A review of the *Canthyporus exilis* group, with the description of two new species (Coleoptera: Dytiscidae)

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Abstract

Canthyporus namaqualacrimus sp. nov. and *Canthyporus pallidus* sp. nov. are described from the Namaqualand region of South Africa, both members of the *exilis* group. A revised key to species of the group is provided, together with details of the external and spermathecal tract morphology of the female of *Canthyporus aenigmaticus* Biström & Nilsson, 2006, a species previously known only from the male holotype. The opportunity is also taken to present new ecological and distributional data on members of the *exilis* group, most of which are primarily associated with springs and seepage habitats.

Key words: Coleoptera, Dytiscidae, *Canthyporus*, new species, new records, ecology, South Africa.

Introduction

Canthyporus Zimmermann, 1919 is one of the most diverse genera of hydroporine diving beetles in the Cape region of South Africa (Biström & Nilsson 2006), where 25 of the 35 known species occur; the remaining 10 being restricted to other parts of the Afrotropical region (Nilsson 2015). The genus represents a relatively basal lineage within Hydroporinae, being recovered as sister to the austral South American *Laccornellus* Roughley & Wolfe, 1987 in most analyses (e.g. Roughley & Wolfe 1987; Ribera *et al.* 2008). These two genera make up the tribe Lacornellini in the phylogeny of Miller & Bergsten (2014), itself sister to all other Hydroporinae, with the exception of *Laccornis* Gozis, 1914. Whilst published data on the ecology of these beetles are sparse, *Canthyporus* species are found in both running and standing waterbodies. Some species are apparently restricted to either lentic or lotic waters, whilst others occur across both habitat types (Biström & Nilsson 2006; D. T. Bilton *pers. obs.*), and the presence of both lentic and lotic taxa in a number of *Canthyporus* species groups suggests that multiple transitions between running and standing waters have occurred during the evolutionary radiation of the genus.

The *Canthyporus exilis* group (sensu Biström & Nilsson 2006) currently includes four species: *C. aenigmaticus* Biström & Nilsson, 2006, *C. brincki* Omer-Cooper, 1965, *C. exilis* (Boheman, 1848) and *C. nebulosus* Omer-Cooper, 1965; of which the first two are known only from the holotypes. Here I describe two new members of the *exilis* group, found during recent fieldwork in Namaqualand, South Africa. I also provide new ecological and distributional data for three of the known species of the group, as well as illustrating the habitus and male genitalia of all known species and the spermathecal tract of all five for which females are now known, alongside a revised key.

Materials and methods

Specimens were studied using a Leica MZ8 and M205C stereomicroscopes, with a Fluopac FP1 fluorescent illuminator. Digital photographs were taken with a Canon EOS 500D camera fitted to a Leica Z6 Apo macroscope, equipped with a 2x objective lens. Specimens were illuminated using two Fluopac FP1 illuminators. Genitalia were mounted on glass slides in Kisser's glycerol gelatine (see Riedel 2005) and imaged using an Olympus CX31 microscope fitted with the same Canon camera. 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 micropins, and the whole abdomen macerated for 20 min in 10% aqueous potassium hydroxide at room temperature. The reproductive tract and associated sclerites were then removed from the abdomen, and stained for 2 min in 1% aqueous chlorazol black, rinsed in distilled water, before observation and imaging of structures in glycerol gelatin using the above Olympus microscope. Terminology of female tract components follows Mazzoldi (1996) and Miller (2001). As shown by Mazzoldi (1996) and Biström & Nilsson (2006), the shape and orientation of the spermatheca and its associated ducts are diagnostic in many Canthyporus. Image stacks were produced by hand, and combined using Zerene Stacker software (www.zerenesystems.com).

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

Abbreviations

Collection D.T. Bilton, Plymouth, UK
Ditsong National Museum of Natural History, Pretoria, South Africa
Iziko South African Museum, Cape Town, South Africa
Lund University Museum of Zoology, Lund, Sweden
Naturhistorisches Museum Wien, Vienna, Austria
South African National Collection of Insects, Pretoria, South Africa
Oxford University Museum of Natural History, Oxford, UK
Dimethyl Hydatoin Formaldehyde, aqueous solution

Taxonomy

Canthyporus namaqualacrimus sp. nov. (Figs 1, 2, 3 & 6)

Type locality. South Africa, Northern Cape Province, Kamiesberg, Johannes se Berg, seepages over sloping rockface below summit, 30°19'54.82"S 18°06'45.26"E, 1,470 m. (Fig. 6A).

