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Phylogenetic analysis of the bee genus *Capicola* with the description of *Capicola hantamensis* sp. nov. (Hymenoptera: Dasypodaidae)

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Abstract

The genus *Capicola* Friese is one of the 8 genera included in the Dasypodaidae. *Capicola* contains 13 species (including the new species *C. hantamensis* **sp. nov.**) restricted to the xeric part of south-western Africa. New cladistic analysis and description of *C. hantamensis* **sp. nov.** complete the recent monographic revision of this genus (Michez *et al*. 2007) and demonstrate that the new species is the sister of all other *Capicola*.

Key words: Hymenoptera, Dasypodaidae, *Capicola*, new species, South Africa

Introduction

The bee genus *Capicola* is one of the 8 genera included in the Dasypodaidae (Michener 1981, 2000; Danforth *et al.* 2006a, b). *Capicola* is restricted to southern Africa, but is closely related to the Neartic genus *Hesperapis* Cockerell (Michener 1981; Engel 2005) and the two were considered congeneric by Michener (2000). Both *Hesperapis* and *Capicola* share morphological features, notably the shape of stigma, the two sub-marginal cells (the first being longer than the second), the galea comb well developed and the scopa restricted to the outer face of hind tibia and basitarsus. The two genera differ in the shape of the pygidial plate, which is flat in *Hesperapis* and displays a strongly elevated longitudinal area in *Capicola* females (except *C. flavicara*). *Capicola* and *Hesperapis* are in the subtribe Hesperapina including also a third genus, the central Asian *Eremaphanta* (Engel 2005; Michez & Patiny 2006).

The genus *Capicola* is represented by 13 species (including the new species *C. hantamensis* **sp. nov.**) (Michener 1981; Michez *et al.* 2007). Most *Capicola* seem to be oligolectic on a few plant families: Asteraceae, Aizoaceae, Campanulaceae and Fabaceae (Michez *et al.* 2007). They probably nest solitarily underground, although the natural history of *Capicola* is still poorly documented. Only *C. braunsiana* Friese has been studied (Rozen 1974). The nesting area was sandy, treeless, with numerous widely spaced desert plants (principally *Mesembryanthemum* sp., Aizoaceae). The nest itself was very simple, consisting in a main ground tunnel that gave rise to linear series of four cells.

During a field trip in 2006, one of us (MK) collected some specimens of a hitherto undescribed *Capicola* in the Hantam Mountains (Northern Cape Province, South Africa). New cladistic analysis of *Capicola* species and description of *C. hantamensis* **sp. nov.** complete the recent monographic revision of *Capicola* (Michez *et al*. 2007).

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Material and method

Description

C. hantamensis is only known from two series of specimens, even though the genus was although reviewed based on a comprehensive study of all *Capicola* material available at that time (including type material) (Michez *et al.* 2007). CKUM and OOLL are respectively used as an acronym for Coll. Kuhlmann at University of Münster (Germany) and Oberösterreichisches Landesmuseums of Linz (Austria). The Holotype is conserved in the National Collection of Insects (SANC), Pretoria (South Africa).

We used Harris (1979) for description of the surface sculpture and Michener (2000) for morphology. Puncture density is given in terms of relationship between puncture diameter (d) and the spaces between them (i), such as i>d. Integumental ultrastructure was studied using SEM (JEOL JSM-6100) and images processed using the software Semafore (JEOL, Sollentuna, Sweden) (Fig. 2). The following abbreviations were used for morphological structures: antennal segment = A (A1 = Scape); tibia = Tb; femur = F; basitarsus = Bt ; metasomal sternum = S; metasomal tergum = T; pygidial plate = Pp; length = L; maximum width = W.

The synthetic distribution map of the genus (Fig. 4) is based on the maps presented by Michez *et al.* (2007). The morphometric values included in the diagnosis and the description are based on 3 females and 7 males. Body lengths were measured from vertex to the apex of T7 for the male and from vertex to the apex of the pygidial plate for the female.

Cladistic analysis

All 13 described *Capicola* species were included in the cladistic analysis (dataset in table 1). *Eremaphanta fasciata* Popov and *Hesperapis regularis* (Cresson) (Dasypodaidae, Dasypodaini, Hesperapina) were used as outgroups. 21 morphological characters were included in the analysis (details see Michez *et al.* 2007). Both sexes share the character if the sex is not specified.

