by the apparent plasticity of characters formerly used to define genera and species groups, such as elytral striation and the presence/absence of strioles or metacoxal lines (Balke *et al*., 2004). Genus-level relationships have previously been investigated by Balke *et al*. (2004) and Shaverdo *et al*. (2008), using a range of mitochondrial DNA markers with somewhat conflicting results. The addition of nuclear DNA sequences in the present study improves our understanding of the interrelationships amongst these beetles, as does inclusion of all but one of the known copelatine genera. The only current genus-level taxon not included in our analyses is *Rugosus*, which was erected for two Neotropical species, largely on the basis of their rugose dorsal sculpture (García, 2001). These taxa appear highly likely to belong to *Aglymbus*, however, which includes other heavily sculptured species in the Neotropics (M. Balke, unpublished data), suggesting that their inclusion would not necessarily change the broader conclusions presented here. All included genera were found to be monophyletic and the internal phylogenetic structure of the subfamily was well-resolved, being largely consistent across different phylogenetic methods. Instead of being nested within *Copelatus*, as has been suggested in most previous molecular analyses, the Oriental genus *Lacconectus* (80 spp.) was found to be sister to remaining Copelatinae, a systematic position first suggested by Brancucci (1986) based on both external and male genital morphology. With over 430 described species and many undescribed taxa, the cosmopolitan *Copelatus* is by far the most species-rich genus of Copelatinae and indeed Dytiscidae. Whilst few species of this genus are included in our phylogeny, these do cover much of the global distribution of *Copelatus*, which was recovered as monophyletic with strong support in all analyses, and sister to remaining copelatine groups, excluding *Lacconectus*. The inclusion of *Agaporomorphus*, a small genus of nine Neotropical species (see Miller, 2014), in our analyses placed this rather than *Aglymbus* sister to the Malagasy *Madaglymbus*; these two genera forming a clade which was supported in all analyses. Our work also forces a re-evaluation of the phylogenetic position of *Liopterus*, made up of two closely-related Palaearctic species which have been considered as either sister to *Madaglymbus* (Balke *et al*., 2004) or sister to all other members of the subfamily based on mtDNA sequence data alone (Shaverdo *et al*., 2008) and which here instead clearly associated with *Capelatus* **gen.n.** and *Exocelina*. Miller & Bergsten (2014) used a combination of molecules and morphology to investigate phylogenetic interrelationships across the Dytiscidae as a whole. These authors clearly demonstrated the monophyly of Copelatinae, although their analyses included representatives of only four genera (*Agaporomorphus*, *Copelatus*, *Exocelina* and *Lacconectus*), which, together with differences in choice of root position, may explain the somewhat different generic inter-relationships suggested in this study.

Capelatus prykei **gen. et sp.n.** was first detected when we received James Pryke's material from Noordhoek Wetlands, where the species is still extant. Subsequent searches in the dytiscid accessions of the BMNH revealed historical material from the Cape Flats, collected in a locality which appears to have been subsequently lost to urban development in the greater Cape Town area. Within an Afrotropical context, the South African dytiscid fauna is relatively well known, the Cape region having been extensively investigated in the past by Joyce Omer-Cooper and others (reviewed by Omer-Cooper, 1966). Whilst a large number of water beetles have been described from the Western Cape in the last 25 years (e.g. Perkins & Balfour-Browne, 1994; Ribera *et al*., 2002; Perkins, 2005, 2008; Bilton, 2013a,b, 2014; Bilton & Gentili, 2014), most of these taxa are non-dytiscids and are small, cryptic and/or occupy madicolous habitats (Vaillant, 1956) largely neglected by earlier workers. The fact that such a large, distinctive diving beetle as *C. prykei* **gen. et sp.n.** has apparently remained undetected for so long strongly suggests that the species has a very narrow geographical and ecological range, unusual in lentic freshwater species (see Ribera, 2008). A similar apparent restriction to the extreme south-west of the Cape is seen in a number of stillwater taxa, however, including the dytiscid *Herophydrus capensis* Régimbart, and the Critically Endangered micro frog *Microbatrachella capensis* (Boulenger) (Harrison *et al*., 2004). Such a pattern may be driven by the combination of strong climatic/ecological gradients, particularly in rainfall, coupled with the relative climatic stability of the region, factors likely to both promote the evolution of narrow-range endemics and to favour their persistence. On the basis of available data, it is suggested that *Capelatus prykei* **gen. et sp.n.** be afforded a provisional IUCN conservation status of Critically Endangered (CR), due to an apparent area of occupancy estimated to be less than 10 km^2, and the observed decline in extent of occurrence, extent and/or quality of habitat, and number of locations or subpopulations due to urban development in the Cape Town area [B2ab (i, iii, iv)] (IUCN, 2012). If the phylogenetic uniqueness of *Capelatus prykei* **gen. et. sp.n.** is also taken into consideration (*sensu* Vane-Wright *et al*., 1991), it is clear that a better understanding of the range and requirements of this newly discovered taxon represents a priority for conservation, in both a regional and global context.

Abbreviations

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

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12128

Figure S1. Maximum-likelihood (A) and maximum parsimony (B) phylogenetic hypotheses for the subfamily Copelatinae as recovered from analyses conducted in RAxML and TNT respectively (see Material and methods for more details on the analyses). Nodal support is given with bootstrap values (BS) in (A) and symmetric resampling values (SR) in (B). The newly described species *Capelatus prykei* is highlighted in green.

Table S1. DNA sequence sampling information with new GenBank accession numbers.

Table S2. Results from the PartitionFinder analyses.

Acknowledgements

We are grateful to James S. Pryke (Stellenbosch University), whose fieldwork on the Cape Peninsula first alerted our attention to this new taxon. Michael Samways (Stellenbosch University), Ruth-Mary Fisher, Deon Hignet, Danelle Kleinhans and Lee-Anne Benjamin (SAN Parks/Cape Nature) are thanked for their continued assistance with sampling permits, and Rebecca Bilton for her help in the field. Roy Moate and Glenn Harper assisted with electron microscopy. Christine Taylor and Max Barclay (BMNH) kindly loaned material for study, Kelly Miller provided information on *Rugosus* and Robert Angus advised regarding an earlier version of this manuscript. Finally Shaun Winterton and four anonymous referees are thanked for their helpful comments on the manuscript.

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Accepted 5 November 2014