Type material. **Holotype** (male): "17/ix/2014 South Africa NC// Kamiesberg – seepages over// rock below summit of Johannes// se Berg ca. 1,470 m D T Bilton leg." (genitalia extracted and mounted in DMHF on same card) with red printed holotype label "Holotype// *Canthyporus namaqualarcimus* sp. nov.// Bilton" (ISAM).

Paratypes: 6m#, 6f# same data as holotype (CDTB, DMSA, ISAM, NMW, SANC, OUMNH). All with red printed paratype labels "Paratype// *Canthyporus namaqualarcimus* sp. nov.// Bilton".

Description. Size: Holotype: body length (to elytral apices) 3.05 mm; maximum width (elytra) 1.65 mm; elytral length 2.5 mm. Same values for paratypes: 3.05–3.15 mm, 1.55–1.65 mm and 2.45–2.60 mm respectively.

Colour (Fig. 1): Dorsal surface predominantly yellowish brown to ferrugineous. Head pale ferrugineous, with anterior margin of clypeus dark ferrugineous. Dark brown patches running along inner margins of compound eyes, separated from eyes by narrow pale ferrugineous area. Dark patches narrow anteriorly, gradually broadening towards posterior margin of head. Pronotum yellowish-pale ferrugineous; narrowly dark brown along anterior and posterior margins. Disc with diffuse dark red-brown central longitudinal marking, and arcuate dark band laterally in posterior 1/2, tracing approximate position of prothoracic gland reservoir. Elytra yellowish to greenish brown, with irregular light brown spots and markings. Antennae with segment 1, proximal 1/2 of segment 2, segments 3–4 and base of segments 5–11 pale yellow; remainder dark brown to black. Maxillary palpi yellowish, apical segment broadly infuscated. Legs yellow to ferrugineous, with segmental junctions and apical segments of pro and mesotarsi infuscated. Venter black; prementum ferrugineous, pronotal hypomera and outer section of elytral epipleura yellowish.

Head: Broad, with large eyes. Anterior margin of clypeus weakly rounded. Shallow, arcuate frontal depressions present, opening anterolaterally towards anterior border of clypeus. Surface shining, with fine isodiametric microreticulation. Punctation extremely fine, almost imperceptible, clearest towards posterior margin. Antennal segments stout; segments 3–4 narrower than remainder.

Pronotum: Rectangular, strongly transverse, broadest at posterior angles. Anterior margin weakly arcuate; posterior margin bisinuate around centre. Lateral margins narrowly bordered; converging towards anterior angles, almost straight in posterior 1/2; more rounded in anterior 1/2. Anterior angles acute; posterior angles obtusely rounded. Surface shining, with fine isodiametric microreticulation; very finely punctate, punctures most clearly visible on disc. Irregular transverse row of coarse punctures along anterior margin, each bearing a fine decumbent seta.

Elytra: Elongate ovate, broadest at middle. Subparallel in anterior 1/2, gradually tapering towards apex in posterior 1/2. Surface shining, with fine isodiametric microreticulation and very fine, sparse punctation. Sutural puncture row effectively obsolete, traces of depressions anteriorly. Discal, dorsolateral and lateral coarse puncture rows distinct and regular, each puncture bearing a short decumbent seta. Punctures in discal row denser than those in dorsolateral and lateral rows, spaced approx. 2–4 puncture widths apart; punctures in outer rows spaced more than 5 puncture widths apart.