TABLE 1. Character-state matrix for cladistic analysis.

	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21
Outgroup																					
Eremaphanta fasciata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hesperapis regularis	1	1	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Ingroup																					
Capicola aliciae	1	1	0	1	1	1	1	0	0	1	1	1	0	1	1	2	0	3	1	1	0
C. braunsiana	0	1	0	1	0	1	1	0	0	1	1	1	0	1	0	1	1	2	0	0	1
C. danforthi	1	0	1	1	0	2	0	1	1	0	0	0	1	1	0	2	1	1	0	0	2
C. flavicara	2	1	0	0	0	1	1	0	0	0	0	1	0	1	0	0	1	2	0	0	1
C. flavitarsis	1	1	1	1	0	2	1	1	0	0	0	1	1	1	0	2	1	1	0	0	2
C. gessorum	1	0	1	1	1	2	1	1	1	0	0	0	1	1	0	1	1	1	0	0	3
C. hantamensis	1	0	1	0	0	3	0	0	0	0	1	0	0	0	0	2	0	2	0	0	3
C. micheneri	1	1	1	1	0	3	1	0	0	1	1	1	0	1	1	2	0	3	1	1	1
C. nanula	1	1	1	1	1	3	1	0	0	1	1	1	0	1	0	1	1	2	0	0	1
C. nigerrima	1	0	1	1	1	2	0	1	1	0	0	1	1	1	0	2	1	1	0	0	2
C. rhodostoma	0	1	0	1	0	1	1	1	0	0	0	1	0	1	0	1	1	2	0	0	1
C. richtersveldensis	1	1	1	1	0	2	0	1	1	0	0	1	1	1	0	2	1	1	0	0	2
C. rufiventris	1	1	1	1	0	1	1	0	0	0	0	1	1	1	0	2	1	1	0	0	3

1. Head: (0) as wide as long; (1) wider than long; (2) longer than wide.
2. Outer surface of galea: (0) smooth; (1) sculptured.
3. Labial palpus: (0) as long as maxillary palpus; (1) shorter than maxillary palpus.
4. Clypeus male: (0) apically yellow; (1) reddish to black.
5. Clypeus male: (0) without median groove; (1) with median groove.
6. Clypeus: (0) width equal to length; (1) twice as wide as long; (2) two and a half times as wide as long; (3) three times as wide as long.
7. A5 male: (0) longer than wide; (1) width subequal to greater than length.
8. Base of propodeal triangle: (0) rugose; (1) shiny.
9. Disc of T2–T4: (0) flat, without basal concavity; (1) with basal concavity.
10. Clypeus female: (0) densely punctate (i<d), at least basally; (1) sparsely punctate (i>3d).
11. Propodeum female seen in profile: (0) with declivous basal area; (1) with horizontal basal area.
12. Inner spur of Tb2 female: (0) finely serrate (1) with outstanding sharp spines.
13. Tb3 male: (0) not expanded apically; (1) expanded apically.
14. Posterior leg male: (0) yellow; (1) black.
15. Outer surface of Tb3 female: (0) without large, blunt spine; (1) with large, blunt spine.
16. Pp female: (0) without median elevated area; (1) with median elevated area weakly raised, consisting of a pair of median subparallel ridges, area between these ridges concave; (2) with a strongly elevated median area.
17. Disc of S6 male: (0) without medio-longitudinal groove; (1) with medio-longitudinal groove.
18. S6 male: (0) without medio-apical process; (1) with medio-apical curved blade; (2) with narrow medio-apical teeth that are half as long as S6 disc; (3) with large medio-apical teeth as long as S6.
19. S7 male: (0) disc not narrowed, apex generally emarginate; (1) main part narrowed medially.
20. S7 male: (0) apical lobes not diverging; (1) apical lobes diverging.
21. Gonostylus: (0) without groove; (1) with narrow hairy groove (with parallel margins); (2) with large hairy groove (margin of groove not parallel); (3) with large hairless groove.

The dataset (table 1) was analysed using PAUP 4.0b10 (Swofford, 2001). A heuristic parsimony search was made with *Eremaphanta fasciata* and *Hesperapis regularis* as outgroups (ingroup= 13 *Capicola* species). The starting tree was obtained by stepwise addition. 10,000 random additional sequences were performed during the search. The branch swapping option was kept as default (TBR). All minimal trees found during branch swapping were kept. The multistate characters (1, 5, 13, 18, 21) are unordered. The most parsimonious trees were used to compute a strict consensus.

Results

Description of Capicola hantamensis Michez & Kuhlmann sp. nov.

Type material. Holotype male SANC, 3 females paratypes, 7 males paratypes, CKUM: “South Africa, 28km N Calvinia, Sandveld, 31°12’09’’S 19°50’05’’E, 885m, 06.X.2006, leg. M. Kuhlmann”.

Additional material. 2 females, 1 male, OOLL: “South Africa, N Cape, 50km Loeriesfontein [30°58’S 19°27’E], 14.X.1999, leg. Marek Halada”.

Etymology. Named after the *locus typicus*, the Hantam Mountains.

Diagnosis. Like other Dasypodaidae, *Capicola hantamensis* has a short pointed glossa with all segments of the labial palpus similar to one another and two submarginal cells (the first longer than the second). Like other *Capicola*, the female Pp has a strong elevated medial area and the male S6 has medio-apical and lateral

processes. *Capicola hantamensis* differs from all other *Capicola* by having yellow legs, yellow clypeus in the male and an inner blade to the gonostylus. Females show the diagnostic combination of rugose propodeal triangle and inner Tb2 spur finely serrate.

Description. ♂(Figs 1a, c; 2a–g). **Body length**: 4.9mm. **Head.** L=1.4mm. W=1.8mm. Head wider than long, mainly black. Mandible base yellow, apex black. Labrum and clypeus yellow. Scape ventrally black, dorsally yellow. Pedicel black. A3–A12 yellow (Figs 1a, c). A13 black. Clypeus, face and genal area with white, erect hairs. Labial palpus two-thirds as long as maxillary palpus, reaching beyond apex of glossa. Maxillary palpus longer than galea. Outer surface of galea smooth. Malar area shorter than A2. Clypeus three times as wide as long; with superficial punctures (i=2d), denser at base. A5 longer than wide. Compound eyes convergent below. Flagellum four times as long as scape. **Mesosoma**. L=1.6mm. W (between tegulae)=1mm. Integument black. Mesoscutum, scutellum, metanotum and mesepisternum with sparse short whitish hairs. Mesoscutum, scutellum and metanotum shiny, with dense, weak punctures that are more than a puncture width apart. Propodeal triangle hairless, mat and rugose; with horizontal basal area (Fig. 1d). **Legs**. Tarsi 1–3 and Tb1–Tb3 yellow. Tb3 and Bt3 with red spot at base of