Venter: Mentum and prementum smooth and shining, lacking microreticulation and with sparse, stout, golden setae. Mentum broadly concave, produced laterally to form a dome around centre. Gula shining, lacking microreticulation. Genae shining, with shallow microreticulation; meshes relatively large and isodiametric to slightly stransverse in posterior 2/3, smaller and more transverse in anterior 1/3 below posterior margin of compound eye. Pronotal hypomeron broad, shining, with shallow, slightly elongate microreticulation. Proepisternum smooth and shining, without microreticulation. Prosternum rugulose and

densely setose. Prosternum and neck of prosternal process forming a more or less continuous angle of approx. 45° with venter; neck of process with stout, erect setae. Prosternal process elongate, spindle-shaped, laterally beaded in anterior 1/2. Medial surface very weakly convex, almost flat, apex located in impression in anterior metaventral process; surface shining, with sparse, medium, shallow punctures, each bearing a recumbent seta. Metaventrite and metepisternum shining, with transverse to isodiametric microreticulation. Metaventrite wrinkled laterally. Elytral epipleura shining, with shallow, isodiametric microreticulation in outer 2/3, with a shining inner ridge lacking microreticulation. Epipleurs as broad as pronotal hypomeron at shoulders, narrowing evenly to level of metacoxae and continuing as narrow ridge to apex. Metacoxae shining, with isodiametric to elongate microreticulation. Metacoxal lines strong, arcuate, diverging anteriorly; punctate, punctures bearing long, decumbent setae. Metacoxal fissure narrow but distinct. Metacoxal process free, lobes broadly rounded and diverging laterally. Abdominal ventrites shining, microreticulate. Ventrites 1-3 fused, junctions weakly visible, but segments distinct due to changes in microreticulation. Microreticulation more or less isodiametric on ventrite 1, elongate on ventrite 2 and transverse on ventrite 3. Ventrites 4–6 with increasingly isodiametric microreticulation; meshes weakly transverse on ventrite 4, weakly transverse to isodiametric on ventrite 6 and distinctly isodiametric on ventrite 6. Ventrites 2–4 with a central tuft of long, stout, recumbent setae, and a transverse row of 4-6 additional smaller recumbent setae running along the centre.

Legs: Basal three segments of pro and mesotarsi somewhat expanded, with suction setae ventrally. Apical segment of mesotarsi elongated, longer than apical segment of protarsi. Tarsal claws elongate, arcuate, simple; equally elongated on pro and meostarsi.

Aedeagus: Median lobe characteristically shaped (Fig. 2D); relatively large and heavily sclerotized, with a truncately rounded apex and median constriction in ventral view. Parameres (Fig. 2D) broad, with distinct apical tuft of setae.

Females: As males except for more strongly impressed microreticulation on dorsum and venter, stronger and slightly coarser punctation on dorsum, particularly on head and pronotum, as well as narrower pro and mesotarsi, which lack suction setae. Apical segment of mesotarsi shorter than in males, equivalent length to apical segment of protarsi. Pro and mesotarsal claws shorter than in males. Spermathecal tract heavily sclerotized, spermatheca robust, curved, relatively elongate (Fig. 3C).

Variation: Paratypes vary slightly in size (see above) and the development of the dorsal pattern, some specimens being somewhat darker or lighter than the holotype.

Differential diagnosis. The new species is a member of the *exilis* group of *Canthyporus* (Biström & Nilsson 2006), characterised by the relatively flattened dorsum, distinctly 5 segmented mesotarsi, dense apical hair tuft on the parameres and a relatively simple median lobe, lacking a dorsal projection. At 3.05–3.15 mm, *C. namaqualacrimus* sp. nov. is the largest member of the group described to date. In size, colouration and aedeagal morphology the new species is closest to *C. aenigmaticus*, from which it can be distinguished by its larger size (3.05–3.15 vs. 2.6–2.7 mm), more elongate body shape, finer dorsal punctation, absence of a distinct anterior depression on the head, as well as details of the aedeagus and spermathecal tract (Figs. 2 & 3).

Distribution and ecology. Known only from the type locality, madicolous seepages at the head of a small stream draining the granite summit dome of Johannes se Berg, close to

Leliefontein in the high Kamiesberg of the Northern Cape province. The highest Kamiesberg summits, including Johannes se Berg, experience much higher rainfall than most of Namaqualand, and support outliers of fynbos vegetation, much of which is endemic to the range (Helme & Desmet 2006). The new species seems likely to be found in similar habitats elsewhere in the Kamiesberg, such as on the summit dome of the Rooiberg. At Johannes se Berg this species occurred together with *C. pallidus* sp. nov., *Anacaena capensis* Komarek, 2004, *Crenitis zimmermanni* Knisch, 1924, *Laccobius praecipuus* Kuwert, 1890, *Hydraena duodecimata* Perkins, 2014, *Parasthetops curidius* Perkins & Balfour-Browne, 2008, *P. striatus* Perkins, 2008 and *Pneuminion velamen* Perkins, 1997.