some setae. Claws 1–3 apically red. F1–F3 basally black, apically yellow. Trochanter 1–3 black. Legs 1–3 shiny, with sparse yellowish hairs. Inner surface of Tb3 with keirotrichia. **Wings**. Surface hyaline. Two submarginal cells, first longer than second. Stigma shorter than first submarginal cell. Basal vein slightly curved. **Metasoma**. L=2.8mm. W=1.5mm. Metasoma black, shiny, with dense weak punctures (i<d). T1–T6 with dense white apical fringe. Disc of terga with few short erect whitish setae. Disc of sterna with brown appressed hairs. Terga and S1–S4 with straight apical margin. S5 with apex emarginate. S6 with two hairy medio-apical lobes and two hairy latero-apical processes (Figs 2a–b). S7 with wide disc and median carina, with sparse long apical hairs (Fig. 2c). Disc of S8 shorter than the column (Fig. 2d). Column of S8 with long hairs (Fig 2d). Apex of S8 triangular. Gonostylus with appressed hairs (Figs 2e–f), with inner blade (Fig. 2g), as long as gonocoxite (Fig. 2f). Digitus as long as cuspis (Fig. 2g). £ (Figs 1b, d). **Body length** (vertex-Pp): 5.8mm. **Head.** L=1.6mm. W=2.1mm. Head wider than long; mainly black. Mandible base reddish; apex red. Labrum and apex of clypeus reddish. Scape black. Flagellum ventrally reddish or yellow, dorsally brownish. Clypeus, face and genal area with white, erect hairs. Vertex shiny. Labial palpus two-thirds as long as maxillary palpus, reaching beyond apex of glossa. Maxillary palpus longer than galea. Outer surface of galea smooth. Malar area shorter than A2. Clypeus glabrous; three times as wide as long; with deep punctures (i=d), denser at base, smooth between punctures. Compound eyes converging slightly below. Flagellum twice as long as scape. **Mesosoma**. L=2.1mm. W (between tegulae)=1.3mm. Integument black. Mesoscutum, scutellum, metanotum, propodeum and mesepisternum with a few short whitish hairs. Mesoscutum, scutellum and metanotum shiny, with dense, weak punctures (i=d). Propodeal triangle hairless, mat and rugose; with horizontal basal area (Fig. 1d). **Legs**. Tarsi 1–3 and Tb1–Tb3 reddish. Tb3 and Bt3 with red spot on the basis of some setae. Claws apically red. F1–F3 basally black, apically reddish. Trochanter 1–3 black. Spurs of Tb2 with 8 sharp outstanding spines. Legs 1 and 3 with sparse yellowish hairs. Tb2 covered with appressed white hairs. Inner surface of Tb3 with keirotrichia. **Wings**. As male. **Metasoma**. L=3.1mm. W=2.1mm. Metasoma reddish. T2–T4 with black lateral spots. Pp reddish at base, red at apex. Disc of terga and sterna shiny. T1–T4 with whitish apical fringe. Prepygidial fimbria yellowish. Terga and sterna with dense weak punctures (i=d) and straight apical margins. Pp with median area strongly elevated.

Floral visitation. All females were collected visiting flowers of *Wahlenbergia* sp. (Campanulaceae). Males were patrolling along patches of *Wahlenbergia* sp.

Biotope. The bees were found along a roadside with shrubs and on the neighbouring sparsely vegetated pasture (Sandveld) with large areas of open sandy ground (Fig. 3).

Distribution. Only known from two localities near Calvinia and Loeriesfontein in the Hantam Mountains (Fig. 4).

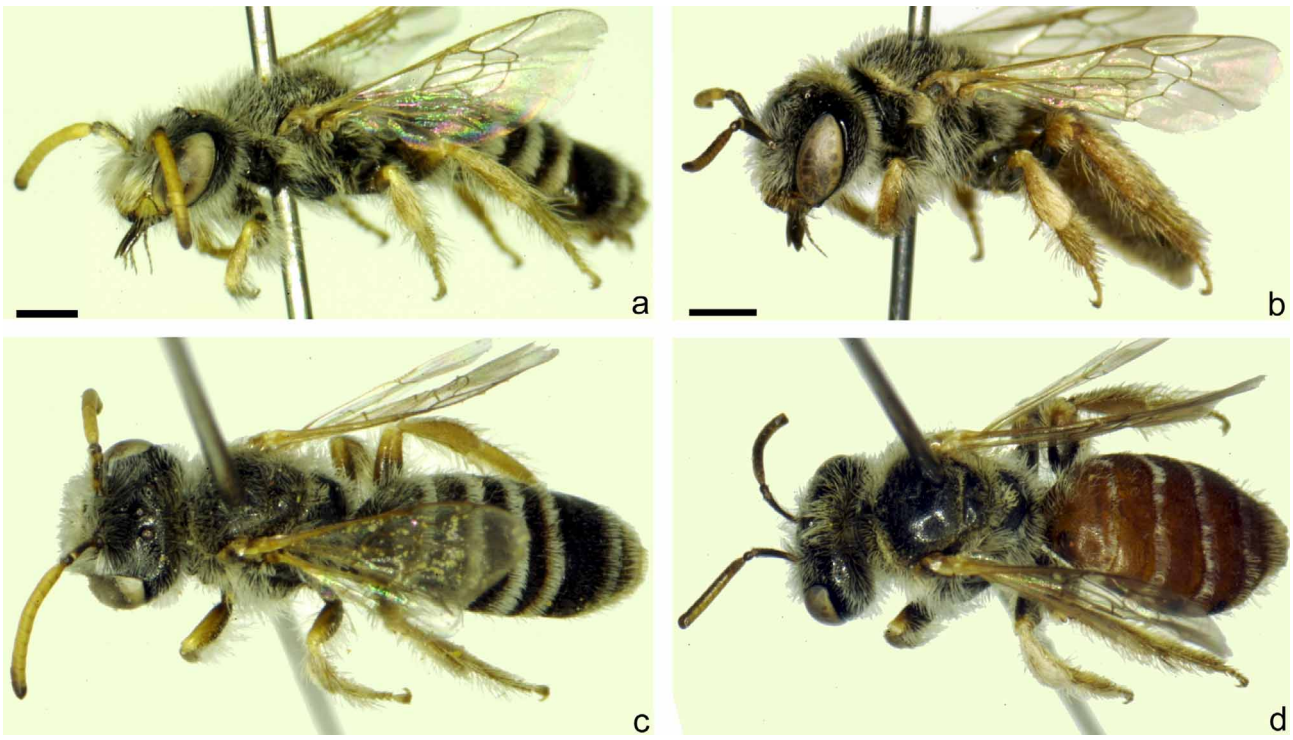

FIGURE 1. *Capicola hantamensis*, general habitus (scale=0.5mm); a. Lateral view of the male; b. Lateral view of the female; c. Dorsal view of the male; d. Dorsal view of the female.

Phylogenetic analysis

The heuristic search based on the data matrix (table 1) yielded two equally parsimonious trees of length=54, CI=0.5370 and RI=0.6835. A cladogram of one tree is displayed in Fig. 5. *Capicola hantamensis* shares many plesiomorphies with *Eremaphanta fasciata* (characters 2, 4–5, 7–10, 12–15, 17, 19, 20). It is the sister species of all other *Capicola*, which share outstanding spines on spur of Tb2 female, black hind leg male and black clypeus male.

Discussion

Morphology and systematics

C. hantamensis shows some notable autapomorphies: the yellow color of the male antenna, the inner blade of the gonostylus and the morphology of proboscides. The male is very easy to identify by its yellow antenna with the last segment black. *C. nanula* Cockerell has a similar antenna (last three segments black) but the colour of its clypeus is black (Michez *et al.* 2007).

Phylogenetically *Capicola hantamensis* is interesting as the males have yellow maculations (on clypeus and legs) like most *Eremaphanta*. This feature increase the hypothesis that *Eremaphanta* and *Capicola* are close relatives (Engel 2005). Moreover, the taxonomic rank of the group *Capicola+Hesperapis+Eremaphanta* needs revaluation in light of the recent phylogenetic result of Danforth *et al.* (2006b). A global phylogenetic study of the Dasypodaidae is in process.

Biogeography and floral choices

The distribution of *C. hantamensis* confirms previous data that *Capicola* species are restricted to the xeric part of south-western Africa (Michener 1981; Michez *et al.* 2007). It also supports previous hypothesis that

the pattern of diversity of *Capicola* is unipolar like some other southern African endemic taxa (e.g. the beetles *Macroderes* Westwood; Frolov & Scholtz 2004). The centre of endemism is clearly in the Western Cape Province's Succulent and Nama Karoo biomes, which have the world's highest temporate floral diversities (Kuhlmann 2005).