Etymology. From Namaqualand, the region in which the Kamiesberg range is situated, and the latin *lacrima* (= tears), in reference to the habitat in trickling seepages over rock. It is an adjective in the nominative singular.

Canthyporus pallidus sp. nov. (Figs 1–5)

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Type locality. South Africa, Western Cape Province, Gifberg, Gifberg Pass, seepages on vertical rockfaces, 31°45'47.93"S 18°46'15.01"E, 485 m. (Fig. 5A).

Type material. **Holotype** (male): "20/ix/2014 South Africa WC// Gifberg – vertical wet rock face// in Gifberg Pass nr. Vanrhynsdorp// D T Bilton leg." (genitalia extracted and mounted in DMHF on same card) with red printed holotype label "Holotype// *Canthyporus pallidus* sp. nov.// Bilton" (ISAM).

Paratypes: 3 m#, 12 f# same data as holotype; 1 m#, 1 f# "20/ix/2014 South Africa WC// Gifberg – stream in Gifberg Pass// above Vanrhynsdorp// rocky stream D T Bilton leg."; 1 m#, 1f# "21/ix/2014 South Africa WC// Matsikammaberg seepage stream// over rock at head of Elandskloof// D T Bilton leg."; 1 f # "21/ix/2014 South Africa WC// Matsikammaberg stream// 1 km NW of Sewefontein farm// D T Bilton leg."; 2 m#, 4 f# "21/ix/2014 South Africa WC// Matsikammaberg stream// 1 km SE of Sewefontein farm// permanent D T Bilton leg."; 1 f# "21/ix/2014 South Africa WC// Matsikammaberg rockpools// on NE edge of plateau// D T Bilton leg."; 2 f# "17/ix/2014 South Africa NC// Kamiesberg – seepages over// rock below summit of Johannes// se Berg ca. 1,470 m D T Bilton leg."; 1 f# "18/ix/2010 South Africa NC// seepages on rockface on R27 road// @ Vanrhynspas D T Bilton leg." (CDTB, DMSA, ISAM, LUMZ, NMW, SANC, OUMNH). All with red printed paratype labels "Paratype// *Canthyporus pallidus* sp. nov.// Bilton".

Description. Size: Holotype: body length (to elytral apices) 2.4 mm; maximum width (elytra) 1.3 mm; elytral length 1.8 mm. Same values for paratypes: 2.3–2.5 mm, 1.25–1.3 mm and 1.65–1.9 mm respectively.

Colour (Fig. 1F): Dorsal surface predominantly yellowish to reddish ferrugineous. Head ferrugineous, infuscated very narrowly around inner margins of compound eyes. Pronotum yellowish-pale ferrugineous, slightly darker in centre; narrowly dark brown along posterior margin. Elytra yellowish, with irregular dark brown spots and markings. Antennae yellow, apical portions of segments infuscated, more so distally. Maxillary palpi yellow, apical segment infuscated in distal 1/3. Legs yellow. Venter of head ferrugineous; pronotal hypomeron, proepisternum and elytral epipleura dark yellowish; remainder of venter pitchy brown to black.

Head: Broad, with large eyes. Anterior margin of clypeus weakly rounded. Frontal depressions very shallow, punctate, opening anteriorly. Surface shining, with moderately shallow isodiametric microreticulation. Punctation fine and sparse; scattered larger punctures close to anterior border of clypeus and around inner margins of compound eyes. Antennal segments short and stout; segments 3–4 narrower than remainder.

Pronotum: Rectangular, strongly transverse, broadest at posterior angles. Anterior margin weakly arcuate; posterior margin bisinuate around centre. Lateral margins converging towards anterior angles; weakly arcuate and narrowly bordered. Anterior angles acute; posterior angles rectangular. Surface shining, with shallow isodiametric microreticulation; very finely and sparsely punctate. Irregular transverse row of coarse punctures along anterior margin, each bearing a fine decumbent seta. Similar punctures present along posterior margin in outer 1/3.