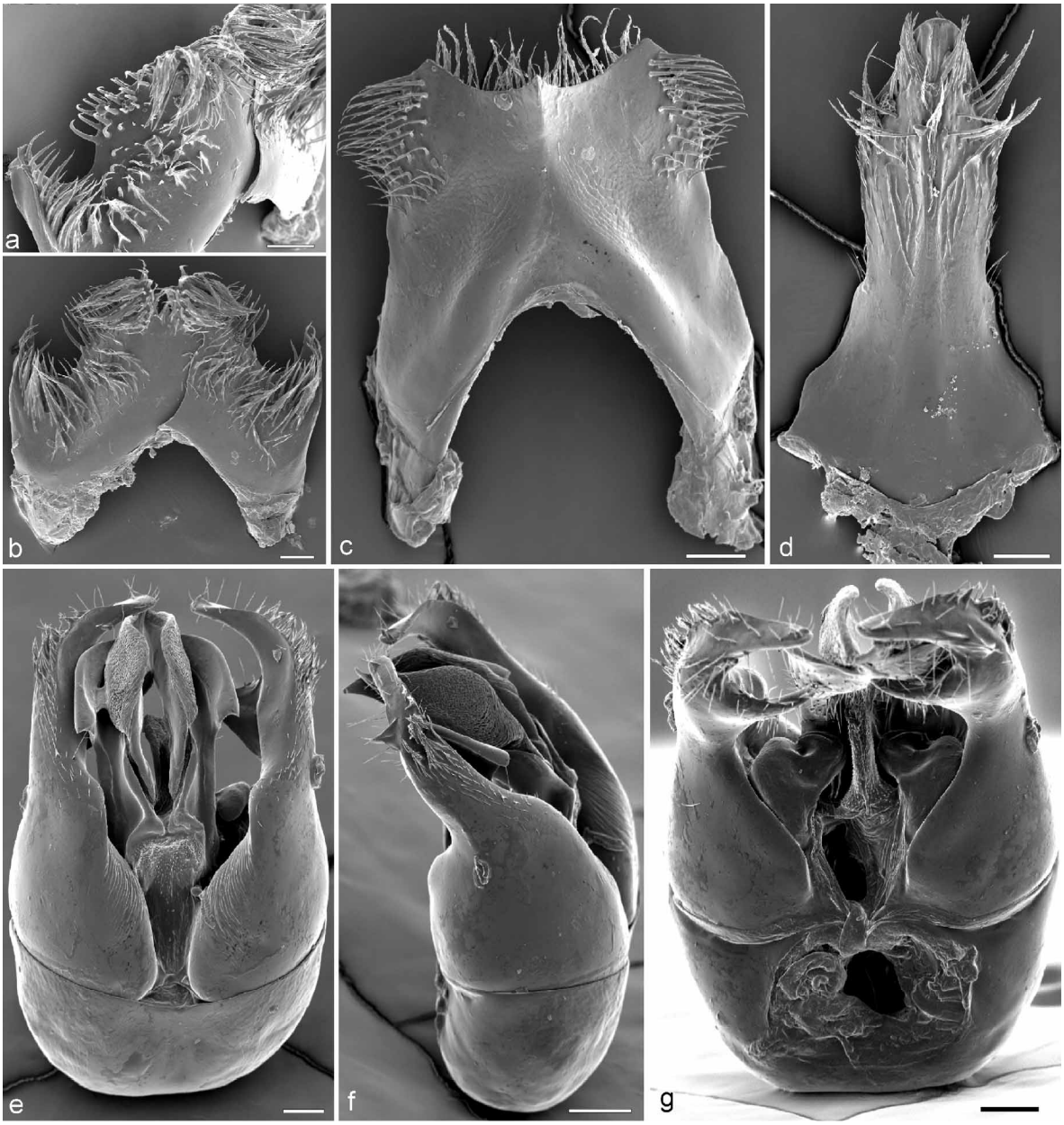

FIGURE 2. *Capicola hantamensis*, male (scale=100µm); a. Apicolateral view of sternum 6; b. Ventral view of sternum 6; c. Ventral view of sternum 7; d. Ventral view of sternum 8; e. Dorsal view of genitalia; f. Lateral view of genitalia; g. Ventral view of genitalia.

Capicola hantamensis seems to prefer the flowers of *Wahlenbergia* sp. (Campanulaceae) as do three other species of *Capicola* (*C. danforthi* Eardley, *C. gessorum* Eardley and *C. richtersveldensis* Patiny & Michez) (Gess & Gess 2004; Michez *et al.* 2007). Michez *et al.* (2007) demonstrated that these 3 species constitute a monophyletic group (with the following synapomorphies: propodeal triangle slanting and shiny, male hind tibia expanded, disc of T2–T4 with basal concavity) (Fig. 5). The morphology of the proboscis of *C. hantamensis* is very close to the morphology of other species of this group: outer surface of galea smooth and labial palpus shorter than maxillary palpus. However, other morphological features clearly show that *C. hantamen-*

sis does not belong to the *C. danforthi* species-group. Thus, the morphology of its proboscis could be regarded as an independently evolved morphological adaptation to forage on *Wahlenbergia* sp.

FIGURE 3. Biotope of *Capicola hantamensis*.

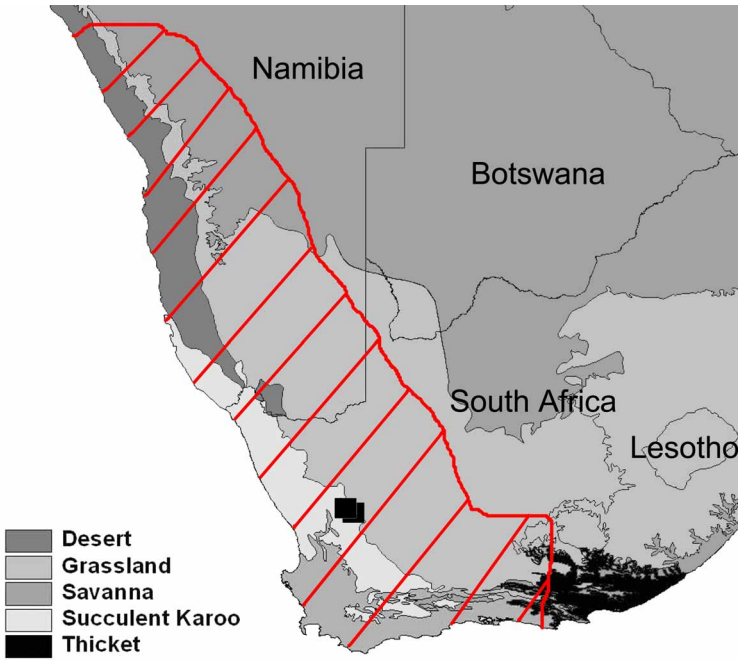

FIGURE 4. Global distribution of the genus *Capicola*. black squares = collecting localities of *Capicola hantamensis*.

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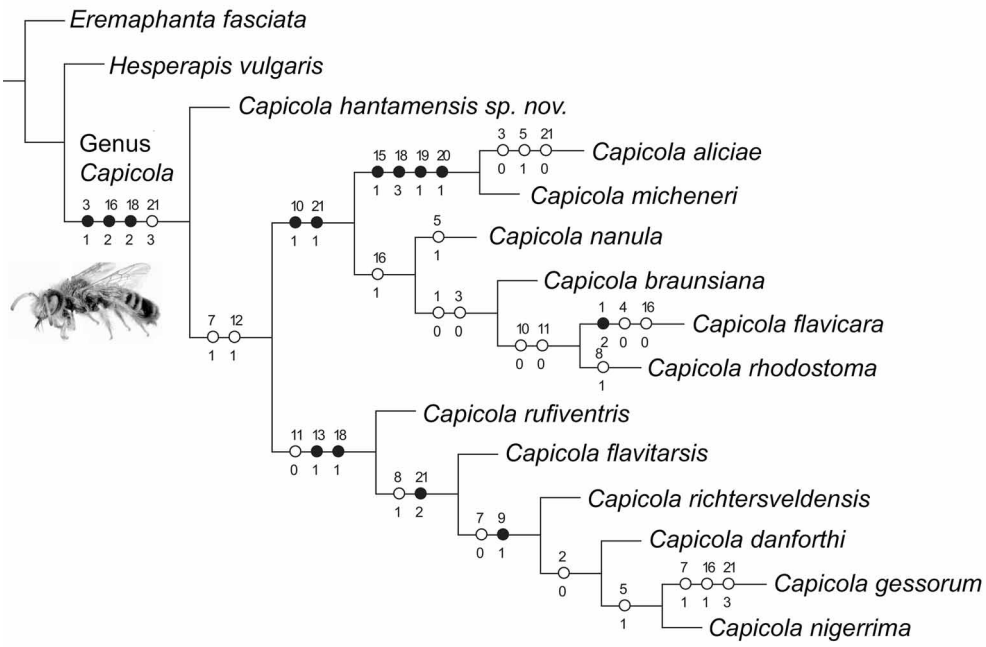

FIGURE 5. Cladogram of *Capicola* from heuristic search (length=54, CI=0.5370 and RI=0.6835). Characters are shown above circles, character states below.

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