Elytra: Slightly elongate ovate, broadest at middle, relatively flat and broad. Rounded at sides, more strongly so in posterior 1/2. Surface shining, with shallow isodiametric microreticulation and fine, sparse punctation. Sutural puncture row distinct, particularly in posterior 2/3; formed by a row of depressions around relatively fine-medium punctures, giving the impression of a shallow stria when viewed from behind. Discal, dorsolateral and lateral puncture rows with somewhat irregular, widely spaced coarse punctures; punctures much larger than in sutural row.

Venter: Prementum shining, finely wrinkled. Mentum shining, with raised, slightly elongate microreticulation on anterolateral projections; weakly wrinkled elsewhere. Mentum broadly concave, produced laterally to form a dome around centre. Gula shining, lacking microreticulation. Genae shining, with shallow transverse microreticulation. Pronotal hypomeron broad; this and proepisternum both shining and finely wrinkled. Prosternum and neck of prosternal process shining, rugose and punctate, punctures with long, recumbent, golden setae. Neck with bunch of erect setae approx. 1/2 distance along length. Prosternum and neck of process forming a more or less continuous angle of approx. 45° with venter. Prosternal process elongate, spathulate, laterally beaded. Lateral bead punctate, punctures bearing fine decumbent setae, which lie on medial surface. Medial surface convex, impunctate, smooth and shining; apex located in impression in metaventrite. Metaventrite and metepisternum shining, finely wrinkled and with very fine, sparse punctation. Metaventrite shining, finely and sparsely punctate, with traces of shallow, transverse microreticulation. Elytral epipleura shining, with shallow, isodiametric microreticulation in outer 2/3, with a shining inner ridge lacking microreticulation. Epipleurs as broad as pronotal hypomeron at shoulders, narrowing evenly to level of metacoxae and continuing as narrow ridge to apex. Metacoxae shining, with shallow isodiametric to elongate microreticulation, more evident that on metaventrite; finely and sparsely punctate. Metacoxal lines strong, arcuate, diverging anteriorly; punctate, punctures bearing long, decumbent setae. Metacoxal fissure narrow but distinct. Metacoxal process free, lobes rounded and strongly diverging laterally. Abdominal ventrites shining, microreticulate. Ventrites 1–3 fused, junctions weakly visible, but segments distinct due to changes in microreticulation. Microreticulation more or less isodiametric on ventrite 2, elongate on ventrite 2 and transverse on ventrite 3. Ventrites 4–6 with increasingly isodiametric microreticulation; meshes weakly transverse on ventrite 4, weakly transverse to isodiametric on ventrite 6 and distinctly isodiametric on ventrite 6. Ventrites 2-4 with a central tuft of long, stout, recumbent setae, and a transverse row of 4-6 additional smaller recumbent setae running along the centre.

Legs: Basal three segments of pro and mesotarsi somewhat expanded, with suction setae ventrally. Apical segment of mesotarsi elongated, longer than apical segment of protarsi. Tarsal claws elongate, arcuate, simple; equally elongated on pro and meostarsi.

Aedeagus: Median lobe characteristically shaped (Fig. 2F); apex relatively truncate in ventral view. Parameres (Fig. 2F) broad, with distinct apical tuft of setae.

Females: As males except for more strongly impressed microreticulation on dorsum and venter, as well as narrower pro and mesotarsi, which lack suction setae. Apical segment of mesotarsi as long as in males; longer than apical segment of protarsi which is shorter than in males. Pro and mesotarsal claws slightly shorter than in males. Spermatheca relatively robust, broad, stout (Fig. 3E).

Variation: Paratypes vary slightly in size (see above) and the development of the dorsal pattern, some specimens being somewhat darker or lighter than the holotype. All specimens lack any distinctly darker dorsal colouration on the head and pronotum. Paratypes vary in the extent to which a sutural puncture row is visible. In some cases this is clear, as in the holotype, in others the row is weak, and only visible as a series of somewhat larger punctures in posterior 1/3.

Differential diagnosis. Another member of the *exilis* group (see above), closest to *C*. *nebulosus* and *C*. *brincki*. Differs from *nebulosus* by the uniformly pale head and pronotum (both always distinctly infuscated in *nebulosus*—see Fig. 1), the somewhat larger size (2.3–2.5 versus 1.94–2.22 mm in *nebulosus*), the broader, flatter dorsum, the shallower microreticulation and finer punctation, especially on the pronotum and elytra, the presence of a sutural puncture row, at least posteriorly, the more elongate apical segment of the male protarsi, as well as the broader median lobe of the aedeagus, which is also much more truncate apically in ventral view (Fig. 2). In females, the spermatheca of *C*. *pallidus* sp. nov. is more robust than that of *C*. *nebulosus*, and shorter and broader (Fig. 3). The new species differs from *brincki* in the more mottled appearance of the elytra (see Fig 1), the less well impressed microreticulation, giving a somewhat more shining appearance, the broader dorsum and slightly larger size (2.3–2.5 vs. 2.06 mm in *brincki*), as well as shape of the apex of the median lobe of the aedeagus in ventral view (rounded in *C*. *brincki*, truncate in *C*. *pallidus* sp. nov.—see Fig. 2).

Distribution and Ecology. Found in the northern part of the Western Cape and the Northern Cape provinces of South Africa. So far known from the Gifberg-Matsikamaberg massif, northwards along the Bokkeveld Escarpment (Vanrhyns Pass), to the high Kamiesberg of Namaqualand. Most records are from seepages over wet rock faces, and although some specimens are from streams, these were mostly located in shallow areas around the margins, particularly over rock. In seepage habitats the new species co-occurred with typical madicoles, such as the hydraenids *Pneuminion velamen* Perkins, 1997 and *Pterosthetops hawequas* Perkins, 2008 (see Bilton 2014).

Etymology. Named in reference to the pale colouration of the head and pronotum. It is an adjective in the in the nominative singular.

New records and notes on described Canthyporus exilis group species

Canthyporus aenigmaticus Biström & Nilsson

Described on the basis of a single male, collected in the Cederberg by Sebastian Endrödy-Younga (Biström & Nilsson 2006). My collections of this species include the first known females. These differ from males in the slightly more strongly impressed microreticulation, particularly on the elytra, the narrower pro and mesotarsi and the shorter apical segment of the mesotarsi. The spermatheca is relatively small, short and stout, with a relatively narrow fertilization duct (Fig. 3A). The spermathecal duct (not shown due to damage during extraction) is coiled, and closely resembles that of other species of the group. I can add the following records, extending the species' distribution north to the Gifberg-Matsikamaberg massif, which represent the northernmost extension of the Cape Fold Mountains, and the adjacent Bokkeveld Escarpment: 27/ix/2010 Northern Cape, temporary pond beside R27 ca. 1 km E of Vanrhyns Pass (1 f#, teneral); 20/ix/2014 Western Cape, Gifberg, stream over sandstone rock in Gifberg pass (1m#, 1f#); 21/ix/2014 Western Cape, Matsikamaberg, temporary rockpools on NE edge of summit plateau (2m#, 4f#, some teneral).

Canthyporus brincki Omer-Cooper

Still only known from the type locality, from Quthing in what is now Lesotho. I have reexamined the holotype, deposited in LUMZ, and illustrate the habitus and male genitalia here for comparison (see Figs. 1 & 2). The species is closest to *C. nebulosus* and *C. pallidus* sp. nov., and is best distinguished by a combination of colour pattern and male genitalia—see key below.

Canthyporus exilis (Boheman)

Known from two localities in the western part of the Eastern Cape Province, and a number of sites in the far southwest of the Western Cape (Biström & Nilsson 2006). I can add the following records, which extend the range far to the north, into the Northern Cape. This species can be found in running water, but in my experience is most abundant in shallow mossy swamps, with or without seepage flow: 27/ix/2008 Western Cape, Table Mountain National Park, Table Mountain, mossy pool behind Woodhead Reservoir (abundant); 25/ix/2011 Western Cape, Cederberg, seepage marsh 3 km SE of Uitkyk Pass (abundant); 25/ix/2011 Northern Cape, Vanrhyns pass, seepage over rock beside R27 (1f#); 2/x/2014 Western Cape, Table Mountain national Park, temporary pools behind dunes at Olifantsbos (1m#).

Canthyporus nebulosus Omer-Cooper

The most widespread member of the group, known from Kwazulu-Natal and both the Eastern and Western Cape Provinces (Biström & Nilsson 2006). A characteristic species of seepages flowing over rock (madicolous habitats—see Bilton 2014; Vaillant 1956), also found in stream margins, and in small temporary pools: September 2002 & 26/ix/2012 Western Cape, Bainskloof Pass above Wellington, seepages over rock beside R301 road on north side of pass (abundant); 23/ix/2009 Western Cape, Garden Route National Park, madicolous seepage beside Salt River nr. Nature's Valley (abundant); 24/ix/2009 & 1/i/2014 Western Cape, Groote Swartberg, stream on R328 2 km N of De Top (abundant); 24/ix/2009 Western Cape, Groote Swartberg, madicolous seepages beside R328, 2 km N of Gamkaskloof turning (abundant); 25/ix/2009 & 25/ix/2010 Western Cape, Franschhoek Pass, wet rock faces beside R45 (abundant); 26/ix/2008, 27/ix/2009, 22/ix/2011 & 26/ix/2012 & 22/ix/2014 Western Cape, Cape, Ceres, seepages over rock (abundant); 21/ix/2010, 24/ix/2012 & 22/ix/2014 Western Cape, Cape, Cape, Uitkyk Pass, seepages over rock face beside road (abundant); 19/ix/2008 &

23/ix/2010 Western Cape, Table Mountain National Park, Silvermine, seepages over rock beside M64 (abundant); 23/ix/2010 Western Cape, Table Mountain National Park, seepage over rock beside M66 at Red Hill above Simonstown (1f#); 24/ix/2010 Western Cape, Table Mountain National park, Table Mountain, seepage over rock in Echo Valley (abundant); 23/ix/2011 & 23/ix/2012 Western Cape, Cederberg, seepages over sloping rock beside stream at 1,200 m below Wolfberg Arch, beside Matjiesrivier-Wupperthal road (abundant); 23/ix/2011 Western Cape, Cederberg, stream in Gabriel's Pass below Wolfberg Arch (abundant); 24/ix/2011, 25/ix/2012 & 4/x/2013 Western Cape, Cederberg, Algeria Waterfall, wet rock seepages (abundant); 1/i/2014 Western Cape, Groote Swartberg, stream on S side of pass below Oliewenberg (abundant on wet rock face); 3/i/2014 Western Cape, Outeniquaberg, wet rock faces in Robinson Pass (abundant).

Revised key to members of the Canthyporus exilis group.

The following key to species of the *exilis* group is modified from that presented in Biström & Nilsson (2006) to accommodate the two new species:

1 Size larger, total length 2.6–3.15 mm. ... 2

- Size smaller, total length less than 2.6 mm. ... 3

2 Body shape shorter and broader. Head with distinct anterior depression running behind the front margin of the clypeus. Punctation of head and pronotum fine but clearly visible throughout. Median lobe of aedeagus characteristic (Fig. 2A), very broad in ventral view. Spermathecal tract as in Fig. 3A. Total length 2.6–2.7 mm. ... *Canthyporus aenigmaticus* - Body shape more elongate. Head without distinct anterior depression. Punctation of head and pronotum very fine, almost imperceptible over much of surface. Median lobe of aedeagus as in Fig 2D. Spermathecal tract as in Fig. 3C. Total length 3.05–3.15 mm. ... *Canthyporus namaqualacrimus* sp. nov.

3 Dorsal colouration dark, blackish ferrugineous to dark piceous, without obvious dark-light mottling. Median lobe of aedeagus narrowing to apex in lateral view (Fig. 2C). Spermathecal tract as in Fig. 3B. Total length 1.85–2.10 mm. ... *Canthyporus exilis*

- Dorsal colouration different, paler with diffuse dark mottling, at least on elytra. Median lobe of aedeagus relatively broad to apex in lateral view (Fig. 2B, E & F). ... 4

4 Head and pronotum distinctly infuscated (Fig. 1E). Body shape relatively short and broad. Microreticulation on dorsum more strongly impressed. Median lobe of aedeagus as in Fig 2E. Spermathecal tract Fig. 3D. Total length 1.95–2.2 mm. ... *Canthyporus nebulosus*

- Head and pronotum paler, lacking obvious infuscation (Fig. 1B & F). Body shape more elongate. Microreticulation on dorsum less strongly impressed ... 5

5 Elytra pale, with limited darker mottling (Fig. 1B). Median lobe of aedeagus with relatively narrow, rounded apex in ventral view (Fig. 2B). Size smaller, total length of holotype 2.06 mm. ... *Canthyporus brincki*

- Elytra with more evident dark mottling (Fig. 1F). Median lobe of aedeagus with apex broader and relatively truncate in ventral view (Fig. 2F). Spermathecal tract Fig. 3E. Size larger, total length 2.3–2.5 mm. ... *Canthyporus pallidus* sp. nov.

Discussion

The two species described here raise the number of known species in the *Canthyporus exilis* group to six. On both external and reproductive morphology, *C. exilis* would appear to be the most isolated member of the group, differing from all other known species in dorsal colour

pattern and the structure of the male genitalia and female spermathecal tract. This species is also unusual in being found in standing waters, particularly pools and swamps with some seepage flow, as well as rivers and streams (Biström & Nilsson 2006).

With the exception of *C. exilis* itself, members of the *exilis* group appear to be largely associated with habitats where shallow water occurs over exposed bedrock, in particular trickles of water, either below springs/seepage lines or beside streams. *C. nebulosus* is the most widespread species, being frequent in such situations over sandstone in the Cape Fold Mountains, where it is often one of the most abundant, or only, diving beetles. To date, *C. aenigmaticus* is known from both temporary rockpools (e.g. Fig. 4A) and stream margins, in the Cederberg and Gifberg-Matsikammaberg mountains, and the Bokkeveld Plateau in the north of the Western Cape Province. Both habitat types provide clear temporary water over rock, and are likely to warm rapidly in the austral spring. *C. namaqualacrimus* sp. nov. and *C. pallidus* sp. nov. are both known largely from madicolous habitats, the former having been found only in the Kamiesberg range, where it may be endemic. Whilst both species were taken in the same seepage stream on Johannes se Berg in the Kamiesberg, they were not microsympatric. *C. pallidus* sp. nov. was present in silty areas with very shallow water (Fig. 4B), whereas *C. namaqualacrimus* sp. nov. was found only in areas with algal growths directly on granite rockfaces (Fig. 6A).

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Figure legends

Fig. 1. *Canthyporus exilis* group, male habitus. A) *C. aenigmaticus*; B) *C. brincki* holotype; C) *C. exilis*; D) *C. namaqualacrimus* sp. nov. holotype; E) *C. nebulosus*; F) *C. pallidus* sp. nov. holotype. Scale bar = 1 mm.

Fig. 2. *Canthyporus exilis* group, male genitalia (ventral and lateral view of median lobe of aedeagus, plus right paramere). A) *C. aenigmaticus*; B) *C. brincki* holotype; C) *C. exilis*; D) *C. namaqualacrimus* sp. nov. holotype; E) *C. nebulosus*; F) *C. pallidus* sp. nov. holotype. Scale bar = 0.25 mm.

Fig. 3. *Canthyporus exilis* group, female spermathecal tracts. A) *C. aenigmaticus* (coils of spermathecal duct not shown); B) *C. exilis*; C) *C. namaqualacrimus* sp. nov.; D) *C.nebulosus*; E) *C. pallidus* sp. nov. Scale bar = 0.25 mm. Spermathecal ducts of *C. nebulosus* and *C. pallidus* sp. nov. snapped on extraction, but shown in entirety.

Fig. 4. *Canthyporus exilis* group habitats. A) Western Cape Province. Matsikammaberg, rockpool on summit close to northeast face—*C. aenigmaticus* and *C. pallidus* sp. nov.; B) Northern Cape Province, Kamiesberg, Johannes se Berg, seepages over sloping rockface below summit, 1,470 m—*C. pallidus* sp. nov. Photos A. Foggo.

Fig. 5. *Canthyporus exilis* group habitats. A) Western Cape Province, Gifberg, seepages over vertical rockface—*C. pallidus* sp. nov.; B) Western Cape Province. Matsikammaberg, stream 1 km NW of Sewefontein Farm—*C. pallidus* sp. nov. Photos D. T. Bilton.

Fig. 6. *Canthyporus exilis* group habitats. A) Northern Cape Province, Kamiesberg, Johannes se Berg, seepages over sloping rockface below summit, 1,470 m—*C. namaqualacrimus* sp. nov.; B) Western Cape Province, Cape Peninsula, temporary pond at Olifantsbos—*C. exilis*. Photos A. Foggo & D. T. Bilton.